COVARIANCES AMONG RELATIVES IN A MAIZE VARIETY (*ZEA MAYS* L.)[1]

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COMSTOCK and ROBINSON (1948, 1952) presented and discussed three mating designs and the associated experimental procedures for estimating genetic variances of quantitative characters in plant populations. These three procedures, designated Experiment I, II, and III, utilize the covariances among full sibs and covariances among half sibs for the estimation of genetic parameters. However, since only two types of covariances among relatives can be calculated from these designs, only two genetic parameters, additive genetic variance and dominance variance, can be estimated. Epistasis must be assumed to be absent for the interpretation of the results although these same authors emphasized that this assumption probably is not realistic. Evidence of epistatic effects for several quantitative characters in maize has been obtained with other estimation procedures (GAMBLE 1962; SPRAGUE *et al.* 1962).

This study utilized 66 phenotypic variances and covariances among relatives for estimating genetic components of variance in an open-pollinated variety of maize (*Zea mays* L.). The relatives were the products of a two-generation mating system similar to that suggested by KEMPTHORNE (1957, pp. 425–426). The estimates of variance components were used to compare the efficiency of four selection methods.

MATERIALS AND METHODS

The open-pollinated variety of maize, Reid Yellow Dent, was used as the original population for this study. This population had been maintained in an isolated nursery near Iowa State University for many generations. It was assumed to be a random-mating population in linkage equilibrium.

Families composed of related individuals from controlled crosses (diagrammed in Figure 1) were produced to provide different degrees of relationship. In 1957 randomly chosen male (m) and female (f) parents from the original population grown in the field were used to produce the first-generation matings. Each of one group of males was crossed to two females to produce progenies of P_i and Q_i. Each of a second group of males was crossed to one female to produce progenies R_i. Each of a third group of plants was self-pollinated to produce inbred progenies S_i. Second-generation matings were made in 1958 among P, Q, R, S, and a bulk of the original population, designated as T. The letters A through K represent the 11 full-sib progenies obtained from

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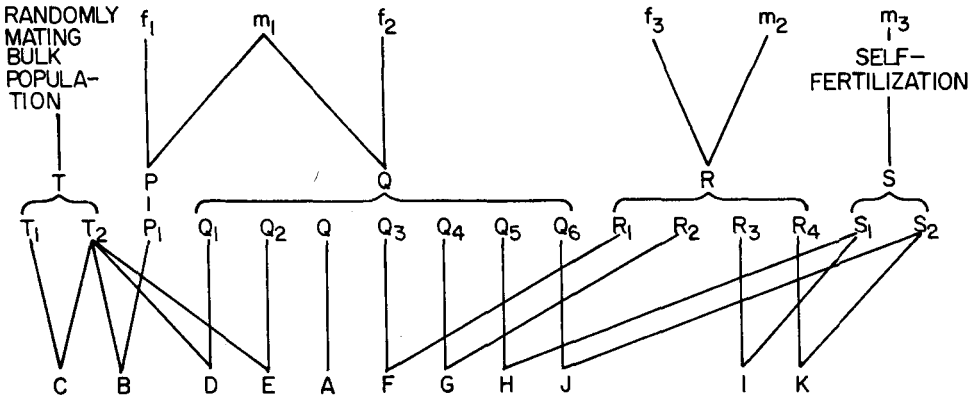

FIGURE 1.—The mating system used in producing the 11 branches of a family.

one first-generation mating and 10 second-generation matings. These 11 full-sib progenies were related by descent and were considered to be 11 branches of a family derived from a random-mating population. Forty-five families of this mating structure were produced and constituted the material grown to obtain estimates of the genetic variances and covariances for the population.

Field experiments were grown at Ames, Iowa, in 1962 and 1963. The 45 families were assigned at random to five sets. Each year three repetitions of each of the five sets were randomly assigned to 15 blocks in the field, and the 99 entries within a set (11 branches of each of nine families) were randomly assigned to plots within the respective block. Individual plots were single rows 101.6 cm apart, with 19 single-plant hills spaced 33.9 cm apart within the row. Soon after plant emergence, hills without plants were replanted with a marker stock characterized by a purple stalk that could be identified at harvest time. These purple plants were grown merely to provide competition for the adjacent plants. Data were obtained only on plants guarded on both sides by other plants.

Seven quantitative characters studied were plant height (cm) measured from the soil to the collar of the uppermost leaf, ear height (cm) measured from the soil to the uppermost ear-bearing node, ear length measured to the nearest 0.5 cm, ear diameter measured to the nearest 0.1 cm at the point of greatest diameter, kernel row number counted at approximately one-third of the distance from the butt to the tip of the ear, kernel weight recorded to the nearest 0.1 g on three samples of 100 randomly drawn kernels, and total shelled grain weight (g) per plant. Ear-character data were obtained after all ears had been dried artificially. The second ears from prolific plants were included in the measurements of yield and kernel weight but not in the measurement of ear length, ear diameter, or kernel row number. Unweighted plot means on a per-plant basis were used for most statistical analyses. An estimate of intraplot variance was obtained from individual plant data from one set of families in 1963.

A total of 66 phenotypic covariances within and among the 11 branches of the families were obtained. By assuming that the pair of individuals, $X_i Y_j$, is a random one from the totality of pairs with the particular relationship from an infinite, random-mating population without linkage and at equilibrium, a genotypic covariance can be derived from each phenotypic covariance. This genotypic covariance was illustrated by KEMPTHORNE (1954, 1957) for the case of one locus as:

$$\mathrm{Cov}(XY) = 2r_{xy}\sigma^2{}_A + u_{xy}\sigma^2{}_D.$$

The theoretical covariance value for the case of n unlinked loci is:

$$\mathrm{Cov}(XY) = 2r_{xy}\sigma^2{}_A + u_{xy}\sigma^2{}_D + \sum_{\substack{t,s=0 \\ 2 \le t+s \le n}}^{n} (2r_{xy})^t (u_{xy})^s \sigma^2{}_{At_Ds}$$

in which the summation extends over all values of t and s so that $t + s = n$, and n is the total

number of loci segregating. Thus, with the assumption of random mating in an equilibrium population with no linkage, the covariances between relatives are simply derived from the covariances in the one-locus case.

The 66 possible relationships among and within the 11 branches of a family in this study may be divided into the following five broad categories: 1) full sibs, 2) half sibs, 3) cousins, 4) uncle-nephew, and 5) no relationship. Because of the differences in the level of inbreeding of the parents and the degree of divergence of the lines of descent among relatives, eight types of covariances were available. The covariation observed between any two relatives may be interpreted in statistical-genetic terms as genotypic covariances among relatives; and accordingly, each genic covariance may be given a series of coefficients of correlation to indicate its degree of genic relationship. These coefficients of correlation are expressed on the basis of the values for ϕ, ϕ', $2r_{xy}$, and u_{xy} (KEMPTHORNE 1954, 1957) (Table 1).

Eleven mean squares (full sibs) and 55 mean cross products were computed from the nine families within each of the sets and then combined over sets. Each observed mean square or mean cross product represents an estimate of a covariance between relatives. Since each covariance of relatives may be translated into genetic components of variance, a series of the covariance of relatives values can be used to estimate genetic variance components by means of least-squares procedures. However, one of the assumptions of using least-squares procedures is that all entries should have equal variances. The variance of a mean square is $\frac{2(\text{E MS})^2}{\text{df}}$ and the variance of a cross product is $\frac{(\text{E MS}_j)(\text{E MS}_j')}{\text{df}} + \frac{(\text{E MP})^2}{\text{df}}$ where E MS is the expected mean square and E MP is the expected cross product. Since E MP is relatively small in comparison to $(\text{E MS}_j)(\text{E MS}_j')$, the weighting of the mean squares by $\sqrt{1/2}$ makes the variances of the mean squares and cross products more nearly equal. The estimate of $(1/r)\sigma_e^2$ is subtracted from the mean square prior to the application of the least-squares procedure for the same reason. If one expresses the

TABLE 1

Coefficients of correlation for different covariances between relatives

Group of relationship	Relatives involving the covariance	Coefficients of correlation ϕ	ϕ'	$2r_{xy}$	u_{xy}
Full sib	HH′, II′, JJ′, KK′	3/4	1/2	5/8	3/8
	AA′, BB′, CC′, DD′, EE′, FF′, GG′	1/2	1/2	1/2	1/4
Half sib	DE	1/2	1/4	3/8	1/8
	HI, JK	3/4	0	3/8	0
	BD, BE	1/2	1/8	5/16	1/16
	BC, CD, CE	1/2	0	1/4	0
Cousin	HJ, IK	1/2	1/4	3/8	1/8
	FG	1/4	1/4	1/4	1/16
	HK, IJ	1/2	0	1/8	0
	DF, DG, DH, DJ, EF, EG, EH, EJ, GH, GI, GJ, FH, FI, FJ, FK	1/4	0	1/8	0
	BF, BG, BH, BJ	1/8	0	1/16	0
Uncle-nephew	AD, AE, AF, AG, AH, AJ	1/2	0	1/4	0
	AB	1/4	0	1/8	0
No relation	AC, AI, AK, BI, BK, CF, CG, CH, CI, CJ, CK, DI, DK, EI, EK	0	0	0	0

equations in the manner, $X\beta = Y$, the parameters (β's) are genetic components of variance namely, σ^2_A, σ^2_D, σ^2_{AA}, σ^2_{AD}, σ^2_{DD}, and σ^2_{AAA}. The elements of X are the coefficients derived from the coefficient of correlation for the genetic components of variance listed in Table 1. When the two known variables (X's and Y's) are available, the unknown parameters (β's) may then be estimated by solving the equations to obtain the unique solution for each parameter.

To examine the significance of the different components of genotypic variance, seven linear regression models were fitted to the observed mean squares (adjusted) and mean cross products. The seven models were

Model	Parameters in the model
1	A
2	A, D
3	A, D, AA
4	A, D, AA, AD
5	A, D, AA, AD, DD
6	A, D, AA, AD, DD, AAA
7	A, D, AA, AAA

in which A, D, AA, AD, DD, and AAA denote σ^2_A, σ^2_D, σ^2_{AA}, σ^2_{AD}, σ^2_{DD}, and σ^2_{AAA}, respectively. The six-parameter model is displayed in matrix form as follows:

$$\sqrt{1/2} \cdot \begin{bmatrix} 5/8 & 3/8 & 25/64 & 15/64 & 9/64 & 125/512 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ 1/2 & 1/4 & 1/4 & 1/8 & 1/16 & 1/8 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \end{bmatrix} \begin{bmatrix} 3/8 & 1/8 & 9/64 & 3/64 & 1/64 & 27/512 \\ 3/8 & 0 & 9/64 & 0 & 0 & 27/512 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ 5/16 & 1/16 & 25/256 & 5/256 & 1/256 & 125/4069 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ 1/4 & 1/16 & 1/16 & 1/64 & 1/256 & 1/64 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ 1/8 & 0 & 1/64 & 0 & 0 & 1/512 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ 1/16 & 0 & 1/256 & 0 & 0 & 1/4096 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \end{bmatrix} \begin{bmatrix} \sigma^2_A \\ \sigma^2_D \\ \sigma^2_{AA} \\ \sigma^2_{AD} \\ \sigma^2_{DD} \\ \sigma^2_{AAA} \end{bmatrix} = \sqrt{1/2} \cdot \begin{bmatrix} MS_1 - (1/r)\sigma_e^2 \\ \cdot \\ MS_{11} - (1/r)\sigma_e^2 \end{bmatrix} = \begin{bmatrix} MP_1 \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ MP_{55} \end{bmatrix}$$

For tests of significance, the normality, independence, and homoscedasticity of the error of each observed mean square and mean cross product were assumed. Since each mean square and mean cross product was estimated with 40 degrees of freedom, the distribution of these variables approaches the normal distribution. Hence, the failure of these assumptions to be completely valid should not influence tests of significance unduly.

The estimates of additive (A) and dominance (D) variance were obtained from the combined data for both years for all branches of all families by fitting regression model 2. The estimates of experimental error ($\hat{\sigma}^2_e$) and intraplot variance ($\hat{\sigma}^2_w$) were used to calculate the expected change (G), in the population mean for one cycle of each of four selection methods, conducted at one location in one year, using a plot size of 12 plants. The selection methods were:

1) Mass selection (M)—Equal quantities of seed from one selected plant from each plot of 12 plants would be used for recombination.
2) Full-sib family selection (F)—Equal quantities of remnant seed from selected full-sib families would be used for recombination.

3) Half-sib family selection (H)—Equal quantities of remnant seed from selected half-sib families would be used for recombination.
4) Modified half-sib family selection (H′)—Equal quantities of seed obtained by self-pollinating the male parents of the selected half-sib families would be used for recombination.

G values were calculated according to the following formulae (k = selection differential in standard deviation units, f = number of females per male, r = number of replications):

$$G(M) = [(n-1)/n]^{1/2} \cdot k \cdot (1/2)A \cdot [(1/2)A + (1/4)D + \hat{\sigma}^2_w]^{-1/2}$$
$$G(F) = k \cdot (1/2)A \cdot [(1/2)A + (1/4)D + (1/r)\hat{\sigma}^2_e]^{-1/2}$$
$$G(H) = k \cdot (1/4)A \cdot [(1/4)A + (1/4f)(A+D) + (1/r)\hat{\sigma}^2_e]^{-1/2}$$
$$G(H') = 2k \cdot (1/4)A \cdot [(1/4)A + (1/4f)(A+D) + (1/r)\hat{\sigma}^2_e]^{-1/2}$$

Genetic parameters are applicable to mass selection only if 12 plant plots are used. Hence, the factor $[(n-1)/n]^{1/2}$ in the numerator of the G(M) formula is a small-sample correction factor. Likewise, a finite population k value ($k = 1.63$) for a selection intensity of 8.33% was used in the G(M) formula. An infinite population k value ($k = 1.84$) for a selection intensity of 8.33% was used in the three family-selection response formulae.

EXPERIMENTAL RESULTS

The grand means, experimental errors, and the coefficients of variation for the seven quantitative characters studied are presented in Table 2. The harmonic mean of guarded plants per plot was 12. Linear regression analyses were computed for seven models differing in their genetic components of variance parameters. The analysis of variance for model 4 (which contained the parameters A, D, AA, and AD presented in Table 3) showed that the mean square due to additive genetic variance accounted for most of the variation among the variance components for all characters in the two experiments. Significant dominance variance was detected in plant height and ear diameter in 1962 and in plant height, ear height, ear diameter, and yield in 1963. The only significant mean squares due to the epistatic variance were those for AD for ear height in 1962 and AA for ear height in 1963. The estimates of σ^2_{AD} in 1962 and σ^2_{AA} in 1963 for ear height were negative, due to chance or invalidity of some assumptions in the models.

Estimates of additive genetic and dominance variance were obtained with the

TABLE 2

Means, errors and coefficients of variation for seven quantitative characters studied in 1962 and 1963

Quantitative character	Mean ($\bar{x}$)		Error (σ^2_e)		C.V. (percent)	
	1962	1963	1962	1963	1962	1963
Plant height (cm)	237	234	45	54	2.8	3.1
Ear height (cm)	119	115	42	39	5.4	5.4
Kernel row number	19	18	.44	.52	3.5	3.9
Ear length (cm)	21	21	1.02	.94	4.7	4.6
Ear diameter (cm)	5.1	5.1	.029	.020	3.3	2.7
Kernel weight (g/100K)	28	30	3.24	3.87	6.5	6.5
Yield (g/plant)	231	240	406	446	8.7	8.8

TABLE 3

Analysis of variance of genetic components of variance for seven quantitative characters in 1962 and 1963 based on the model which contained the Additive (A), Dominance (D), Additive × Additive (AA), and Additive × Dominance (AD) parameters

Source of variation		df	Plant height ($\times 10^{-4}$)	Ear height ($\times 10^{-4}$)	Kernel row number	Ear diameter	Ear length	Kernel weight	Yield ($\times 10^{-4}$)
A	1962	1	13611**	10057**	39738**	11.32**	32787**	57294**	49841**
	1963	1	10253**	10003**	32207**	10.39**	30695**	68468**	79300**
D	1962	1	1296**	100	438	.43*	148	113	1906
	1963	1	2029**	390*	257	1.16*	341	2	5640**
AA	1962	1	5	149	1	.17	131	1023	1046
	1963	1	3	301(*)†	31	.15	21	169	578
AD	1962	1	82	222(*)†	180	.03	31	175	846
	1963	1	13	17	115	.06	2	7	234
Deviation									
	1962	1	139	52	158	.07	131	127	624
	1963	1	94	57	132	.06	113	250	784

** Significant at 1% probability level.
* Significant at 5% probability level.
† Significant at 5% probability level but the estimates of AA or AD were negative.

model having only two genetic parameters, σ^2_A and σ^2_D (Table 4). Estimates obtained from all 11 branches and from only the seven branches derived from non-inbred parents (i.e., A, B, C, D, E, F, and G) are shown separately. The estimates from the two sets of relatives showed very good agreement. The standard deviations of the two estimates were also similar although they were slightly larger when the matings involved only non-inbred parents. Significant additive genetic variance was detected for all characters. Significant dominance variance was found for plant height, ear diameter, and yield only.

Estimates of genetic covariances and the genetic correlations of yield with the other six characters are shown in Table 5. Ear length showed a higher correlation with yield than did ear diameter, kernel weight, or kernel row number.

Since the estimates of σ^2_w and σ^2_e were obtained from plots containing approximately 12 bordered plants per plot, a similar sample size was used in predicting progress from mass selection. Selection for this system would be based solely upon the phenotype of individual plants, the highest-yielding plant being chosen from each of the 12-plant plots in which bulked seed of the variety had been planted. The three family-selection systems all are based upon progeny evaluation in replicated trials. The expected progress from selection for the four selection methods is shown in Table 6, both on a per-cycle basis and a per-year basis, with the assumptions that years per cycle for mass, full-sib, and half-sib selection would be one, two and three years, respectively. The full-sib and modified half-sib family methods were calculated to be the most effective methods for use in this population under the specified conditions.

DISCUSSION

The analyses of variance obtained by fitting a model with the parameters of

TABLE 4

Estimates of additive and dominance components of variance for seven characters from all progenies and from progenies of non-inbred parents only

Quantitative character	Year	From 11 branches		From 7 branches with non-inbred parents	
		σ^2_A	σ^2_D	σ^2_A	σ^2_D
Plant height (cm)	1962	96 ± 26	202 ± 66	116 ± 32	192 ± 86
	1963	58 ± 21	224 ± 56	66 ± 35	276 ± 94
	Pooled	80 ± 17	225 ± 43	91 ± 24	234 ± 64
Ear height (cm)	1962	120 ± 17	56 ± 42	144 ± 19	228 ± 52
	1963	99 ± 17	108 ± 42	141 ± 23	71 ± 62
	Pooled	110 ± 12	82 ± 30	143 ± 15	47 ± 40
Kernel row number	1962	2 ± .3	1.0 ± .7	3 ± .4	.9 ± 1
	1963	2 ± .3	0.9 ± .6	3 ± .4	.5 ± 1
	Pooled	2 ± .2	1.0 ± .5	3 ± .3	.7 ± 1
Ear length (cm)	1962	2 ± .3	0.7 ± .6	2 ± .3	1 ± .9
	1963	2 ± .2	1.0 ± .6	2 ± .2	1 ± .6
	Pooled	2 ± .2	0.9 ± .4	2 ± .2	1 ± .5
Ear diameter (cm)	1962	.03 ± .01	.04 ± .01	.04 ± .01	.04 ± .02
	1963	.03 ± .01	.06 ± .01	.05 ± .01	.02 ± .02
	Pooled	.03 ± .01	.05 ± .01	.05 ± .01	.03 ± .01
Kernel weight (g/100K)	1962	11 ± 0.9	2 ± 2	12 ± 0.9	2 ± 2
	1963	11 ± 1.0	3 ± 2	11 ± 1.0	1 ± 4
	Pooled	11 ± .7	1 ± 1	12 ± 0.8	2 ± 2
Yield (g/plant)	1962	229 ± 54	246 ± 135	228 ± 71	451 ± 191
	1963	247 ± 61	411 ± 152	304 ± 101	471 ± 273
	Pooled	239 ± 41	329 ± 102	266 ± 62	461 ± 167

additive (A), dominance (D), additive × additive (AA) and additive × dominance (AD) components of variance are summarized in Table 3. The mean squares due to A were much larger than those for either D or any of the epistatic parameters in both years. However, the mean squares due to D were significant at the 1% probability level for plant height in both years and for yield in 1963 and

TABLE 5

Combined estimates of genetic covariances and genetic correlations of yield with other quantitative characters

Yield with	Genetic covariances $\sigma_{A_iA_j}$	Genetic correlation $r_{A_iA_j}$
Plant height	56 ± 18	.40
Ear height	41 ± 41	.25
Kernel row number	1.89 ± .72	.04
Ear length	9.97 ± 1.82	.43
Ear diameter	.38 ± .32	.14
Kernel weight	2.88 ± 3.51	.06

TABLE 6

Expected progress from selection for yield when the selection intensity is 8.33%

Method	Expected progress		
	g per plant	Percent of mean	
		Per cycle	Per year
Mass selection 12 plants per plot	2.96	1.25	1.25
Full-sib family selection 4 replications, 1 female per male	11.45	4.84	2.42
Half-sib family selection 4 replications, 6 females per male	8.45	3.59	1.20
Modified half-sib family selection 4 replications, 6 females per male	16.95	7.17	2.39

significant at the 5% level for ear diameter in both years and for ear height in 1963. The estimates of A and D (Table 4) indicated that additive gene action accounted for a major part of the total genetic variance for the characters ear height, ear length, kernel row number, and 100 kernel weight. However, for plant height, ear diameter, and yield, the estimates of dominance variance were greater than those of additive genetic variance. This situation is not surprising since the occurrence of heterosis in the expression of plant height, ear diameter, and yield in F_1 hybrids indicates some degree of dominance (ROBINSON, COMSTOCK and HARVEY 1949). No evidence for epistatic variance was found for any of the characters studied. EBERHART *et al.* (1966) also obtained no evidence that epistatic variance was important in two North Carolina varieties of maize.

The estimates of all the genetic components of variance included genotype-by-environmental interactions. Upward biases from these interactions may or may not increase the probability of detecting epistatic variance but should not reduce the probability.

The least-squares procedure was employed to obtain the estimates of genetic components of variance. Theoretically, the least-squares procedure would provide the best linear unbiased estimates of the parameters if the variances of the observations were equal and independent. The least-squares estimates obtained with the observed mean products and adjusted mean squares (see METHODS) were unbiased. However, they were not minimum-variance estimates since all of the observations on mean products were not independent. Covariances between mean products involving the same branch of a family, for example MP(AB), MP(AC), . . . , MP(AK) for branch (A) of the families in the present case, would not equal zero, i.e.,

$$E\{\text{Cov}\,[\text{MP(AB)}, \text{MP(AC)}]\} \neq 0 \text{ and}$$

similarly for other pairs of mean products. The assumption that the effects of the small covariances would be negligible seems reasonable, however.

One main problem of the linear model involving covariances among relatives is that the coefficients of the second- and the third-order genetic components of

variance (σ^2_{AA}, σ^2_{AD}, σ^2_{DD}, σ^2_{AAA}) are highly correlated with those of the first-order genetic variances (σ^2_A, σ^2_D). The coefficients of the second-order and the third-order genetic components of variance in the theoretical values for covariance among relatives are generated by squaring or multiplying of the coefficients of the first-order genetic components of variance. This inherent property of the covariance model reduces the sensitivity of the model for detecting epistasis. Evidence of this can be seen in the "correlation" matrix for the six parameters involved in this estimation:

Parameter	A					
A	1.0000	D				
D	.7533	1.0000	AA			
AA	.9162	.9298	1.0000	AD		
AD	.7133	.9848	.9195	1.0000	DD	
DD	.6692	.9537	.8931	.9931	1.0000	AAA
AAA	.8076	.9581	.9722	.9762	.9701	1.0000

The high correlations of the coefficients obviously will give larger standard errors of the estimates of the genetic variances. This is true for all designs involving covariances among relatives, however.

This model also assumed (1) diploid inheritance, (2) no linkage, (3) no maternal effect, and (4) environmental effects additive to the genotypic values. No evidence has been found in maize for the invalidity of (1), (3), and (4). But linkage cannot be assumed absent. COCKERHAM (1956) and SCHNELL (1963) showed that the effect of linkage is to increase the coefficient of epistatic variance components in the covariances among relatives. This would increase the correlations among genetic variance components and further decrease ability to partition the effect of epistasis from additive and dominance variance. However, the effect of linkage is probably negligible except for extremely tight linkages among loci.

SUMMARY

Covariances among relatives including full sibs, half sibs, cousins, and uncle-nephews for 45 families from the Reid Yellow Dent variety of maize were used to estimate genetic variances for plant height, ear height, kernel row number, ear length, ear diameter, kernel weight and yield. Sixty-six phenotypic covariances were computed from the pooled mean squares and mean cross products. For each phenotypic covariance, the expectation was derived in terms of genetic variances, and the estimates of genetic variances (σ^2_A, σ^2_D, σ^2_{AA}, σ^2_{AD}, σ^2_{DD}, σ^2_{AAA}) were obtained for this variety by the least-squares procedure. The results indicated that epistatic variances were negligible in relation to the additive and dominance variance components for the seven quantitative characters studied. The additive genetic variance constituted the major part of the total genetic variance for ear height, ear length, kernel row number and kernel weight. The dominance variance exceeded the additive genetic variance for plant height, ear diameter and yield. The high correlations among the coefficients of the genetic parameters inevitably reduced the sensitivity for detecting epistasis. These correlations also exist for all

known designs involving covariances among relatives. The estimates of the additive and dominance variance were used to compare four breeding methods for Reid Yellow Dent. Full-sib and modified half-sib selection should be the most effective when only one crop per year is possible.

LITERATURE CITED

COCKERHAM, C. C., 1956 Analysis of quantitative gene action. Brookhaven Symp. Biol. **9**: 53–68.

COMSTOCK, R. E., and H. F. ROBINSON, 1948 The components of genetic variance in populations of biparental progenies and their use in estimating the average degree of dominance. Biometrics **4**: 254–266. —— 1952 Estimation of average dominance of genes, pp. 494–516. In: *Heterosis*. Edited by J. W. GOWEN. Iowa State College Press, Ames, Iowa.

EBERHART, S. A., R. H. MOLL, H. F. ROBINSON, and C. C. COCKERHAM, 1966 Epistatic and other genetic variances in two varieties of maize. Crop Sci. **6**: 275–280.

GAMBLE, E. E., 1962 Gene effects in corn (*Zea mays* L.) I. Separation and relative importance of gene effects for yield. Can. J. Plant Sci. **42**: 339–348.

KEMPTHORNE, O., 1954 The correlation between relatives in a random mating population. Proc. Roy. Soc. London B **143**: 103–113. —— 1957 *An Introduction to Genetic Statistics*. Wiley, N. Y.

ROBINSON, H. F., R. E. COMSTOCK, and P. H. HARVEY, 1949 Estimates of heritability and degree of dominance in corn. Agron. J. **41**: 353–359.

SCHNELL, F. W., 1963 The covariance between relatives in the presence of linkage. Statistical Genetics and Plant Breeding. Natl. Acad. Sci.—Natl. Res. Council Publ. **982**: 468–483.

SPRAGUE, G. F., W. A. RUSSELL, L. H. PENNY, R. W. HORNER, and W. D. HANSON, 1962 Effect of epistasis on grain yield in maize. Crop Sci. **2**: 205–208.