

AN ABSTRACT OF THE THESIS OF

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Title: THE INHERITANCE OF TEN QUANTITATIVE CHARACTER-
ISTICS IN SWEET CORN (ZEA MAYS L.)

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The inheritance of ten characteristics of sweet corn was studied by quantitative genetic analysis. Characters studied were tassel date, silk date, plant height, ear height, shank length, husk extension, tip blanking, number of kernel rows, ear length, and weight of the first ear.

Diallel crosses were made between seven inbred parents. The ten characters were measured on the seven parents and 21 F_1 crosses in two years and on the 21 reciprocal F_1 crosses and 21 F_2 families in one year. A fixed model of the diallel analysis was used to partition genetic variation into general combining ability (GCA) and specific combining ability (SCA). F_1 data were combined over years to evaluate genotype by year interactions. Regressions of progeny on parents were calculated to compare the results of covariance among relatives with results based on variance components. Combining ability effects and genotypic correlations between characters were also estimated.

Both GCA and SCA were involved in the inheritance of all ten characters. This was consistent for the F_1 crosses in both years and for the F_2 families.

Variance components were extracted from expectations of mean squares and expressed as ratios of V_{SCA}/V_{GCA} to compare the relative importance of GCA and SCA. SCA was more important than GCA for ear length and weight of the first ear in the F_1 . Ratios for these characters were slightly larger than 1.0.

GCA was more important than SCA for all other characters in the F_1 . Ratios ranged from .047 for number of kernel rows to .566 for plant height.

Variance ratios for most characters decreased in the F_2 . The failure of some ratios to decrease in the F_2 was attributed to either differential interactions of GCA and SCA with the environment or inadequate sampling of the F_2 families. Analyses of heterosis and inbreeding depression were in general agreement with variance component ratios.

Genotype by year interactions influenced the expression of most characters. A greater portion of the genotype by year interaction was contained in estimates of SCA than in estimates of GCA.

Heritability estimates from parent-progeny regression and from variance components were generally in close agreement, although those from regression were generally larger than those from variance

components. This supports the use of the combining ability analyses in this study.

Large positive genotypic correlations were found between tassel date and silk date, plant height and ear length, ear height and shank length, ear height and tip blanking, ear height and ear length, number of kernel rows and ear weight, and ear length and ear weight. Large negative genotypic correlations were found between plant height and husk extension, ear length and husk extension, and ear weight and husk extension. Characters with large genotypic correlations also had large phenotypic correlations.

Reciprocal F_1 crosses differed for all characters except weight of the first ear. These differences were large enough in some crosses to have important breeding implications. The cause of these reciprocal differences could not be definitely established in this study.

The Inheritance of Ten Quantitative Characteristics
in Sweet Corn (Zea mays L.)

by

Leon Afton Hansen

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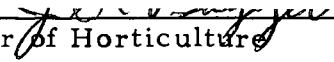
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TABLE OF CONTENTS

	<u>Page</u>
INTRODUCTION	1
REVIEW OF LITERATURE	4
Gene Action	4
Diallel Analysis and Combining Ability	5
Genotype X Environment Interactions	7
Estimates of Genetic Variances for Plant and Ear	
Characteristics in Corn	9
Tassel Date	9
Silk Date	10
Plant Height	11
Ear Height	11
Shank Length	12
Husk Extension	13
Tip Blanking	13
Number of Kernel Rows	13
Ear Length	14
Weight of First Ear	15
Heritability	15
Character Associations	20
Reciprocal Differences	23
MATERIALS AND METHODS	26
General Procedures	26
Measurement of Characters	26
Tassel Date	27
Silk Date	27
Plant Height	27
Ear Height	27
Shank Length	28
Husk Extension	28
Tip Blanking	28
Number of Kernel Rows	28
Ear Length	29
Weight of First Ear	29
Plant Material and Chronology of Field Studies	29
Statistical Analysis of Data	34
EXPERIMENTAL RESULTS	40
Performance of Inbred Parents	40
Performance of F ₁ Crosses (Preliminary Analysis with Reciprocals)	40

	<u>Page</u>
Reciprocal Differences	47
Performance of F ₁ Crosses	50
Performance of F ₂ Families	55
Relative Importance of GCA and SCA	55
Interactions of GCA and SCA with Years	64
Combining Ability Effects	65
Phenotypic and Genotypic Correlations	78
Heritability Estimates	84
 DISCUSSION	 87
Genetic Variances	87
Reciprocal Differences	92
Character Associations	93
Breeding Implications	95
 SUMMARY AND CONCLUSIONS	 97
 BIBLIOGRAPHY	 99

LIST OF TABLES

<u>Table</u>		<u>Page</u>
1	Degree of inbreeding and previous ratings for tip blanking and husk extension of 20 sweet corn inbred lines included in the diallel crossing block in 1973	30
2	Mean measurements made in 1973 for tip blanking and husk extension of 18 sweet corn inbred lines	32
3	Mean values for ten characters measured on seven sweet corn inbred lines in 1974	41
4	Mean squares from the analyses of variance for ten characters of seven sweet corn inbred lines grown in 1974	41
5	Mean values for ten characters measured on seven sweet corn inbred lines in 1975	42
6	Mean squares from the analyses of variances for ten characters of seven sweet corn inbred lines grown in 1975	42
7	Mean squares from the combined analyses of variance for ten characters of seven sweet corn inbred lines grown in 1974 and 1975	43
8	Mean values for ten characters measured on 21 F_1 sweet corn hybrids grown in 1974	44
9	Mean values for ten characters measured on 21 reciprocal F_1 sweet corn hybrids grown in 1974	45
10	Mean squares from the diallel analyses of variance (method 3 - model I) for ten characters of 21 F_1 and 21 reciprocal F_1 sweet corn hybrids grown in 1974	47
11	Differences between reciprocal means (F_1 mean minus reciprocal F_1 mean) for nine characters of 21 F_1 and 21 reciprocal F_1 sweet corn hybrids grown in 1974	48

<u>Table</u>	<u>Page</u>
12 Mean squares from the diallel analyses of variance (method 4 - model I) for ten characters of 21 F ₁ sweet corn hybrids grown in 1974	51
13 Mean values for ten characters measured on 21 F ₁ sweet corn hybrids grown in 1975	52
14 Mean squares from the diallel analyses of variance (method 4 - model I) for ten characters of 21 F ₁ sweet corn hybrids grown in 1975	53
15 Mean squares from the combined analyses of variance (method 4 - model I) for ten characters of 21 F ₁ sweet corn hybrids grown in 1974 and 1975	54
16 Mean values for ten characters measured on 21 F ₂ sweet corn families grown in 1975	56
17 Mean squares from the diallel analyses of variance (method 4 - model I) for ten characters of 21 F ₂ sweet corn families grown in 1975	57
18 Components of GCA and SCA variance (V) for ten characters of sweet corn	58
19 Ratio of SCA variance to GCA variance $\left(\frac{V_{SCA}}{V_{GCA}}\right)$ for ten characters in sweet corn	58
20 Heterosis for ten characters of 21 F ₁ sweet corn crosses measured in 1974	61
21 Heterosis for ten characters of 21 F ₁ sweet corn crosses measured in 1975	62
22 Inbreeding depression for ten characters of 21 F ₂ sweet corn families measured in 1975	63
23 Variance components for GCA X years and SCA X years interactions and their ratios with GCA and SCA, respectively	66
24 Estimates of GCA effects for ten characters derived from the analyses of 21 F ₁ sweet corn crosses grown in 1974	67

<u>Table</u>	<u>Page</u>
25 Estimates of GCA effects for ten characters derived from the analyses of 21 F ₁ sweet corn crosses grown in 1975	68
26 Estimates of GCA effects for ten characters derived from the combined analyses of 21 F ₁ sweet corn crosses grown in 1974 and 1975	69
27 Estimates of GCA effects for ten characters derived from the analyses of 21 F ₂ sweet corn crosses grown in 1975	70
28 Estimates of SCA effects for ten characters derived from the analyses of 21 F ₁ sweet corn crosses grown in 1974	73
29 Estimates of SCA effects for ten characters derived from the analyses of 21 F ₁ sweet corn crosses grown in 1975	74
30 Estimates of SCA effects for ten characters derived from the combined analyses of 21 F ₁ sweet corn crosses grown in 1974 and 1975	75
31 Estimates of SCA effects for ten characters derived from the analyses of 21 F ₂ sweet corn crosses grown in 1975	76
32 Estimates of variances of GCA and SCA effects and variances of plot means derived from the combined analyses of 21 F ₁ sweet corn crosses grown in 1974 and 1975	77
33 Phenotypic correlations between ten characters of sweet corn calculated from three generations in two years	79
34 Genotypic correlations between ten characters of sweet corn estimates by: (1) regression of progeny on parents, and (2) components of variance and covariance from the analyses of variance	81
35 Heritability estimates (%) for ten characters of sweet corn estimated by: (1) regression of progeny on parents, and (2) components of variance from the analyses of variance	85

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THE INHERITANCE OF TEN QUANTITATIVE
CHARACTERISTICS IN SWEET CORN
(ZEA MAYS L.)

INTRODUCTION

Sweet corn, Zea mays L., is one of the most important vegetable crops in the United States. It is grown extensively by the home gardener, the market gardener, and for commercial processing. Superior F_1 hybrids have largely replaced open-pollinated cultivars because of their higher yield and increased uniformity. New cultivars, to be accepted, must meet certain criteria for plant and ear characteristics as well as exhibit improved yield and quality. A new cultivar defective for one or more plant or ear characters will not be accepted into commerce even though it may be superior for other horticultural attributes.

A basic understanding of the inheritance of characters under selection is a prerequisite for a successful plant breeding program. The purpose of this study was to analyze the inheritance and interrelationships of ten plant and ear characters in a population of seven selected sweet corn inbreds. The following characters were included:

1. length of time from planting to anthesis (tassel date)
2. length of time from planting to silk emergence (silk date)
3. plant height
4. ear height

5. shank length
6. husk extension beyond the tip of the ear
7. tip blanking
8. number of kernel rows
9. ear length
10. weight of first ear

Variation in each of these characters is continuous and was assumed to be under quantitative genetic control.

Tip blanking was a character of primary interest and may be defined as the failure of kernels to develop at the tip of the ear. This defect can be intensified by unfavorable environmental conditions or improper plant nutrition. However, tip blanking is genetically controlled and is expressed by inferior genotypes even when environmental and nutritional conditions are optimum. No reports concerning the inheritance of tip blanking have been found in the literature.

Husk extension and shank length were additional characters of interest. Husk extension has been associated with resistance to the corn earworm (Heliothis zea (Boddie) and dusky sap beetle (Carpophilus lugubris Murr.) in sweet corn and field corn (Snyder, 1967) and with resistance to bird damage in field corn (Thompson, 1963). Inheritance of husk extension has been studied in limited populations of sweet and field corn. (Robinson, Comstock, and Harvey, 1949; Thompson, 1963; and Snyder, 1967).

The shank is the lateral branch that attaches the ear to the stalk. Short shanks are more desirable because cultivars with long shanks are difficult to harvest. Studies on the inheritance of shank length have not been reported.

The remaining characters included in the present study have been studied extensively in field corn but studies in sweet corn have been limited. These characters were included in this study to provide more information about inheritance in sweet corn germplasm and to study their interrelationships with the characters of primary interest.

The objectives of this study were as follows:

1. Determine the relative importance of additive versus non-additive genetic variance for each of the ten characters studied.
2. Determine the heritability of each character by two different methods:
 - a. variance components
 - b. parent-progeny regression.
3. Determine if reciprocal crosses behave differently.
4. Determine phenotypic and genotypic associations among characters.
5. Determine the stability of types of genetic variance between years.

REVIEW OF LITERATURE

Gene Action

Gene action involved with quantitative characters is studied in terms of the gross gene system. Types of gene action have been reviewed by Allard (1960) and Brewbaker (1964). Genetic variation can be partitioned into additive and non-additive gene action. Additive gene action is characterized by alleles that express themselves regardless of their allele mate and the expression of the F_1 heterozygote is intermediate to the two homozygous parents. Non-additive gene action involves deviation from the additive scheme. These deviations may arise from intra-allelic interactions (dominance) or inter-allelic interactions (epistasis).

An individual character may be controlled by a combination of additive and non-additive gene action. The relative proportions of these types of gene action dictates the type of breeding program that will be the most effective for accumulating desirable alleles. The effects of additive gene action can be fixed by selection during inbreeding. Non-additive gene effects can not be fixed and must be utilized through favorable combinations in the heterozygous state. Moll and Stuber (1974) have reviewed the role of quantitative genetics in plant breeding.

Diallel Analysis and Combining Ability

Sprague and Tatum (1942) discussed combining ability in terms of the breeding behavior of a particular character within a population of plants. General combining ability (GCA) is associated with additive gene action and specific combining ability (SCA) is associated with non-additive gene action. In this context, Sprague and Tatum (1942) defined general combining ability as the average performance of a line in hybrid combinations. Specific combining ability designates those cases in which certain combinations do relatively better or worse than would be expected on the basis of the average performance of the lines involved.

Sprague and Tatum (1942) were the first to use the diallel cross to evaluate combining ability in terms of gene action. They used a statistical analysis of F_1 progeny yields from all possible crosses among ten field corn inbred lines to arrive at variance estimates for GCA and SCA. GCA was determined by the variation among parents when averaged over single crosses and compared to the grand mean of all single crosses. The more a parental average deviated from the grand mean, the greater its contribution to GCA. SCA was determined by the relative performance of an individual cross compared to the performance of the parents and the other crosses involving those parents.

The genetic theory of the diallel analysis was later detailed by Jinks and Hayman (1953), Hayman (1954a, 1954b), and Griffing (1956a, 1956b). It was defined in terms of gene action, combining ability, and was also related to the methods of covariances between relatives in terms of additive and non-additive genetic variances.

Griffing (1956a) pointed out that if the diallel analysis is used to estimate genetic parameters of a population from which inbred lines were derived, the following assumptions must be met: (1) random mating and gene equilibrium in the parent population; (2) inbred lines used in the analysis must be a random sample from a population of inbred lines derived from an inbreeding system which did not change gene frequencies; (3) a modified diallel analysis in which the parental lines are not included must be used.

If these assumptions are met, the total variation measured in the experiment can be partitioned into genotypic variance and environmental variance. The genotypic variance can then be partitioned into GCA and SCA components of variance which estimate the additive and non-additive components of variance respectively. The GCA variance contains one-half of the additive gene action plus one-quarter of the additive X additive epistasis plus one-eighth of the additive X additive X additive epistasis etc. The SCA variance contains all of the dominance gene action plus one-half of the additive X additive epistasis plus all of the additive X dominance and dominance X dominance

epistasis etc. The GCA variance is equal to the covariance between parents and progeny which illustrates the genetic relationship between the diallel method and methods involving covariances between relatives.

In a second paper, Griffing (1956b) extended the theory of the diallel analysis, in terms of combining ability, to cover the case of a chosen or fixed set of parental lines. The case of a fixed set of parents was designated Model I; the case of a random set of parents was designated Model II. Conclusions based on the random model apply to the population represented by the randomly chosen parental lines; whereas, conclusions based on the fixed model are confined to only those parental lines that were included in the analysis.

Griffing (1956b) also outlined four methods to be used under each model based on whether or not reciprocal F_1 's and/or parents were included in the analysis. Details of the eight possible analyses were presented along with procedures for obtaining combining ability effects and variances of effects to provide specific information about each parental line.

Genotype X Environment Interactions

Quantitative characters controlled by polygenes are strongly influenced by the environment. Gardner (1963) warned that gene action estimates based on experiments conducted in a single environment

would be biased upward because the genotype X environment interaction can not be separated from the genotypic effects. Experiments conducted in two or more environments provide more realistic estimates because a large part of the genotype X environment interaction can be separated from the genotypic effects.

Rojas and Sprague (1952) reported a study of the interaction of GCA and SCA for yield in corn with locations and years. Inbred parents previously selected for GCA were used in the analysis. They found that the interactions with locations and years were consistently larger for SCA than for GCA. Additive effects were more constant from location to location and from year to year than non-additive effects. They concluded that SCA includes a considerable portion of the genotype X environment interaction.

Matzinger, Sprague, and Cockerham (1959) conducted a similar experiment using S_1 lines that had not been selected for yield. They found significant variances of interactions for GCA X years, GCA X years X locations, and SCA X locations. In general, larger interactions with environments were found for GCA than for SCA.

These conflicting results reaffirm the necessity of repeating experiments under different environments when studying types of genetic effects conditioning a quantitative genetic trait.

Estimates of Genetic Variances for Plant
and Ear Characteristics in Corn

Numerous estimates of genetic variance in corn for characteristics such as plant height, ear height, ear length, and yield have been reported. Most of these estimates have involved field corn germplasm derived from open pollinated varieties, synthetic varieties, unselected inbred lines, or selected inbred lines. The most widely used mating designs and their underlying assumptions have been reviewed by Gardner (1963).

The results of these studies must be viewed in terms of the kinds of populations analyzed. As pointed out by Griffing (1956b), conclusions are restricted to the parent population in the case of random selection of experimental material or to the experimental material itself in the case of fixed selection. Therefore, results from different populations are not directly comparable and can not be extrapolated to untested populations. However, the relative magnitude of additive genetic variance versus non-additive genetic variance for a character, established in several populations, may be useful for predicting the outcome of analyses in previously untested populations.

Tassel Date

Mohamed (1959) studied tassel date in the F_1 , F_2 , and backcross generations of two inbred field corn lines and concluded that the

difference between the two parents was controlled by two major genes. In a similar study, Giesbrecht (1960a) found the difference in tassel date between two inbreds to be controlled by about five genes.

Stuber, Moll, and Hanson (1966) analyzed a cross between two field corn populations and found the additive genetic variance to be almost twice as large as the dominance variance.

Silk Date

Mohamed (1959) found that the difference in days to silk between two field corn inbreds was controlled by three major genes.

Giesbrecht (1960a) estimated that the difference between the two inbreds in his study was controlled by four or five genes. Hallauer (1965) found the difference between two inbreds to be controlled by three genes.

Additive genetic variance was found to be the most important for days to silk by Robinson, Comstock, and Harvey (1955), Hallauer (1965), and Wright et al. (1971). Daniel (1965), using sweet corn inbreds, estimated additive variance to be nine times more important than non-additive variance. Partial dominance for earliness was reported by Gardner et al. (1953) and Gardner and Lonquist (1959). Giesbrecht (1960b) reported partial to complete dominance for days to silk and also indicated that epistasis may have been important.

Darrah and Hallauer (1972) found significant additive effects but concluded that non-additive effects were more important in determining days to silk.

Plant Height

Plant height was found to be controlled largely by additive genetic variance by Robinson et al. (1949), Robinson et al. (1955), Rumbaugh and Lonquist (1959), Stuber et al. (1966), and Wright et al. (1971). Both Robinson et al. (1949) and Stuber et al. (1966) reported little or no dominance for plant height. Daniel (1965) reported that additive variance for plant height was about five times larger than non-additive variance in a diallel analysis of 18 sweet corn inbred lines.

In contrast, partial dominance for plant height was reported by Gardner et al. (1953) and Gardner and Lonquist (1959). Darrah and Hallauer (1972) found significant additive effects for plant height but concluded that non-additive effects were more important. Gamble (1962) found significant additive, dominant, and epistatic effects and concluded that they were all important.

Ear Height

Additive variance was found to be the most important for controlling ear height in studies by Robinson et al. (1949), Robinson et al. (1955), Rumbaugh and Lonquist (1959), Stuber et al. (1966), and

Wright et al. (1971). Robinson et al. (1949) and Stuber et al. (1966) reported that the amount of dominance was insignificant.

Partial dominance for greater ear height was reported by Gardner et al. (1953), Rumbaugh and Lonquist (1959), and Giesbrecht (1961). Darrah and Hallauer (1972) found non-additive effects to be more important than additive effects. Thompson, Hanson, and Shaw (1971) reported additive and dominance components to be of about equal importance.

Significant epistasis for ear height was reported by Giesbrecht (1961) and Ahmad (1968). Bauman (1959) found significant epistasis for ear height in individual experiments. However, when experiments were combined over years epistasis was non-significant indicating that values had been inflated by genotype X environment interactions within years.

Thompson and Rawlings (1960) studied ear height in crosses between 26 inbreds and four single cross testers of different ear heights and concluded that effective selection for ear height could be based on the ear height of the inbred parents per se.

Shank Length

The relative importance of types of gene action controlling the inheritance of shank length have not been reported in the literature.

Husk Extension

Robinson et al. (1949), using F_3 progenies of F_2 biparental crosses derived from three field corn single crosses, found approximately complete dominance of genes affecting husk extension. The direction of dominance was not indicated. Snyder (1967) reported partial dominance for short husk extension in both sweet corn and field corn lines. Thompson (1963) noted negative heterosis for husk extension in field corn. However, it was thought that positive heterosis for ear length may have contributed to the apparent expression of negative heterosis for husk extension.

Tip Blanking

Investigations concerning the inheritance of tip blanking in corn have not been reported in the literature.

Number of Kernel Rows

Daniel (1965) reported that additive variance was approximately five times larger than non-additive variance for kernel row number in a diallel analysis of 18 sweet corn inbred lines. Likewise, Robinson et al. (1955), Hallauer (1968), and Wright et al. (1971) found additive variance to be larger than non-additive variance for kernel row number in field corn.

Darrah and Hallauer (1972) found significant additive effects but concluded non-additive effects were more important. Partial dominance was reported by Gardner et al. (1953) and nearly complete dominance for high row number was reported by Leng (1953).

Gamble (1962) concluded that additive, dominance, and epistatic effects contributed equally to the genetic component of kernel row number. Bauman (1959) found significant epistasis for kernel row number in experiments within years. However, epistasis was non-significant when experiments were combined over years.

Ear Length

The additive component of genetic variance for ear length was found to be relatively more important than the non-additive component by Robinson et al. (1955), Hallauer (1968), and Wright et al. (1971) in field corn. Daniel (1965) reported that additive and non-additive variances were almost equal in importance in sweet corn.

Partial dominance for increased ear length was indicated in studies by Robinson et al. (1949), Gardner et al. (1953), and Gardner and Lonquist (1959). Gardner et al. (1953) also found indications of overdominance for ear length in a second F_2 population derived from inbred lines. Gamble (1962) reported significant additive, dominance, and epistatic effects for ear length. Dominance and epistasis were relatively more important than additive gene effects.

Weight of First Ear

Data concerning genetic variance of ear weight at the "table stage" of maturity are not available for either sweet corn or field corn. However, this character would be expected to respond in a similar manner to grain yield which has been studied extensively in field corn.

Sprague and Tatum (1942) suggested that in material previously selected for yield, non-additive variance would be expected to be relatively more important than additive variance. However, in unselected material the reverse situation would be expected. More recently, Wright et al. (1971) found additive genetic variance to be the most important for yield in an analysis of unselected inbred lines.

Heritability

Heritability was defined by Lush (1949) as "the fraction of the observed or phenotypic variance which was caused by differences between the genes or the genotypes of the individuals." The phenotypic variance is composed of a portion due to genetic effects and a portion due to environmental influences. Heritability for a character in a population is then a ratio of genetic variation to total variation. If the total genetic variation, composed of additive genetic effects, intra-allelic interactions, and inter-allelic interactions, is used in

the numerator, the heritability estimate is termed "broad sense." Whereas if only the additive genetic variance is used in the numerator the estimate is termed "narrow sense." A narrow sense heritability estimate is usually more useful in selection work because it is an index of transmissibility and reflects the fraction of the phenotypic differences between parents that may be expected to be recovered in their offspring (Lush, 1949). For maximum benefit, heritability estimates should be used with a selection differential to predict gain from selection and to suggest the best breeding method for the problem at hand (Allard, 1960).

Warner (1952) reported that techniques for estimating heritability fall into three main categories: "(1) parent-offspring regressions, (2) variance components from an analysis of variance, and (3) approximation of nonheritable variance from genetically uniform populations to estimate total genetic variance." Parent progeny regressions estimate heritability in the narrow sense because the degree to which the progeny resemble the parents is reflected. This is a function of additive gene action but, depending on the circumstances, may be biased upward by including a portion of the inter-allelic interactions. Variance components from an analysis of variance can be used to estimate either broad or narrow sense heritability depending on the methods used to partition genetic variance and the components used in the calculation. Heritabilities obtained

from approximation of nonheritable variance from genetically uniform populations to estimate total genetic variance are normally broad sense estimates because additive and non-additive portions can not be separated.

Warner (1952), working with corn, developed a method to estimate heritability by using only the F_2 generation and backcrosses of the F_1 to both parents. The problem of differential expression of environmental variation by the non-vigorous inbred parents, the uniformly vigorous F_1 generation, and the segregating F_2 generation was avoided. This method was based on total within-population variances and did not require estimates of environmental variance or of total genetic variance. Heritability was calculated as $H = \frac{(1/2)D}{VF_2}$ where $1/2D$ is the additive genetic component in the F_2 determined by two times the variance in the F_2 minus the variance in the backcross to one parent plus the variance in the backcross to the other parent. V_{F_2} is the total within variance of the F_2 population.

Frey and Horner (1957) proposed a modification of the conventional parent-progeny regression method termed "heritability in standard units." This method is a parent-progeny regression on data coded in terms of standard deviation units and identical to a correlation calculated on the original data. The advantage of the standard unit method is to reduce the scaling effect of year to year environmental influences on parents grown one year and progeny

grown the next. This method also imposes a ceiling of 100% on heritability estimates.

Jenkins (1929) conducted an extensive study dealing with correlations between the inbred parents and their hybrid F_1 progenies for several characteristics in field corn. These correlations are comparable to narrow sense heritability estimates in terms of the standard unit method defined by Frey and Horner (1957). Jenkins (1929) reported correlations of .43 for tassel date, .45 for plant height, .43 for ear length, and .20 for yield.

Robinson et al. (1949) analyzed biparental F_3 progenies derived from three field corn single cross hybrids. Heritabilities in the narrow sense were estimated for several plant and ear characteristics by three methods: (1) components of variance from the analysis of variance, (2) regression of F_3 progenies on the F_2 female parent, and (3) regression of F_3 progenies on the F_2 male parent. Heritability estimates of .70, .43, and .60 for plant height; .55, .41, and .47 for ear height; .50, .72, and .62 for husk extension; .17, .16, and .13 for ear length; and .20, .10, and .16 for yield were obtained by the three methods respectively.

Warner (1952) used both backcrosses and the F_2 generation from two field corn inbreds to estimate heritability in the narrow sense for plant and ear characteristics. Values of .43 for tassel date, .32 for silk date, .56 for number of kernel rows, .32 for ear

length, and .29 for yield were reported.

Giesbrecht (1961) used Warner's method to calculate heritability for ear height in two field corn inbreds and obtained an estimate of .82. Daniel (1965) obtained narrow sense estimates of .73 for number of kernel rows and .26 for ear length using variance components from an analysis of 18 sweet corn lines.

Lush (1949) pointed out that heritability applies to a particular character in a particular population. An estimate of heritability can be altered by changes in either the numerator or the denominator. Since environmental variation enters into the denominator of all heritability estimates, profound differences in the magnitude of heritability estimates for a character in a given population can be obtained from an environment that varies widely compared to an environment that varies slightly. On the other hand, two different populations under equally variable environments may yield extremely different heritability estimates because of differences in the amount of genetic variability for a character present in those populations. It is generally accepted that segregating populations with the greatest range tend to give the highest heritability estimates (Frey and Horner, 1955). Therefore, heritability estimates for a character from different populations or different environments are not directly comparable.

Dudley and Moll (1969) noted that for maximum usefulness, heritability values should be calculated in terms of the type of selection

unit to be used in the selection program for which progress is being predicted. The type of selection to be used and the type of variety to be produced should also determine the type of genetic variance to be included in the numerator of the heritability estimate.

Character Associations

Successful new cultivars of any crop must be superior to existing cultivars for one or more economically important characteristics. The remaining important characters must meet or exceed some threshold level of acceptability. Because of this, selection in a breeding program must be practiced for several characters simultaneously; or at least, when one character is being selected, the effect on other characters must be known.

One approach to this problem is the use of a selection index to consider the economically important characters. Sprague (1966) indicated that the following information is needed for each character to construct a selection index: "(1) relative economic value, (2) genetic and phenotypic variance, and (3) phenotypic and genetic correlations for each pair of traits." In practice, relative economic value of several traits may not be definable. Some informal selection index or an alternate procedure, such as tandem selection, may be of greater value to the breeder in many cases. In any event, knowledge of phenotypic and genotypic correlations between traits will lead to

a more efficient improvement program.

Several workers have reported phenotypic and genetic correlations for plant and ear characters in corn. Hayes and Johnson (1939) calculated phenotypic correlations between characters of 110 field corn inbred lines developed by the pedigree breeding method. Correlation values exceeding 0.19 were significant at the 95 percent level of probability; those exceeding 0.25 were significant at the 99 percent level. The following values were reported: silk date and plant height, .51; silk date and ear height, .61; silk date and ear length, -.06; silk date and grain yield, .07; plant height and ear height, .76; plant height and ear length, .08; plant height and grain yield, .25; ear height and ear length, -.01; ear height and grain yield, .15; and ear length and grain yield, .64.

Robinson, Comstock, and Harvey (1951) calculated correlations between traits of F_3 biparental progenies of field corn. The following phenotypic and genetic correlations, respectively, were reported; plant height and ear height, .749 and .840; plant height and husk extension, .157 and .299; plant height and ear length, .054 and .049; ear height and husk extension, .072 and .157; ear height and ear length, -.058 and .028; and husk extension and ear length, -.254 and -.037. Important genetic associations with yield were established for ears per plant, plant height, and ear height.

Thompson and Rawlings (1960) found a significant phenotypic correlation of .65 between ear height and yield in test cross progenies of 26 field corn inbred lines. Stuber et al. (1966) calculated genetic correlations between traits in a cross of two field corn populations grown in two years and at two locations. Values ranged from .42 to .62 for tassel date and plant height, from .43 to .62 for tassel date and ear height, and from .69 to .82 for plant height and ear height. Hallauer (1968) also reported a strong association between plant height and ear height in field corn.

Snyder (1967) found phenotypic correlations of .233 and .446 between husk extension and tip blanking in 14 sweet and field corn lines grown in two different years. Daniel (1965) reported the following genetic correlations from a diallel analysis of 18 sweet corn lines; silk date and plant height, .443; silk date and ear length, .057; silk date and number of kernel rows, .720; plant height and ear length, .612; plant height and number of kernel rows, .476; and ear length and number of kernel rows, .114.

Reciprocal Differences

Reciprocal crosses are crosses in which the source of male and female gametes are reversed. A reciprocal difference is a differential expression of a trait between progeny of such crosses.

If the parents differ only by chromosomal genes that are not sex linked and preferential segregation of chromosomes does not occur at meiosis, the progeny from such crosses should be identical in phenotype. In such cases, reciprocal differences must be explained in terms of extrachromosomal factors.

Reciprocal differences may be a result of either maternal effects or true cytoplasmic inheritance. Maternal effects arise from the greater contribution of the maternal parent to the embryo during the early stages of development. Cytoplasmic inheritance is conditioned by hereditary factors carried in the cytoplasm. In corn, essentially all of the cytoplasm is contributed by the maternal parent.

Maternal effects would be expected either to disappear after one generation or to appear with a diminished effect in successive generations. Differences caused by cytoplasmic inheritance would be expected to persist undiminished in successive generations.

Reciprocal differences have been assumed to be nonexistent in most plant inheritance studies (Griffing, 1956b). This assumption has been routinely made in many designs of quantitative genetic analysis (Hayman, 1954b; Gardner, 1963). However, recent evidence indicates that reciprocal differences may be a common occurrence for some quantitative characters in corn.

Fleming, Kozelnicky, and Browne (1960) studied the effects of four different cytoplasms on quantitative traits in two double cross

field corn hybrids. Four lots of seed were prepared for each hybrid in which each lot had the same genotype but cytoplasm from a different inbred. Significant cytoplasmic effects were obtained for yield, silk date, ear height, plant height, number of erect plants, and budworm damage. Differential interactions between a given genotype and various cytoplasms were noted. Brown (1961) reported striking reciprocal differences in F_1 hybrids involving the popcorn inbred P2. When P2 was used as the female parent in crosses with four dent corn inbreds and one popcorn line, progenies exhibited defective phenotypes such as reduced plant height, reduced ear size, reduced number of leaves, chlorophyll streaking, and varying degrees of pollen abortion. A substitution of chromosomes from the dent corn inbred, WF9, into the P2 cytoplasm resulted in expression as abnormal as the original F_1 hybrid. The author concluded the abnormal behavior exhibited in crosses, with P2 as the female parent, was due to a factor or factors contained in the cytoplasm of the inbred P2.

Singh (1965 and 1966) studied reciprocal crosses involving nine exotic cytoplasm sources and a corn belt cytoplasm source. Reciprocal differences were detected for tassel date, silk date, plant height, ear height, ear length, and yield. Bhat and Dhawan (1969 and 1970) found reciprocal differences between maize cultivars from different geographic regions in India for maturity, plant height, ear height, and grain yield. Sayed-Galal, Hini, and El-Fattah (1973)

studied reciprocal differences in 112 reciprocal F_1 crosses between two Egyptian open pollinated cultivars and 28 divergent open pollinated cultivars. Each set of reciprocals exhibited significant differences for one or more of the 12 characters studied. Characters studied included tassel date, silk date, plant height, ear height, ear height to plant height ratio, ear length, ear diameter, number of kernel rows, kernel weight, ears per plant, and grain yield. Baynes and Brawn (1973) found significant reciprocal differences for silk date, ear height, plant height, and ear moisture content at harvest in a diallel analysis of eight field corn inbred lines.

The cause of most of these reciprocal differences has been explained by a "plasmon-sensitive genes" hypothesis in which an interaction between the cytoplasm and genome occurs (Bhat and Dhawan, 1971). Abdalla (1974) reviewed these findings and concluded that genome-cytoplasm interactions were only one of several possible explanations. "Maternal effects" was suggested as a more likely explanation in some cases. The possibilities of accidental differences and dauermodifications were also discussed as explanations. Mechanisms of cytoplasmic inheritance as well as other possible explanations for reciprocal differences have been reviewed by Jinks (1964).

MATERIALS AND METHODS

General Procedure

Field experiments were conducted at the sweet corn research farm of Rogers Brothers Seed Company, Nampa, Idaho from 1973 to 1975. Plots were grown on a Baldock loam soil of high fertility. Fertilizer was banded along the row during preplant corrugation each year at the following rates (Kg/hectare): 1973-210.5 N, 120.4 P₂O₅, 120.3 K₂O; 1974-182 N, 119.3 P₂O₅, 75.6 K₂O; 1975 - 120 N, 129.6 P₂O₅, 105 K₂O. An additional 112 Kg/hectare N was plowed down for the 1975 crop.

Moisture was applied by furrow irrigation at intervals required to maintain good plant growth. Weeds were controlled with a preplant application of Alachlor (3.36 Kg/hectare) plus cultivation and hand weeding as required. The corn earworm (Heliothus zea (Boddie)) was controlled with six applications of Methomyl insecticide (.28 Kg/hectar/application) each year. Applications were made at three to four day intervals beginning at mid-silk on the earliest lines.

Measurement of Characters

Plant and ear characters were measured by the criteria and methods described below.

Tassel Date

Tassel date was measured as the number of days from planting until 50 percent of the plants in a plot were shedding pollen. Shedding tassels were counted daily from the beginning of anthesis until the 50 percent figure was reached. A tassel was counted as shedding pollen when anthers were extruded for a linear distance of 3 cm along the main spike.

Silk Date

Silk date was measured as the number of days from planting until 50 percent of the plants in a plot had silked. Plants with silk extended were counted daily from first silk until the 50 percent figure was reached. A plant was counted as silked when silk was visible for a distance of 3 cm beyond the husk leaves of the uppermost ear shoot.

Plant Height

Plant height was measured as the distance in cm from the soil surface to the point of attachment of the lowest lateral tassel branch.

Ear Height

Ear height was measured as the distance in cm from the soil surface to the butt of the uppermost ear.

Shank Length

Shank length was measured as the distance in cm from the butt of the ear to the point of attachment to the stalk.

Husk Extension

Husk extension was measured as the distance in cm from the tip of the ear to the collar attaching the flag leaf of the longest husk sheath. The collar and flag leaf were absent on some ears and the husk sheath terminated in a long tapered point. In these cases, the measurements were made to the midpoint between the longest and next longest husk sheaths. Measurement of husk extension was facilitated by first removing the silk so that a small ruler could be inserted through the husk opening to rest firmly on the tip of the ear.

Tip Blanking

Tip blanking was measured as the distance in cm from the tip of the ear back to the last developed kernels. Ears that were perfectly filled to the tip were measured as zero.

Number of Kernel Rows

Number of kernel rows was measured by an actual count of the number of rows on each ear.

Ear Length

Ear length was measured as the distance in cm from the butt to the tip of the ear, and included any blank tip portions.

Weight of First Ear

The husked, first ears from the ten measured plants in each F_1 and parent plot and from the 20 measured plants in each F_2 plot were bulked and weighed. All weights were expressed as kg/ten ears.

Plant Materials and Chronology of Field Studies

The initial plant material for this study consisted of 20 mis-season, yellow sweet corn inbred lines chosen from the closed pedigree sweet corn inbreds of Rogers Brothers Seed Company. Inclusion in this study was based on subjective ratings for tip blanking and husk extension made in previous years. Inbreds were selected to represent a wide range of expression for tip blanking and husk extension (Table 1).

Six row plots of each inbred were planted in the diallel crossing block in 1973. Rows were 9.14 m long, 81.28 cm apart, and plants were spaced 22.86 cm within rows. Planting dates were adjusted according to maturity to insure that all lines would be tasseling and silking at the same time. The 380 possible crosses, including

Table 1. Degree of inbreeding and previous ratings for tip blanking and husk extension of 20 sweet corn inbred lines included in the diallel crossing block in 1973.

Inbred No.	Inbred Generation	Tip Blanking ^a	Husk Extension ^b
320	S ₁₅	3	4
323	S ₁₅	3	3 - 4
327	S ₁₀	4 - 5	2 - 2.5
328	S ₇	5	2.5 - 3
333	S ₈	2 - 3	2.5
334	S ₁₀	5	4
355	S ₉	3 - 5	4
362-A	S ₇	3 - 4	2.5 - 3
363-A	S ₈	2 - 2.5	5
364	S ₁₀	4	3
368	S ₈	4 - 5	4
368-C	S ₁₃	3 - 4	4
372	S ₁₁	3 - 4	2
372-A	S ₁₁	1 - 4	3
376	S ₇	5	3
379	S ₁₆	3 - 5	3
393-D	S ₉	3 - 4	5
395-B	S ₁₃	5	5
397-A	S ₅	5	2
T42-S	S ₇	1	5

^a Subjective rating scale 1 - 5; 1 = over 2.5 cm. tip blank, 5 = perfect fill over ear tips.

^b Subjective rating scale 1 - 5; 1 = no husk extension - ear protrudes from husk, 5 = husk extension 7.5 cm. beyond ear tip.

reciprocals, between the 20 lines were made by hand pollination. Each cross was replicated four times to insure an adequate supply of F_1 hybrid seed for the experiment. It was assumed that all plants of a particular inbred line were genotypically identical so the same individual plants were not necessarily used in reciprocal crosses. Four plants of each inbred were also self pollinated by hand to provide adequate seed for further analysis of the parents. F_2 seed was obtained by selfing F_1 plants during the summer of 1974.

Tip blanking and husk extension were measured on ten randomly selected plants of each inbred at the table stage of maturity in 1973. Mean values for 18 inbreds are shown in Table 2. Some crosses involving 379 and 393-D failed to yield enough F_1 seed and as a result these inbreds were eliminated from the study.

Because of sample size requirements for F_1 and F_2 analysis, it was necessary to restrict the experiment to seven inbred parents and their progeny. Inbreds were again selected to represent different levels of expression for tip blanking and husk extension based on measurements made in 1973 (Table 2). The following inbreds were selected: 320, 327, 362-A, 368, 372, 376, and T42-S.

In 1974, the seven inbred parents and the 42 single crosses between them, were planted in five replications of a randomized block design. Each plot consisted of a row 457 cm long with plants spaced 22.86 cm within the row. Rows were 81.28 cm apart. Some seeds

Table 2. Mean measurements made in 1973 for tip blanking and husk extension of 18 sweet corn inbred lines.

Inbred	Tip Blanking (cm)	Husk Extension (cm)
320*	2.46	6.84
323	3.29	7.01
327*	.37	1.56
328	.64	6.24
333	3.53	6.30
334	3.08	8.94
355	1.65	5.80
362-A*	3.25	5.55
363-A	2.17	3.00
364	3.13	4.38
368*	1.20	11.30
268-C	3.87	7.57
372*	2.05	2.71
372-A	2.82	4.08
376*	2.85	5.45
395-B	1.69	11.67
397-A	.14	4.75
T42-S*	5.90	7.95
s	0.686	1.205
$s_{\bar{x}}$	0.217	0.381
$s_{\bar{d}}$	0.307	0.539
C. V.	28.07	19.46
Error d. f.	162	162
LSD _{.05}	0.606	1.065

* = Inbreds selected for further study.

did not germinate in the cool, wet weather following planting, and were subsequently replaced to provide equal competition. The replacement plants were not included in the sample for character measurements.

Measurements were made on ten equally competitive plants in each plot. Plant height and ear height were measured ten days past mid-silk. Several plots were remeasured 25 days past mid-silk to confirm that extension growth had been completed at the time of the first measurement. No measurable changes were detected.

The remaining characters were measured at 25 days past mid-silk. Ears at this time were just past the prime edible stage and dimensional ear characters had reached maximum.

Based on a preliminary analysis of 1974 data, the decision was made not to continue the study of reciprocal crosses in 1975. Reasons for this will be discussed in the results and discussion sections. It was also concluded that four replications would be adequate for controlling field error. During the 1974 growing season, it became apparent that the inbred parents could not compete on an equal basis with the more vigorous F_1 hybrids when randomized together in the same block. Because of this, the parents were planted in separate blocks adjacent to the F_1 's and F_2 's in 1975.

The 21 F_1 crosses and the corresponding 21 F_2 's were planted in four replications of a randomized block design in 1975. Each parent

and F_1 plot consisted of a single row 609.6 cm long. Each F_2 plot consisted of two rows 609.6 cm long. An equal distance of 81.28 cm was maintained between rows. All plots were planted double and thinned to a uniform spacing of 22.86 cm within the row. Measurements, as described for 1974, were made on ten equally competitive plants in each parent F_1 plot and on 20 equally competitive plants in each F_2 plot.

Growing conditions were extremely different in 1974 and 1975. In 1974, plots were planted on May 7 which is a normal planting date for the area. Several abnormally cool days followed planting. However, the remainder of the growing season was generally favorable for rapid crop development.

Planting in 1975 was delayed by cool wet weather until May 29; approximately three weeks later than normal. The ensuing growing season included abnormally hot and abnormally cool periods.

Statistical Analysis of Data

Data from 1974 F_1 's were subjected to an analysis of variance as described by Griffing (1956b). Since the parents had been selected and reciprocal F_1 's were included, experimental method three - model I was used. Plot means were used in the analyses of all characters except weight of first ear, for which plot totals were used.

The replication X crosses mean square was used as the error term

to test significance of all other mean squares.

Combining ability effects were calculated by the following formulas:

$$\text{Mean effects } (\hat{\mu}) = \frac{1}{P(P-1)} X_{..}$$

$$\text{GCA effects } (\hat{g}_i) = \frac{1}{2P(P-2)} [P(X_{i.} + X_{.i}) - 2X_{..}]$$

$$\text{SCA effects } (\hat{s}_{ij}) = 1/2(x_{ij} + x_{ji}) - \frac{1}{2(P-2)} (X_{i.} + X_{.i} + X_{.j} + X_{j.}) + \frac{1}{(P-1)(P-2)} X_{..}$$

$$\text{Reciprocal effects } (\hat{r}_{ij}) = 1/2(x_{ij} - x_{ji})$$

where P equals the number of parents, x_{ij} denotes a plot mean, and X denotes a sum as indicated by the subscripts.

Combining ability variances (V) were extracted from mean squares; based on expectations of mean squares for method three - model I (Griffing, 1956b); by the following formulas:

$$V_{\text{GCA}} = \frac{\text{GCA mean square} - \text{reps X crosses mean square}}{2(P-2)(\text{reps})}$$

$$V_{\text{SCA}} = \frac{\text{SCA mean square} - \text{reps X crosses mean square}}{2(\text{reps})}$$

$$V_{\text{reciprocals}} = \frac{\text{reciprocals mean square} - \text{reps X crosses mean square}}{2(\text{reps})}$$

Additive genetic covariances were derived as follows:

1. An analysis of covariance was calculated for each pair of characters.

2. The reps X crosses mean square obtained from this analysis was subtracted from the GCA mean square and the resulting value was divided by $2(P-2)(\text{reps})$.
3. The GCA variances for each character individually were then subtracted from this value and the result divided by two, to yield the additive genetic covariance ($\text{COV}_{\text{GCA}_{1,2}}$) for these two characters.

Genotypic correlations were calculated from components of variance and covariance by the formula:

$$r_{\text{GCA}_{1,2}} = \frac{\text{COV}_{\text{GCA}_{1,2}}}{\left(\sqrt{V_{\text{GCA}_1}}\right)\left(\sqrt{V_{\text{GCA}_2}}\right)}$$

Genotypic correlations were calculated from parent-offspring regressions by the formula (Hazel, 1943):

$$r_{G_{1,2}} = \sqrt{\frac{(b_{o_1 p_2})(b_{o_2 p_1})}{(b_{o_1 p_1})(b_{o_2 p_2})}}$$

where G is the additive genetic component corresponding to GCA, $b_{o_1 p_2}$ is the regression coefficient of character 1 of the offspring (o) on character 2 of the parent (p), etc. Offspring family means and mid-parent values were used to calculate the regression coefficients. Phenotypic correlations were calculated by the standard method using the mean of all replications for each line or family.

Narrow sense heritability estimates were calculated from variance components using the following formula:

$$H = \frac{2V_{GCA}}{2V_{GCA} + V_{SCA} + V_{reciprocals} + V_E}$$

This formula was suggested by Rojas and Sprague (1952). According to Gardner (1963), V_{GCA} equals one-half of the additive genetic effects and V_{SCA} equals all of the non-additive genetic effects in the F_1 when homozygous lines are used.

After the decision was made to discontinue the study of reciprocal crosses, data on reciprocal F_1 's were omitted and the 1974 data reanalyzed. Method four - model I (Griffing, 1956b) was used for this analysis and also for the analyses of 1975 F_1 and F_2 data.

Effects were estimated as follows:

$$\text{Mean effects } (\hat{\mu}) = \frac{2}{P(P-1)} X_{..}$$

$$\text{GCA effects } (\hat{g}_i) = \frac{1}{P(P-2)} [pX_{i.} - 2X_{..}]$$

$$\text{SCA effects } (\hat{s}_{ij}) = x_{ij} - \frac{1}{P-2} (X_{i.} + X_{j.}) + \frac{2}{(P-1)(P-2)} X_{..}$$

Combining ability variance were extracted from the expected mean squares as follows:

$$V_{GCA} = \frac{\text{GCA mean square} - \text{reps X crosses mean square}}{(P-2)(\text{reps})}$$

$$V_{SCA} = \frac{\text{SCA mean square} - \text{reps X crosses mean square}}{\text{reps}}$$

Average SCA effects for series of crosses involving individual lines were determined by:

$$V_{s_i} = \frac{1}{P-2} \sum_{j \neq i} \hat{s}_{ij}^2 \frac{P-3}{P-2} V_E$$

Comparable values for GCA effects were calculated by:

$$V_{g_i} = (\hat{g}_i)^2 - \frac{P-1}{P(P-2)} V_E$$

Additive genetic covariances were obtained as previously described except the quantity, $2(P-2)(\text{reps})$, was replaced by $(P-2)(\text{reps})$. Genotypic and phenotypic correlations were also determined as previously described.

The formula, $H = \frac{2V_{GCA}}{2V_{GCA} + V_{SCA} + V_E}$, was used to obtain

narrow sense heritability estimates from variance components of F_1 data. Variance components from F_2 data were used to obtain narrow sense heritability estimates by the formula:

$$H = \frac{2V_{GCA}}{2V_{GCA} + 4V_{SCA} + V_E}$$

This formula is based on Allard's (1960) statement that the variance of an F_2 segregating for many genes is equal to one-half of the additive effects plus one quarter of the non-additive effects plus the experimental error. Thus, the coefficients of two and four are assigned to the variance components of GCA and SCA, respectively, to obtain a ratio of additive genetic variation to total variation. Regressions of F_2 on F_1 and F_1 on mid-parent were also used to estimate the heritability of each character.

The interactions of GCA and SCA with years were evaluated by a combined analysis of 1974 and 1975 F_1 data. The combined analysis was patterned after those described by Rojas and Sprague (1952) and Matzinger et al. (1959). Because of the extreme differences between growing seasons and the later-than-normal planting date in 1975, years were considered as fixed. The expectations of mean squares used to derive components of variance and covariance are shown below.

Source	d. f.	Expectations of mean squares
Years (y)	1	
GCA	6	$V_E + ry(P-2)V_{GCA}$
SCA	14	$V_E + ryV_{SCA}$
Years X GCA	6	$V_E + r(P-2)V_{GCA \cdot y}$
Years X SCA	14	$V_E + rV_{SCA \cdot y}$
Reps (r) within years	7	
Error	140	V_E

EXPERIMENTAL RESULTS

Performance of Inbred Parents

Parental means for each character in 1974 are shown in Table 3. The seven parents encompassed a wide range of expression for all characters measured. Table 4 shows mean squares from the analysis of variance for each character. Line differences were significant at the .01 level for all characters.

Similar results were obtained in 1975 (Table 5, and Table 6). Mean squares from a combined analysis of the two years data are shown in Table 7. The significant differences between years were expected because of the extreme differences in growing conditions during the two seasons. The significance of the year X line interaction for most characters was probably enhanced by the differential competition provided by adjacent F_1 plots in 1974 versus the separate blocking of inbreds in 1975.

Performance of F_1 Crosses (Preliminary Analysis with Reciprocals)

Mean values for the ten measured characters of each F_1 in 1974 are shown in Table 8. Corresponding values for reciprocal F_1 crosses are shown in Table 9. Mean squares from the diallel analysis of variance (Griffing, (1956b) method three - model I) for each

Table 3. Mean values for ten characters measured on seven sweet corn inbred lines in 1974.

Line	Tassel Date	Silk Date	Plant Height (cm)	Ear Height (cm)	Shank Length (cm)	Husk Extension (cm)	Tip Blanking (cm)	Row Number	Ear Length (cm)	Weight of First Ear (kg)
320	72.6	77.2	166.24	91.74	6.312	6.054	2.232	13.62	16.282	1.5956
327	74.4	79.4	199.86	77.14	12.180	4.680	.088	15.84	15.862	1.7364
362-A	81.2	90.8	172.06	94.98	10.786	7.256	5.108	21.34	17.474	1.6062
368	82.0	87.8	155.26	68.90	5.558	9.562	.282	18.26	12.800	1.5612
372	78.6	81.0	197.42	110.34	15.730	1.352	1.690	16.32	19.114	2.0698
376	81.0	84.4	179.22	73.32	8.634	7.402	2.778	16.64	17.564	1.8824
T42-S	82.4	87.0	163.82	93.76	10.570	7.908	4.498	10.60	15.868	.8562
s	1.050	1.563	6.487	3.880	1.168	.496	.278	.494	.603	.1480
s _x	.470	.699	2.901	1.735	.522	.222	.124	.221	.270	.0662
s _d	.664	.988	4.103	2.454	.739	.314	.176	.312	.382	.0936
C.V. (%)	1.34	1.86	3.68	4.45	11.72	7.85	11.67	3.07	3.67	9.16
LSD _{.05}	1.37	2.04	8.47	5.06	1.524	.648	.362	.645	.788	.1932
LSD _{.01}	1.86	2.76	11.48	6.86	2.066	.878	.491	.874	1.067	.2628

Table 4. Mean squares from the analyses of variance for ten characters of seven sweet corn inbred lines grown in 1974.

Source	df	Tassel Date	Silk Date	Plant Height	Ear Height	Shank Length	Husk Extension	Tip Blanking	Row Number	Ear Length	Weight of First Ear
Reps	4	.688	5.543	121.620*	53.593*	5.237*	.127	.058	.132	.730	.0466
Lines	6	79.495**	121.848**	1439.370**	1073.650**	61.433**	35.434**	18.533**	57.442**	19.514**	.7268**
Rep x Line	24	1.102	2.443	42.083	15.056	1.364	.246	.077	.244	.364	.0219

* ** Significant at .05 and .01 level of probability, respectively.

Table 5. Mean values for ten characters measured on seven sweet corn inbred lines in 1975.

Line	Tassel Date	Silk Date	Plant Height (cm)	Ear Height (cm)	Shank Length (cm)	Husk Extension (cm)	Tip Blanking (cm)	Row Number	Ear Length (cm)	Weight of First Ear (kg)
320	60.5	67.2	138.60	79.85	6.345	8.190	1.660	13.85	16.892	1.9988
327	61.5	68.8	172.75	66.50	12.712	6.430	.095	17.35	15.330	1.5950
362-A	67.5	76.0	166.22	88.50	12.990	5.175	3.120	20.45	18.558	2.1760
368	70.5	75.5	136.38	61.50	9.205	11.015	.670	17.65	12.885	1.5738
372	65.8	69.0	169.78	98.20	15.628	1.292	1.430	14.95	19.938	1.9915
376	68.8	73.2	162.28	66.68	10.010	6.755	2.568	16.05	18.478	2.0485
T42-S	71.0	80.0	140.78	77.18	13.170	10.385	4.728	9.95	15.238	.8010
s	.837	.713	4.726	2.804	1.118	.573	.195	.506	.313	.0823
s \bar{x}	.458	.356	2.363	1.402	.559	.286	.097	.253	.157	.0412
s \bar{d}	.647	.504	3.342	1.982	.790	.405	.138	.358	.222	.0582
C. V. (%)	1.26	0.98	3.04	3.64	9.78	8.14	9.57	3.21	1.87	4.73
LSD .05	1.359	1.059	7.022	4.164	1.660	.851	.290	.752	.466	.1223
LSD .01	1.862	1.451	9.618	5.704	2.274	1.166	.397	1.030	.639	.1675

Table 6. Mean squares from the analyses of variances for ten characters of seven sweet corn inbred lines grown in 1975.

Source	df	Tassel Date	Silk Date	Plant Height	Ear Height	Shank Length	Husk Extension	Tip Blanking	Row Number	Ear Length	Weight of First Ear
Reps	3	.810	.702	10.196	15.881	.216	.231	.064	.131	.171	.0067
Lines	6	69.250**	87.476**	1020.030**	697.932**	38.366**	43.518**	9.896**	44.160**	23.782**	.8972**
Rep x Line	18	.837	.508	22.333	7.861	1.249	.328	.038	.256	.098	.0068

* **, Significant at .05 and .01 level of probability, respectively.

Table 7. Mean squares from the combined analyses of variance for ten characters of seven sweet corn inbred lines grown in 1974 and 1975.

Source	df	Tassel Date	Silk Date	Plant Height	Ear Height	Shank Length	Husk Extension	Tip Blanking	Row Number	Ear Length	Weight of First Ear
Years	1	2286.26 **	1924.01 **	6869.80 **	1635.67 **	33.61 **	8.03 **	1.84 **	1.78 *	1.76 *	.24 **
Lines	6	146.83 **	196.63 **	2318.43 **	1741.25 **	95.36 **	72.65 **	27.03 **	99.62 **	42.20 **	1.46 **
Year x Line	6	1.91	12.69 **	140.98 **	30.32 *	4.44 **	6.30 **	1.40 **	1.98 **	1.09 **	.16 **
Reps within Years	7	.74	3.47	73.87	37.43 **	3.08 *	.17	.06	.13	.49	.03
Error	42	.99	1.61	33.62	11.97	1.31	.28	.06	.25	.25	.015

* **, Significant at .05 and .01 level of probability, respectively.

Table 8. Mean values for ten characters measured on 21 F₁ Sweet corn hybrids grown in 1974.

Cross	Tassel Date	Silk Date	Plant Height (cm)	Ear Height (cm)	Shank Length (cm)	Husk Extension (cm)	Tip Blanking (cm)	Row Number	Ear Length (cm)	Weight of First Ear (kg)
320 x 327	70.8	75.6	211.88	96.20	13.570	3.414	.878	15.84	21.342	2.9596
320 x 362-A	70.6	76.0	214.30	112.52	13.040	1.370	1.660	17.48	21.320	3.0390
320 x 368	71.6	75.6	202.36	98.26	11.728	6.002	1.376	15.84	19.850	2.6706
320 x 372	71.0	75.0	224.08	119.90	16.190	1.516	2.144	14.40	22.478	3.0164
320 x 376	72.8	76.4	227.72	112.86	13.740	2.222	2.134	15.68	21.760	2.9314
320 x T42-S	74.2	79.8	197.24	114.30	21.040	4.772	1.734	12.98	19.308	2.2340
327 x 362-A	73.0	78.0	220.20	106.26	15.306	2.598	.500	18.48	21.978	3.0788
327 x 368	74.0	78.2	193.20	80.22	12.246	4.280	.252	18.40	18.838	2.6594
327 x 372	69.8	76.2	206.64	96.02	23.128	1.236	.188	16.96	22.826	3.1128
327 x 376	75.0	78.6	222.02	96.74	15.522	3.276	.466	15.80	21.662	2.9086
327 x T42-S	73.8	79.0	207.68	105.84	20.864	3.902	.852	13.84	20.050	2.2566
362-A x 368	75.0	80.2	195.62	99.42	15.790	6.858	.540	21.24	19.138	3.0164
362-A x 372	76.4	82.4	213.50	116.34	21.970	2.648	2.076	20.24	19.936	2.4098
362-A x 376	75.4	80.6	223.12	103.34	18.258	2.442	2.464	19.04	23.158	3.2150
362-A x										
T42-S	75.0	81.8	206.74	117.58	18.152	2.820	2.142	17.00	22.324	2.7612
368 x 372	74.2	78.6	212.70	106.78	15.518	4.050	1.682	18.76	20.380	2.9824
368 x 376	77.0	80.6	202.56	81.40	9.102	4.108	1.336	17.88	19.230	2.4948
368 x										
T42-S	77.8	83.6	199.72	115.04	15.032	8.176	1.416	15.48	18.138	2.2058
372 x 376	75.6	79.6	224.18	112.00	18.806	.140	2.302	17.92	22.710	2.8464
372 x										
T42-S	74.0	79.6	228.90	136.48	23.604	1.642	1.916	15.00	23.468	2.5798
376 x										
T42-S	76.2	80.8	217.12	111.36	18.624	4.492	1.118	14.56	20.970	2.4326
s	1.185	1.181	5.753	5.069	1.846	.472	.321	.513	.401	.1241
s _x	.530	.528	2.573	2.267	.826	.211	.144	.229	.179	.0555
s _d	.749	.747	3.638	3.206	1.167	.298	.203	.324	.253	.0785
C.V. (%)	1.60	1.50	2.71	4.75	11.04	13.77	23.11	3.05	1.91	4.51
LSD .05	1.491	1.486	7.240	6.380	2.322	.593	.404	.645	.503	.1562
LSD .01	1.976	1.971	9.597	8.457	3.078	.786	.536	.855	.667	.2071

Table 9. Mean values for ten characters measured on 21 reciprocal F_1 Sweet corn hybrids grown in 1974.

Crosses	Tassel Date	Silk Date	Plant Height (cm)	Ear Height (cm)	Shank Length (cm)	Husk Extension (cm)	Tip Blanking (cm)	Row Number	Ear Length (cm)	Weight of First Ear (kg)
327 x 320	70.4	74.6	212.32	97.30	15.554	2.870	.606	15.80	21.980	2.9656
362-A x 320	72.0	76.6	216.02	116.60	13.344	2.888	1.608	17.24	21.022	2.9822
368 x 320	72.8	77.6	195.22	94.80	13.042	5.566	1.112	15.72	19.730	2.6592
372 x 320	70.0	74.6	224.14	121.94	15.328	.878	2.006	15.36	22.130	2.9426
376 x 320	73.4	76.4	228.04	116.36	14.916	2.134	2.120	15.32	22.350	2.9372
T42-S x 320	74.2	78.2	209.12	126.38	18.902	5.094	2.090	13.16	19.380	2.0978
362-A x 327	72.2	78.4	211.18	97.70	16.528	3.410	.224	19.48	21.272	3.0448
368 x 327	75.8	80.6	193.46	83.06	10.166	4.932	.202	17.36	19.150	2.6196
372 x 327	70.2	76.0	215.06	98.54	20.414	1.468	.158	17.24	22.056	3.0788
376 x 327	75.4	79.6	214.82	89.00	11.288	2.646	.670	16.48	21.786	2.8124
T42-S x 327	73.6	78.2	203.66	107.28	20.428	2.546	.342	14.56	20.894	2.3870
368 x 362-A	77.2	81.6	199.66	108.20	15.226	4.382	1.254	22.28	19.252	2.8574
372 x 362-A	76.4	83.2	207.72	117.18	22.686	2.460	2.398	19.28	20.822	2.5176
376 x 362-A	76.2	81.0	226.74	107.18	17.632	2.506	2.758	20.00	22.984	3.1810
T42-5 x										
362-A	76.4	82.4	218.48	126.84	17.598	3.988	2.702	18.76	21.192	2.5684
372 x 368	72.6	77.2	206.66	102.88	17.002	3.784	1.550	18.80	20.394	3.0958
376 x 368	76.6	79.8	199.12	83.60	11.448	4.098	1.086	17.96	19.368	2.6252
T42-5 x 368	76.4	82.2	194.40	112.66	16.670	7.340	1.424	15.16	18.536	2.2058
376 x 372	75.0	78.6	222.18	112.06	17.430	.300	1.778	17.48	22.734	2.8578
T42-5 x 372	74.4	80.0	225.92	133.46	23.006	1.286	1.756	15.16	23.348	2.7272
T42-5 x 376	77.4	81.4	225.38	119.04	18.744	5.098	1.698	15.12	20.658	2.3586

character are shown in Table 10. Crosses were significantly different at the .01 level for all characters. Thus, variation due to crosses was partitioned into general combining ability (GCA), specific combining ability (SCA), and reciprocal effects. Both GCA and SCA were significant for all characters at the .01 level. This indicates that both additive and non-additive genetic variation are involved in the inheritance of these characters. Significant differences between reciprocal crosses for all characters except weight of the first ear were indicated by the analysis.

Reciprocal Differences

Differences between reciprocal means for the nine characters showing significant differences in the analyses of variance are shown in Table 11. Since the difference between the mean of any F_1 cross and the mean of its reciprocal constitutes a single degree-of-freedom comparison, the LSD test was used to detect significant differences between reciprocal means of individual crosses.

Reciprocal differences at the .05 level were found for one or more characters in each cross except 372 x T42-S. The crosses 362-A x 368 and 362-A x T42-S showed significant reciprocal differences for the largest number of characters (six each) while the crosses 320 x 327, 320 x 368, 320 x 376, 362-A x 376, 368 x 376, and 372 x 376 showed significant reciprocal differences for the fewest

Table 10. Mean squares from the diallel analyses of variance (method 3 - model I) for ten characters of 21 F₁ and 21 reciprocal F₁ sweet corn hybrids grown in 1974.

Source	df	Tassel Date	Silk Date	Plant Height	Ear Height	Shank Length	Husk Extension	Tip Blanking	Row Number	Ear Length	Weight of First Ear
Reps	4	3.183 *	6.424 **	122.619 *	41.976	3.966	.252	.004	.716	.167	.0696 **
Crosses	41	25.563 **	29.738 **	603.942 **	897.500 **	67.764 **	16.589 **	2.879 **	22.966 **	10.676 **	.4649 **
GCA	6	136.246 **	159.816 **	3027.295 **	5353.574 **	359.796 **	90.262 **	15.760 **	145.280 **	50.410 **	1.9844 **
SCA	14	12.322 **	14.154 **	333.046 **	224.470 **	33.907 **	7.128 **	1.246 **	3.038 **	8.715 **	.4770 **
Reciprocals	21	2.767 **	2.962 **	92.153 **	73.024 **	6.897 **	1.846 **	.286 **	1.305 **	.631 **	.0226
Error	164	1.186	1.094	40.186	26.399	3.139	.221	.105	.302	.146	.0171

* , ** Significant at .05 and .01 level of probability, respectively.

Table 11. Differences between reciprocal means (F_1 mean minus reciprocal F_1 mean) for nine characters of 21 F_1 and 21 reciprocal F_1 sweet corn hybrids grown in 1974.

F_1	Reciprocal F_1	Tassel Date	Silk Date	Plant Height	Ear Height	Shank Length	Husk Extension	Tip Blanking	Row Number	Ear Length
320 x 327	- 327 x 320	.4	1.0	-.44	-1.10	-1.984	.544	.264	.04	-.638**
320 x 362-A	- 362-A x 320	-1.4*	-.6	-1.72	-4.08	-.304	-1.518**	.052**	.24	.298
320 x 368	- 368 x 320	-1.2	-2.0**	7.14	3.38	-1.314	.436	.264	.12	.120
320 x 372	- 372 x 320	1.0	-.4	-.06	-2.04	.862	.638*	.138	-.96**	.348
320 x 376	- 376 x 320	-.6	0.0	-.32	-3.50	-1.176	.088	.014	.36	-.590*
320 x T42-S	- T42-S x 320	0.0	1.6*	-11.88**	-12.08**	2.138	-.322	-.356	-.18	-.072
327 x 362-A	- 362-A x 327	.8	-.4	9.02*	8.56**	-1.222	-.812**	.276	-1.00**	.706**
327 x 368	- 368 x 327	-1.8**	-2.4**	-.26	-2.84	2.080	-.652*	.050	1.04**	-.312
327 x 372	- 372 x 327	-.4	.2	-8.42*	-2.52	2.714*	-.232	.030	-.28	.770**
327 x 376	- 376 x 327	-.4	-1.0	6.40	7.74*	4.234**	.630*	-.204	-.68	-.124
327 x T42-S	- T42-S x 327	.2	-.8	4.02	-1.44	.436	1.356**	.510*	-.72*	-.844**
362-A x 368	- 368 x 362-A	-2.2**	-1.4*	-4.04	-8.78**	.564	2.476**	-.714**	-1.04**	-.114
362-A x 372	- 372 x 362-A	0.0	-.8	5.78	-.84	-.716	.188	-.322	.96**	-.886**
362-A x 376	- 376 x 362-A	-.8	-.4	-3.62	-3.84	.626	-.064	-.294	-.96**	.174
362-A x T42-S	- T42-S x 362-A	-1.4*	-.6	-11.74**	-9.26**	.554	-1.168**	-.560**	-1.76	1.132
368 x 372	- 372 x 368	1.6*	1.4*	6.04	3.90	-1.484	.266	.132	-.04	.014
368 x 376	- 376 x 368	.4	.8	3.44	-2.20	-2.346*	.010	.250	-.08	-.138
368 x T42-S	- 368 x T42-S	1.4*	1.4*	5.32	2.38	-1.638	.836**	-.008	.32	-.398
372 x 376	- 376 x 372	.6	1.0	2.00	-.06	1.376	-.160	.524*	.44	-.024
372 x T42-S	- T42-S x 372	-.4	-.4	2.98	3.02	.598	.256	.160	.16	.120
376 x T42-S	- T42-S x 376	-1.2	-.6	-8.26*	-7.68*	-.120	.606*	-.580**	-.56	.312
s^2_d		.689	.662	4.009	3.250	1.121	.297	.204	.348	.248
LSD .05		1.360	1.307	7.918	6.417	2.213	.587	.404	.686	.478
LSD .01		1.795	1.725	10.451	8.471	2.921	.774	.533	.906	.630

*, ** Significant reciprocal difference at the .05 and .01 level of probability, respectively.

characters (one each). Significant differences were found in the largest number of crosses (ten) for husk extension and in the smallest number of crosses (three) for shank length.

The largest reciprocal difference for each character was as follows: tassel date, 2.2 days; silk date, 2.4 days; plant height, 11.88 cm; ear height, 12.08 cm; shank length, 4.234 cm; husk extension, 2.476 cm; tip blanking, .714 cm; number of kernel rows, 1.76 rows; and ear length, .886 cm. The magnitude of these differences, for most characters, is large enough to be of economic importance. The differences for some characters, e.g. husk extension and tip blanking, are large enough to have a significant influence on whether or not an F_1 hybrid would be commercially acceptable.

The cause of these reciprocal differences can not be definitely established in this experiment. Differences may be due to cytoplasmic inheritance, maternal effects, or artifacts in experimental procedure. Since the same individual plants were not involved in a reciprocal cross and all plots of each cross were established from seed of an individual ear, reciprocal differences could have arisen from small plant to plant genotypic differences within an inbred line. Because of this, results from a second years data would still be inconclusive.

The main objective of this study was to determine the relative importance of additive versus non-additive genetic variance for each

of the ten characters. It was concluded that more useful information would be gained by increasing the sample size of the F_2 generation than from obtaining a second year's data on reciprocal differences. Thus, the study of reciprocal crosses was discontinued. However, the preliminary finding of reciprocal differences with potential economic significance points out the need for a detailed study of this phenomenon in the future.

Performance of F_1 Crosses

Data on reciprocal F_1 crosses were removed and the 1974 F_1 data were reanalyzed using method four - model I (Griffing, 1956b). Mean squares from the analysis of variance for each character are shown in Table 12. The purposes of this reanalysis were to establish a common basis with 1975 data and to facilitate a combined analysis over years.

Table 13 shows mean values for each character of the 21 F_1 crosses in 1975. Mean squares from the diallel analysis of variance (Griffing, 1956b, method four - model I) for each character are shown in Table 14. GCA and SCA were both significant at the .01 level for all characters. These results are in agreement with 1974 results.

A diallel analysis of variance was calculated for each character on combined F_1 data from 1974 and 1975. Mean squares from these analyses are shown in Table 15. Both GCA and SCA were significant

Table 12. Mean squares from the diallel analyses of variance (method 4 - model I) for ten characters of 21 F₁ sweet corn hybrids grown in 1974.

Source	df	Tassel Date	Silk Date	Plant Height	Ear Height	Shank Length	Husk Extension	Tip Blanking	Row Number	Ear Length	Weight of First Ear
Reps	4	2,033	4.105*	86.958*	38.599	3.274	.410	.029	.842**	.097	.0176
Crosses	20	24,572**	29,007**	600.013**	830.606**	77.108**	19.121**	2.608**	22.987**	12.301**	.4944**
GCA	6	63.619**	78.027**	1355.477**	2296.347**	208.061**	50.783**	6.745**	71.925**	26.908**	1.0065**
SCA	14	7.838**	7.998**	276.242**	202.432**	20.985**	5.552**	.836**	2.014**	6.041**	.2749**
Error	80	1.403	1.395	33.098	25.698	3.407	.223	.103	.263	.160	.0154

*, ** Significant at .05 and .01 level of probability, respectively.

Table 13. Mean values for ten characters measured on 21 F1 sweet corn hybrids grown in 1975.

Cross	Tassel Date	Silk Date	Plant Height (cm)	Ear Height (cm)	Shank Length (cm)	Husk Extension (cm)	Tip Blanking (cm)	Row Number	Ear Length (cm)	Weight of First Ear (kg)
320 x 327	58.8	63.2	207.38	101.55	11.830	4.278	.610	15.55	21.850	2.8350
320 x 362-A	60.0	66.8	209.12	106.12	11.390	2.072	1.380	18.60	21.948	3.2250
320 x 368	60.0	65.8	191.80	94.65	9.115	5.300	1.305	17.10	20.325	2.7002
320 x 372	58.8	62.8	217.20	120.80	13.110	.835	1.528	15.05	22.375	2.9128
320 x 376	60.2	66.2	218.78	109.75	12.735	3.012	1.832	15.95	22.232	3.0192
320 x T42-S	61.8	69.5	191.20	109.70	16.132	6.450	2.295	13.10	19.628	2.2678
327 x 362-A	61.0	68.0	208.45	99.38	12.502	4.482	.470	21.60	21.068	3.0758
327 x 368	62.0	66.5	186.58	85.78	8.228	5.538	.222	19.80	18.425	2.5092
327 x 372	59.8	64.0	215.22	107.15	16.160	1.660	.102	18.15	22.270	3.1468
327 x 376	61.8	67.2	219.75	91.30	13.250	4.605	.288	18.00	21.508	3.0405
327 x T42-S	62.0	69.8	197.95	101.28	20.285	6.248	1.105	15.45	20.088	2.2892
362-A x 368	63.5	69.8	192.02	96.15	11.430	7.010	1.030	22.35	18.805	2.8702
362-A x 372	64.0	70.2	207.18	114.72	16.312	2.770	1.512	20.25	20.000	2.4732
362-A x 376	64.5	72.0	214.08	101.98	14.618	2.532	2.540	20.10	23.000	2.9978
362-A x T42-S	63.2	72.2	203.15	106.72	15.830	6.062	3.538	17.95	21.300	2.6295
368 x 372	63.8	69.0	206.15	98.88	14.518	3.788	1.340	19.40	20.910	3.0898
368 x 376	66.8	70.2	197.45	82.88	9.508	4.588	1.138	17.75	19.502	2.6650
368 x T42-S	67.0	75.8	190.85	94.42	11.778	8.630	1.690	15.65	18.202	2.1475
372 x 376	64.5	68.0	222.28	123.55	14.915	1.735	1.942	17.25	21.862	2.7358
372 x T42-S	63.0	71.0	221.32	131.45	21.690	2.832	2.642	15.15	23.740	2.6510
376 x T42-S	66.5	72.8	211.52	114.15	16.510	6.755	1.942	14.65	20.522	2.3742
s	.738	.866	5.421	4.234	1.267	.462	.240	.503	.337	.1281
s _x	.369	.433	2.710	2.117	.634	.231	.120	.251	.168	.0640
s _d	.522	.613	3.833	2.994	.896	.326	.170	.356	.238	.0906
C.V. (%)	1.18	1.26	2.63	4.06	9.12	10.64	16.55	2.86	1.61	4.66
LSD _{.05}	1.044	1.226	7.666	5.988	1.792	.652	.340	.712	.476	.1812
LSD _{.01}	1.388	1.631	10.196	7.964	2.383	.867	.452	.947	.633	.2410

Table 14. Mean squares from the diallel analyses of variance (method 4 - model I) for ten characters of 21 F₁ sweet corn hybrids grown in 1975.

Source	df	Tassel Date	Silk Date	Plant Height	Ear Height	Shank Length	Husk Extension	Tip Blanking	Row Number	Ear Length	Weight of First Ear
Source	3	3,345**	3,567**	95,340*	46,388	2,338	.126	.034	.310	.435*	.0364
Crosses	20	25,012**	43,214**	509,126**	593,141**	45,948**	17,280**	3,030**	23,735**	9,015**	.3977**
GCA	6	74,695**	132,531**	1412,826**	1759,443**	129,985**	50,404**	8,453**	77,022**	18,866**	.8240**
SCA	14	3,719**	4,936**	121,826**	93,297**	9,933**	3,084**	.706**	.898**	4,792**	.2150**
Error	60	.545	.751	29,385	17,926	1,606	.213	.058	.253	.113	.0164

*,** Significant at .05 and .01 level of probability, respectively.

Table 15. Mean squares from the combined analyses of variance (method 4 - model I) for ten characters of 21 F₁ sweet corn hybrids grown in 1974 and 1975.

Source	df	Tassel Date	Silk Date	Plant Height	Ear Height	Shank Length	Husk Extension	Tip Blanking	Row Number	Ear Length	Weight of First Ear
Years	1	6118,117**	4912,032**	1576,447**	228,908**	373,183**	39,085**	.172	27,192**	.180	.0026
Crosses	20	47,696**	69,333**	1059,470**	1280,376**	112,708**	33,889**	5,125**	45,035**	20,394**	.8518**
GCA	6	137,849**	202,705**	2742,271**	3803,206**	323,706**	95,564**	13,968**	146,279**	44,018**	1,8040**
SCA	14	9,060**	10,313**	338,270**	199,163**	22,281**	7,456**	1,335**	1,645**	10,270**	.4437**
Years x Crosses	20	1,937*	4,466**	39,570	116,987**	6,886**	2,308**	.561**	1,771**	.556**	.0296*
GCA x Years	6	1,696	9,566**	32,404	192,929**	5,665	5,580**	1,420**	3,234**	.863**	.0063
SCA x Years	14	2,040*	2,281*	42,642	84,440**	7,409**	.906**	.193**	1,144**	.425**	.0396**
Reps within years	7	2,596*	3,874**	90,550**	41,937	2,873	.289	.031	.614*	.242	.0257
Error	140	1,036	1,119	31,507	22,367	2,635	.219	.084	.259	.140	.0158

*, ** Significant at .05 and .01 level of probability, respectively.

at the .01 level for all characters. These results reaffirm the conclusion that both additive and non-additive genetic effects are involved in the inheritance of these characters.

Performance of F₂ Families

F₂ families, derived from selfing each F₁, were evaluated in 1975. Mean values for each of the ten measured characters are shown in Table 16. Mean squares from the diallel analyses of variance (model four - method I) are shown in Table 17. GCA mean squares were significant at the .01 level for all characters. SCA mean squares were significant at the .01 level for all characters except tip blanking; which was significant at the .05 level.

Relative Importance of GCA and SCA

Estimates of the components of variance for GCA and SCA were derived from the expectations of mean squares (Griffing, 1956b). These components for each character from the 1974, 1975, and combined F₁ analyses, and the 1975 F₂ analysis are shown in Table 18. Ratios of V_{SCA}/V_{GCA} are shown in Table 19 and provide a measure of the relative importance of GCA and SCA. Values less than one indicate a greater importance of GCA in the determination of that character. Increasing values indicate an increasing importance of SCA and a value of one suggests equal contributions of GCA and SCA.

Table 16. Mean values for ten characters measured on 21 F₂ sweet corn families grown in 1975.

Family Derived From Cross	Tassel Date	Silk Date	Plant Height (cm)	Ear Height (cm)	Shank Length (cm)	Husk Extension (cm)	Tip Blanking (cm)	Row Number	Ear Length (cm)	Weight of First Ear (kg)
320 x 327	61.2	67.0	189.30	94.08	8.802	5.788	.970	16.05	18.470	2.1690
320 x 362-A	61.5	69.5	189.32	96.35	9.340	3.938	1.940	18.50	18.395	2.5053
320 x 368	63.0	69.8	179.68	90.85	7.855	7.578	1.630	16.88	17.235	2.1440
320 x 372	61.8	67.2	200.25	115.38	10.630	2.785	1.570	14.70	19.690	2.3495
320 x 376	62.2	68.5	204.55	100.78	8.655	4.150	1.772	16.18	19.115	2.2473
320 x T42-S	65.0	73.0	177.60	105.08	14.790	8.280	2.875	12.75	16.770	1.6053
327 x 362-A	63.5	70.5	190.20	90.65	11.455	3.272	1.128	19.85	18.810	2.2255
327 x 368	63.2	68.0	174.65	75.70	7.935	6.180	.375	18.52	16.522	2.0378
327 x 372	61.2	68.2	183.48	81.40	15.192	2.398	.695	16.98	20.630	2.4235
327 x 376	63.5	68.2	204.05	86.92	11.320	6.468	.820	16.98	18.288	2.1935
327 x T42-S	65.5	73.8	185.12	93.88	16.575	6.228	2.138	14.62	17.480	1.7470
362-A x 368	65.8	72.8	176.48	86.70	11.010	8.120	1.910	21.32	16.778	2.2848
362-A x 372	66.0	72.2	198.15	111.38	17.310	2.708	1.835	19.28	18.650	2.0130
362-A x 376	66.2	73.0	203.30	94.55	12.790	3.930	2.022	19.95	19.062	2.4593
362-A x T42-S	67.5	77.0	193.95	107.32	15.965	6.570	3.162	15.85	18.532	1.9280
368 x 372	64.0	69.0	188.62	93.30	11.265	4.718	1.222	17.98	17.985	2.1015
368 x 376	68.0	72.2	182.58	74.35	8.600	5.850	.920	17.68	17.042	2.1300
368 x T42-S	68.8	78.0	166.75	83.00	11.818	10.558	2.200	14.85	15.680	1.5523
372 x 376	65.8	69.2	204.45	105.35	14.402	1.795	1.960	17.00	20.348	2.3003
372 x T42-S	64.8	73.0	199.25	116.98	18.118	4.195	2.538	14.48	20.745	2.1335
376 x T42-S	68.0	75.0	201.25	103.10	15.508	7.690	2.672	13.82	18.085	1.7225
s	.726	.938	4.870	4.401	1.013	.601	.273	.521	.437	.1140
s _x	.363	.469	2.435	2.201	.506	.301	.136	.260	.218	.0570
s _d	.513	.663	3.443	3.112	.716	.425	.193	.368	.309	.0806
C.V.(%)	1.12	1.32	2.56	4.60	8.20	11.15	15.77	3.09	2.39	5.41
LSD .05	1.026	1.326	6.886	6.224	1.432	.850	.386	.736	.618	.1612
LSD .01	1.364	1.764	9.158	8.278	1.904	1.130	.513	.979	.822	.2144

Table 17. Mean squares from the diallel analyses of variance (method 4 - model I) for ten characters of 21 F₂ sweet corn families grown in 1975.

Source	df	Tassel Date	Silk Date	Plant Height	Ear Height	Shank Length	Husk Extension	Tip Blanking	Row Number	Ear Length	Weight of First Ear
Reps	3	.302	1.663	33.270	3.987	1.118	.657	.007	.882*	.119	.0104
Crosses	20	21.987**	39.490**	507.483**	584.777**	42.866**	20.967**	2.229**	19.862**	7.494**	.2882**
GCA	6	64.495**	123.190**	1390.036**	1645.135**	131.170**	60.280**	7.042**	64.206**	20.330**	.7153**
SCA	14	3.769**	3.619**	129.245**	130.337**	5.021**	4.119**	.166*	.857**	1.992**	.1051**
Error	60	.526	.879	23.714	19.370	1.026	.362	.075	.271	.191	.0130

*, ** Significant at .05 and .01 level of probability, respectively.

Table 18. Components of GCA and SCA Variance (V) for ten characters of sweet corn.

Character	1974 F ₁ analysis		1975 F ₁ analysis		Combined F ₁ analysis		1975 F ₂ analysis	
	V _{GCA}	V _{SCA}	V _{GCA}	V _{SCA}	V _{GCA}	V _{SCA}	V _{GCA}	V _{SCA}
Tassel Date	2.489	1.287	3.708	.793	1.520	.446	3.198	.811
Silk Date	3.096	1.321	6.589	1.046	2.240	.511	6.116	.685
Plant Height	52.895	48.629	69.172	23.110	30.120	17.042	68.316	26.383
Ear Height	90.826	35.347	87.076	18.843	42.009	9.822	81.288	27.742
Shank Length	8.186	3.516	6.419	2.082	3.568	1.091	6.507	.999
Husk Extension	2.022	1.066	2.510	.718	1.059	.402	2.996	.939
Tip Blanking	.266	.146	.420	.162	.154	.070	.348	.024
Number of kernel rows	2.866	.350	3.838	.161	1.622	.077	3.197	.146
Ear Length	1.070	1.176	.938	1.170	.488	.563	1.007	.450
Weight of First Ear	.040	.052	.040	.050	.020	.024	.035	.023

Table 19. Ratio of SCA variance to GCA variance $\left(\frac{V_{SCA}}{V_{GCA}}\right)$ for ten characters in sweet corn.

Character	1974 F ₁ analysis	1975 F ₁ analysis	Combined F ₁ analysis	1975 F ₂ analysis
	V _{SCA} /V _{GCA}	V _{SCA} /V _{GCA}	V _{SCA} /V _{GCA}	V _{SCA} /V _{GCA}
Tassel Date	.517	.214	.293	.253
Silk Date	.426	.158	.228	.112
Plant Height	.919	.334	.566	.386
Ear Height	.389	.216	.234	.341
Shank Length	.429	.324	.306	.153
Husk Extension	.527	.286	.380	.314
Tip Blanking	.551	.387	.450	.066
Number of Kernel Rows	.123	.042	.047	.045
Ear Length	1.098	1.248	1.154	.447
Weight of First Ear	1.311	1.228	1.196	.656

Values greater than one indicate that SCA is relatively more important than GCA for that character.

GCA was more important than SCA for all characters in the F_1 generation except ear length and weight of the first ear. SCA was least important in the inheritance of number of kernel rows and became increasingly more important in the inheritance of characters such as plant height, shank length, husk extension, and tip blanking. SCA was relatively more important than GCA in the determination of ear length and weight of the first ear.

GCA in relation to SCA, in the F_1 generation, was relatively more important for most characters in 1975 than in 1974. However, the reverse was true for ear length.

The ratio of V_{SCA} / V_{GCA} was expected to be smaller in the F_2 generation because of the loss of non-additive gene action accompanying inbreeding. This was found to be the case for silk date, shank length, tip blanking, ear length, and weight of the first ear. However, this reduction was not observed for the other characters and in some cases, the ratio was substantially larger than in the corresponding F_1 .

The failure of the variance ratios for some characters to respond as expected in the F_2 analysis may be caused by a larger contribution of the genotype-environment interaction to SCA variance than to GCA variance as demonstrated in the combined F_1 analysis. Inadequate sampling of F_2 families (in which plants, with a preponderance of heterozygous loci for those characters, were

unintentionally selected for evaluation) could also contribute to the discrepancy.

Ratios of SCA variance to GCA variance are in general agreement with data on heterosis and inbreeding depression (Tables 20, 21, and 22). Heterosis and inbreeding depression were observed for all characters; reflecting the significant contribution of SCA variance to their expression. Substantial heterosis occurred for ear length and weight of the first ear in agreement with the large proportion of SCA variance associated with these characters. The least heterosis and smaller ratios of SCA variance to GCA variance occurred for number of kernel rows, tassel date, and silk date. These results confirm the large contribution of GCA variance to these characters.

Some characters, such as husk extension, exhibited considerably more heterosis and inbreeding depression, percentagewise, than would have been expected based on SCA to GCA variance ratios. This may be the result of an interaction between metrical components of a character. For example, husk extension in the F_1 may be largely predictable based on the parents and their performance in a series of crosses. Minor deviations from this additive scheme would result in a relatively low proportion of SCA variance. However, heterosis for longer ears would result in a higher average expression of heterosis for less husk extension when the F_1 is compared to the mean of the parents.

Table 20. Heterosis for ten characters of 21 F₁¹ sweet corn crosses measured in 1974.

Cross	Tassel Date	Silk Date	Plant Height	Ear Height	Shank Length	Husk Extension	Tip Blanking	Row Number	Ear Length	Weight of First Ear
Direction of Heterosis	Earlier	Earlier	Taller	Higher	Longer	Less	Less	Higher	Longer	Heavier
320 x 327	3.7	3.5	15.7	13.9	46.8	36.4	24.4	7.5	32.8	77.6
320 x 362-A	8.2	9.6	26.7	20.5	52.5	79.5	54.8	0.0	26.3	89.8
320 x 368	7.4	8.4	25.9	22.3	97.6	23.2	-9.4	-0.7	36.5	69.2
320 x 372	5.0	5.2	23.2	18.7	46.9	59.1	-9.3	-3.8	27.0	64.6
320 x 376	5.3	5.5	31.8	36.8	83.9	67.0	14.9	3.6	28.6	68.6
320 x T42-S	4.3	2.9	19.5	23.2	149.3	31.7	48.5	7.2	20.1	82.2
327 x 362-A	6.2	8.4	18.4	23.5	33.3	56.5	80.8	-0.6	31.8	84.2
327 x 368	5.4	6.5	8.8	9.9	38.1	39.9	-36.2	7.9	31.4	61.3
327 x 372	7.7	5.0	4.0	2.4	65.7	59.1	78.9	5.5	30.5	63.6
327 x 376	3.5	4.1	17.1	28.6	49.1	45.8	67.5	-2.7	29.6	60.7
327 x T42-S	5.9	5.1	14.2	23.9	83.4	28.1	62.9	4.7	26.4	74.1
362-A x 368	8.1	10.2	19.5	21.3	93.2	18.5	80.0	7.3	26.4	90.5
362-A x 372	3.3	4.1	15.6	13.3	65.7	38.5	39.0	7.5	9.0	31.1
362-A x 376	7.1	8.0	27.0	22.8	88.0	66.7	37.6	0.3	32.2	84.3
362-A x T42-S	8.4	8.0	23.1	24.6	70.0	62.9	55.5	6.4	33.9	124.3
368 x 372	6.6	6.9	20.6	19.1	45.8	25.8	-70.1	8.5	27.7	64.3
368 x 376	5.6	6.4	21.1	14.5	28.3	51.6	12.7	2.5	26.7	44.9
368 x T42-S	5.4	4.4	25.2	41.4	86.4	6.4	40.8	7.3	26.5	82.5
372 x 376	4.2	3.8	19.0	22.0	54.4	96.9	-3.0	8.7	23.8	44.0
372 x T42-S	7.1	5.3	26.7	33.7	79.5	64.6	38.1	11.4	34.2	76.3
376 x T42-S	6.8	5.8	26.6	33.3	94.0	41.4	69.3	6.9	25.4	77.6
Average	3.7	6.0	20.3	22.3	67.8	45.7	58.3	4.4	27.8	70.4

¹ Percent of F₁ mean above mid parent.

Table 21. Heterosis¹ for ten characters of 21 F₁ sweet corn crosses measured in 1975.

Cross	Tassel Date	Silk Date	Plant Height	Ear Height	Shank Length	Husk Extension	Tip Blanking	Row Number	Ear Length	Weight of First Ear
Direction of Heterosis	Earlier	Earlier	Taller	Higher	Longer	Less	Less	Higher	Longer	Heavier
320 x 327	3.6	7.1	33.2	38.8	24.2	41.5	30.5	-0.3	35.6	57.7
320 x 362-A	6.2	6.7	37.2	26.1	17.8	69.0	42.3	8.4	23.8	54.5
320 x 368	8.4	7.8	39.5	33.9	17.2	44.8	-12.0	8.6	36.5	51.2
320 x 372	7.0	7.8	40.9	35.7	19.3	82.4	1.1	4.5	21.5	46.0
320 x 376	6.8	5.7	45.4	49.8	55.7	59.7	13.3	6.7	25.7	49.2
320 x T42-5	6.1	5.6	36.9	39.7	65.3	30.6	28.2	10.1	22.2	62.0
327 x 362-A	5.4	6.1	23.0	28.2	-2.7	22.8	70.8	14.3	24.3	63.1
327 x 368	6.1	7.9	20.7	34.0	-24.9	36.5	41.9	13.1	30.6	58.4
327 x 372	6.0	7.1	25.7	30.1	14.0	57.0	86.6	12.4	26.3	75.5
327 x 376	5.2	5.4	31.2	37.1	16.6	30.2	78.4	7.8	27.2	66.9
327 x T42-5	6.4	6.2	26.3	41.0	56.7	25.7	54.2	13.2	31.4	91.1
362-A x 368	8.0	7.9	26.9	28.2	3.0	13.4	45.6	17.3	19.6	53.1
362-A x 372	3.9	3.2	23.3	22.9	14.0	14.4	33.5	14.4	3.9	18.7
362-A x 376	5.4	3.5	30.3	31.4	27.1	57.6	10.7	10.1	24.2	41.9
362-A x T42-S	8.7	7.4	32.3	28.8	21.0	22.1	9.8	18.1	26.0	76.6
368 x 372	6.5	4.4	34.7	23.8	16.9	38.4	-27.6	19.0	27.4	73.3
368 x 376	4.0	5.6	32.2	29.3	-1.0	48.4	29.7	5.3	24.3	47.1
368 x T42-5	5.4	2.6	37.7	36.2	5.3	19.4	37.4	13.4	29.4	80.8
372 x 376	4.2	4.4	33.9	49.9	16.4	56.9	2.9	11.3	13.8	35.4
372 x T42-5	7.9	4.7	42.5	49.9	50.6	51.5	15.0	21.7	35.0	89.9
376 x T42-S	4.9	5.0	39.6	58.7	42.4	21.5	46.8	12.7	21.7	64.5
Average	6.0	5.8	32.8	30.6	21.5	38.2	28.9	11.5	24.9	57.7

¹ Percent of F₁ mean above mid parent.

Table 22. Inbreeding depression¹ for ten characters of 21 F₂ sweet corn families measured in 1975.

Cross	Tassel Date	Silk Date	Plant Height	Ear Height	Shank Length	Husk Extension	Tip Blanking	Row Number	Ear Length	Weight of First Ear
320 x 327	4.1	6.0	8.7	7.4	25.6	35.3	59.0	-3.2	15.5	23.5
320 x 362-A	2.5	4.0	9.5	9.2	18.0	90.1	40.6	0.6	16.2	22.3
320 x 368	5.0	6.1	6.3	4.0	13.8	43.0	24.9	1.3	15.2	20.6
320 x 372	5.1	7.0	7.8	4.5	18.9	233.5	2.7	2.3	12.0	19.3
320 x 376	3.3	3.5	6.5	8.2	32.0	37.8	-3.3	-1.4	14.0	25.6
320 x T42-S	5.2	5.0	7.1	4.2	8.3	28.4	28.3	2.7	14.6	29.2
327 x 362-A	4.1	3.7	8.8	8.8	8.4	27.0	140.0	8.1	10.7	27.6
327 x 368	1.9	2.3	6.4	11.8	3.6	-11.6	68.9	6.5	10.3	18.8
327 x 372	2.3	6.6	14.7	24.0	6.0	-44.4	581.4	6.4	7.4	23.0
327 x 376	2.8	1.5	7.2	4.8	14.6	-40.4	184.7	5.7	15.0	27.9
327 x T42-S	5.6	5.7	6.5	7.3	18.3	0.3	93.5	5.4	13.0	23.7
362-A x 368	3.6	4.3	8.1	9.8	3.7	-15.8	85.4	4.6	10.8	20.4
362-A x 372	3.1	2.8	4.4	2.9	-6.1	2.2	21.4	4.8	6.7	18.6
362-A x 376	2.6	1.4	5.0	7.3	12.5	55.2	-20.4	0.8	17.1	18.0
362-A x T42-S	6.8	6.6	4.5	-0.6	-0.8	8.4	-10.6	11.7	13.0	26.7
368 x 372	0.3	0.0	8.5	5.6	22.4	24.6	-8.8	7.3	14.0	32.0
368 x 376	1.8	2.8	7.5	10.3	9.6	27.5	-19.2	0.4	12.6	20.1
368 x T42-S	2.7	2.9	12.6	12.1	-0.3	22.3	30.2	5.1	13.9	17.7
372 x 376	2.0	1.8	8.0	14.7	3.4	3.4	0.9	1.4	6.9	15.9
372 x T42-S	2.8	2.8	10.0	11.0	16.5	48.1	-3.9	4.4	12.6	19.5
376 x T42-S	2.3	3.0	4.9	9.7	6.1	13.8	37.6	5.7	11.9	27.4
Average	3.3	3.8	7.8	4.9	11.1	24.1	19.4	4.0	12.6	23.2

¹ Percent of F₂ mean below F₁ mean.

A differential response of the inbred parents and the vigorous F_1 's to the environment would also lead to a difference between the level of heterosis expressed and that expected based on variance ratios.

Interactions of GCA and SCA with Years

The combined analysis of 1974 and 1975 F_1 data (Table 15) was used to study the interactions of GCA and SCA with years for each character. GCA by years was significant at the .01 level for silk date, ear height, husk extension, tip blanking, number of kernel rows, and ear length. SCA by years was significant at the .01 level for ear height, shank length, tip blanking, number of kernel rows, ear length, and weight of the first ear and at the .05 level for tassel date and silk date.

Mean squares for the interactions of GCA and years were generally much smaller than mean squares for GCA main effects and even though most interactions were statistically significant, the interpretation of main effects is probably not significantly affected. Mean squares for the interactions of SCA and years, in some cases, were relatively large in relation to mean squares for SCA main effects. Interpretations of SCA effects must be viewed with this in mind.

The relationship between GCA and SCA over years can be evaluated by comparing the ratio of $V_{GCA \cdot y} / V_{GCA}$ to the ratio

of $V_{SCA \cdot y} / V_{SCA}$ (Table 23). For most characters, the ratio of $V_{SCA \cdot y} / V_{SCA}$ is substantially larger than the ratio of $V_{GCA \cdot y} / V_{GCA}$. This indicates that a substantial portion of the genotype by year interaction is contained in the estimate of SCA.

Combining Ability Effects

The breeding value of each parent for each character can be evaluated by estimating the combining ability effects. Each F_1 or F_2 mean value is a linear function of the effects defined by method four - model I (Griffing, 1956b). The linear function is $x_{ij} = \hat{u} + \hat{g}_i + \hat{g}_j + \hat{s}_{ij}$ where x_{ij} is the cross mean value, \hat{u} is the population mean, \hat{g}_i is the GCA effect for one parent, \hat{g}_j is the GCA effect for the other parent, and \hat{s}_{ij} is the SCA effect for the cross. Maximum expression of a character can be achieved by identifying two parents each with large GCA effects in the desirable direction and a large SCA effect in the same direction. For example, an earlier silk date is desirable and maximum earliness would be identified in the cross between the two parents with the largest negative GCA effects and a large negative SCA effect.

GCA effects for each character of each of the seven parents are presented in Tables 24, 25, 26, and 27 and identified from 1974 F_1 's, 1975 F_1 's, combined F_1 's, and 1975 F_2 's, respectively. The most important effects are those that exceed their standard errors by two

Table 23. Variance components for GCA x Years and SCA x Years interactions and their ratios with GCA and SCA, respectively.

Character	$V_{GCA \cdot y}$	$\frac{V_{GCA \cdot y}}{V_{GCA}}$	$V_{SCA \cdot y}$	$\frac{V_{SCA \cdot y}}{V_{SCA}}$
Tassel Date	.015	.010	.112	.251
Silk Date	.188	.084	.129	.252
Plant Height	.020	.001	1.235	.072
Ear Height	3.790	.090	6.897	.702
Shank Length	.067	.019	.530	.486
Husk Extension	.119	.112	.076	.189
Tip Blanking	.030	.195	.012	.171
Number of Kernel Rows	.066	.041	.098	1.273
Ear Length	.016	.033	.032	.057
Weight of First Ear	0.0 ¹	-	.003	.125

¹ Negative variance component (-.0002) set to zero.

Table 24. Estimates of GCA effects for ten characters derived from the analyses of 21 F₁ sweet corn crosses grown in 1974.

Parent	Tassel Date	Silk Date	Plant Height	Ear Height	Shank Length	Husk Extension	Tip Blanking	Row Number	Ear Length	Weight of First Ear
\bar{x}	73.962	78.867	211.980	106.610	16.725	3.427	1.389	16.801	20.994	2.7529
320	-2.554**	-2.960**	+1.146	+2.873	-2.209*	-.253	+3.18*	-1.717**	+0.019	+0.0667
327	-1.474**	-1.520**	-2.046	-11.679**	+0.057	-.371	-1.040**	-.297	+0.147	+0.0917
362-A	+0.326	+1.160*	+0.326	+3.157	+0.433	-.365	+0.209	+2.535**	+0.379*	+0.2005**
368	+1.166*	+0.720	-13.138**	-11.711**	-4.187**	+2.583**	-.347*	+1.359**	-2.077**	-.0976
372	-.554	-.360	+7.630**	+9.569	+3.773**	-1.866**	+0.394*	+0.495*	+1.167**	+0.0860
376	+1.646**	+0.680	+8.974**	-4.395*	-1.260	-.776**	+0.297*	+0.015	+0.706**	+0.0623
T42-S	+1.444*	+2.280**	-2.892	+12.186**	+3.393**	+1.048**	+0.169	-2.390**	-.341*	-.4096**
$\text{Var}(\hat{g}_i - \hat{g}_j)$.561	.558	13.239	10.279	1.363	.089	.041	.105	.064	.0062
$\text{SE}(\hat{g}_i - \hat{g}_j)$.749	.747	3.638	3.206	1.167	.298	.202	.324	.253	.0787
$\text{Var}(\hat{g}_i)$.241	.239	5.674	4.405	.585	.038	.018	.045	.028	.0026
$\text{SE}(\hat{g}_i)$.490	.489	2.382	2.099	.765	.195	.133	.212	.166	.0515

*, ** Exceeds its standard error by two and three or more times, respectively.

Table 25. Estimates of GCA effects for ten characters derived from the analyses of 21 F_1 sweet corn crosses grown in 1975.

Parent	Tassel Date	Silk Date	Plant Height	Ear Height	Shank Length	Husk Extension	Tip Blanking	Row Number	Ear Length	Weight of First Ear
\bar{x}	62.512	68.607	206.160	104.400	13.897	4.342	1.450	17.564	20.931	2.7455
320	-3.114 **	-3.479 **	-.301	+3.238	-1.814 **	-.821 **	+.050	-2.007 **	+.554 **	+.0974
327	-1.964 **	-2.579 **	-.331	-7.992 **	-.226	+.152	-1.181 **	+.633 **	-.076	+.0847
362-A	+.236	+1.471 **	-.596	-.262	-.260	-.224	+.354 **	+3.093 **	+.106	+.1597 **
368	+1.586 **	+1.071 *	-14.426 **	-14.727 **	-3.762 **	+1.760 **	-.395 **	+1.333 **	-1.884 **	-.0982
372	-.264	-1.329 **	+10.474 **	+14.033 **	+2.664 **	-2.486 **	+.073	-.027	+1.114 **	+.1073 *
376	+1.836 **	+.971 *	+9.374 **	-.557	-.370	-.565 *	+.196	-.337	+.608 **	+.0719
T42-S	+1.684 **	+3.874 **	-4.194	+6.267 **	+3.768 **	+2.184 **	+.903 **	-2.688 **	-.422 **	-.4228 **
$\text{Var}(\hat{g}_i - \hat{g}_j)$.2181	.3003	11.7540	7.1705	.6424	.0852	.0231	.1012	.0454	.00656
$\text{SE}(\hat{g}_i - \hat{g}_j)$.4670	.5480	3.4284	2.6778	.8015	.2919	.1518	.3181	.2131	.08099
$\text{Var}(\hat{g}_i)$.093	.129	5.037	3.073	.275	.036	.010	.043	.019	.0028
$\text{SE}(\hat{g}_i)$.306	.359	2.244	1.753	.525	.191	.099	.208	.139	.0530

*, ** Exceeds its standard error by two and three or more times, respectively.

Table 26. Estimates of GCA effects for ten characters derived from the combined analyses of 21 F₁ sweet corn crosses grown in 1974 and 1975.

Parent	Tassel Date	Silk Date	Plant Height	Ear Height	Shank Length	Husk Extension	Tip Blanking	Row Number	Ear Length	Weight of First Ear
\bar{x}	68.237	73.737	209.069	105.505	15.311	3.884	1.420	17.183	20.962	2.7492
320	-2.834**	-3.219**	+.422	+3.056	-2.012*	-.537*	+.184	-1.862**	+.286	+.0820
327	-1.719**	-2.049**	-1.188	-9.836**	-.084	-.110	-1.110**	+.168	+.035	+.0882
362-A	+.281	+1.316**	-.135	+1.448	+.086	-.295	+.282	+2.814**	+.242	+.1801**
368	+1.376**	+.896*	-13.782**	-13.219**	-3.974**	+2.171**	-.371**	+1.346**	-1.980**	-.0979
372	-.409	-.844	+9.052**	+11.801**	+3.218**	-2.176**	+.234	+.234	+1.140**	+.0966
376	+1.741**	+.826	+9.174**	-2.467	-.815	-.670**	+.246*	-.161	+.657**	+.0671
T42-S	+1.564**	+3.074**	-3.543	+9.217**	+3.581**	+1.617**	+.535**	-2.539**	-.380*	-.4161**
$\text{Var}(\hat{g}_i - \hat{g}_j)$.414	.448	12.603	8.947	1.054	.087	.033	.104	.056	.0063
$\text{SE}(\hat{g}_i - \hat{g}_j)$.644	.669	3.550	2.991	1.027	.296	.183	.322	.237	.0796
$\text{Var}(\hat{g}_i)$.178	.192	5.401	3.834	.452	.037	.014	.044	.024	.0027
$\text{SE}(\hat{g}_i)$.421	.438	2.324	1.958	.672	.194	.120	.211	.155	.0521

*, ** Exceeds its standard error by two and three or more times, respectively.

Table 27. Estimates of GCA effects for ten characters derived from the analyses of 21 F₂ sweet corn crosses grown in 1975.

Parent	Tassel Date	Silk Date	Plant Height	Ear Height	Shank Length	Husk Extension	Tip Blanking	Row Number	Ear Length	Weight of First Ear
\bar{x}	64.595	71.202	190.140	95.575	12.349	5.390	1.731	16.867	18.301	2.1082
320	-2.564**	-2.443**	-.030	+5.810**	-2.805**	+.035	+.074	-1.230**	-.026	+.0742
327	-1.864**	-2.293**	-2.810	-10.165**	-.563	-.402	-.852**	+.360	+.079	+.0294
362-A	+.586	+1.557**	+2.110	+2.700	+.755	-.761**	+.322	+2.710**	+.085	+.1533**
368	+1.036**	+.507	-14.420**	-13.910**	-3.123**	+2.132**	-.426**	+1.205**	-1.712**	-.0798
372	-.814*	-1.643**	+6.670**	+10.065**	+2.564**	-2.749**	-.113	-.160	+1.649**	+.1344*
376	+1.236**	-.193	+11.865**	-1.680	-.564	-.492	-.044	+.080	+.427*	+.0807
T42-S	+2.384**	+4.508**	-3.385	+7.180**	+3.736**	+2.237**	+1.039**	-2.965**	-.502*	-.3922**
$\text{Var}(\hat{g}_i - \hat{g}_j)$.211	.352	9.485	7.748	.410	.145	.030	.108	.076	.0052
$\text{SE}(\hat{g}_i - \hat{g}_j)$.459	.593	3.080	2.784	.641	.380	.173	.329	.276	.0721
$\text{Var}(\hat{g}_i)$.090	.151	4.065	3.321	.176	.062	.013	.046	.033	.0022
$\text{SE}(\hat{g}_i)$.300	.388	2.016	1.822	.419	.249	.113	.216	.181	.0472

*, ** Exceeds its standard error by two and three or more times, respectively.

and three or more times and are identified in the tables. Sign of an effect is important and desirable effects for each character are in the following directions: tassel date and silk date - negative effects identify earliness; plant height and ear height - negative effects identify shorter plants and lower ear set; shank length - negative effects identify shorter shanks; husk extension - positive effects identify better husk coverage; tip blanking - negative effects identify better tip filling; number of kernel rows - positive effects identify higher row number; ear length and weight of first ear - positive effects identify longer and heavier ears.

For each character (except husk extension) it was possible to identify a single parent which excelled in both years. In the case of husk extension, 368 transmitted the greatest husk extension in the 1974 F_1 's and the combined F_1 's but was exceeded by T42-S in the 1975 F_1 's and F_2 's. The ranking of GCA effects for each character, with minor exceptions, was similar in both years and both generations. However, in most cases, the parent with the largest desirable effect for each character and the ranking of parents could be established by examining parental means.

These results confirm the stability of GCA in different environments, suggested by the combined F_1 analysis. They also emphasize the major role of GCA in the inheritance of these characters.

SCA effects for each character for each cross are presented in Tables 28, 29, 30, and 31. Desirable effects are in the same direction as described for GCA effects. Relatively few SCA effects exceeded their standard errors by two or three or more times. More large SCA effects were measured in the F_1 generation than in the F_2 . This was expected because of the rapid loss of non-additive gene action associated with inbreeding. Large SCA effects were more numerous for those characters exhibiting the most heterosis and large SCA variances in relation to GCA variances.

No crosses were identified as consistently having the largest desirable SCA effect in different years and different generations. Ranking of crosses for SCA effects were also inconsistent and in some cases the sign of an effect differed from year to year and generation to generation. These results correspond with the relatively large SCA X years interaction found for most characters in the combined F_1 analysis.

Average SCA of a series of crosses involving one parent can be compared with that of a different parent by calculating variances of SCA effects. These values can also be compared with variances of GCA effects and errors of plot means. Such data for the combined F_1 's are shown in Table 32.

Variances of GCA effects were generally positive with a majority exceeding the variances of plot means by several times. Many of the

Table 28. Estimates of SCA effects for ten characters derived from the analyses of 21 F₁ sweet corn crosses grown in 1974.

Crosses	Tassel Date	Silk Date	Plant Height	Ear Height	Shank Length	Husk Extension	Tip Blanking	Row Number	Ear Length	Weight of First Ear
320 x 327	+ .867	+1.213	+ .805	-1.607	-1.004	-.611**	+ .211	+1.053*	+ .182	+ .0483
320 x 362-A	-1.133	-1.067	+ .853	-.123	-1.910	-1.439**	-.257	-.139	-.071*	+ .0189
320 x 368	-.973	-1.027	+2.377	+ .485	+1.399	+ .246	+ .015	-.603	+ .915	-.0514
320 x 372	+ .147	-.547	+3.329	+ .845	-2.100	+ .208	+ .042	-1.179*	+ .298	+ .1108
320 x 376	-.253	-.187	+5.625*	+7.769	+ .483*	-.176	+ .130	+ .581	+ .041**	+ .0495
320 x T42-S	+1.347	+1.613	-12.991*	-7.371	+3.131*	+ .550	-.142	+ .285	-1.364**	-.1761
327 x 362-A	+ .187	-.507	+9.945*	+8.169	-1.909	-.093	-.059	-.559	+ .459	+ .0337
327 x 368	+ .347*	+ .133	-3.591*	-3.003*	-.349	-1.358**	+ .249*	+ .537	-.225	-.0875
327 x 372	-2.133*	-.787	-10.919*	-8.483*	+2.573	+ .046*	-.556*	-.039	-.518	+ .1822
327 x 376	+ .867	+ .573	+3.117	+6.201	-.0003	+ .996*	-.180	-.719	-.184	+ .0018
327 x T42-S	-.133	-.627	+ .642	-1.279	+ .689	-.202**	+ .334*	-.275	+ .286	-.1785
362-A x 368	-.453	-.547*	-3.543	+1.361	+2.819	+1.214**	-.712	+ .545	-.157**	+ .1606
362-A x 372	+2.667*	+2.733*	-6.431	-2.999	+1.039	+1.452**	+ .083*	+ .409	-2.604**	-.6297**
362-A x 376	-.533	-.107	+1.845	-2.035	+2.360	+ .156**	+ .569	-.311	+1.080**	+ .1993
362-A x T42-S	-.733	-.506	-2.670	-4.375	-2.399	-1.290**	+ .375	+ .053	+1.293**	+ .2173*
368 x 372	-.373	-.627	+6.233	+2.309*	-.793	-.094*	+ .245	+ .105	+2.965**	+ .2411*
368 x 376	+ .227	+ .333	-5.251	-9.107*	-2.176	-1.125*	-.003	-.295	-.392**	-.2228*
368 x T42-S	+1.227	+1.733	+3.774	+7.953	-.899	+1.118*	+ .205	-.291	-3.106**	-.0400
372 x 376	+ .546	+ .414	-4.398*	+ .214	-.432	-.645*	+ .221	+ .609	-1.789**	-.0548
372 x T42-S	-.853	-1.187	+12.185*	+8.113	-.287	-.9676*	-.036*	+ .093	+1.648**	+ .1504
376 x T42-S	-.853	-1.027	-.939	-3.043	-.235	+ .7928*	-.737	+ .133	+1.244**	+ .0269
SE($\hat{s}_{ij} - \hat{s}_{ik}$)	1.498	1.494	7.277	6.412	2.335	.597	.406	.649	.507	.1572
(i ≠ j, k; j ≠ k)										
SE($\hat{s}_{ij} - \hat{s}_{kl}$)	1.298	1.294	6.302	5.553	2.022	.517	.352	.562	.439	.1361
(i ≠ j, k, l; j ≠ k, l; k ≠ l)										
Var(\hat{s}_{ij})	.936	.930	22.066	17.132	2.272	.1486	.0687	.175	.107	.0103
SE(\hat{s}_{ij})	.967	.964	4.697	4.139	1.507	.385	.262	.419	.327	.1015

*, ** Exceeds its standard error by two and three or more times, respectively.

Table 29. Estimates of SCA effects for ten characters derived from the analyses of 21 F₁ sweet corn crosses grown in 1975.

Crosses	Tassel Date	Silk Date	Plant Height	Ear Height	Shank Length	Husk Extension	Tip Blanking	Row Number	Ear Length	Weight of First Ear
320 x 327	+1.317*	+.700	+1.843	+1.907	-.027	+.605**	+.291*	-.640	+.441	-.0926*
320 x 362-A	+.367	+.150	+3.858	-1.248	-.433	-1.224	-.474*	-.050	+.356*	+.2224*
320 x 368	-.983	-.450	+.363	+1.742	+.794	+.019	+.200	+.210	+.724*	-.0444
320 x 372	-.383	-1.050	+.863	-.868	-1.637	-.200	-.046	-.480	-.224	-.0374
320 x 376	-.983	+.150	+3.538	+2.672	+1.022	+.056	+.136	+.730	+.140**	+.1044
320 x T42-S	+.667**	+.500	-10.467*	-4.203	+.281	+.744	-.107	+.230	-1.436**	-.1524
327 x 362-A	+2.167**	+.500	+3.213	+3.232	-.909	+.213	-.153	+.310	+.106	+.0858*
327 x 368	-.133	-.600	-4.832	+4.097	-1.682	-.716	+.348	+.270	-.546	-.2228*
327 x 372	-.533	-.700	-1.082	-3.288	-.176	-.347	-.240	-.020	+.301	+.2093*
327 x 376	-.633	+.250	+4.543	-4.548	-.052	+.676	-.178	+.140	+.044	+.1384
327 x T42-S	-.233	-.150	-3.687	-1.399	+2.845*	-.431**	-.067	-.060	-.346	-.1182
362-A x 368	-.833	-1.400*	+.883	+6.742	+1.555	+1.132**	-.379	+.360	-.349	+.0632**
362-A x 372	+1.517*	+1.500*	-8.867*	-3.443	+.011	+1.139**	-.365*	-.380	-2.152**	-.5392**
362-A x 376	-.083	+.950*	-.867	-1.603	+1.350	-1.020*	+.540*	-.220	+1.354**	+.0206
362-A x T42-S	-1.183	-1.700*	+1.778	-3.679	-1.575	-.240	+.831**	-.020	+.684*	+.1470*
368 x 372	-.083	+.650	+3.938	-4.828	+1.718	+.172*	+.212	+.530	+.748*	+.3352**
368 x 376	+.817*	-.400**	-3.662	-6.238	-.258*	-.950*	-.114	-.810	-.153	-.0542
368 x T42-S	+1.217*	+2.200**	+3.308	-1.514	-2.126*	+.343	-.267	-.560	-.424*	-.0770
372 x 376	+.417	-.250	-3.736*	+5.676	-1.276	+.444**	+.223	+.050	-.790**	-.1889*
372 x T42-S	-.933	-.150	+8.883*	+6.752	+1.360	-1.208**	+.217*	+.300	+2.116**	+.2210*
376 x T42-S	+.467	-.700	+.183	+4.042	-.786	+.793*	-.606**	+.110	-.595*	-.0204
SE($\hat{\sigma}_{ij}^2 - \hat{\sigma}_{ik}^2$) (i ≠ j, k; j ≠ k)	.934	1.096	6.857	5.356	1.603	.584	.304	.636	.426	.1620
SE($\hat{\sigma}_{ij}^2 - \hat{\sigma}_{kl}^2$) (i ≠ j, k, l; j ≠ k, l; k ≠ l)	.809	.949	5.938	4.638	1.388	.506	.263	.551	.369	.1403
Var($\hat{\sigma}_{ij}^2$)	.363	.501	19.590	11.951	1.071	.142	.038	.169	.076	.0109
SE($\hat{\sigma}_{ij}^2$)	.603	.707	4.426	3.457	1.035	.377	.196	.411	.275	.1046

*, ** Exceeds its standard error by two and three or more times, respectively.

Table 30. Estimates of SCA effects for ten characters derived from the combined analyses of 21 F₁ sweet corn crosses grown in 1974 and 1975.

Crosses	Tassel Date	Silk Date	Plant Height	Ear Height	Shank Length	Husk Extension	Tip Blanking	Row Number	Ear Length	Weight of First Ear
320 x 327	+1.092	+.957	+1.324	+.150	-.515	+.608**	+.251	+.207	+.312	-.0221
320 x 362-A	-.383	-.458	+2.356	-.686	-1.171	-1.331**	-.365	-.094	+.142*	+.1206
320 x 368	-.978	-.738	+1.370	+1.114	+1.096	+.132	+.108	-.196	+.819*	-.0479
320 x 372	-.118	-.798	+2.096	-.012	-1.868	+.004	-.002	-.829	+.037	+.0367
320 x 376	-.618	-.018	+4.582*	+5.220	+.752	-.060	-.133	+.656	+.090**	+.0770
320 x T42-S	+1.007	+1.057	-11.729*	-5.787	+1.706	+.647	+.141	+.258	-1.400**	-.1643
327 x 362-A	+.202	-.003	+6.579	+5.700	-1.409	+.060	-.106	-.124	+.282	+.0598
327 x 368	+.107	-.233	-4.211	+.547	-1.016	-1.037*	+.299	+.404	-.386	-.1552
327 x 372	-1.333	-.743	-6.000	-5.886	+1.199	-.150*	-.390	-.029	+.410	+.1958
327 x 376	+.117	+.412	+3.830	+.826	-.026	+.836	-.179	-.289	-.070	+.0701
327 x T42-S	-.183	-.388	-1.523	-1.338	+1.767	-.317	+.126	-.167	-.548	-.1483
362-A x 368	-.064*	-.973*	-1.330	+4.052	+2.187	+1.173**	-.545*	+.453	-.253	+.1119
362-A x 372	+2.092*	+2.117*	-7.649	-3.221	+.525	+1.295**	-.141*	+.015	-2.377**	-.5844**
362-A x 376	-.308	+.422	+.489	-1.819	+1.855	-.432*	+.554*	-.265	-1.217**	+.1100
362-A x T42-S	-1.537	-1.103	-.446	-4.026	-1.987	-.765	+.603*	+.017	+3.423**	+.1822*
368 x 372	-.228	+.012	+5.086	-1.260	+.624	+.039*	+.228	+.318	+.522	+.2882*
368 x 376	+.522	-.033*	-4.456	-7.672	-1.217	-1.037*	-.058	-.552	-.272	-.1385
368 x T42-S	+.643	+1.967*	+3.541	+3.220	-1.674	+.730	-.031	-.425	-.430	-.0585
372 x 376	-.097	+.082	-4.068*	+2.945	-1.016	-.100*	+.480*	+.330	+1.961**	-.1219
372 x T42-S	-.314	-.668	+10.534*	+7.432	+.537	-1.088*	-.176*	+.197	-.552	+.1857
376 x T42-S	+.386	-.863	-.378	+.500	-.348	+.793*	-.664*	+.122	-.492	+.0033
SE($\hat{s}_{ij} - \hat{s}_{ik}$)	1.287	1.338	7.100	5.982	2.053	.591	.366	.643	.474	.1592
(i ≠ j, k; j ≠ k)										
SE($\hat{s}_{ij} - \hat{s}_{kl}$)	1.115	1.159	6.149	5.181	1.778	.512	.317	.557	.410	.1379
(i ≠ j, k, l; j ≠ k, l; k ≠ l)										
Var(\hat{s}_{ij})	.690	.746	21.005	14.912	1.757	.146	.056	.172	.094	.0106
SE(\hat{s}_{ij})	.831	.864	4.583	3.862	1.325	.382	.236	.415	.306	.1028

*, ** Exceeds its standard error by two and three or more times, respectively.

Table 31. Estimates of SCA effects for ten characters derived from the analyses of 21 F₂ sweet corn crosses grown in 1975.

Crosses	Tassel Date	Silk Date	Plant Height	Ear Height	Shank Length	Husk Extension	Tip Blanking	Row Number	Ear Length	Weight of First Ear
320 x 327	+1.083	+.533	+1.998	+2.855*	-.179	+.764	+.017	+.053	+.116	-.0428
320 x 362-A	-1.117	-.817	-2.897	-7.735*	-.960	-.727	-.187	+.153	+.035	+.1696
320 x 368	-.067	+.483	+3.983	+3.375	+1.433	+.020	+.251	+.033	+.672	+.0414
320 x 372	+.533	+.133	+3.468	+3.925	-1.479	+.108	-.122	-.777	-.234	+.0327
320 x 376	-1.017	-.067	+2.573*	+1.070	-.326	-.784	+.011	+.458	+.413	-.0158
320 x T42-S	+.583	-.267	-9.126*	-3.490	+1.510	+.619	+.030	+.078	-1.003*	-.1850
327 x 362-A	+.183	+.033	+.758	+2.540	-1.086	-.955	-.073	-.087	+.345	-.0654
327 x 368	-.517	-1.417	+1.738*	+4.200**	-.728	-.941	-.079	+.093	-.145	-.0200
327 x 372	-.667	+.983	-10.527*	-14.075**	+.842	+.158**	-.070	-.092	+.601	+.1515
327 x 376	-.467	-.467	+4.853	+3.195	+.098	+1.971*	-.015	-.332	-.520	-.0248
327 x T42-S	+.383	+.333	+1.179	+1.285	+1.054	-.997*	+.219	+.363	-.398	+.0016
362-A x 368	-.467*	-.517	-1.357	+2.335	+1.028*	+1.358*	+.283	+.543	+.104**	+.1030**
362-A x 372	+1.633*	+1.133	-.772	+3.035	+1.642*	+.827	-.105	-.142	-1.384**	-.3829**
362-A x 376	-.167	+.433	-.817	-2.045	+.250	-.208	+.013	+.293	+.250	+.1170
362-A x T42-S	-.067	-.267	+5.083	+1.870	-.874	-.295	+.070	-.762	+.649	+.0586
368 x 372	-.817	-1.067	+6.233	+1.570	-.526	-.056*	+.031	+.063	-.252	-.0613
368 x 376	+1.133	+.733*	-5.012	-5.635	-.062	-1.181*	-.341	-.477	+.027	+.0209
368 x T42-S	+.733	+1.783*	-5.586	-5.845	-1.144	+.799	-.145	-.257	-.406	-.0840
372 x 376	+.734*	-.117	-4.226	+1.390	+.053	-.355	+.386	+.213	-.029	-.0230**
372 x T42-S	-1.417*	-1.067	+5.823	+4.155	-.532	-.682	-.120	+.733	+1.298**	+.2830**
376 x T42-S	-.217	-.517	+2.628	+2.025	-.013	+.556	-.054	-.157	-.141	-.0742
SE($\hat{s}_{ij} - \hat{s}_{ik}$)	.918	1.186	6.160	5.567	1.281	.761	.345	.659	.553	.1442
(i ≠ j, k; j ≠ k)										
SE($\hat{s}_{ij} - \hat{s}_{kl}$)	.795	1.027	5.334	4.821	1.110	.659	.299	.570	.479	.1249
(i ≠ j, k, l; j ≠ k, l; k ≠ l)										
Var(\hat{s}_{ij})	.351	.586	15.809	12.914	.684	.241	.050	.181	.127	.0087
SE(\hat{s}_{ij})	.592	.766	3.976	3.594	.827	.491	.223	.425	.357	.0931

*, ** Exceeds its standard error by two and three or more times, respectively.

variances of SCA effects were negative or smaller than the variances of plot means. Exceptions were found for husk extension, ear length, and weight of the first ear in which several variances of SCA effects substantially exceeded the variance of the plot means for that character.

In general, large variances of GCA effects were accompanied by small variances of SCA effects and vice-versa. Notable exceptions were the cases of parent 372 for ear length and parent 362-A for weight of the first ear. In these cases, variances of both GCA and SCA effects were relatively large. These parents should thus be outstanding for ear length and ear weight, respectively, in specific F_1 combinations. Above average performance of F_1 's for other characters should be predictable based on the evaluations of those characters in the parents.

Phenotypic and Genotypic Correlations

The 45 possible phenotypic correlations between the ten characters were calculated for parents, F_1 's, and F_2 's for each year and are shown in Table 33. Data were plotted for each correlation and examined for isolated points or distinct clustering which would result in an erroneous relationship. A few such situations were found, especially in the parents where only seven data points were available.

Table 33. Phenotypic correlations between ten characters of sweet corn calculated from three generations in two years.

Characters Correlated		1974	1975	1975	1974	1975
		F ₁	F ₁	F ₂	Parents	Parents
Tassel Date	Silk Date	.92**	.86**	.86**	.92**	.88**
Tassel Date	Plant Ht	-.13	-.18	-.11	-.49	-.27
Tassel Date	Ear Ht	.04	-.12	-.005	-.22	-.16
Tassel Date	Shank Ln	.04	.11	.40*	-.14	.24
Tassel Date	Husk Ext	.40	.43	.46*	.62	.35
Tassel Date	Tip Blank	.21	.35	.53*	.45	.54
Tassel Date	Row No	.21	.08	-.10	.21	-.11
Tassel Date	Ear Ln	-.38*	-.40*	-.38**	-.22	-.20
Tassel Date	Wt of 1st Ear	-.53*	-.49*	-.59*	-.40	-.40
Silk Date	Plant Ht	-.22	-.25	-.24	-.49	-.33
Silk Date	Ear Ht	.19	-.03	.11*	-.13	-.17
Silk Date	Shank Ln	.28	.30**	.51**	-.12	.21
Silk Date	Husk Ext	.38	.58**	.56**	.61	.50
Silk Date	Tip Blank	.21	.55**	.73**	.54	.71
Silk Date	Row No	.22	.01	-.23	.45	-.15
Silk Date	Ear Ln	-.32*	-.34**	-.37**	-.21	-.32
Silk Date	Wt of 1st Ear	-.54*	-.56**	-.65**	-.37	-.56
Plant Ht	Ear Ht	.52*	.64**	.61**	.29*	.33
Plant Ht	Shank Ln	.24**	.42**	.27**	.81*	.65*
Plant Ht	Husk Ext	-.70*	-.74**	-.62**	-.85	-.82*
Plant Ht	Tip Blank	.46*	.14	.14	-.31	-.23
Plant Ht	Row No	-.12**	-.10**	-.03**	.08	.47
Plant Ht	Ear Ln	.80**	.87**	.74**	.63	.62
Plant Ht	Wt of 1st Ear	.40**	.53**	.40**	.62	.45
Ear Ht	Shank Ln	.58**	.68**	.55**	.66	.52
Ear Ht	Husk Ext	-.26**	-.49*	-.33**	-.66	-.73
Ear Ht	Tip Blank	.62**	.52*	.65**	.43	.28
Ear Ht	Row No	-.32	-.39**	-.40*	-.15	-.07
Ear Ht	Ear Ln	.41	.62**	.53	.70	.75
Ear Ht	Wt of 1st Ear	-.16	-.02	-.04	.04*	.31
Shank Ln	Husk Ext	-.33	-.13*	-.15**	-.81*	-.59
Shank Ln	Tip Blank	.16	.44*	.59**	.09	.19
Shank Ln	Row No	-.18	-.35	-.33	.01	.02
Shank Ln	Ear Ln	.40	.42	.38	.72	.38
Shank Ln	Wt of 1st Ear	-.18	-.23	-.34	.30	-.17
Husk Ext	Tip Blank	-.32	.04	.29	.22	.18
Husk Ext	Row No	-.02**	-.10**	-.30**	.07	-.29*
Husk Ext	Ear Ln	-.82*	-.76**	-.83**	-.72	-.85*
Husk Ext	Wt of 1st Ear	-.48*	-.66**	-.70*	-.58	-.61
Tip Blank	Row No	-.06	-.32	-.45	-.02	-.47
Tip Blank	Ear Ln	.32	.26	-.003*	.40	.21
Tip Blank	Wt of 1st Ear	-.04	-.30	-.45	-.45	-.36
Row No	Ear Ln	-.07*	-.15*	-.02**	.06	.11
Row No	Wt of 1st Ear	.45**	.47**	.60**	.55	.67
Ear Ln	Wt of 1st Ear	.60**	.59**	.59**	.46	.64
n		21	21	21	7	7

*, ** Significant at .05 and .01 levels of probability, respectively.

However, no abnormalities were found in plots of correlations that were of sufficient magnitude to be significant.

Genotypic correlations (Table 34) were calculated using both regression of progeny on parents and components of variance and covariance from the analyses of variance. In general, genotypic correlations calculated by different methods and on different generations were in close agreement. Characters with consistently high genotypic correlations also had high phenotypic correlations. However, genotypic correlations were usually larger than corresponding phenotypic correlations.

The most important character associations identified in this study were those between tassel date and silk date, plant height and husk extension, plant height and ear length, ear height and shank length, ear height and tip blanking, ear height and ear length, husk extension and ear length, husk extension and ear weight, number of kernel rows and ear weight, and ear length and ear weight. Griffing (1956b) indicated that genotypic correlations depend primarily on pleiotropic effects of genes rather than on linkage. These correlations are consistent with pleiotropy and most of them can be explained according to logical biological relationships within the plant. For example, tassel date and silk date are both expressions of time-to-flowering and would be expected to have a majority of genes in common.

Table 34. Genotypic correlations between ten characters of sweet corn estimated by: (1) regression of progeny on parents, and (2) components of variance and covariance from the analysis of variance.

Characters Correlated	Regression			Variance Components					
	1974 F ₁ on Mid Parent	1975 F ₁ on Mid Parent	1975 F ₁ on F ₂	1974 F ₁ with Reciprocals	1974 F ₁	1975 F ₁	Combined		
							F ₁	1975 F ₂	
Tassel Date	Silk Date	.95	.89	.86	.93	.92	.89	.94	.89
Tassel Date	Plant Ht	-.41	-.24	-.17	-.13	-.13	-.15	-.14	-.08
Tassel Date	Ear Ht	*	-.16	-.12	.03	.02	-.11	-.04	-.02
Tassel Date	Shank Ln	*	.25	.26	.02	.06	.17	.12	.42
Tassel Date	Husk Ext	.58	.40	.47	.44	.46	.45	.44	.50
Tassel Date	Tip Blank	.33	.53	.44	.26	.18	.46	.36	.58
Tassel Date	Row No	.20	*	*	.29	.22	.23	.17	-.08
Tassel Date	Ear Ln	-.78	-.26	-.42	-.30	-.26	-.39	-.33	-.35
Tassel Date	Wt of 1st Ear	-.41	-.46	-.59	-.43	-.47	-.48	-.49	-.59
Silk Date	Plant Ht	-.47	-.40	-.24	-.16	-.17	-.29	-.22	-.21
Silk Date	Ear Ht	*	-.13	.03	.20	.25	-.01	.14	.17
Silk Date	Shank Ln	.01	.30	.43	.27	.31	.34	.32	.54
Silk Date	Husk Ext	.53	.57	.60	.39	.34	.62	.54	.60
Silk Date	Tip Blank	.37	.70	.68	.25	.18	.66	.51	.79
Silk Date	Row No	.23	*	-.11	.36	.21	.02	.12	-.23
Silk Date	Ear Ln	-.17	-.33	-.39	-.26	-.19	-.41	-.29	-.40
Silk Date	Wt of 1st Ear	-.38	-.63	-.68	-.45	-.57	-.69	-.51	-.74
Plant Ht	Ear Ht	*	.44	.60	.50	.42	.70	.56	.57
Plant Ht	Shank Ln	.70	.47	.37	.50	.49	.50	.50	.36
Plant Ht	Husk Ext	-.99	-.89	-.73	-.87	-.93	-.83	-.90	-.73
Plant Ht	Tip Blank	*	*	*	.56	.54	.14	.34	.15
Plant Ht	Row No	*	*	-.22	-.16	-.10	-.13	-.12	-.03
Plant Ht	Ear Ln	1.09	.91	.92	.95	.96	.96	.97	.85
Plant Ht	Wt of 1st Ear	.71	.67	.50	.33	.42	.49	.45	.49
Ear Ht	Shank Ln	.66	.63	.68	.77	.78	.80	.81	.64
Ear Ht	Husk Ext	-.51	-.71	-.45	-.28	-.36	-.57	-.37	-.41
Ear Ht	Tip Blank	.84	.52	.67	.77	.75	.60	.77	.70
Ear Ht	Row No	-.22	*	-.42	-.33	-.35	-.45	-.41	-.45
Ear Ht	Ear Ln	.64	.80	.69	.39	.47	.79	.64	.65
Ear Ht	Wt of 1st Ear	*	.15	*	-.35	-.31	-.11	-.17	.01
Shank Ln	Husk Ext	-.76	-.33	-.05	-.48	-.53	-.14	-.35	-.21
Shank Ln	Tip Blank	.12	.30	.56	.34	.28	.52	.41	.60
Shank Ln	Row No	*	*	-.32	-.19	-.24	-.42	-.33	-.36
Shank Ln	Ear Ln	.74	.40	.36	.56	.63	.49	.56	.49
Shank Ln	Wt of 1st Ear	*	-.22	-.34	-.24	-.24	-.39	-.31	-.36
Husk Ext	Tip Blank	-.15	.17	.17	-.24	-.33	.11	-.14	.30
Husk Ext	Row No	*	-.28	-.24	-.04	-.02	-.12	-.09	-.32
Husk Ext	Ear Ln	-.93	-.90	-.82	-.97	-.98	-.85	-.92	-.92
Husk Ext	Wt of 1st Ear	-.61	-.78	-.75	-.63	-.60	-.79	-.71	-.81
Tip Blank	Row No	-.05	-.43	-.41	-.006	-.07	-.36	-.26	-.49
Tip Blank	Ear Ln	.52	.22	.12	.33	.40	.19	.31	-.01
Tip Blank	Wt of 1st Ear	*	-.35	-.38	-.06	-.02	-.46	-.04	-.55
Row No	Ear Ln	*	*	-.06	-.06	-.05	-.21	-.13	-.05
Row No	Wt of 1st Ear	.67	.64	.55	.60	.62	.56	.60	.69
Ear Ln	Wt of 1st Ear	.50	.57	.63	.48	.46	.50	.48	.53

* Differences in sign of the regression coefficients in the numerator of the formula resulted in the square root of a negative number which has not been defined.

Shank length is a component of ear height and the genes controlling shank length would be a portion of those controlling ear height.

The strong negative association between ear length and husk extension can be explained by examining the components of husk extension. Husk extension is determined by the difference between the length of the ear and the length of the husk sheaths. If the length of the husk sheaths varies by a small amount in relation to a relatively large variation in ear length, from cross to cross, then husk extension will vary inversely with ear length. Thus, the genes controlling ear length play a major role in controlling husk extension. The strong negative association between plant height and husk extension is probably a result of the strong positive association between plant height and ear length. Plant height and ear length apparently have a majority of genes in common in the genetic material used in this study.

Ear length contributes to ear weight so the strong positive association between these characters was expected. Likewise, ear diameter, which was not measured in this study, contributes to ear weight. Larger ear diameter results when kernel row number increases substantially, resulting in the positive correlation between number of kernel rows and ear weight. The large negative correlation between husk extension and ear weight is probably a result of the positive correlation between ear length and ear weight.

The positive correlation between ear height and tip blanking is difficult to explain in terms of the biological system. If this genotypic correlation is a result of pleiotropic effects of genes and not the result of linkage, sampling error, or chance, then we must assume that tip blanking and ear height have some genes in common. The action of these genes is obscured by an incomplete understanding of the physiological components affecting tip blanking. Had the correlation between tip blanking and ear length been stronger, the correlation with ear height could have resulted indirectly through the association between ear height and ear length. Conceivably, ear length could increase beyond the capacity of the plant to support all kernels. Thus, the youngest kernels, at the tip, would fail to fill.

Other genotypic correlations such as those between tassel date and husk extension, tassel date and weight of the first ear, silk date and husk extension, silk date and weight of the first ear, plant height and ear height, plant height and shank length, plant height and weight of the first ear, and shank length and ear length were generally consistent over methods and generations and were suggestive of relationships. However, correlation values were not large enough to be predictive. Nevertheless, these relationships should be considered in any selection program involving this genetic material.

Heritability Estimates

Regressions of 1974 F_1 on 1974 mid-parent, 1975 F_1 on 1975 mid-parent, and 1975 F_2 on 1975 F_1 were calculated to estimate heritability in the narrow sense for each character. Components of variance from the analyses of 1974 F_1 's with reciprocals, 1974 F_1 's without reciprocals, 1975 F_1 's, 1974 and 1975 combined F_1 's, and 1975 F_2 's were also used to estimate heritability in the narrow sense. Heritability estimates are given in Table 35.

Heritability estimates from the two methods were generally in close agreement although those from regression were generally larger than those from variance components. Estimates within methods were also in general agreement with a few minor exceptions. In 1974, regression estimates for some characters, such as tip blanking, were out of line with comparable estimates in other years and generations. This was probably a result of the 1974 parents not expressing their true potential because of unequal competition arising from adjacent F_1 's in a common block. Several of the heritability estimates from regression were greater than 100 percent which indicates that they were subject to considerable sampling error.

These heritability estimates have not been evaluated by establishing a selection differential and comparing actual gain with predicted gain in selection experiments. The primary objective of

Table 35. Heritability estimates (%) for ten characters of sweet corn estimated by: (1) regression of progeny on parents, and (2) components of variance from the analyses of variance.

Character	Regression			Variance Components				
	1974 F ₁ on Mid Parent	1975 F ₁ on Mid Parent	1975 F ₁ on F ₂	1974 F ₁ with Reciprocals	1974 F ₁	1975 F ₁	Combined F ₁	1975 F ₂
Tassel Date	77.1 ± 11.0*	90.1 ± 8.7	87.6 ± 8.1	68.7	64.9	84.7	65.2	62.9
Silk Date	62.8 ± 11.2	107.6 ± 9.1	88.1 ± 8.6	71.0	69.5	88.0	67.7	77.2
Plant Height	50.8 ± 21.2	71.1 ± 20.8	88.3 ± 10.7	61.5	56.4	72.5	54.7	51.4
Ear Height	113.6 ± 20.2	119.0 ± 21.2	88.7 ± 10.2	80.7	74.8	82.6	64.3	55.5
Shank Length	142.4 ± 26.4	122.2 ± 29.9	86.2 ± 9.0	68.4	70.3	77.7	61.9	72.2
Husk Extension	88.4 ± 18.6	86.2 ± 12.9	102.2 ± 9.4	77.0	75.8	84.4	69.4	59.3
Tip Blanking	34.5 ± 11.6	76.6 ± 11.0	75.1 ± 9.5	72.5	68.0	79.2	57.9	80.7
Number of Kernel Rows	98.1 ± 7.4	112.9 ± 9.1	88.3 ± 5.5	89.6	90.3	94.9	85.1	88.2
Ear Length	102.3 ± 18.3	72.3 ± 16.0	81.4 ± 9.4	65.7	61.6	59.4	56.0	50.3
Weight of First Ear	87.1 ± 23.6	81.0 ± 16.6	75.9 ± 8.8	55.2	54.1	55.0	48.5	40.0

$$* sb = \sqrt{\frac{S_y^2 - (S_{xy})^2}{S_x^2}}{\frac{(n-2) S_x^2}}$$

where sb is the standard error of the regression coefficient, S_y^2 is the sum of squares of the progeny, S_{xy} is the sum of cross products, and S_x^2 is the sum of squares of the parents.

calculating heritability in this study was to provide a means for comparing the results of the combining ability analysis with the method of covariance among relatives.

Heritabilities by regression for the most part confirm the results of the combining ability analysis. Relatively high heritability estimates by both methods substantiate the conclusion that genes acting in an additive manner are more important than non-additive gene interactions in the inheritance of most characters. However, larger heritabilities by regression for ear length and ear weight, in relation to heritabilities of other characters, may suggest that the importance of SCA for these characters was over estimated by the combining ability analyses.

DISCUSSION

Genetic Variances

The concept of fixed and random statistical genetic models creates a dilemma in setting up a study to estimate genetic variances. Theoretically, a random model results in more detailed genetic information about a character in a population because assumptions concerning gene frequency and linkage equilibrium can be met. This is accomplished by deriving a random sample from the random mating parent population without imposing selection pressure in any direction. The results obtained from the analysis can then be applied to the source population. However, very little immediately useful breeding material can be produced in this manner and results obtained from such studies can not be extrapolated to selected populations.

On the other hand, estimates of genetic variance for a character, based on selected material, yields less detailed genetic information about the character because the fixed model must be used. Specific information can be obtained for the breeding lines included in the study, in relation to each other, but estimates of genetic variances for the character apply only to those lines.

A fixed model was used in the present study and the validity of extracting variance components may be questioned. It is recognized that some unknown biases are present in the estimates of these

variance components, especially those obtained from F_2 data. However, the agreement between heritability estimates obtained from parent-progeny regressions and those obtained from variance components indicate that these biases are not serious. It is possible that differential interactions of the non-vigorous parents, the vigorous F_1 's, and the variable F_2 's with the environment may render estimates obtained from parent-progeny regressions less reliable than those obtained from variance components.

Absence of epistasis is an underlying assumption of this type of analysis. This assumption has probably also been violated in the present study because the presence of epistasis in corn for several of these characters has been reported (Bauman, 1959; Gamble, 1962; and Wright et al., 1971). The occurrence of epistasis in this material would inflate GCA by the amount of additive types of epistasis present and would inflate SCA by the amount of non-additive types of epistasis present. This violation is not considered to be serious for two reasons. First, if epistasis is present, a portion of the additive epistasis will become fixed by random chance during inbreeding and will contribute to improvement of the character. Second, while epistasis has been reported to be present in corn, Moll and Stuber (1974) have reviewed these reports and have concluded that epistasis contributes very little to genetic variation in relation to additive and dominance variances.

My estimates of genetic variance are in general agreement with results of others cited. Additive effects comprise a major portion of the genetic variation for tassel date, silk date, plant height, ear height, and number of kernel rows but non-additive effects are also important, indicating partial dominance. The relatively greater importance of non-additive effects for ear length found in this study was not reported by the majority of previous workers (Robinson et al., 1949; Gardner et al., 1953; Robinson et al., 1955; Gardner and Lonquist, 1959; Hallauer, 1968; and Wright et al., 1971). However, an adjustment of SCA variance for the relatively large SCA by years interaction may bring this estimate into closer agreement with previous reports. Unfortunately, this is not possible in this case because years must be considered fixed.

Variance estimates for weight of the first ear were comparable to those of Sprague and Tatum (1942) for yield in previously selected field corn lines but were in opposition to those of Wright et al. (1971) in a study of unselected material. The significant SCA by years interaction and non-significant GCA by years interaction may somewhat modify the indicated relationship between GCA and SCA variances. The component of ear diameter, not measured in this study, may also have a major impact on the expression of weight of the first ear.

Variance estimates for characters receiving little or no previous study (shank length, husk extension, and tip blanking) were in line with results for other characters. The proportions of additive effects to non-additive effects are roughly comparable to trends for plant and ear height. Additive effects comprise the majority of the genetic variation but non-additive effects are important for all three characters.

Thompson's (1963) report of negative heterosis for husk extension and its relationship with positive heterosis for ear length were confirmed by this study. The strong negative association between these two characters is most likely a result of component interactions.

Comparisons of F_1 analyses in individual years with F_1 analyses of combined data validates Gardner's (1963) warning that gene action estimates based on experiments conducted in a single environment will be biased upward because of the genotype x environment interactions contained in estimates of genotypic effects. The conclusion that estimates of SCA, for most characters, are inflated more by genotype x year interactions than are estimates of GCA is in agreement with the results of Rojas and Sprague (1952) but in conflict with the results of Matzinger et al. (1959). However, Matzinger et al. (1959) were studying material previously unselected while the

materials in both this study and that of Rojas and Sprague (1952) were highly selected.

General support for the greater importance of additive effects found in this study is contained in a recent comprehensive review by Moll and Stuber (1974). These authors reviewed the results of experiments to estimate genetic variance in a wide range of crop species. Additive genetic variance has been found to be relatively more important than non-additive genetic variance for most characters in a range of crops including cross-pollinated species, self-pollinated species, and polyploid species.

Reports of major importance of non-additive effects including epistasis and overdominance, for some characters are not surprising in view of the complex nature of characters being studied. These complex characters of economic importance are many steps away from the actions of the individual genes that determine their expression. It is conceivable that a majority of the non-additive effects revealed in estimates of genetic variance are a result of interactions among the components of a character rather than interactions among the genes themselves. Grafius (1964) has demonstrated that apparent overdominance for a complex trait can be explained by the interaction of two component traits that are strictly additive. This implies that a clearer understanding of the inheritance of a complex character may be gained by studying components rather than the character

itself. An understanding of gene action governing simple components coupled with an understanding of component interactions may ultimately lead to more rapid breeding progress.

In terms of the present study, husk extension is obviously an interaction of husk sheath length and ear length. It is probably also affected by the number of husk sheaths and the distance between the nodes of attachment to the shank and the butt of the ear. Likewise, shank length can be subdivided into components such as number of nodes and length of internodes. Components of characters such as tip blanking may be physiological in nature necessitating a more complex method of measurement. Future studies of these characters may yield more useful information if estimates of genetic variance are made on components and interpreted in terms of the complex characters.

Reciprocal Differences

The finding of apparent reciprocal differences for nine of the ten characters studied is supported by the results of others (Fleming et al., 1960; Brown, 1961; Singh, 1965, and 1966; Bhat and Dhawan, 1969, and 1970; Sayed-Galal et al., 1973; and Baynes and Brawn, 1973) for several of the same characters. Possible explanations for these differences have been discussed previously and the present results must be considered inconclusive. However, if the observed

differences are the result of either maternal effects or true cytoplasmic inheritance, they have some important implications to sweet corn improvement.

Significant improvement of a character may be achieved by simply reversing the parents of promising F_1 hybrids. It is realized that in many cases there are compelling reasons to use a particular inbred as either a male or female. These reasons include ability to shed pollen, relative maturity, seed yield, disease resistance, and seed quality. Nevertheless, in situations where the role of a parent is arbitrary, testing of reciprocal F_1 hybrids is recommended. This recommendation is based on the assumption that the material included in this study is not unique and represents selected sweet corn inbreds in general. Such an assumption is subject to considerable criticism because of the "fixed" selection of parent inbreds for this experiment.

Character Associations

As discussed previously, unknown biases present in estimating variance components from a fixed model were not considered to be serious. These biases introduced into estimates of components of covariance, used to calculate genotypic correlations, are potentially more misleading; especially if linkage between characters is strong.

In this case, results of genotypic correlations calculated from regression and from components of variance and covariance could be in close agreement and both be subject to considerable linkage bias. The implication by Griffing (1956b) that genotypic correlations are primarily due to pleiotropic effects of genes, with a random model, seems logical to explain the strong genotypic associations found in this study. However, it should be recognized that under the present fixed model, linkage rather than pleiotropy may be the basis for the true explanation.

For these reasons, genotypic correlations obtained in this experiment must be considered a function of the particular inbred parents involved. These character associations should be valuable in any selection program with these parents as the source but should not be extrapolated to selection from untested material.

At the outset, it was hoped that a strong genetic relationship could be established between other characters and husk extension and also between other characters and tip blanking. These characters are difficult to select for phenotypically during inbreeding because of hand pollination procedures. The tip of the husk is normally removed to accommodate the shoot bag and to allow more uniform silk emergence. This procedure precludes any accurate evaluation of husk extension. Complete pollination is seldom achieved on hand

pollinated ears; thus, the true expression of tip blanking is obscured. Second ears can be used to evaluate these characters but in inbred material under close competition, second ears do not always develop. Strong correlation with other more readily accessible characters would be a valuable selection aid.

The strong negative correlation between ear length and husk extension in this material could be used for indirect selection. However, both characters are economically important and since the association was negative, a compromise within economically acceptable limits would be necessary.

Correlations between tip blanking and other characters were not strong enough for reliable correlated selection. Either a strong relationship with some character not included in this study could be sought, or a top cross progeny test with a broad based tester could be used.

Breeding Implications

A selection program based on the lines included in this study as a source population could be expected to yield improved inbred lines for the characters evaluated. Selection for these characters during inbreeding based on the phenotypes of individual plants is consistent with the findings of predominately additive genetic effects and high narrow sense heritabilities. Mass selection and recurrent

selection for GCA should also be effective for increasing the level of characters in the source population before extracting inbreds.

The use of breeding procedures such as recurrent selection for SCA or reciprocal recurrent selection are probably not warranted for these characters in most situations. However, if major emphasis is placed on ear length or weight of the first ear, these procedures may be justified.

Resulting inbreds should be tested in single cross combinations to evaluate SCA. However, because of the major effects of GCA for most characters, it should not be necessary to test all possible single crosses. Crosses with a selected series of tester lines should be sufficient to characterize an inbred. Only those crosses expected to perform above some specified level for a character, based on parental and test cross data, would require evaluation.

SUMMARY AND CONCLUSIONS

1. Tassel date, silk date, plant height, ear height, shank length, husk extension, tip blanking, number of kernel rows, ear length, and weight of the first ear are heritable quantitative characteristics of sweet corn.
2. Mean squares for both general combining ability (GCA) and specific combining ability (SCA) were statistically significant for all characters as measured in the F_1 and F_2 generations of a seven parent diallel cross.
3. A comparison of variance components for SCA and GCA revealed that GCA was relatively more important than SCA for all characters except ear length and weight of the first ear.
4. Data on heterosis and inbreeding depression were in general agreement with variance component ratios and supported conclusions concerning the relative importance of GCA and SCA.
5. Heritability estimates based on covariance among relatives were generally in close agreement with estimates based on variance components. This agreement confirms the results of the combining ability analyses.
6. Estimates of SCA variances contained a substantially larger portion of the genotype by year interaction than did estimates of GCA variances.

7. GCA effects for individual lines were consistent from year to year. Thus, parents could be ranked by either GCA effects or parental means.
8. SCA effects for individual crosses were not consistent from year to year. This was reflected in the relatively large interaction of SCA with years.
9. Variances of SCA effects for a series of crosses involving a single parent were generally smaller than the variances of plot means. Exceptions were found for husk extension, ear length, and weight of the first ear for certain parents.
10. Large positive genotypic correlations were found between tassel date and silk date, plant height and ear length, ear height and shank length, ear height and tip blanking, ear height and ear length, number of kernel rows and ear weight, and ear length and ear weight. Large negative genotypic correlations were found between plant height and husk extension, ear length and husk extension, and ear weight and husk extension. Phenotypic correlations between these characters were also large.
11. Significant differences between means of reciprocal crosses were found for all characters except weight of the first ear. The underlying cause of these differences was not determined.

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