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GENETIC VARIANCES IN AN OPEN-POLLINATED

VARIETY OF CORN ESTIMATED FROM

FULL-SIB AND HALF-SIB PROGENIES

by

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INTRODUCTION

In a plant breeding program the ability to predict effects of alternative procedures on rate of progress and potential improvement is a key factor in developing superior plant populations. Reliable prediction depends upon the relative magnitudes of various genetic parameters, including genotype-environment interactions and the types of gene action involved. For quantitative characters, phenotypes commonly are measured in terms of statistics such as means, variances, and covariances. On the basis of the genetic expectations of these statistics for specified models estimates of genetic parameters having utility for making breeding decisions are obtained.

A considerable number of estimates of some of the genetic parameters for corn have been obtained experimentally. Estimates have been obtained by analysis of segregating generations of hybrids between a pair of inbred lines, by analysis of a set of diallel crosses, by analysis of crosses among individuals of an open-pollinated variety, and so forth. Many of the estimates were strictly applicable to very restricted populations, and their predictive values were quite limited. In a few cases the population considered was not even clearly defined. Various models and genetic assumptions were used in obtaining the estimates. In some cases genotype-environment interactions were not estimated or taken into account. The diversity of the approaches used and the populations studied has been such that critical comparisons of the methods used and results obtained have not been feasible. Furthermore, information on the genetic parameters of corn continues to be inadequate for acceptable generalization.

An extensive mathematical methodology concerned with the inheritance of quantitative characters has been derived and presented in the literature. In recent years the methodology has been extended to include such things as general epistacy. Also in recent years a considerable amount of data has been accumulated by application of the methodology to experimental situations. The estimation of some of the genetic parameters in terms of second-order statistics, i.e., variances and covariances, has been especially productive. However, most of the estimates for crops, and in particular, corn, have been of total phenotypic variance or genetic variances of parent-offspring, full-sib, and half-sib relationships only.

The present study is the initial stage of an experiment designed to provide estimates of genetic variances utilizing a series of degrees of relationship such as full-sibs, half-sibs, uncle-nephews, first cousins, double first cousins, and so forth. The estimates are confined to a single population of corn, an open-pollinated variety.

The various estimates of the genetic variances confined to a single population should provide information useful not only from the standpoint of understanding the genetics of the specific population but also from the standpoint of critical evaluation of the techniques and models used. In the present study estimates of covariances of parent and offspring, covariance of full-sibs, and covariances of half-sibs are obtained. Some of the uses of these estimates of genetic parameters are discussed.

REVIEW OF LITERATURE

Lack of basic information about the genetics of plant populations has meant that plant breeding is largely empirical. Sprague (1955) summarized and discussed some of the problems in the estimation and utilization of genetic variability, especially with reference to corn breeding. He pointed out that two courses are available for the evaluation of a multitude of breeding schemes which may be devised. One would involve critical contrasts of the various schemes and laborious collection of data for choosing among them. This course has not been particularly popular. The alternative course would be to obtain adequate estimates of a series of genetic parameters which enable the breeder to compare genetic expectations for a series of breeding systems. Sprague further pointed out that various mathematical models have been devised for estimating certain genetic parameters; but even so, critical information on some of the parameters is still inadequate.

Many approaches to the estimation of the various genetic parameters for corn have been and are being used. The methods fit into three general categories, namely, (1) analysis of diallel crosses, (2) analysis of F_2 generations of single crosses, and (3) analysis of crosses within or among open-pollinated varieties. Since breeding schemes in corn are mainly centered around the relative importance of various types of gene action involved in heterosis, a brief review of these is in order.

Types of Gene Action Involved in Heterosis in Corn

Sprague (1953) gave an extensive review of the literature pertaining to the manifestation of heterosis and to the theories proposed to explain it. No attempt will be made here to review the voluminous literature concerned

with this phenomenon. Suffice it to say that from common usage two quite
different types of gene action have been postulated generally to account
for heterosis in corn. These are:

1. Dominant favorable growth factor hypothesis usually attributed
    to Bruce (1910) and Jones (1917).

2. Divergent alleles or overdominance hypothesis usually attri-
    buted to East (1936) and Hull (1945) although Fisher (1918)
    used the term superdominance for the same phenomenon as
    early as 1918.

Hull (1945) suggested that overdominance (Aa > AA) would account for
the breeding results of corn and proposed recurrent selection for specific
combining ability to capitalize on this type of gene action. Later (1952),
he gave additional evidence from a series of twenty-five experiments to
support his contention.

Crow (1948, 1952) presented an argument suggesting that in crosses
involving members of equilibrium populations increases in vigor much greater
than 5 percent cannot be explained satisfactorily by the dominance hypothesis
where vigor is measurable in terms of selective value. The basis of his
argument was that in an equilibrium population the average decrease in
selective value due to homozygous recessives is equal to the product of the
number of gene loci (n) and the average mutation rate ($\bar{u}$) assuming that the
beneficial genes are completely dominant and all deleterious factors are
recessive. Hence, the increase in vigor, as measured by selective advantage,
that would result from replacing all the homozygous recessive loci with
dominants would be $n\bar{u}$. He used prevailing estimates of n and $\bar{u}$ as 5000 and
10^{-5}, respectively, and suggested that the selective advantage accruing to

members of a population, if all homozygous recessive factors were replaced, would be of the order of 5 percent. For increases in vigor larger than this he suggested the alternative hypothesis that the increase is due to certain gene loci where the heterozygote is superior to either homozygote. In the latter case the average reduction in selective advantage of the population due to the two inferior homozygous genotypes would be of the order of magnitude of the selection coefficients. Since selection coefficients are in general much larger than mutation rates, the selective advantage accruing to members of a population, if homozygous gene loci were replaced with superior heterozygotes, would be quite large and could exceed the 5 percent advantage hypothesized for the complete dominance case. It should be pointed out that Crow's entire argument is predicated upon the assumptions that an equilibrium population applies and that vigor is measurable in terms of selective value.

Fisher (1949) presented an argument similar to that of Crow in support of the overdominance (or superdominance) hypothesis. He suggested that since it is reasonable with grain crops to equate chance of survival to yield, the depression in yield in a cross-bred crop due to a depression in yield of seed associated with a homozygous recessive gene defect be equated to the total mutation rate to which the crop is subject inasmuch as the great majority of mutants are deleterious. He went on to state that

"it would appear that the total elimination of deleterious
recessives would make less difference to the yield of
cross-bred commercial crops than the total mutation rate
would suggest. Perhaps no more than a 1 per cent. improve-
ment could be looked for from this cause. Differences of
the order of 20 per cent. remain to be explained.

"Factors in which selection favors the heterozygote
over both homozygotes will establish a stable polymorphism

, in which a considerable fraction of the population will
be below optimum. Such factors, if frequent, might
explain a great advantage in some first-cross hybrids,
but scarcely in later crosses, unless a multiplicity of
alleles, all deleterious when homozygous, were assumed."

Brieger (1950) arrived at conclusions similar to those of Crow. He

calculated the number of sub-viable or lethal mutants which would have to

be accumulated to explain the effects of selfing in a population exhibiting

heterosis. He concluded that there were not enough loci in the corn plant

to accumulate the required mutants to account for the dominance hypothesis,

but it was possible to have an accumulation sufficient to account for

heterotic gene pairs and hence overdominance.

Robinson et al. (1955) pointed out that if overdominance is the major

type of gene action in corn as suggested by Hull, Crow, and Brieger above,

then the genetic variance produced by segregation of alleles exhibiting this

phenomenon is mostly dominance variance with a trivial amount of additive

genetic variance. Clearly, the ratio of dominance variance to additive

genetic variance or level of dominance would provide a means of determining

if the overdominance theory were correct. Robinson, et al. (1949) and

Gardner, et al. (1953) discussed the degree of dominance in relation to these

theories.

In the review that follows, some attention will be directed toward the

magnitude of "dominance" since it has a bearing on this problem.

Diallel Crosses

The term "diallel crosses" will be used here in a loose sense to denote

any of the four techniques listed by Griffing (1956). They vary depending

upon whether the parents and reciprocal F_1's are included.

Earlier use of diallel crosses was concerned with the concept of combining ability as it relates to the evaluation of inbred lines of corn in hybrid combination. Sprague and Tatum (1942) divided combining ability or performance of lines in hybrid combination into two categories, general combining ability and specific combining ability. They related these to additive gene action and deviations from the additive scheme, respectively. They found that in previously tested and selected lines the variance of specific combining ability was larger than that for general combining ability. In previously unselected material the variance of general combining ability was the larger component.

Rojas and Sprague (1952) extended the analysis for general and specific combining ability to include interactions with years and locations. The single cross yield trials reported involved two groups of material which had been tested previously for general combining ability. The variance for specific combining ability, σ_s^2, was consistently larger than that for general combining ability, σ_g^2, which was in agreement with the results of Sprague and Tatum above. Interaction components involving specific combining ability were also higher than those for general combining ability, and it was suggested that genotype-environment interactions may be an important contributing factor to the variance of specific combining ability. The authors also noted that the interaction components were not necessarily proportional to σ_g^2 and σ_s^2, i.e. $\sigma_{gd}^2/\sigma_g^2 \neq \sigma_{sd}^2/\sigma_g^2$ and $\sigma_{gp}^2/\sigma_g^2 \neq \sigma_{sp}^2/\sigma_s^2$, where the subscripts $\underline{d}$ and $\underline{p}$ denote location and year interaction components, respectively.

Jinks (1955) and Hayman (1957) reported degree or level of dominance in corn estimated from some diallel cross data reported earlier for another

purpose by Kinman and Sprague (1945). The data involved 10 inbred lines

and their 45 possible F_1's and F_2's. They used a ratio of their H_1/D as

level of dominance or their $(H_1/D)^{1/2}$ as degree of dominance. H_1 and D

were weighted sums of h^2 and d^2, where d, h, and - d were genotypic values

for AA, Aa, and aa, respectively. They reported ratios for yield in the

overdominance range $(H_1 > D)$ for this 10 x 10 diallel. However, they

pointed out that the ratios were biased by epistasis in a non-systematic

way. After removal of lines producing significant epistatic interactions,

the ratios were still in the overdominance range. They further pointed out

though that linkage or other interactions may bias the estimates.

Jink's and Hayman's results may be criticized from two additional

standpoints as pointed out by Kempthorne (1956). The lines used initially

did not represent a pertinent or definite population, being merely

individual inbred lines from several geographical areas of the United States.

Therefore, the relevance of the results obtained to any appropriate popula-

tion seemed somewhat obscure. Secondly, removal of some of the lines pro-

ducing epistatic interactions on the basis of the experimental data at

hand voids interpretation of the estimates of additive genetic and dominance

variances with respect to any definite population. Kempthorne also pointed

out that the analysis of variance of the diallel table used by Hayman and

Jinks was of little use unless epistacy could be ignored.

Matzinger, et al. (1959) reported yields for 45 F_1's from 10 parents

selected at random from a random mating synthetic variety and tested at 3

locations for 3 years. Estimates of variance components from both the indi-

vidual experiments and the combined analysis in most cases gave considerably

more variance of specific combining ability than general combining ability.

The second order interaction of general combining ability with years and locations was significant as well as the interaction of specific combining ability and locations. They discussed estimates of the variances of general and specific combining ability with respect to their expectations in terms of additive genetic and dominance variances. Assuming epistatic components negligible, the ratio of dominance variance to additive genetic variance was greater than 1, possibly indicating overdominance. There was non-proportionality of general and specific combining ability variances with their respective interactions with years and locations. The results of this experiment were discussed more completely with respect to estimates of additive genetic and dominance variances by Matzinger (1956).

Jensen (1959) studied yields of 116 of the F_1's among 29 inbred lines originating without intentional selection from the open-pollinated variety Krug in what was termed an incomplete diallel series. Two locations in one year were used. The mean square for specific combining ability was greater than that for general combining ability at one location, and the reverse was true for the other location. Only specific combining ability effects were significant in the combined analysis.

F_2 Analysis

Byrd (1955) used six inbred lines of corn, their 15 single crosses or F_1's, their 15 F_2's and their 30 backcrosses to obtain estimates of heritability for yield and several other characters from experiments at two locations for two years. Both variances within F_1 generations and the average of variances of P_1, P_2, and F_1 were used to estimate environmental variance. Variances of F_2 generations and a function of variances of F_2 and backcrosses

were used to estimate heritability in both the narrow and broad sense. The estimates of heritability for yield ranged from - 100 to + 89. The estimates were quite inconsistent from one experiment to another, and the author stated that they were of questionable value.

Using the same data as Byrd used, Gamble (1957) found evidence of epistatic gene action, but non-epistatic gene action was relatively more important. Epistatic gene action interacted with environment and lines. Both Byrd's and Gamble's results would be restricted in application to the lines studied.

Robinson, et al. (1949) obtained estimates of heritability in the narrow sense and estimates of the degree of dominance (their "a") from biparental crosses among F_2 generation plants within three single-cross corn hybrids. Both variance components and parent-offspring regression were used to estimate heritability. Plant height, ear height, husk extension, and husk score had relatively high heritabilities. Ears per plant, ear length, ear diameter, and yield had relatively low heritabilities. The possibility of overdominance was indicated for yield. Plant and ear height had very little dominance. The other characters were in the partial to complete dominance range. The authors indicated that linkage would bias the estimates upward.

Later, Robinson and Comstock (1955) reported results from second and third cycle recurrent selection progenies for two of the above hybrid populations. The estimates of dominance for yield were essentially zero by the third cycle of selection. They suggested recombinations had dissipated the linkage biases found in first cycle progenies which had indicated a degree of overdominance.

Comstock and Robinson (1952) gave a discussion of three designs of experiments to determine the degree of dominance. The results discussed above were results from use of their Design I.

Gardner, et al. (1953) reported estimates of average dominance ($\bar{a}$) for two hybrid corn populations by using Design III of Comstock and Robinson. F_2 generation plants were backcrossed to each parent and variance components representing σ_A^2 and σ_D^2 obtained from an analysis of the data. Values of $\bar{a}$ in the overdominance range were obtained for yield in both hybrids. One of the populations was the same as Robinson, et al. (1949) used. Upward biases in $\bar{a}$ due to linkage were discussed. Epistatic biases were considered to be negligible. It should be pointed out that the estimates obtained by Robinson, et al. (1949) and Gardner, et al. (1953) apply only to the hybrids actually used.

Gwynn (1959) obtained estimates of heritabilities and average degrees of dominance ($\bar{a}$) from ten sets of biparental crosses among S_1 generation plants, each set tracing back to an S_0 generation plant chosen at random from a synthetic made up from lines from the variety Krug. Since the S_1's were related to a definite S_0 plant, they corresponded to F_2 generations with respect to genic content. There was a significant amount of σ_A^2 in all of the sets and a significant amount of σ_D^2 in most of them. Many of the sets had significant genotype-environment interactions. Estimates of heritabilities were quite inconsistent from set to set, ranging from - 4.5 to 121 percent for yield. However, most of them were quite low for yield. Heritabilities for number of kernel rows, ear length, ear diameter, and weight of 100 kernels were more consistent. Estimates of the degree of dominance also varied considerably over the various sets of progenies. Some of the values

appeared to be in the overdominance range and some were negative as $(\bar{a})^2$.

These results were applicable to the Krug synthetic from which the 10

original S_0 plants were drawn although 10 plants were a rather small sample.

The sample of plants used to make the biparental crosses in each set of

S_1's was also small and led to considerable sampling difficulty in the

results.

Crosses in Open-Pollinated Varieties

For estimates of genetic parameters in corn to have any general appli-

cability in the interpretation of corn breeding problems they must be related

inferentially to the more general populations such as open-pollinated

varieties or synthetics instead of to specified crosses only. Some of the

reports already cited had this characteristic and some others follow.

Robinson, et al. (1955) obtained estimates of additive genetic variance,

dominance variance, and relative magnitude of dominance variance to additive

genetic variance from biparental crosses made within three open-pollinated

varieties. In all varieties and for all characters the dominance variance

was considerably less than that for additive genetic variance; however, each

of the varieties had a considerable amount of additive genetic variance.

They discussed the implication of this with respect to yield and showed that

gene action appeared to be in the partial to complete dominance range, or it

was a mixture of partial dominance and overdominance such that the average

dominance was in the partial dominance range. They indicated that their

estimates were based on the assumptions of no multiple alleles, no effect

of linkage on the relative frequencies of genotypes, and no epistasis.

They suggested that multiple allelism would not change the interpretation

of the estimates. Linkage and epistasis could cause considerable bias in their estimates; however, the conclusions they reached were not seriously affected by such biases.

In a slightly later paper Robinson and Comstock (1955) gave estimates of additive genetic variances and dominance variances for additional samples of two of the varieties cited above by Robinson, et al. (1955). The results were analagous. In a second cycle of selection inconsistent estimates were obtained. They summarized the information from their research as follows:

1. Genes affecting yield show dominance ranging from partial to complete. Overdominance may exist only at a portion of effective loci.

2. The level of dominance in some F_2 generations of hybrids differs from that of open-pollinated varieties. Upward bias due to linkage may account for this.

3. An appreciable amount of additive genetic variance remains in the open-pollinated varieties.

Robinson, et al. (1956) and Robinson, et al. (1958) obtained estimates of heterosis from variety crosses of corn of 20 percent above midparent on the average. This was in excess of the 5 percent increases which Crow (1948, 1952) had indicated were possible if complete dominance were assumed. They pointed out that Crow's argument applied to "equilibrium populations" only and was not pertinent to crosses of varieties which were not the same equilibrium populations. They developed equations and tables which indicated that the estimates of level of dominance obtained were in the partial to complete dominance range for yield.

In addition to the above models and techniques, Kempthorne (1957, p. 426) described a plan for getting a number of independent estimates of the covariances between pairs of individuals which would in turn provide estimates of the composition of the genotypic variance. The plan was not outlined in detail but a diagram showing the types and composition of matings to be made was given. The present study is somewhat of an outgrowth of that plan.

MATERIALS AND METHODS

Conduct of Experiment

The source of material for this experiment was the Reid Yellow Dent variety maintained in isolation at Ames, Iowa. At one time this stock of the variety was used extensively in the corn breeding program at Iowa State College. The isolation consisted of 15,000 to 30,000 plants per year grown in a nursery free of contaminating pollen. The variety was maintained from seed of a very large number of open-pollinated ears chosen at random from the isolation each year. As part of an earlier experiment a large sample of plants in the variety was selfed, and the progenies of the plants examined for visible seed and seedling mutants. Remnant self-pollinated seed of those plants failing to show visible mutants in their seed or seedling progenies were bulked and planted in isolation to form a reconstituted variety. However, the reconstituted variety was grown in isolation and maintained from open-pollinated ears as described above for five years prior to its use in the present experiment.

In 1957 a bulk population of the Reid Yellow Dent variety was grown at Ames. A sample of 96 plants were designated as pollen parents, hereafter referred to as males. Each of the males was crossed to 2 other plants designated as ear parents, hereafter referred to as females, within the same variety. No intentional selection was exercised in choosing these plants and the pollinations were made by hand. The ears were identified and harvested separately. The seed from these crosses were used to plant the progenies from which the estimates of this experiment were obtained. This material was designated Sample I. The progeny from a cross of a particular male and a

particular female consisted of plants which were full-sibs. A pair of

progenies with a common male parent but two different female parents con-

sisted of plants which were half-sibs.

In addition to the above crosses each of the 96 male plants was self-

pollinated. In order to obtain measurements of the ears which were satis-

factory for estimating the covariances of parent and offspring, it was

necessary to obtain a full set of kernels on the self-pollinated ears. To

do this the self-pollinated ears were pollinated after one or two days with

a stock containing genes for purple aleurone. After two or three more days

the ear bags were raised and open-pollination permitted to take place. The

band of kernels around the ear, easily recognized by the purple aleurone,

served to separate the self-pollinated seed at the base of the ear from the

open-pollinated seed at the tip of the ear. The ears were artificially

dried after harvest and measurements taken on yield of shelled grain, ear

length, ear diameter, number of kernel rows, and weight of 100 kernels. The

self-pollinated seed were retained for further use.

In 1958 another sample of crosses similar to the first was produced in

a nursery of the Reid Yellow Dent variety grown at Ames. The nursery con-

sisted of 96 plots planted from remnant seed of the Reid Yellow Dent variety

used in producing the crosses in 1957 and 192 plots planted from the 192

crosses of Sample I produced in 1957. This nursery was used to produce

crosses to be used in another experiment. However, it was possible to obtain

a set of crosses by a procedure identical to that used in 1957 to produce

Sample I. A sample of 96 males was crossed to 2 females each to produce

progenies of full-sibs and progenies of half-sibs. The procedure was such

that no other relationships were established. The crosses were made by hand

and no intentional selection was exercised in choosing plants to be crossed. The seed from these crosses were used to plant progenies from which a second group of estimates of the present experiment were obtained. This group of material was designated Sample II. Ears of the male plants were not harvested or measured.

The 192 progenies of Sample I were grown in randomized block designs with 4 replications at Ankeny, Iowa, in 1958 and 1959. Different randomizations were used for each year. The plots consisted of 16 plants spaced 13 inches apart in single rows 40 inches apart. Five consecutive and competitive plants were harvested separately from each plot. The ears were placed in a heated forced-air dryer for 10 days thereby reducing the moisture content of the grain to approximately 8 percent. No corrections for moisture content were made in the data. Data were collected on each of the individual ears, the identity of the ears being maintained throughout for the various characters measured. Data were taken on weight of shelled grain or yield (grams), ear length (mm.), ear diameter (mm.), weight of 100 kernels (grams), and number of kernel rows. A few plants had two ears both of which were included in yield.

The 192 progenies of Sample II were grown at Ankeny in 1959. The design and procedure was the same as that for Sample I except a different randomization of the randomized block design was used. The data on the ears were taken as for Sample I except that the weight per 100 kernels was obtained on only 2 replications in the case of Sample II. Analysis of the data was adjusted accordingly.

Statistical Procedures

A partition of the variance leading to estimates of genetic parameters was obtained by the analysis of variance. The analysis used was similar to that given by Kempthorne (1957, p. 458) and that given as Experiment I by Comstock and Robinson (1952). The model used for a single sample of the progenies grown in one year was:

$$y_{ijkp} = \mu + m_i + f_{ij} + r_k + e_{ijk} + d_{ijkp}$$

where
$$i = 1, 2, \ldots, a$$
$$j = 1, 2, \ldots, b$$
$$k = 1, 2, \ldots, c$$
$$p = 1, 2, \ldots, n$$

and y_{ijkp} was the observed value for the p-th plant of a progeny grown in the k-th replication, the progeny having arisen from a cross of the i-th male and j-th female per male. In this model μ is the common mean of all plants of all progenies grown in all replications; m_i is the average effect of the i-th male to all progeny; f_{ij} is the average effect of the j-th female to the progeny of the i-th male; r_k is the average effect of all progenies grown in the k-th replication; e_{ijk} is the error effect associated with a plot in the k-th replication and common to all individuals in the plot; d_{ijkp} is the error effect specific to each individual in a plot. It is assumed that μ is a constant, the m_i's are NID $(0, \sigma_m^2)$, the f_{ij}'s are NID $(0, \sigma_f^2)$, the r_k's are fixed constants ($\Sigma_k r_k = 0$), the e_{ijk}'s are NID $(0, \sigma_e^2)$, and the d_{ijkp}'s are NID $(0, \sigma_d^2)$. The assumptions of normality are necessary only to make tests of significance.

Analysis for one year

The form of the analysis of variance and expected mean squares used for a single sample grown in one year is given in Table 1. This form applies to

Table 1. Analysis of variance and expected mean squares for a single sample in one year[a]

Source	d.f.	S.S.	M.S.	E.M.S.
Replications	c-1	$\frac{1}{abn}\Sigma_k Y_{..k.}^2 - \frac{1}{abcn}Y_{....}^2$		
Males	a-1	$\frac{1}{bcn}\Sigma_i Y_{i...}^2 - \frac{1}{abcn}Y_{....}^2$	M_1	$\sigma_w^2 + n\sigma_e^2 + cn\sigma_f^2 + bcn\sigma_m^2$
Females in males	a(b-1)	$\frac{1}{cn}\Sigma_{ij}Y_{ij..}^2 - \frac{1}{bcn}\Sigma_i Y_{i...}^2$	M_2	$\sigma_w^2 + n\sigma_e^2 + cn\sigma_f^2$
Males-females x replications	(ab-1)(c-1)	$\frac{1}{n}\Sigma_{ijk}Y_{ijk.}^2 - \frac{1}{abn}\Sigma_k Y_{..k.}^2$ $-\frac{1}{cn}\Sigma_{ij}Y_{ij..}^2 + \frac{1}{abcn}Y_{....}^2$	M_3	$\sigma_w^2 + n\sigma_e^2$
Plants in plots	abc(n-1)	$\Sigma_{ijkp}Y_{ijkp}^2 - \frac{1}{n}\Sigma_{ijk}Y_{ijk.}^2$	M_4	σ_w^2

[a] a = males; b = females per male; c = replications; n = plants per plot; y_{ijkp} = observed value

$Y_{....} = \Sigma_{ijkp}y_{ijkp}$; i = 1, 2, ..., a; j = 1, 2, ..., b; k = 1, 2, ..., c; p = 1, 2, ..., n

$Y_{ijk.} = \Sigma_p y_{ijkp}$

$Y_{ij..} = \Sigma_{kp}y_{ijkp}$

$Y_{i...} = \Sigma_{jkp}y_{ijkp}$

$Y_{..k.} = \Sigma_{ijp}y_{ijkp}$

σ_w^2 = within plot variance = σ_d^2 + genotypic variance within full-sib families

σ_d^2 = intraplot error variance

σ_e^2 = variance of plot effects

σ_f^2 = variance of female effects

σ_m^2 = variance of male effects

the case when everything is balanced, i.e., the same number of females is

crossed to each male and the same number of plants occurs in each plot.

On the basis of the expectations of the model, estimates of the

individual variance components were obtained from linear functions of the

mean squares as follows:

$$\hat{\sigma}_m^2 = \frac{1}{bcn} [M_1 - M_2]$$

$$\hat{\sigma}_f^2 = \frac{1}{cn} [M_2 - M_3]$$

$$\hat{\sigma}_e^2 = \frac{1}{n} [M_3 - M_4]$$

$$\hat{\sigma}_w^2 = M_4$$

Tests of the null hypotheses that σ_m^2, σ_f^2, and σ_e^2 were equal to zero were

made by comparison with the F-distribution. The tests were:

$F = M_1/M_2$ with $(a-1)$ and $a(b-1)$ degrees of freedom,

$F = M_2/M_3$ with $a(b-1)$ and $(ab-1)(c-1)$ degrees of freedom,

$F = M_3/M_4$ with $(ab-1)(c-1)$ and $abc(n-1)$ degrees of freedom.

The utility of the estimates depends upon their genetic expectations.

In order to get estimates of genetic parameters for the population of

interest, i.e., the variety, the males and females from which the crosses

were made were considered to be non-inbred random members of a random mating

population. Derivation of the genetic expectations is contingent upon the

following assumptions:

1. Regular diploid behavior at meiosis.

2. No maternal effects.

3. Either no linkage or linkage at equilibrium with respect

to coupling and repulsion phases.

4. No selection of individuals from which estimates were

obtained.

The procedure for getting the genetic expectations of the mean squares is to find the genetic expectations of the sums of squares and divide by the appropriate degrees of freedom. The derivation given here is for the genetic portions of the expectations only. Constants such as μ and r_k cancel out in each derivation because of the summing procedures followed. The error terms come out directly from application of the procedure; however, since they are uncorrelated with the genetic portions of the expectations, they are not considered in the following description.

The structure of the entries or progenies in the experiment is as follows:

      1. Individual plants within a plot are full-sibs.

      2. Individual plants resulting from a particular cross

      but grown in different replications are full-sibs.

      3. Individual plants in the same or different replications

      having a common male parent but different female parents

      are half-sibs.

Because of the structure of the entries it is important to consider the plants or genotypes individually or in pairs in the derivations in order to account for family relationships. It is useful to let the plants of a given cross have genotypic effects g_1, g_2, ..., g_z where the g_i's have expectation 0 and variance σ_G^2, and σ_G^2 is the total genotypic variance in the original random mating population.

Referring to Table 1, all of the sums of squares are obtained from the quantities:

$$\Sigma_{ijkp} y_{ijkp}{}^2$$

$$\frac{1}{n} \Sigma_{ijk} Y_{ijk.}{}^2$$

$$\frac{1}{cn} \Sigma_{ij} Y_{ij..}{}^2$$

$$\frac{1}{abn} \Sigma_k Y_{..k.}{}^2$$

$$\frac{1}{abcn} Y_{....}{}^2$$

y_{ijkp} is the observation on a single plant which has genotypic effect g_i. There are abcn plants in the entire set of entries. Hence, the genetic expectation of the first quantity above is:

$$E(\Sigma_{ijkp} y_{ijkp}{}^2) = \Sigma_{ijkp} E(y_{ijkp}{}^2) = abcn \; \sigma_G{}^2.$$

$Y_{ijk.}$ is a plot sum containing values for n plants. The genetic expectation of its square is:

$$E(g_1 + g_2 + \ldots + g_n)^2$$

which contains n $g_i{}^2$ terms and $n(n-1)g_i g_j$ terms and is equal to

$$n \; \sigma_G{}^2 + n(n-1) \; Cov(FS)$$

where Cov(FS) is covariance full-sibs. Hence,

$$E(\frac{1}{n} \Sigma_{ijk} Y_{ijk.}{}^2) = \frac{abc}{n} \; [n\sigma_G{}^2 + n(n-1)Cov(FS)]$$

$$= abc \; [\sigma_G{}^2 + (n-1) \; Cov(FS)].$$

$Y_{ij..}$ is the sum of n plants per plot over c replications. The cn plants have a common pair of parents and are full-sibs. The genetic expectation of the square of the sum is

$$E(g_1 + g_2 + \ldots + g_{cn})^2$$

which contains cn g_i^2 terms and $cn(cn-1)$ $g_i g_j$ terms and is equal to

$$cn \ \sigma_G^2 + cn(cn-1) \ \text{Cov(FS)}.$$

Therefore,

$$E(\frac{1}{cn} \Sigma_{ij} Y_{ij..}^2) = \frac{ab}{cn} \ [cn\sigma_G^2 + cn(cn-1) \ \text{Cov(FS)}]$$

$$= ab \ [\sigma_G^2 + (cn-1) \ \text{Cov(FS)}].$$

Continuing in the same manner $Y_{i...}$ is the sum of values for bcn plants. There are b families containing cn full-sib plants each, and plants in the b families have a common male parent and are half-sibs to one another. The expectation of its square is

$$E[(g_1 + g_2 + \ldots + g_{cn}) + (g_1^* + g_2^* + \ldots + g_{cn}^*)$$

$$+ \ldots + (g_1^{**} + g_2^{**} + \ldots + g_{cn}^{**})]^2$$

where the g_i's are genotypic effects in one full-sib family, the g_i^*'s are genotypic effects in a second full-sib family, and the g_i^{**}'s are genotypic effects in the b-th full-sib family. The superscripts * and ** are only a notation device to distinguish full-sib families. There are bcn terms of the type

$$E(g_i^2) = E(g_i^{*2}) = E(g_i^{**2}) = \sigma_G^2,$$

$bcn(cn-1)$ terms of the type

$$E(g_i g_j) = E(g_i^* g_j^*) = E(g_i^{**} g_j^{**}) = \text{Cov(FS)},$$

and $(cn)^2$ terms of the type

$$E(g_i g_j^*), \ E(g_i g_j^{**}), \ \text{or} \ E(g_i^* g_j^{**}).$$

There are $b(b-1)$ sets of terms of the latter type so that there are a total of $b(b-1)(cn)^2$ terms of the type

$$E(g_i g_j^{\,*}) = E(g_i g_j^{\,**}) = E(g_i^{\,*} g_j^{\,**}) = Cov(HS)$$

where Cov(HS) is covariance half-sibs. Therefore,

$$E(\frac{1}{bcn} \Sigma_i Y_{i...}^{\,2}) = \frac{a}{bcn} \, [bcn \, \sigma_G^2 + bcn(cn-1) \, Cov(FS)$$

$$+ b(b-1)(cn)^2 \, Cov \, (HS)]$$

$$= a[\sigma_G^2 + (cn-1) \, Cov(FS) + (b-1)cn \, Cov(HS)].$$

The sum, $Y_{..k.}$, contains ab plots of n plants. There are a sets of families with a common male parent and b female parents per male. For one set there are b(b-1) families with the half-sib relationship and n plants in each of the families with the full-sib relationship. The genetic expectation of the square for one set is

$$bn \, \sigma_G^2 + bn(n-1) \, Cov(FS) + b(b-1)n^2 \, Cov(HS)$$

and for the a sets is

$$abn \, \sigma_G^2 + abn(n-1) \, Cov(FS) + ab(b-1)n^2 \, Cov(HS).$$

Therefore,

$$E(\frac{1}{abn} \Sigma_k Y_{..k.}^{\,2}) = \frac{c}{abn} \, [abn \, \sigma_G^2 + abn(n-1)Cov(FS) + ab(b-1)$$

$$n^2 Cov(HS)]$$

$$= c[\sigma_G^2 + (n-1)Cov(FS) + (b-1)nCov(HS)],$$

$Y_{....}$ is the sum of abcn plants. There are abcn genotypic effects, ab families containing cn(cn-1) full-sib relationships, and a families containing $b(b-1)(cn)^2$ half-sib relationships. Then,

$$E(\frac{1}{abcn} Y_{....}^{\,2}) = \frac{1}{abcn} \, [abcn \, \sigma_G^2 + abcn(cn-1)Cov(FS) +$$

$$ab(b-1)(cn)^2 \, Cov(HS)]$$

$$= \sigma_G^2 + (cn-1)Cov(FS) + (b-1)cn \, Cov(HS).$$

Substituting the genetic expectations of the observations and sums
into the functions for the sums of squares of Table 1 gives the expected
sums of squares. Division by the corresponding degrees of freedom gives
the genetic expectations of the mean squares as follows:

$$M_1 = \frac{1}{a-1} \Big(a[\sigma_G^2 + (cn-1) \; Cov(FS) + (b-1)cn \; Cov(HS)]$$

$$- [\sigma_G^2 + (cn-1) \; Cov(FS) + (b-1)cn \; Cov(HS)] \Big)$$

$$= \sigma_G^2 - Cov(FS) + cn[Cov(FS) - Cov(HS)] + bcn \; Cov(HS)$$

$$M_2 = \frac{1}{a(b-1)} \Big(ab[\sigma_G^2 + (cn-1) \; Cov(FS)] - a[\sigma_G^2 +$$

$$(cn-1) \; Cov(FS) + (b-1)cn \; Cov(HS)] \Big)$$

$$= \sigma_G^2 - Cov(FS) + cn[Cov(FS) - Cov(HS)]$$

$$M_3 = \frac{1}{(ab-1)(c-1)} \Big(abc[\sigma_G^2 + (n-1) \; Cov(FS)] - c[\sigma_G^2 + (n-1) \; Cov(FS)$$

$$+ (b-1)n \; Cov(HS)] - ab[\sigma_G^2 + (cn-1) \; Cov(FS)]$$

$$+ [\sigma_G^2 + (cn-1) \; Cov(FS) + (b-1)cn \; Cov(HS)] \Big)$$

$$= \sigma_G^2 - Cov(FS)$$

$$M_4 = \frac{1}{abc(n-1)} \Big(abcn \; \sigma_G^2 - abc[\sigma_G^2 + (n-1) \; Cov(FS)] \Big)$$

$$= \sigma_G^2 - Cov(FS).$$

Attaching the error variances σ_d^2 to all expected mean squares and
$n \; \sigma_e^2$ to all except M_4, the expected mean squares now appear as in Table 2.
The similarity between Tables 1 and 2 is evident and in fact is

$$\sigma_w^2 = \sigma_d^2 + \sigma_G^2 - Cov(FS)$$

$$\sigma_e^2 = \sigma_e^2$$

$$\sigma_f^{\,2} = \text{Cov(FS)} - \text{Cov(HS)}$$

$$\sigma_m^{\,2} = \text{Cov(HS)}.$$

Table 2. Analysis of variance and genetic expectations of mean squares for a single sample in one year

Source	d.f.	M.S.	E.M.S.
Replications	(c-1)		
Males	(a-1)	M_1	$[\sigma_d^{\,2} + \sigma_G^{\,2} - \text{Cov(FS)}] + n\ \sigma_e^{\,2} + cn$ $[\text{Cov(FS)} - \text{Cov(HS)}] + bcn\ \text{Cov(HS)}$
Females in males	a(b-1)	M_2	$[\sigma_d^{\,2} + \sigma_G^{\,2} - \text{Cov(FS)}] + n\ \sigma_e^{\,2} + cn[\text{Cov}$ $(FS) - \text{Cov(HS)}]$
Male-females x replications	(ab-1)(c-1)	M_3	$[\sigma_d^{\,2} + \sigma_G^{\,2} - \text{Cov(FS)}] + n\ \sigma_e^{\,2}$
Plants in plots	abc(n-1)	M_4	$[\sigma_d^{\,2} + \sigma_G^{\,2} - \text{Cov(FS)}]$

On the basis of the expectations of Table 2, the estimates obtained from the analysis in Table 1 had the following genetic constitution:

$$\hat{\sigma}_m^{\,2} = \frac{1}{bcn}\,[M_1 - M_2] = \widehat{\text{Cov(HS)}}$$

$$\hat{\sigma}_f^{\,2} = \frac{1}{cn}\,[M_2 - M_3] = \widehat{\text{Cov(FS)}} - \widehat{\text{Cov(HS)}}$$

$$\hat{\sigma}_f^{\,2} + \hat{\sigma}_m^{\,2} = \widehat{\text{Cov(FS)}}.$$

Fisher (1918) gave the genetic composition of Cov(FS) and Cov(HS) for the single locus case which is applicable in the general case in the absence of epistacy. Kempthorne (1954, 1957) extended Fisher's results to the case

of general epistacy, but in the present experiment an additional assumption of no epistasis was added at this point so that the estimates had the following interpretation:

$$Cov(HS) = 1/4 \ \sigma_A^2$$

$$Cov(FS) - Cov(HS) = 1/4 \ \sigma_A^2 + 1/4 \ \sigma_D^2$$

$$Cov(FS) = 1/2 \ \sigma_A^2 + 1/4 \ \sigma_D^2$$

where σ_A^2 is the additive genetic variance and σ_D^2 is the dominance variance. These relationships are true regardless of multiple alleles. In turn σ_A^2 and σ_D^2 were estimated as follows:

$$\hat{\sigma}_A^2 = 4 \ \widehat{Cov(HS)}$$

$$\hat{\sigma}_D^2 = 4 \ [\widehat{Cov(FS)} - 2 \ \widehat{Cov(HS)}].$$

Heritability in the narrow sense is the fraction of the total phenotypic variance due to the additive genetic effects and was estimated for the population from which these samples were drawn as

$$\hat{H}_1 = \frac{4 \ \hat{\sigma}_m^2}{\hat{\sigma}_w^2 + \hat{\sigma}_e^2 + \hat{\sigma}_f^2 + \hat{\sigma}_m^2} \ \times \ 100 = \frac{\hat{\sigma}_A^2}{\hat{\sigma}_P^2} \ \times \ 100$$

where σ_P^2 is total phenotypic variance. This estimate is on an individual plant basis whereas the magnitude of the quantity changes with the units for which it is calculated.

As indicated in the literature review, the ratio σ_D^2/σ_A^2 has properties related to the type of gene action involved in heterosis. An estimate of this quantity was obtained as

$$\frac{\hat{\sigma}_f^2 - \hat{\sigma}_m^2}{\hat{\sigma}_m^2} = \frac{1/4 \ (\widehat{\sigma_A^2 + \sigma_D^2}) - 1/4 \ \hat{\sigma}_A^2}{1/4 \ \hat{\sigma}_A^2} = \frac{\hat{\sigma}_D^2}{\hat{\sigma}_A^2} \ .$$

To illustrate the relationship between this ratio and the degree of dominance, the simple case of two alleles at a single locus may be considered. Let the genotypic array $p^2AA + 2pqAa + q^2aa$ have genotypic values u, au, and -u respectively. Substitution of these values in formulae given by Kempthorne (1957) gives

$$\sigma_A^2 = 2pq \; [p(u-au) + q(au + u)]^2$$

$$= 2pq \; [1 - (p-q)a]^2 u^2$$

$$\sigma_D^2 = p^2 q^2 \; (u - 2au-u)^2$$

$$= 4p^2 q^2 (au)^2.$$

The ratio is now

$$\frac{\sigma_D^2}{\sigma_A^2} = \frac{4p^2 q^2 (au)^2}{2pq[1 - (p-q)a]^2 u^2} = \frac{2pqa^2}{[1 - (p-q)a]^2}$$

and is in terms of gene frequency and the measure of dominance a, interpreted as follows:

a = 0	No dominance
-1 < a < 0 or 0 < a < 1	Partial dominance
a = ± 1	Complete dominance
-1 > a > 1	Overdominance

Under the assumptions of no linkage and no epistacy, the totals of σ_D^2 and σ_A^2 for all loci are sums of the above quantities. Since the gene frequencies and a values in this experiment were unknown, interpretation of the estimated ratio was based on averages. It was indicated earlier that multiple alleles did not change the expected values of σ_A^2 and σ_D^2.

Variances of the estimates

The estimates of σ_A^2, σ_D^2, and H_1 are linear functions of mean squares. To get some idea about the reliability of these estimates, variances of the linear functions were obtained by use of formulae given by Kempthorne (1957, p. 246). The usual formulae for variances of linear functions hold and mean squares are independent. This experiment was balanced and the terms of the model were assumed to be normally and independently distributed. Thus, the variance of a mean square M with k degrees of freedom was estimated unbiasedly as $2M^2/(k + 2)$. The standard errors of the estimates were obtained as square roots of the variances.

The variances of $\hat{\sigma}_A^2$ and $\hat{\sigma}_D^2$ were obtained as

$$V\left(\hat{\sigma}_A^2\right) = V\left(\frac{4}{bcn}\left[M_1 - M_2\right]\right)$$

$$= \frac{16}{(bcn)^2}\left[\frac{2M_1^2}{a + 1} + \frac{2M_2^2}{a(b-1) + 2}\right]$$

$$V\left(\hat{\sigma}_D^2\right) = \left\{4\left[\frac{1}{cn}(M_2 - M_3) - \frac{1}{bcn}(M_1 - M_2)\right]\right\}$$

$$= \frac{16}{(bcn)^2}\left[(b + 1)^2\frac{2M_2^2}{a(b-1) + 2} + b^2\frac{2M_3^2}{(ab-1)(c-1) + 2}\right.$$

$$\left. + \frac{2M_1^2}{a + 1}\right].$$

Heritabilities are ratios and approximate variances are given by the formula

$$V\left(\frac{X}{Y}\right) = \frac{V(X)}{Y^2} - \frac{2X\text{Cov}(X, Y)}{Y^3} + \frac{X^2 V(Y)}{Y^4}.$$

The estimate of H_1 was

$$\frac{\frac{4}{bcn} [M_1 - M_2]}{\frac{1}{bcn} [bc(n-1) M_4 + b(c-1) M_3 + (b-1) M_2 + M_1]}$$

so that

$$X = \frac{4}{bcn} [M_1 - M_2] = \hat{\sigma}_A^2$$

$$Y = \frac{1}{bcn} [bc(n-1)M_4 + b(c-1)M_3 + (b-1)M_2 + M_1]$$

$$V(X) = V(\hat{\sigma}_A^2) \text{ given above}$$

$$V(Y) = \frac{1}{(bcn)^2} [(bc)^2(n-1)^2 \frac{2M_4^2}{abc(n-1) + 2} + b^2(c-1)^2 \frac{2M_3^2}{(ab-1)(c-1)}$$

$$(b-1)^2 \frac{2M_2^2}{a(b-1) + 2} + \frac{2M_1^2}{a + 1}]$$

$$Cov(X, Y) = \frac{4}{(bcn)^2} [\frac{2M_1^2}{a + 1} - \frac{(b-1) 2M_2^2}{a(b-1) + 2}].$$

Variances of the ratio $\hat{\sigma}_D^2/\hat{\sigma}_A^2$ were not obtained because the approximate

formula above did not appear to be adequate. In general, variances of this

ratio would be quite large.

Parent-offspring regressions

For Sample I twice the regression of the means of the progenies with a

common male parent on the male parent itself was obtained as an estimate of

heritability.

$$\hat{H}_2 = 2b \times 100$$

where b is the parent offspring regression. The standard error of b is

$$S.E.(b) = \sqrt{\frac{\text{Mean square for deviations from regression}}{\Sigma(X-\bar{X})^2}}$$

where X is the male parent observation.

Genotypic and phenotypic correlations between pairs of attributes

Estimates of covariance components were obtained from an analysis of covariance for pairs of characters. The structure of the analysis of covariance is given in Table 3. P_1, P_2, P_3 and P_4 are mean products and the E.M.P. are expected mean products. The procedure used here was similar to that given by Robinson, et al. (1951).

Table 3. Form of the analysis of covariance for characters 1 and 2

Source	d.f.	M.P.	E.M.P.[a]
Replications	c-1		
Males	a-1	P_1	$\sigma_{w12} + n\ \sigma_{e12} + cn\ \sigma_{f12} + bcn\ \sigma_{m12}$
Females in males	a(b-1)	P_2	$\sigma_{w12} + n\ \sigma_{e12} + cn\ \sigma_{f12}$
Males-females x replications	(ab-1)(c-1)	P_3	$\sigma_{w12} + n\ \sigma_{e12}$
Plants in plots	abc(n-1)	P_4	σ_{w12}

[a] σ_{m12} = covariance of characters 1 and 2 due to male differences

σ_{f12} = covariance of characters 1 and 2 due to female differences

σ_{e12} = covariance of characters 1 and 2 due to plot differences

σ_{w12} = covariance of characters 1 and 2 due to plants in plots differences

Estimates of covariance components analogous in meaning to those of variance components were obtained as

$$\hat{\sigma}_{m12} = \frac{1}{bcn}\ [P_1 - P_2]$$

$$\hat{\sigma}_{f12} = \frac{1}{cn} [P_2 - P_3]$$

$$\hat{\sigma}_{e12} = \frac{1}{n} [P_3 - P_4]$$

$$\hat{\sigma}_{w12} = P_4 .$$

Genotypic correlations were estimated as

$$r_A = \frac{\hat{\sigma}_{m12}}{\sqrt{(\hat{\sigma}_{m1}^2)(\hat{\sigma}_{m2}^2)}}$$

where $\hat{\sigma}_{m12}$ is the estimated additive genetic covariance component for characters 1 and 2, $\hat{\sigma}_{m1}^2$ is the estimated additive genetic variance component for character 1, and $\hat{\sigma}_{m2}^2$ is the estimated additive genetic variance component for character 2.

In a similar manner the phenotypic correlation was estimated as

$$r_P = \frac{\hat{\sigma}_{w12} + \hat{\sigma}_{e12} + \hat{\sigma}_{f12} + \hat{\sigma}_{m12}}{\sqrt{(\hat{\sigma}_{w1}^2 + \hat{\sigma}_{e1}^2 + \hat{\sigma}_{f1}^2 + \hat{\sigma}_{m1}^2)(\hat{\sigma}_{w2}^2 + \hat{\sigma}_{e2}^2 + \hat{\sigma}_{f2}^2 + \hat{\sigma}_{m2}^2)}}$$

where the terms have definitions analogous to those for the genotypic correlation except they are total phenotypic variances and covariances.

Combined analysis for t years

Sample I was grown in 2 years and a combined analysis of the data was made. This type of analysis provided estimates of two genotype-environment interactions, viz., a component due to "males x years" interaction and a component due to "females in males x years" interaction. The structure of the analysis of variance for t years is given in Table 4. The model includes terms for years, interaction of males and years, and interaction of females in males and years, all of which are assumed to be normally and independently

distributed with means and variances $(0, \sigma_y^2)$, $(0, \sigma_{my}^2)$, and $(0, \sigma_{fy}^2)$, respectively.

Table 4. Form of the analysis of variance for a single sample combined over t years

Source	d.f.[a]	M.S.	E.M.S.[b]
Years	t-1		
Replications in years	t(c-1)		
Males	a-1	M_1	$\sigma_w^2 + n\,\sigma_e^2 + cn\,\sigma_{fy}^2 + bcn\,\sigma_{my}^2 + cnt\,\sigma_f^2 + bcnt\,\sigma_m^2$
Females in males	a(b-1)	M_2	$\sigma_w^2 + n\,\sigma_e^2 + cn\,\sigma_{fy}^2 + cnt\,\sigma_f^2$
Males x years	(a-1)(t-1)	M_3	$\sigma_w^2 + n\,\sigma_e^2 + cn\,\sigma_{fy}^2 + bcn\,\sigma_{my}^2$
Females in males x years	a(b-1)(t-1)	M_4	$\sigma_w^2 + n\,\sigma_e^2 + cn\,\sigma_{fy}^2$
Pooled error	t(ab-1)(c-1)	M_5	$\sigma_w^2 + n\,\sigma_e^2$
Plants in plots	abct(n-1)	M_6	σ_w^2

[a] t = years; c = replications; a = males; b = females per male; n = plants per plot

[b] σ_w^2 = intraplot variance = $\sigma_d^2 + \sigma_G^2$ - Cov(FS) in previous terminology

σ_e^2 = interplot variance

σ_{fy}^2 = variance due to the interaction of female effects and years

σ_{my}^2 = variance due to the interaction of male effects and years

σ_f^2 = variance of female effects = Cov(FS) - Cov(HS) = $1/4\,\sigma_A^2 + 1/4\,\sigma_D^2$

σ_m^2 = variance of male effects = Cov(HS) = $1/4\,\sigma_A^2$

Estimates of the variance components were obtained as follows:

$$\hat{\sigma}_m^2 = \frac{1}{bcnt} [M_1 - M_2 - M_3 + M_4]$$

$$\hat{\sigma}_f^2 = \frac{1}{cnt} [M_2 - M_4]$$

$$\hat{\sigma}_{my}^2 = \frac{1}{bcn} [M_3 - M_4]$$

$$\hat{\sigma}_{fy}^2 = \frac{1}{cn} [M_4 - M_5]$$

$$\hat{\sigma}_e^2 = \frac{1}{n} [M_5 - M_6]$$

$$\hat{\sigma}_w^2 = M_6 .$$

Tests of hypotheses to determine if the components were zero were made as follows:

$$\sigma_e^2 : \quad F = \frac{M_5}{M_6}$$

$$\sigma_{fy}^2 : \quad F = \frac{M_4}{M_5}$$

$$\sigma_{my}^2 : \quad F = \frac{M_3}{M_4}$$

$$\sigma_f^2 : \quad F = \frac{M_2}{M_4}$$

where the calculated values were compared to the F-distribution with corresponding degrees of freedom given in Table 4. The approximate test for $\sigma_m^2 = 0$ was

$$F = \frac{M_1 + M_4}{M_2 + M_3}$$

which was compared with the F-distribution with degrees of freedom determined

from formulae given by Snedecor (1956, p. 362).

Estimates of the additive genetic and dominance variances were

$$\hat{\sigma}_A^2 = 4 \hat{\sigma}_m^2$$

$$\hat{\sigma}_D^2 = 4 (\hat{\sigma}_f^2 - \hat{\sigma}_m^2)$$

and their variances were computed as

$$V(\hat{\sigma}_A^2) = \frac{16}{(bcnt)^2} \left[\frac{2M_1^2}{a+1} + \frac{2M_2^2}{a(b-1)+2} + \frac{2M_3^2}{(a-1)(t-1)+2} + \frac{2M_4^2}{a(b-1)(t-1)+2} \right]$$

$$V(\hat{\sigma}_D^2) = \frac{16}{(bcnt)^2} \left[(b+1)^2 \frac{2M_2^2}{a(b-1)+2} + \frac{2M_3^2}{(a-1)(t-1)+2} + \frac{2M_1^2}{a+1} + (b+1)^2 \frac{2M_4^2}{a(b-1)(t-1)+2} \right].$$

Estimates of heritability on an individual plant basis were obtained as

$$\hat{H}_1 = \frac{4 \hat{\sigma}_m^2}{\hat{\sigma}_w^2 + \hat{\sigma}_e^2 + \hat{\sigma}_{fy}^2 + \hat{\sigma}_{my}^2 + \hat{\sigma}_f^2 + \hat{\sigma}_m^2} \times 100.$$

The variance of this estimate was again of the form $V(X/Y)$ where

$$X = \frac{4}{bcnt} [M_1 - M_2 - M_3 + M_4] = \hat{\sigma}_A^2$$

$$Y = \frac{1}{bcnt} [M_1 + (b-1)M_2 + (t-1)M_3 + (b-1)(t-1)M_4$$

$$+ bt(c-1)M_5 + bct(n-1)M_6]$$

$$V(X) = V(\hat{\sigma}_A^2) \text{ given above}$$

$$V(Y) = \frac{1}{(bcnt)^2} \left[\frac{2M_1^2}{a+1} + (b-1)^2 \frac{2M_2^2}{a(b-1)+2} + (t-1)^2 \frac{2M_3^2}{(a-1)(t-1)+2} \right.$$

$$+ (b-1)^2(t-1)^2 \frac{2M_4^2}{a(b-1)(t-1)+2} + (bt)^2(c-1)^2 \frac{2M_5^2}{t(ab-1)(c-1)+2}$$

$$\left. + (bct)^2(n-1)^2 \frac{2M_6^2}{abct(n-1)+2} \right]$$

$$Cov(X,Y) = \frac{4}{(bcnt)^2} \left[\frac{2M_1^2}{a+1} - (b-1) \frac{2M_2^2}{a(b-1)+2} - (t-1) \right.$$

$$\frac{2M_3^2}{(a-1)(t-1)+2} + (b-1)(t-1) \frac{2M_4^2}{a(b-1)(t-1)+2} \right].$$

The ratio σ_D^2/σ_A^2 was estimated as

$$\frac{\hat{\sigma}_D^2}{\hat{\sigma}_A^2} = \frac{\hat{\sigma}_f^2 - \hat{\sigma}_m^2}{\hat{\sigma}_m^2} \ .$$

The analysis of covariance for pairs of characters was obtained for the combined two-year analysis also. The structure of this analysis is analogous to that for the analysis of variance for t years except mean products and expected values in terms of covariances are substituted for mean squares and expected mean squares. Estimates of the covariance components are obtained by substitution of mean products for mean squares in the formulae given earlier for estimation of variance components. Genotypic and phenotypic correlations were obtained as in the single year case except the phenotypic variances and covariances contain the interaction components and are

$$\hat{\sigma}_P^2 = \hat{\sigma}_w^2 + \hat{\sigma}_e^2 + \hat{\sigma}_{fy}^2 + \hat{\sigma}_{my}^2 + \hat{\sigma}_f^2 + \hat{\sigma}_m^2$$

$$\hat{\sigma}_{P12} = \hat{\sigma}_{w12} + \hat{\sigma}_{e12} + \hat{\sigma}_{fy12} + \hat{\sigma}_{my12} + \hat{\sigma}_{f12} + \hat{\sigma}_{m12}$$

Expected genetic advance due to selection

The expected genetic change in the mean of a character due to selection on the basis of phenotype is obtained from the formula

$$\text{Expected change} = k\sigma_P \frac{\sigma_A^2}{\sigma_P^2} = k\frac{\sigma_A^2}{\sqrt{\sigma_P^2}}$$

where $k\sigma_P$ is the selection differential or average superiority of the selected individuals over the population mean and σ_A^2/σ_P^2 is the heritability for the selection units involved. σ_A^2 is the additive genetic variance among the selection units and σ_P^2 is the total phenotypic variance among the selection units, both of which were replaced by the appropriate estimates in the present study. The expected change applies to a normal population of infinite size but is a reasonable approximation for samples the size of those in this experiment. The formula is also based on the assumption that the genes are additive in their effects, i.e., that there is a linear regression of genotypic value on phenotypic value. In the case of the normal distribution and for the common type of truncation or mass selection, k is the selection differential in standard units with an expected value equal to z/p where z is the value of the ordinate of the normal curve corresponding to the fraction of the population selected and p is the fraction selected. For example, if 5 percent of a large sample were selected, p = .05 and z = .1031. The value of z may be obtained from a table of areas and ordinates of the normal curve of error by selecting the value of the ordinate corresponding to an area under the normal curve of 0.95. The value of k in this case would be .1031/.05 = 2.06. Under the assumptions given, the mean of the population obtained by random mating of the selected individuals would be greater than the original mean by the amount of the calculated change.

In this experiment the expected changes were calculated for the combined two-year analysis of Sample I only. Certainly this would be a minimum of testing in most cases and served to illustrate the procedure. Selection was assumed to be among the plant means of the 192 full-sib families grown for t years with n plants per plot in c replications per year. The variance among full-sib families contains $1/2\ \sigma_A^2 + 1/4\ \sigma_D^2$ in the absence of linkage and epistasis. For selection units of this composition the appropriate formula was

$$\text{Expected change} = k\ \frac{1/2\ \hat{\sigma}_A^2}{\sqrt{\hat{\sigma}_P^2}} = k\ \frac{2\ \hat{\sigma}_m^2}{\sqrt{\hat{\sigma}_P^2}}$$

where

$$\hat{\sigma}_P^2 = \frac{\hat{\sigma}_w^2}{cnt} + \frac{\hat{\sigma}_e^2}{ct} + \frac{\hat{\sigma}_{fy}^2 + \hat{\sigma}_{my}^2}{t} + \hat{\sigma}_f^2 + \hat{\sigma}_m^2$$

and $c = 4$, $n = 5$, $t = 2$, and $k = 2.06$ in this specific case.

When the individual plant is the basic selection unit, which it almost always is, selection of a plant on the basis of one character will quite naturally result in some distribution of all other characters for that plant since they can not be separated from the plant. In the case when a genetic correlation exists between the character selected and another character, selection for one leads to changes in the other. This change is

$$\text{Expected change in character 2 when selection is for character 1} = k\ \frac{\sigma_{A12}}{\sqrt{\sigma_{P1}^2}}$$

where k is the selection differential in standard units, σ_{A12} is the covariance estimate of additive genetic effects between characters 1 and 2 among specified selection units, and σ_{P1}^2 is the phenotypic variance among the selection units for the selected character 1.

Expected changes in unselected characters were calculated for this experiment on the basis of the same selection units given for direct selection above. The specific formula was

$$(2.06) \quad \frac{2\,\hat{\sigma}_{m12}}{\sqrt{\hat{\sigma}_{P1}^{2}}}$$

where $\hat{\sigma}_{m12}$ was the male covariance component for characters 1 and 2 and $\hat{\sigma}_{P1}^{2}$ was the total phenotypic variance of the specified selection units for the selected character.

EXPERIMENTAL RESULTS

The analyses of variance for yield, ear length, ear diameter, number

of kernel rows, and weight per 100 kernels are presented in Tables 5, 6

and 7. The analyses for Sample I for each of the two years, 1958 and 1959,

are given in Table 5. The analyses for Sample I for 1958 and 1959 combined

are given in Table 6. The analyses for Sample II for the single year 1959

are given in Table 7. The mean squares given in these tables were used to

estimate the pertinent variance components as outlined previously. Under

the assumptions of normality in the models, F-tests were applied to ratios

of the mean squares to determine if the variance components deviated from

zero. Those components deviating from zero at the 5 and 1 percent levels of

probability are indicated in Tables 5, 6 and 7.

The estimates of the variance components obtained from the mean squares

are presented in Table 8. For all the characters the intraplot variance,

σ_w^2, was a relatively large fraction of the total phenotypic variance, σ_p^2.

This was expected since data on individual plants is known to be quite

variable usually. In this case the intraplot variance contained a component

for the genotypic variance within full-sib families as well as a component

for the errors specific to each plant.

The interplot error variance, σ_e^2, was relatively large for yield and

ear length, characters which are known to be subject to considerable environ-

mental fluctuation. Ear diameter, number of kernel rows, and weight per 100

kernels were reasonably consistent from replication to replication, which was

reflected in somewhat lower interplot variances. However, σ_e^2 significantly

deviated from zero in practically every case. There were a few irregularities

Table 5. Mean squares for 5 characters, Sample I, 1958 and 1959

Year	Source	d.f.	M.S.				
			Yield	Ear length	Ear diameter	Number kernel rows	Weight per 100 kernels
1958							
	Replications	3	21,444	2,833	45.6	3.0	147.7
	Males	95	14,804[a]	4,397[a]	114.1[a]	53.7[a]	232.2[a]
	Females in males	96	7,872[a]	2,216[a]	47.7[a]	20.8[a]	100.5[a]
	Males-females x replications	573	3,378[a]	576	11.8[a]	4.4	37.8[a]
	Plants in plots	3072	2,816	543	10.1	4.7	29.9
1959							
	Replications	3	119,255	25,117	359.0	44.3	269.0
	Males	95	8,113	4,334[a]	99.9[a]	48.9[a]	155.3[a]
	Females in males	96	6,081[a]	2,698[a]	41.0[a]	20.4[a]	76.9[a]
	Males-females x replications	573	4,127[a]	1,086[a]	15.4[a]	5.5[a]	25.1[a]
	Plants in plots	3072	1,709	530	9.3	4.4	17.2

[a] Denotes significance at 1 percent level

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Table 6. Mean squares for 5 characters, Sample I, combined analysis 1958 and 1959

Source	d.f.	M.S.				
		Yield	Ear length	Ear diameter	Number kernel rows	Weight per 100 kernels
Years	1	3,212,655	542,321	4,499.0	92.0	12,085.0
Replications in years	6	70,349	13,975	202.3	23.7	208.3
Males	95	16,573^a	7,280^b	191.5^b	92.9^b	340.5^b
Females in males	96	8,704^b	3,853^b	76.1^b	36.1^b	141.2^b
Males x years	95	6,344	1,452	22.5^b	9.7^b	47.1
Females in males x years	96	5,249^b	1,061^a	12.6	5.1	36.2
Pooled error	1146	3,753^b	831^b	13.6^b	4.9^a	31.5^b
Plants in plots	6144	2,262	537	9.7	4.5	23.5

[a] Denotes significance at 5 percent level

[b] Denotes significance at 1 percent level

Table 7. Mean squares for 5 characters, Sample II, 1959

Source	d.f.	M.S.				
		Yield	Ear length	Ear diameter	Number kernel rows	Weight per 100 kernels
Replications	3 (1)[a]	32,253	2,906	167.3	4.3	47.0
Males	95 (95)	8,748	3,649	107.6[b]	59.0[b]	97.0[c]
Females in males	96 (96)	10,185[b]	3,154[b]	45.6[b]	20.2[b]	65.3[b]
Males-females x replications	573 (191)	3,752[b]	921[b]	13.8[b]	5.0	32.8[b]
Plants in plots	3072 (1919)	1,981	580	9.8	4.8	17.9

[a] Degrees of freedom in parentheses refer to weight per 100 kernels only

[b] Denotes significance at 1 percent level

[c] Denotes significance at 5 percent level

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Table 8. Estimates of variance components for Sample I and Sample II, 1958 and 1959

Character	Sample	Year	σ_m^2	σ_f^2	σ_{my}^2	σ_{fy}^2	σ_e^2	σ_w^2	σ_P^2
Yield	I	1958	173.3	224.7	--	--	112.5	2815.7	3326.2
		1959	50.8	97.7	--	--	483.7	1708.6	2340.8
		Combined	84.7	86.4	27.4	74.8	298.1	2262.2	2833.6
	II	1959	(-35.9)	321.7	--	--	354.2	1981.3	2622.2
Ear length	I	1958	54.5	82.0	--	--	6.5	543.3	686.4
		1959	40.9	80.6	--	--	111.1	530.2	762.8
		Combined	37.9	69.8	9.8	11.5	58.8	536.8	724.6
	II	1959	12.4	111.7	--	--	68.1	580.0	772.2
Ear diameter	I	1958	1.66	1.80	--	--	.34	10.12	13.92
		1959	1.47	1.28	--	--	1.22	9.33	13.30
		Combined	1.32	1.59	.25	(-.05)	.78	9.73	13.62
	II	1959	1.55	1.59	--	--	.80	9.78	13.72
Number kernel rows	I	1958	.82	.82	--	--	(-.06)	4.66	6.24
		1959	.71	.75	--	--	.22	4.37	6.05
		Combined	.65	.78	.12	.01	.08	4.51	6.14
	II	1959	.97	.76	--	--	.04	4.83	6.53
Weight per 100 kernels	I	1958	3.29	3.14	--	--	1.58	29.88	37.89
		1959	1.96	2.59	--	--	1.58	17.17	23.30
		Combined	2.36	2.63	.27	.24	1.60	23.52	30.61
	II	1959	1.59	3.25	--	--	2.98	17.86	25.68

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such as a negative estimate of the component for number of kernel rows in

the 1958 portion of Sample I and an unusually low estimate for ear length

in the 1958 portion of Sample I. Since the variance component estimates

were expected to have rather high sampling errors, some irregular estimates

were expected. The negative estimates indicated the magnitude of some of

the sampling deviations since variances are not negative.

For each character and for each analysis the females in males component,

σ_f^2, was significant at the 1 percent probability level. In the absence of

linkage and epistasis this component was an estimate of $1/4\ \sigma_A^2 + 1/4\ \sigma_D^2$

and under those assumptions was also an estimate of one quarter of the total

genotypic variance in the population. Since this component was consistently

significant for all five characters, genetic differences measurable in experi-

ments of the size used here existed in this population for each of the

characters. As will be indicated later, it was possible to obtain an estimate

of the dominance variance from this component.

The estimates for the males component, σ_m^2, were somewhat irregular.

In the case of ear diameter, number of kernel rows, and weight per 100 kernels,

the component was significant at least at the 5 percent probability level and

in most cases at the 1 percent level. In the absence of linkage and epistacy

this component was an estimate of $1/4\ \sigma_A^2$, and apparently a relatively large

amount of additive genetic variance was present in the population for these

characters. This component was also significant at the 1 percent probability

level for ear length except for the Sample II estimate. This could have been

merely a chance or sampling variant although there was some tendency for the

Sample II estimates to differ from those of Sample I in some cases.

The males component for yield was extremely irregular. The Sample II estimate was actually a relatively large negative value. This clearly illustrated the sampling errors attached to these estimates. The 1959 estimate of this component for Sample I was not significant also. However, it was just short of the F-value for the 5 percent probability level and was considered to be a non-zero estimate since strict adherence to probability levels is not necessary. On the other hand, when this estimate and the Sample II estimate were considered together, there was an indication that little or no additive genetic variance existed in this population. The Sample I estimates from the 1958 and combined analyses were significant at the 1 and 5 percent probability levels, respectively. Two alternative conclusions seemed appropriate. Either there was no additive genetic variance for yield in this population, the two significant estimates being sampling deviations, or there was additive genetic variance, the two non-significant estimates being sampling deviations. As pointed out, one of the non-significant values was for practical purposes considered significant. Only the unusual estimate obtained from Sample II remained to be explained. Examination of the progeny means for Sample II disclosed that many of the pairs of progenies with a common male parent but different female parents were quite divergent in their yields. On the other hand, the range of the progeny means grouped on the basis of males was similar to that of Sample I. This situation would lead to anomalous estimates such as obtained and probably indicates the problem of adequately sampling a population so that experimental data provide consistent estimates.

The combined two-year analysis of Sample I provided estimates of the males x years, σ_{my}^2, and females in males x years, σ_{fy}^2, interaction

components of variance given in Table 8. Weight per 100 kernels was reasonably consistent from year to year, and neither of the interaction components was significant for this character. The females in males x years interaction components for ear diameter and number of kernel rows were small and non-significant. The males x years interaction components for the same characters were significant at the 1 percent probability level though they were relatively small compared to some of the other components. The males x years interactions were estimates of the interaction of additive genetic effects with years.

In the case of yield and ear length the components for the interaction females in males x years deviated significantly from zero at the 1 and 5 percent probability levels, respectively, whereas the males x years interaction components did not. However, for ear length the component σ_{my}^2 was almost as large as σ_{fy}^2 and was just short of the value necessary for significance at the 5 percent level. The interaction females in males x years involved differences due to an interaction of both additive genetic effects and dominance deviations with years. For yield σ_{my}^2 was quite small and did not deviate significantly from zero so that the interaction of additive genetic effects for yield and years appeared to be negligible in the experiment.

Although estimates of the interaction components could not be made from data for a single year, the interactions were still in reality a part of the expected mean squares for males and for females in males. Thus, estimates of these components made from the analyses for a single year tended to have an upward bias. In fact, the estimate of σ_m^2 for a single year has expectation

$$\sigma_m^{\,2} + \sigma_{my}^{\,2} \;,$$

and the estimate of $\sigma_f^{\,2}$ for a single year has expectation

$$\sigma_f^{\,2} + \sigma_{fy}^{\,2} \;.$$

The estimates agreed in general with these expectations, the few exceptions being well within possible sampling variation. It might be pointed out, though, that biases such as these would not seriously affect the estimate of a genetic parameter such as

$$\frac{\hat{\sigma}_D^{\,2}}{\hat{\sigma}_A^{\,2}} = \frac{\hat{\sigma}_f^{\,2} - \hat{\sigma}_m^{\,2}}{\hat{\sigma}_m^{\,2}} = \frac{\hat{\sigma}_f^{\,2}}{\hat{\sigma}_m^{\,2}} - 1$$

provided the interaction components were proportional to the components for their respective main effects, i.e.,

$$\frac{\sigma_{my}^{\,2}}{\sigma_m^{\,2}} = \frac{\sigma_{fy}^{\,2}}{\sigma_f^{\,2}} \;.$$

The above estimate is that described in the discussion of procedures previously under the assumption of no linkage and no epistasis. The data indicated that the interaction components were not in general proportional to the components for their corresponding main effects. However, in view of the sampling variability associated with the estimation of the components, an observation of this sort is not too critical.

The estimates of the genetic variances and some relationships among them are summarized in Table 9. To indicate the reliability of the estimates of the additive genetic and dominance variances, estimates of their standard errors are shown. While the distributions of estimates obtained in this way

Table 9a. Estimates of additive genetic variance, dominance variance, the ratio of dominance variance to additive genetic variance, and the ratio of additive genetic variance to genotypic variance

Character	Sample	Year	σ_A^2	σ_D^2	$\dfrac{\sigma_D^2}{\sigma_A^2}$	$\dfrac{\sigma_A^2}{\sigma_G^2}$
Yield	I	1958	693.2 ± 240.0	205.6 ± 401.0	.30	.77
		1959	203.2 ± 142.0	187.5 ± 273.0	.92	.52
		Combined	338.7 ± 147.0	6.8 ± 252.0	.02	.98
	II	1959	(-143.8)± 192.0	1430.4 ± 456.0	--[a]	--
Ear length	I	1958	218.2 ± 71.0	109.8 ± 114.0	.50	.67
		1959	163.7 ± 73.0	158.7 ± 132.0	.97	.51
		Combined	151.8 ± 60.0	127.5 ± 101.0	.84	.54
	II	1959	49.6 ± 69.0	397.1 ± 145.0	8.01	.11
Ear diameter	I	1958	6.64 ± 1.78	.56 ± 2.62	.08	.92
		1959	5.88 ± 1.55	(-.76)± 2.28	--	1.15
		Combined	5.28 ± 1.49	1.08 ± 2.16	.20	.83
	II	1959	6.20 ± 1.68	.16 ± 2.49	.03	.97
Number kernel rows	I	1958	3.29 ± .83	(-.012)± 1.18	--	1.00
		1959	2.84 ± .76	.16 ± 1.12	.06	.95
		Combined	2.61 ± .72	.49 ± 1.03	.19	.84
		1959	3.88 ± .89	(-.84) ± 1.21	--	1.28
Weight per 100 kernels	I	1958	13.16 ± 3.63	(-.60) ± 5.47	--	1.05
		1959	7.84 ± 2.49	2.52 ± 3.99	.32	.76
		Combined	9.42 ± 2.68	1.08 ± 3.98	.11	.90
	II	1959	6.34 ± 1.68	6.66 ± 3.20	1.05	.49

[a] -- indicates ratio had negative value

are not known, it is customary to take 2.5 times the estimated standard

errors to set approximate confidence limits for the true values. The

standard errors were relatively high indicating again the sampling vari-

ability attached to estimates of components of variance. Since estimates

of σ_A^2 were computed directly from $\hat{\sigma}_m^2$, the standard deviations were some-

what smaller than those for the estimates of σ_D^2 which were obtained from

$\hat{\sigma}_m^2$ and $\hat{\sigma}_f^2$, both of which contributed to the standard deviations. All of

the negative estimates of σ_A^2 and σ_D^2 were less than one standard deviation

in absolute value which indicated that they could easily be estimates of

true values of zero or more.

Assuming that the genotypic variance consisted entirely of additive

genetic variance and dominance variance, the ratios of the estimates of

additive genetic variance to the genotypic variance given in Table 9 indi-

cated that with the exception of the Sample II estimates for yield and ear

length the genetic variance in the population was predominantly the additive

genetic type for all five of the characters. There was very little dominance

variance for ear diameter and number of kernel rows or for weight per 100

kernels except in the Sample II estimate. Values of the ratio exceeding one

were merely a result of negative estimates for σ_D^2.

The ratios of the estimates of σ_D^2 to σ_A^2 which are related to the level

of dominance were all less than one with two exceptions, viz., the Sample II

estimates for ear length and weight per 100 kernels. The latter, estimated

as 1.05, indicated that the additive genetic variance and dominance variance

were approximately equal in magnitude. The estimate of 8.01 for ear length

indicated considerably more dominance variance than additive genetic variance.

There were several cases where the estimate of the dominance variance was negative and was considered to be negligible in amount. The Sample II ratio for yield, however, was negative because the estimate of σ_A^2 was negative and not because the estimate of σ_D^2 was negative. If, as the data tended to indicate, σ_A^2 was near zero in this case, then in reality the ratio would be very large.

An empirical interpretation of the ratio σ_D^2/σ_A^2 with respect to the degree of dominance was obtained by comparison of the estimated value with some theoretical values given in Table 9a. Under the assumptions of no linkage and no epistasis the theoretical values given for the single locus case may be an average over all segregating loci and for the purposes here $\underline{a}$ and $\underline{p}$ in Table 9a were considered to be average values. With the exception of the two values 8.01 and 1.05 the estimates in Table 9 fell in one of three general areas of Table 9a, low average gene frequency and any level of dominance, partial dominance and any gene frequency, and very high gene frequency with overdominance. It seemed reasonable to reject the latter on the basis that past selection in the variety for any of the characters would not have resulted in gene frequencies near 1.0 for all favorable genes. On the other hand it seemed reasonable also to argue that the frequencies of the favorable genes would not be very low in a corn variety with a performance record such as Reid Yellow Dent had in the past. The most reasonable explanation is that most of the estimates of the ratio were in the partial dominance range. However, since the level of dominance was discussed on the basis of average effects, the above explanation was not to be construed as implying that the level of dominance was in general in the partial dominance range only.

Table 9b. Theoretical values of σ_D^2/σ_A^2 for a single locus with two alleles and for various values of a and p as described in the text

P	a				
	0	.8	1.0	1.5	2.0
.1	0	.04	.05	.08	.11
.2	0	.09	.13	.20	.26
.3	0	.15	.21	.37	.51
.4	0	.23	.33	.64	.98
.5	0	.32	.50	1.13	2.00
.6	0	.44	.75	2.20	5.33
.7	0	.58	1.17	5.91	42.00
.8	0	.76	2.00	72.00	32.00
.9	0	.89	4.50	10.13	2.00
.99	0	.27	49.50	.20	.09

The value of 1.05 for weight per 100 kernels did not deviate enough from the majority of the ratios to warrant special attention. It deviated only slightly from a value less than one which would have put it in the category discussed above. The value of 8.01 for ear length, however, was definitely in the complete dominance or overdominance range.

The estimates of the individual plant heritabilities and their standard errors are given in Table 10. The method involving the use of estimates of components of variance agreed quite well with that of regression of offspring on parent. The heritabilities were higher for ear diameter, number of kernel rows, and weight per 100 kernels than for yield and ear length. The

Table 10. Estimates of heritabilities on an individual plant basis obtained by the method of components of variance and the method of parent-offspring regression, Sample I and Sample II, 1958 and 1959

Character	Method of estimation[b]	Sample I			Sample II[a]
		1958	1959	Combined	1959
Yield	V.C.	20.8 ± 7.0	8.7 ± 6.0	12.0 ± 5.1	(-5.5) ± 7.3
	P.O.	8.8 ± 9.0	6.3 ± 6.7	7.6 ± 6.7	
Ear length	V.C.	31.8 ± 9.8	21.5 ± 9.4	20.9 ± 8.1	6.4 ± 8.9
	P.O.	34.2 ± 8.3	29.9 ± 8.4	32.0 ± 7.5	
Ear diameter	V.C.	47.8 ± 12.3	44.3 ± 10.9	38.8 ± 10.2	45.2 ± 11.3
	P.O.	46.9 ± 9.9	43.1 ± 9.3	45.0 ± 9.0	
Number kernel rows	V.C.	52.4 ± 12.0	46.7 ± 11.6	42.5 ± 10.9	59.4 ± 12.2
	P.O.	56.0 ± 9.6	56.9 ± 8.9	56.9 ± 8.6	
Weight per 100 kernels	V.C.	34.7 ± 9.0	33.6 ± 10.2	30.8 ± 8.3	24.7 ± 6.0
	P.O.	33.7 ± 11.0	38.2 ± 8.5	36.5 ± 9.1	

[a] Method of parent-offspring regression not used for Sample II

[b] V.C. denotes variance components
P.O. denotes parent-offspring regression

heritability estimates for the combined two-year analyses were somewhat lower than the individual year analyses. Genotype-environment interactions would tend to bias heritabilities for a single year upwards.

Tables 11, 12, 13, and 14 present the estimates of the components of covariance for the ten possible pairs of the five characters. Tables 11, 12, and 13 give the estimates for Sample I for each year individually and combined. The Sample II estimates are given in Table 14. Little comment about the estimates seemed necessary. The estimates of the component σ_{w12} were particularly large and indicated the large intraplot differences. Negative values of the covariance components were possible and were to be expected where inverse associations between pairs of characters existed. The estimates of σ_{m12} were used where genetic statistics for pairs of characters were to be computed. This component represented the additive genetic effects of association between the pairs of characters.

The components of covariance were used to compute genetic and pheno-typic correlations between the characters. The correlations are given in Table 15. The genetic correlation between yield and ear length was con-siderably less than the phenotypic correlation in this population. The genetic correlation estimates for ear length and ear diameter were quite inconsistent. Previously the very low estimate of σ_m^2 for ear length in Sample II was pointed out. Reference to Table 14 shows also that the esti-mate of σ_{m12} for ear length and ear diameter had an unusually large nega-tive value as contrasted to the other covariance components for the same pair of characters. Therefore, the genetic correlation of -1.18 for this pair of characters was considered suspect. It seemed likely that large sampling errors had led to rather unusual estimates for this pair of characters.

Table 11. Estimates of covariance components for pairs of characters, Sample I, 1958

	Component	Yield	Ear length	Ear diameter	Number kernel rows
Ear length	σ_{m12}	46.8			
	σ_{f12}	72.4			
	σ_{e12}	22.1			
	σ_{w12}	833.2			
Ear diameter	σ_{m12}	10.62	1.71		
	σ_{f12}	7.50	-5.54		
	σ_{e12}	5.40	1.76		
	σ_{w12}	89.64	12.47		
Number kernel rows	σ_{m12}	4.13	-1.11	.67	
	σ_{f12}	2.16	-1.70	.51	
	σ_{e12}	.72	.38	-.04	
	σ_{w12}	14.97	-3.95	3.13	
Weight per 100 kernels	σ_{m12}	7.87	3.30	.47	-.80
	σ_{f12}	8.09	-.29	1.14	-.71
	σ_{e12}	9.76	3.40	.56	.06
	σ_{w12}	139.86	34.03	5.44	-4.11

Table 12. Estimates of covariance components for pairs of characters, Sample I, 1959

	Component	Yield	Ear length	Ear diameter	Number kernel rows
Ear length	σ_{m12}	11.94			
	σ_{f12}	53.55			
	σ_{e12}	213.84			
	σ_{w12}	689.0			
Ear diameter	σ_{m12}	6.10	-1.75		
	σ_{f12}	2.32	-5.66		
	σ_{e12}	20.70	9.10		
	σ_{w12}	71.42	8.89		
Number kernel rows	σ_{m12}	1.74	-2.20	.62	
	σ_{f12}	1.26	-1.99	.39	
	σ_{e12}	8.18	2.94	.44	
	σ_{w12}	16.06	-.98	3.05	
Weight per 100 kernels	σ_{m12}	4.07	1.89	.40	-.45
	σ_{f12}	4.50	-.12	.84	-.66
	σ_{e12}	18.64	8.28	.76	.18
	σ_{w12}	64.96	14.06	3.28	-3.61

Table 13. Estimates of covariance components for pairs of characters, Sample I, 1958 and 1959 combined

	Component	Yield	Ear length	Ear diameter	Number kernel rows
Ear length	σ_{m12}	20.70			
	σ_{f12}	38.93			
	σ_{my12}	8.67			
	σ_{fy12}	24.04			
	σ_{e12}	117.98			
	σ_{w12}	761.1			
Ear diameter	σ_{m12}	6.35	-.43		
	σ_{f12}	3.50	-5.92		
	σ_{my12}	2.01	.41		
	σ_{fy12}	1.41	.33		
	σ_{e12}	13.06	5.42		
	σ_{w12}	80.53	10.68		
Number kernel rows	σ_{m12}	2.46	-1.52	.505	
	σ_{f12}	1.65	-1.76	.500	
	σ_{my12}	.48	- .130	.143	
	σ_{fy12}	.055	- .080	-.050	
	σ_{e12}	4.46	1.66	.200	
	σ_{w12}	15.52	-2.47	3.09	
Weight per 100 kernels	σ_{m12}	5.03	2.27	.419	-.595
	σ_{f12}	4.51	-1.33	.960	-.543
	σ_{my12}	.94	.33	.017	-.028
	σ_{fy12}	1.78	1.13	.025	-.140
	σ_{e12}	14.22	5.84	.660	.140
	σ_{w12}	102.41	24.05	4.36	-3.86

Table 14. Estimates of covariance components for pairs of characters, Sample II, 1959

	Component	Yield	Ear length	Ear diameter	Number kernel rows
Ear length	σ_{m12}	-42.0			
	σ_{f12}	150.2			
	σ_{e12}	152.4			
	σ_{w12}	776.9			
Ear diameter	σ_{m12}	4.17	-5.19		
	σ_{f12}	10.13	.21		
	σ_{e12}	15.86	6.34		
	σ_{w12}	83.48	10.62		
Number kernel rows	σ_{m12}	2.47	-2.02	.70	
	σ_{f12}	2.54	-2.19	.66	
	σ_{e12}	- .040	- .18	.060	
	σ_{w12}	22.00	-2.84	3.41	
Weight per 100 kernels	σ_{m12}	-.80	- .82	.32	-.80
	σ_{f12}	10.29	6.20	.15	-.90
	σ_{e12}	31.44	14.82	1.34	-.14
	σ_{w12}	69.99	22.10	3.60	-3.54

Table 15. Genetic and phenotypic correlations for the 5 characters in Sample I and Sample II, 1958 and 1959[a]

Character	Sample	Year	Yield	Ear length	Ear diameter	Number kernel rows	Weight per 100 kernels
Yield	I	1958		.48	.63	.35	.33
		1959		.26	.71	.29	.41
		Combined		.37 [b]	.60	.33	.36
	II	1959		--	--	--	--
Ear length	I	1958	.65		.18	-.17	.25
		1959	.73		-.20	-.41	.21
		Combined	.68		-.06	-.31	.24
		1959	.73		-1.18	-.58	-.18
Ear diameter	I	1958	.53	.11		.57	.20
		1959	.57	.10		.61	.24
		Combined	.54	.11		.54	.24
	II	1959	.60	.12		.57	.20
Number kernel rows	I	1958	.15	-.10	.45		-.49
		1959	.23	-.03	.51		-.38
		Combined	.19	-.06	.48		-.48
	II	1959	.21	-.10	.51		-.64
Weight per 100 kernels	I	1958	.47	.25	.33	-.36	
		1959	.40	.18	.30	-.38	
		Combined	.44	.22	.32	-.37	
	II	1959	.43	.30	.29	-.41	

[a] Genetic correlations in upper right corner of table
Phenotypic correlations in lower left corner of table

[b] -- indicates where $\hat{\sigma}_m^2$ for yield was negative and square root could not be taken

The genetic correlation between ear length and number of kernel rows was higher than the phenotypic correlation. The genetic and phenotypic correlations for the other pairs of characters were similar in magnitude.

Some of the genetic correlations between yield and the other characters were sufficiently high to bear scrutiny as possible bases of selection for yield itself. All four of the other characters had positive genetic correlations with yield ranging from .26 to .71. The correlation with ear diameter was .60 to .71 and indicated that there was a possibility in this material of using ear diameter as a selection criterion for yield at least in the initial stages of a selection program.

A few uses of the information obtained on the genetic parameters are illustrated in the following examples. The combined two-year analysis of Sample I only was used for this purpose because it constituted what might be considered minimum testing in a practical breeding program and because it was thought that it adequately demonstrated the procedures and results. Actually, no case in which only 5 plants were used in a plot for making tests of this type in corn was known to the author. It is clear from statistical procedures outlined previously that the expected results would be quite dependent on actual techniques used in the testing phases. As long as the necessary estimates of the genetic parameters were available, the progress under any specified breeding procedure could be determined. The entire concept is dependent of course upon certain basic assumptions outlined in the statistical procedures.

Changes expected due to selection were computed on the basis of selection of the superior 5 percent of the full-sib progenies which were the progenies

obtained from the cross of any individual male with any individual female.

Selection was based on the mean plant performance of the full-sib progenies

for two years with 4 replications per year and 5 plants per plot. The

changes expected in each of the characters if selection were for that

character per se are given in Table 16. The means for the original popula-

tion indicated that the variety itself was relatively quite good for these

5 characters. Even so, selection for the individual characters would result

in increases of 6 to 14 percent of the original means. There was enough

additive genetic variance in the population to result in yield increase of

9.32 bushels per acre for the selected offspring over that of the original

population which was an 8.6 percent increase over the rather high yield of

108.5 bushels per acre. It should be noted here that the original yields

in terms of grams per plant were multiplied by .47489 to get bushels per

acre.

Table 16. Expected genetic advance in the means of the 5 characters on the basis of selection of the superior 5 percent of the 192 full-sib families of Sample I when their performance was measured as the mean of 5 plants per plot grown in 4 replications per year for 2 years

Character	Mean	Expected change	
		Units	Percent of mean
Yield bushels/acre	108.5	9.32	8.6
Ear length mm./ear	119.2	13.25	11.1
Ear diameter mm./ear	49.8	2.97	6.0
Number of kernel rows number/ear	17.9	2.12	11.9
Weight per 100 kernels g./100	30.0	4.14	13.8

In view of the correlations obtained previously, it was worthwhile to compute the expected changes in each of the characters when selection was for one of the other characters. These are given in Table 17. Selection for some of the characters would be quite effective in changing other characters. For instance, selection for ear diameter would increase yield 6.3 percent above the mean yield of the population. Selection for number of kernel rows would result in a 4.1 percent decrease in the mean ear length, etc. Selection for yield itself would make positive changes in each of the other four characters. It was interesting to note that selection for ear length, ear diameter, and number of kernel rows would all make increases in yield of 3.2 to 6.3 percent.

Table 17. Expected genetic advance in the means of 5 characters resulting from selection for other characters when selection is based on the mean performance of the superior 5 percent of the 192 progenies in Sample I grown in plots of 5 plants, 4 replications per year, and 2 years

| Selection for | Expected change in[a] | | | | |
	Yield bushels/acre	Ear length mm./ear	Ear diameter mm./ear	Number kernel rows number/ear	Weight per 100 kernels g./100
Yield		4.80 (4.0)	1.47 (3.0)	.57 (3.2)	.12 (.4)
Ear length	3.43 (3.2)		-.15 (.3)	-.53 (3.0)	.79 (2.6)
Ear diameter	6.79 (6.3)	-.97 (.8)		1.14 (6.4)	.94 (3.1)
Number kernel rows	3.79 (3.5)	-4.93 (4.1)	1.64 (3.3)		- 1.93 (6.4)
Weight per 100 kernels	.42 (.4)	3.99 (3.4)	.74 (1.5)	-1.05 (5.9)	

[a] Change as percent of mean given in parentheses

Since yield was the character of primary economic importance, the effect of selection for each of the other characters was computed and is given in Table 18. The increases expected are the same as those of Table 17, but in addition, the increases were given as the percent of change in yield if selection had been for yield itself. The four characters would change yield from 4.5 to 72.9 percent as much as selection for yield itself would do. It was interesting that selection for ear diameter would change yield 73 percent as much as selection for yield. This indicated that it might be useful and possible to select in this population on the basis of ear diameter and make a substantial increase in yield. Ear diameter is quite easily determined and less elaborate experimental designs would be necessary to adequately measure it since it is less subject to environmental fluctuations.

Table 18. Expected change in yield due to selection for each of the other 4 characters on the basis of the mean performance of the superior 5 percent of the 192 progenies of Sample I grown in plots of 5 plants, 4 replications, and 2 years

Selection for	Expected change in yield	
	Bushels/acre	Percent of yield[a]
Ear length	3.43	36.8
Ear diameter	6.79	72.9
Number kernel rows	3.79	40.7
Weight per 100 kernels	.42	4.5

[a] Expressed as percent of change due to selection for yield itself = 9.32 bushels per acre

DISCUSSION

Estimates of the type furnished by this study, sufficiently precise and applicable to a broad population of corn, would provide a basis for the interpretation of many problems in corn breeding and maximization of the progress to be realized from selection. While what may be learned about quantitative genetics is less than total understanding, acquisition of information sufficient for the formulation of efficient breeding programs appears to be attainable. Various mathematical models are available for the estimation of genetic parameters. Invariably, certain assumptions are necessary to apply the models to the biological situation. Adequacy of these models for describing a population in terms of genetic parameters becomes critical in view of the assumptions which must be made. Information suitable for the evaluation of some of the models used is needed.

A study the size of the one reported here could not provide by any means an adequate evaluation of a model. This is merely the initial study of a series designed to provide estimates of enough different types to permit some degree of critical comparison. However, two samples of progenies were drawn from a single population providing estimates of a few of the genetic parameters for the population and perhaps indicating some of the sampling difficulties to be encountered in the procedure. A few differences in the estimates for the two samples apparently were due to sampling inadequacies.

Estimates of the components of variance were readily obtained from the mean squares and expected mean squares for the random model. The structure

of the progenies was such that each individual analysis had 192 full-sib

families with 96 pairs of half-sib families. Because of this breeding

structure the partition of the degrees of freedom was such that the compo-

nent of variance for males was Cov (HS) and the component of variance for

females in males was Cov (FS) - Cov (HS), both of which were estimated.

The genetic interpretation of the estimated components when the males and

females are non-selected random individuals from a non-inbred random mating

population has been given by Kempthorne (1957) as

$$\text{Cov (HS)} = 1/4 \ \sigma_A^2 + 1/16 \ \sigma_{AA}^2 + 1/64 \ \sigma_{AAA}^2 + \dots$$

$$\text{Cov (FS)} = 1/2 \ \sigma_A^2 + 1/4 \ \sigma_D^2 + 1/4 \ \sigma_{AA}^2 + 1/8 \ \sigma_{AD}^2 + 1/16 \ \sigma_{DD}^2 + \dots$$

The above formulae were based on the assumption that there is absence of

linkage, an assumption used throughout this study in obtaining estimates.

However, it was not necessary to assume that there were only two alleles

per locus. The assumptions concerning diploid behavior and maternal effects

should have caused no difficulty in corn and at any rate would probably be

negligible relative to some of the other factors.

To make the estimates more useful and interpretable it was further

assumed that there was no epistacy. With this assumption, however, the

assumption of no linkage could be relaxed to one of linkage equilibrium

with respect to frequencies of coupling and repulsion heterozygotes.

Cockerham (1956) showed that covariance between relatives of the type here

were affected by recombination frequencies less than one half even in a

random mating population whose genotypic frequencies are in linkage equilib-

rium. The biases were in the epistatic components and not in the additive

genetic and dominance components. Since the progenies were a random sample
from a variety which had undergone random mating for a considerable number
of generations, the assumption of linkage equilibrium appeared to be
appropriate. The assumption of no epistacy was not founded on a priori
knowledge of the actual facts, and in reality any interpretation of the
data was subject to serious limitations because of the assumption. From
an operational viewpoint though, it appeared that use of the simplified
model would lead to useful interpretations. It is reasonable that the
simple model may be adequate in some situations. Also, it was possible to
determine the probable biases due to the assumptions and to show in some
cases that the interpretations were not changed by removing the assumptions.

With the assumption of no epistacy the component of variance for males
was an estimate of $1/4 \ \sigma_A^2$ and the component for females in males was an
estimate of $1/4 \ \sigma_A^2 + 1/4 \ \sigma_D^2$. The dominance variance was estimated by
taking the difference between them. For the Sample I estimates, the
additive genetic variance was a relatively large amount of the total geno-
typic variance for each of the five characters, yield, ear length, ear
diameter, number of kernel rows, and weight per 100 kernels. The Sample I
data provided the more complete analyses of the two samples. It involved
individual analyses for two years as well as combined analyses for the two
years. The three estimates for each character were fairly consistent and
reliable. These estimates indicated that there was additive genetic vari-
ance of sufficient magnitude to result in reasonable increases in each of
the characters by selection. It also implied that selection for general
combining ability should be relatively important in this variety, and that

possibly preliminary evaluation of lines taken from the variety could be made by use of a test of general combining ability such as the top-cross test. These estimates for yield agreed with those obtained from similar experiments reported by Robinson and Comstock (1955). The estimates for ear length, ear diameter, and number of kernel rows also apparently agreed with that of the same authors although they did not report actual data but rather a statement concerning the results obtained.

The estimates for Sample II differed from those of Sample I for yield, ear length, and weight per 100 kernels. The estimates of the additive genetic variance and dominance variance for weight per 100 kernels were essentially equal in magnitude. This could very easily have been sampling variation in obtaining the estimate. The estimate of additive genetic variance for yield was actually negative and if taken as a zero estimate was in direct contrast to the estimates in Sample I. The Sample II estimate would indicate that only dominance variance was present in this variety and that selection should be for specific combining ability. The estimate of additive genetic variance for ear length was very low also. It was not clear why the Sample II estimates differed so much from those of Sample I. The plot technique did not appear to be faulty. In fact, the estimates of the interplot and intraplot variances were consistent with those of Sample I. The major difference apparently lay in the highly divergent response of the pair of half-sib families of many of the males in Sample II. The performance of the two full-sib progenies of a particular male over a large number of the 96 pairs of male progenies tended to be of a specific nature perhaps overemphasizing the non-additive genetic effects.

Perhaps the extremes of the half-sib family distributions were drawn more frequently than would normally be the case. If so, the use of more females per male should tend to improve the sampling problem involved here.

The Sample II estimates were obtained from data for only one year and would not be considered adequate by most corn breeders. However, the differences between Sample I and Sample II do point out some of the sampling difficulties encountered in obtaining estimates of genetic parameters. Inconsistencies of this magnitude can not be ignored. Both adequate sampling of the individuals of the population to be studied as well as adequate sampling in the testing phases of the experiment would appear to be quite important.

Significant genotype x year interactions were obtained for all characters except weight per 100 kernels on the basis of the combined two-year analysis of Sample I. In no case though were both the males x years and females x years interactions significant. The full-sib progenies were genetically heterogeneous being on the average as heterogeneous as the open-pollinated variety itself. Sprague and Federer (1951) showed that genotype x environment interaction components were smaller for heterogeneous materials than for the more homogeneous materials. Also, the years 1958 and 1959 had similar growing seasons for corn and yield performance was relatively high in both years. Therefore, the interaction components in this experiment may have been somewhat smaller than often encountered.

The interactions did not appear to be proportional to the main effects for males and females in males in this study. Comstock (1955) pointed out that such proportionality may be critical in studies of the nature of gene action in quantitative inheritance. If the assumption of proportionality

is not valid, then the cost of obtaining data of sufficient scope to pro-
vide satisfactory estimates of the genetic parameters may be prohibitive.

The average degree of dominance could not be obtained from the present
data because the exact gene frequencies in the random mating population
were unknown. Robinson, et al. (1955) pointed out, however, that the ratio
σ_D^2/σ_A^2 is related to the type of gene action involved in heterosis. Hull
(1945) suggested overdominance as the reason intra-variety selection for
yield in open-pollinated varieties of corn was ineffective. Crow (1948)
and Brieger (1950) gave supporting arguments for the overdominance hypothe-
sis on the basis of equilibrium random mating populations. Robinson, et al.
(1955) pointed out that if the overdominance hypothesis is correct, gene
frequencies gravitate toward an equilibrium at intermediate values for the
alleles. Furthermore, they stated that the genetic variance produced by
segregation of such alleles would be mostly dominance variance with only a
trivial amount of additive genetic variance. Hence, to find considerable
dominance variance in a population but only negligible additive genetic
variance would support the overdominance hypothesis.

The estimates of σ_D^2/σ_A^2 obtained in the present experiment were in
quite different categories for Sample I and Sample II. The estimates for
Sample I were less than one for all of the characters and were very near
zero for ear diameter, number of kernel rows, and weight per 100 kernels.
This was in agreement with results obtained by Robinson and Comstock (1955).
On the other hand, the estimates of the ratio for yield, ear length, and
weight per 100 kernels in Sample II were greater than one. The estimate of
8.01 for ear length was especially large. An estimate for yield was not
actually given because the estimate of σ_A^2 was negative and the relative

magnitude of a negative ratio would have little meaning. However, if the negative estimate of σ_A^2 indicated a trivial amount of additive genetic variance for yield, the ratio $\hat{\sigma}_D^2/\hat{\sigma}_A^2$ would be a very large number. Large estimates such as these for yield and ear length lend support to the over-dominance hypothesis. Conflicting results such as these for a single population seriously limited any definite conclusions about the type of gene action in the Reid Yellow Dent variety.

The estimates of σ_D^2/σ_A^2 were empirically compared to theoretical values possible with different gene frequencies and degrees of dominance for the simple case of a single locus with two alleles. It was indicated that all of the estimates less than one fell in the partial dominance and no dominance range. The large estimates of the ratio for yield and ear length in Sample II fell in the overdominance range. The comparison was absolutely dependent upon the assumptions of no linkage and no epistacy so that the parameters for gene frequency and degree of dominance could be considered as average. As such, Robinson, et al. (1955) pointed out that there are two explanations for values of σ_D^2/σ_A^2 less than one. The first is that there is no overdominance at any locus, i.e., a < 1.0 at all loci. The second is that there is both partial dominance at some loci and over-dominance at other loci, the former producing mostly additive genetic variance and the latter mostly dominance variance, so that the net or average result is estimates of the ratio between zero and one.

Due to what is known about the past history of the variety and about the five characters studied, low or extremely high gene frequencies and negative levels of dominance, i.e., a < 0, were not considered in the above

comparison. The variety was rather widely grown on a commercial basis at one time and various strains had undergone appreciable selection so that it is likely the frequencies of the favorable genes were reasonably high. Furthermore, each of the five characters studied here would have been considered important in the choice of seed ears by the early breeders. For these five characters the variety compares favorably with some of the better hybrids grown today. The mean performance of the progenies used in this experiment certainly supported the latter statement. On the other hand, it is unlikely that any past selection would have been intense enough to produce gene frequencies greater than 0.9. Therefore, it appeared reasonable to consider gene frequencies between 0.5 and 0.9 only.

Negative levels of dominance were not considered because the expression of heterosis in corn in the majority of cases is of the positive type. Most of the results concerning heterosis concerned yield only. Recently, Robinson, et al. (1956) reported results for yield which indicated that varietal hybrids had higher yields than the better of the two parents. While very little data on the expression of heterosis has been reported for ear length, ear diameter, number of kernel rows, and weight per 100 kernels, Byrd (1955) reported data on each of these characters for a rather comprehensive set of crosses. His results indicated that single cross hybrids were better than the best parent for each of the characters.

Linkage and epistasis cause biases in the ratio $\hat{\sigma}_D^2/\hat{\sigma}_A^2$. The ratio was estimated as

$$\frac{\hat{\sigma}_f^2 - \hat{\sigma}_m^2}{\hat{\sigma}_m^2} \quad \text{or} \quad \frac{\widehat{\text{Cov}}\,(FS) - 2\,\widehat{\text{Cov}}\,(HS)}{\widehat{\text{Cov}}\,(HS)}$$

Robinson and Comstock (1955) gave the biases in σ_m^2 and σ_f^2 due to linkage when there are two alleles per locus. Since the formulae are long and require considerable definition, they are not given here. In general, the effect of linkage is as follows. The bias in σ_m^2 is related to the quantity (pt-rs) where pt is the frequency of coupling heterozygotes and rs is the frequency of repulsion heterozygotes in the progenies studied. The term is positive for linked gene pairs that enter the cross in the coupling phase and negative when they enter in the repulsion phase. Also, for a large group of crosses it is possible to obtain equal frequencies of cases when the term is positive or when it is negative for a pair of loci so that the effects of coupling and repulsion linkage are equivalent and result in no effect on σ_m^2. For σ_f^2 an additional bias is due to the term $(pt-rs)^2$ which is always positive unless there is linkage equilibrium, i.e., pt = rs. The net effect of this is to cause an upward bias in the ratio.

The composition of Cov (HS) and Cov (FS) for arbitrary epistacy was given earlier in the discussion. In the case of epistacy the ratio $\dfrac{\hat{\sigma}_f^2 - \hat{\sigma}_m^2}{\hat{\sigma}_m^2}$ would become an estimate of

$$\frac{1/4\ \sigma_D^2 + 1/8\ \sigma_{AA}^2 + 1/8\ \sigma_{AD}^2 + 1/16\ \sigma_{DD}^2 + \ldots}{1/4\ \sigma_A^2 + 1/16\ \sigma_{AA}^2 + 1/64\ \sigma_{AAA}^2 \ldots}.$$

Again the bias in the estimate of σ_D^2/σ_A^2 would be upward and could be appreciable if simple inter-locus interactions such as additive effects by additive effects were sizable.

It is evident that the possible sources of bias tend to cause the estimated ratio to be larger than the true σ_D^2/σ_A^2. For the cases when

the estimates of the ratio were less than one, linkage and epistasis would not change the interpretation. If anything, the estimates are larger than the true parameter. Linkage, epistacy, or a combination of linkage and epistacy could cause overestimation of the true ratio. Some of the values of the ratio greater than one could be a result of such overestimation. As mentioned earlier the assumption of no epistacy makes it next to impossible to draw definite conclusions about the genetic parameters, especially when the results are as inconsistent as in the present case.

The estimates of heritability for this population were of sufficient magnitude to suggest that sizable increases in each of the five characters could be obtained by selection. To illustrate the possible effects of a selection procedure in which the superior 5 percent of the progenies would be intercrossed to produce a new population, the expected changes due to selection were computed on the basis of the performance of the progenies for the combined two-year analyses of Sample I. The assumptions involved in this type of computation were outlined in the statistical procedures.

Although the performance of the variety used in this study with respect to the five characters studied was relatively good, the estimates of the expected changes due to selection indicated that increases of 6.0 to 13.8 percent of the respective means could be obtained. For instance, even though the estimate of heritability for yield was quite small, a genetic advance of 8.6 percent per cycle of selection was indicated by the data. However, many attributes not considered here such as disease resistance, insect resistance, and seed quality must be considered in a selection program. For example, this population had very poor stalk quality and

lodged seriously as compared to recently selected hybrids growing in the same field. It should be pointed out again that estimates such as this are based on certain assumptions concerning the formula used, and the expected values may not be attained at all. It would seem, though, that from a breeding standpoint, the utility of the estimates of genetic parameters lies in their value for making predictions of this sort.

The correlations between the pairs of characters were quite interesting and some of them appeared to be sufficiently high to be useful in selection programs. The genetic and phenotypic correlations for yield, ear length, and ear diameter were higher than those obtained by Robinson, et al. (1951) from a study of the F_2 generations of three populations. In the present study ear length, ear diameter, number of kernel rows, and weight per 100 kernels had positive genetic correlations with yield. Since such correlations could provide a useful tool in selection programs for yield, the changes in yield due to selection of the superior 5 percent of the progenies on the basis of each of the other characters were computed. The results indicated that selection for ear diameter, for example, would lead to an increase in yield 72 percent of that due to selection for yield itself. Since ear diameter is easily measured, selection of ears with large diameters in this variety could very well produce in initial stages of selection appreciable increases in yield. Selection for ear length and number of kernel rows also would lead possibly to appreciable increases in yield. Such results indicate some of the uses of the estimates of the genetic parameters.

Although some of the estimates obtained in this study were inconsistent, due to sampling difficulties, they did provide information on the

reliability of the approach used. They indicated that considerable diffi-

culty may be encountered in obtaining adequate estimates of at least some

of the genetic parameters such as level of dominance. The series of

studies planned as a continuation of this one should provide relatively

complete information on the reliabilities of estimates of genetic para-

meters obtained by the approach used here as well as the magnitude of the

biases due to the genetic assumptions made, particularly that of absence

of epistacy.

SUMMARY

1. Estimates of the additive genetic and dominance variance for yield of shelled grain, ear length, ear diameter, number of kernel rows, and weight per 100 kernels were obtained for the open-pollinated variety of corn, Reid Yellow Dent. The estimates were based on replicated tests of full-sib and half-sib progenies obtained by crossing random and non-inbred individuals of the open-pollinated variety which was assumed to be a random mating population. Two samples of progenies from the single variety were studied. Each sample consisted of 192 progenies obtained by crossing each of 96 plants designated males to 2 other plants designated females. Sample I was grown at one location for two years; Sample II was grown at the same location for one year only.

2. The additive genetic and dominance variances were estimated under the assumptions of equilibrium linkage with respect to coupling and repulsion phases and no epistacy. The Sample I estimates indicated that the additive genetic variance was a large part of the total genotypic variance, i.e., the sum of the additive genetic and dominance variances, for all five characters. The dominance variance was less, and in many cases considerably less, than the additive genetic variance. In contrast, the Sample II estimates indicated that the dominance variance was the principal component of the total genotypic variance for yield and ear length and to a lesser extent for weight per 100 kernels. The estimates for ear diameter and number of kernel rows were similar to those of Sample I. These conflicting results reflect the magnitude of the problem of adequately estimating genetic variances.

3. The ratio σ_D^2/σ_A^2 was estimated and related empirically to the type of gene action involved in heterosis. In view of the conflicting esti-mates of the genetic variance obtained for Sample I and Sample II, con-clusions were in two categories. Where the estimate of σ_D^2/σ_A^2 was less than 1.0 there could be either no overdominance, or a combination of partial dominance and overdominance, i.e., partial dominance at some loci and overdominance at others. Where the estimate was greater than 1.0 over-dominance was indicated. The Sample II estimates for yield and ear length were appreciably greater than 1.0.

4. Linkage and epistacy could cause considerable upward bias in the estimates of σ_D^2/σ_A^2. A brief discussion of this was given. The upward bias would have little effect on the interpretation for values of ratio less than 1.0. Such bias, however, could account for the ratio being greater than 1.0 when in reality there was no overdominance.

5. Estimates of the genotype x year interactions were obtained for the Sample I crosses. There were sizable and significant interactions for yield, ear length, ear diameter, and number of kernel rows. The inter-actions for the different types of genetic effects were not proportional to their respective main effects. This indicated that extensive testing may be necessary to adequately and reliably estimate some of the genetic parameters such as σ_D^2/σ_A^2.

6. Heritability in terms of the proportion of additive genetic variance to the total phenotypic variance was computed from the components of variance and in the case of Sample I from the regression of offspring on parent. The estimates were quite low for yield but ranged from 25 to 50 percent for the other characters. The two methods of computation agreed reasonably well.

7. Genetic and phenotypic correlations between pairs of the characters were obtained by analyses of covariance. The genetic and phenotypic correlations differed in magnitude for some of the characters, but the various estimates for pairs of characters were reasonably consistent in the case of both correlations. The genetic correlations between yield and each of the other four characters ranged from .32 for number of kernel rows to .65 for ear diameter.

8. The heritabilities and genetic correlations for the combined two-year analysis of Sample I were used to compute the expected genetic changes due to selection when the selection criterion was each of the characters per se and when it was each of the other four characters. The change in yield per cycle of selection when the superior 5 percent of the progenies of full-sibs are intercrossed to produce the new population was estimated to be 8.6 percent of the mean yield when the selection criterion was yield itself. The expected changes were based on the assumptions of normal distribution of the progeny means and linear regression of phenotypic value on genotypic value. Sizable changes could also be obtained for the other characters if selection were practiced for them. The change in yield due to selection for each of the other characters was estimated as the percent of the change in yield itself. It ranged from 4.5 percent when weight per 100 kernels was the selection criterion to 72.9 percent when ear diameter was the selection criterion. It was suggested that in the initial stages of a selection program a sizable increase in yield for this population could be obtained by selection for ear diameter.

LITERATURE CITED

Brieger, F. G. 1950. The genetic basis of heterosis in maize. Genetics 35:420-445.

Bruce, A. B. 1910. The Mendelian theory of heredity and the augmentation of vigor. Science 32:627-628.

Byrd, W. P. 1955. Genetic and environmental variances in segregating and non-segregating maize populations. Unpublished Ph.D. Thesis. Ames, Iowa, Library, Iowa State University of Science and Technology.

Cockerham, C. C. 1956. Effects of linkage on the covariances between relatives. Genetics 41:138-141.

Comstock, R. E. 1955. Theory of quantitative genetics: Synthesis. Cold Spring Harbor Symposia on Quantitative Biol. 20:93-102.

Comstock, R. E. and Robinson, H. F. 1952. Estimation of average dominance of genes. In Gowen, J. W., ed. Heterosis. pp. 494-516. Ames, Iowa, Iowa State College Press.

Crow, J. F. 1948. Alternative hypotheses of hybrid vigor. Genetics 33: 477-487.

Crow, J. F. 1952. Dominance and overdominance. In Gowen, J. W., ed. Heterosis. pp. 282-297. Ames, Iowa, Iowa State College Press.

East, E. M. 1936. Heterosis. Genetics 21:375-397.

Fisher, R. A. 1918. The correlation between relatives on the supposition of Mendelian inheritance. Trans. Roy. Soc. Edin. 52:399-433.

Fisher, R. A. 1949. The theory of inbreeding. Edinburgh, Oliver and Boyd.

Gamble, E. E. 1957. Relative importance of epistatic and nonepistatic gene effects in maize. Unpublished Ph.D. Thesis. Ames, Iowa, Library, Iowa State University of Science and Technology.

Gardner, C. O., Harvey, P. H., Comstock, R. E., and Robinson, H. F. 1953. Dominance of genes controlling quantitative characters in maize. Agron. Jour. 45:186-191.

Griffing, B. 1956. Concept of general and specific combining ability in relation to diallel crossing systems. Australian Jour. Biol. Sci. 9:463-493.

Gwynn, G. R. 1959. Relation between means and components of genotypic variance in biparental progenies of a variety of maize. Unpublished Ph.D. Thesis. Ames, Iowa, Library, Iowa State University of Science and Technology.

Hayman, B. I. 1957. Interaction, heterosis and diallel crosses. Genetics 42:336-355.

Hull, F. H. 1945. Recurrent selection for specific combining ability in corn. Jour. Amer. Soc. Agron. 37:134-145.

Hull, F. H. 1952. Recurrent selection and overdominance. In Gowen, J. W., ed. Heterosis. pp. 451-473. Ames, Iowa, Iowa State College Press.

Jensen, S. D. 1959. Combining ability of unselected inbred lines of corn from incomplete diallel and top-cross tests. Unpublished Ph.D. Thesis. Ames, Iowa, Library, Iowa State University of Science and Technology.

Jinks, J. L. 1955. A survey of the genetical basis of heterosis in a variety of diallel crosses. Heredity 9:223-238.

Jones, D. F. 1917. Dominance of linked factors as a means of accounting for heterosis. Genetics 2:466-479.

Kempthorne, O. 1954. The correlation between relatives in a random mating population. Proc. Roy. Soc. London, B, 143:103-113.

Kempthorne, O. 1956. The theory of the diallel cross. Genetics 41:451-459.

Kempthorne, O. 1957. An introduction to genetic statistics. New York, N. Y., John Wiley and Sons, Inc.

Kinman, M. L. and Sprague, G. F. 1945. Relation between number of parental lines and theoretical performance of synthetic varieties of corn. Jour. Amer. Soc. Agron. 37:341-351.

Matzinger, D. F. 1956. Components of variance of diallel crosses of maize in experiments repeated over locations and years. Unpublished Ph.D. Thesis. Ames, Iowa, Library, Iowa State University of Science and Technology.

Matzinger, D. F., Sprague, G. F., and Cockerham, C. C. 1959. Diallel crosses of maize in experiments repeated over locations and years. Agron. Jour. 51:346-350.

Robinson, H. F. and Comstock, R. E. 1955. Analysis of genetic variability in corn with reference to probable effects of selection. Cold Spring Harbor Symposia on Quantitative Biol. 20:127-136.

Robinson, H. F., Comstock, R. E., and Harvey, P. H. 1949. Estimates of heritability and the degree of dominance in corn. Agron. Jour. 41:353-359.

Robinson, H. F., Comstock, R. E., and Harvey, P. H. 1951. Genotypic and phenotypic correlations in corn and their implications in selection. Agron. Jour. 43:282-287.

Robinson, H. F., Comstock, R. E., and Harvey, P. H. 1955. Genetic variances in open-pollinated varieties of corn. Genetics 40:45-60.

Robinson, H. F., Comstock, R. E., Khalil, A., and Harvey, P. H. 1956. Dominance versus over-dominance in heterosis: Evidence from crosses between open-pollinated varieties of maize. Amer. Nat. 90:127-131.

Robinson, H. F., Khalil, A., Comstock, R. E., and Cockerham, C. C. 1958. Joint interpretation of heterosis and genetic variances in two open-pollinated varieties of corn and their cross. Genetics 43:868-877.

Rojas, B. A. and Sprague, G. F. 1952. A comparison of variance components in corn yield trials: III. General and specific combining ability and their interaction with locations and years. Agron. Jour. 44:462-466.

Snedecor, G. W. 1956. Statistical methods. 5th ed. Ames, Iowa, Iowa State College Press.

Sprague, G. F. 1953. Heterosis. In Loomis, W. E., ed. Growth and differentiation in plants. pp. 113-136. Ames, Iowa, Iowa State College Press.

Sprague, G. F. 1955. Problems in the estimation and utilization of genetic variability. Cold Spring Harbor Symposia on Quantitative Biol. 20:87-92.

Sprague, G. F. and Federer, W. T. 1951. A comparison of variance components in corn yield trials: II. Error, year x variety, location x variety, and variety components. Agron. Jour. 43:535-541.

Sprague, G. F. and Tatum, L. A. 1942. General vs. specific combining ability in single crosses of corn. Jour. Amer. Soc. Agron. 34:923-932.

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