GENETIC VARIANCES IN OPEN POLLINATED VARIETIES OF CORN¹*

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INVESTIGATIONS of quantitative inheritance in corn have been in progress at the North Carolina Experiment Station for the past seven years. While data have been collected on a number of characters, the primary objectives have been (a) measurement of the additive genetic variance in grain yield in corn populations and (b) estimation of the level of dominance involved in the action of genes affecting grain yield. Previous reports, ROBINSON *et al.* (1949) and GARDNER *et al.* (1953) have related to studies on hybrid populations derived from single crosses of inbred lines. They have been consistent and can be briefly summarized.

- (a) Estimates of additive genetic variance have been large enough to indicate that selection, either single plant or among progenies, should be effective in improving the yield of such hybrid populations. Selection studies, designed for comparison of actual with predicted progress and to indicate the rate at which additive genetic variance is dissipated, are in progress.
- (b) Estimates of the average dominance of yield genes have been in the overdominance range. However, it was recognized from the outset that both linkage and interaction of non-allelic genes were possible sources of upward bias in these estimates. Thus, strictly speaking, the results serve only to indicate an upper limit for dominance in yield inheritance and by themselves do not constitute final evidence for overdominance.

Complementary work with open-pollinated varieties was initiated in 1949. Early corn breeding experience had led to the widespread belief that selection for yield in adapted varieties is essentially ineffective. However, there is known to be considerable intra-variety genetic variation. Why should selection be ineffective? A possible explanation has been provided by HULL (1945) who postulates in effect that the genetic variance in such populations is largely non-additive and hence that progress through selection should not be expected. He points out that corn and corn varieties have been under selection for yield for years past. Assuming partial or complete dominance, the effect of continued selection on the population frequencies of a pair of alleles should be to cause the frequency of the more favorable, the plus, allele to approach ever closer to *one* until very little genetic variation of any sort remains. However, assuming overdominance the result is different. Because the heterozygote is favored, the effect of selection is toward holding both alleles in the population, rather than toward eliminating one of them; the population gene frequencies gravitate toward an equilibrium at intermediate values for both alleles.

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When this equilibrium is reached, selection has no further effect. Both alleles remain in the population, but, while it was not stated in these terms by HULL, the genetic variance produced by their segregation is dominance variance; at most only a trivial amount of additive genetic variance remains.

This explanation, for which supporting arguments have been advanced by CROW (1948), BRIEGER (1950), and some of the contributions to HETEROSIS (1952), immediately suggests that the nature of genetic variance in open-pollinated varieties be examined. Clearly, to find considerable dominance variance but only a negligible amount of additive genetic variance would constitute strong supporting evidence for the overdominance theory. Because of the extended opportunities for recombinations to bring linkage relations in varieties to equilibrium, no complications from linkages are to be expected. By equilibrium in the linkage relation between two loci is meant a state where the relative frequency of the four kind of gametes AB , Ab , aB , and ab is q_Aq_B , $q_A(1 - q_B)$, $(1 - q_A)q_B$ and $(1 - q_A)(1 - q_B)$ as when there is independent segregation. q_A is the frequency of A and q_B the frequency of B .

MATERIALS AND METHODS

Biparental progenies were made within the Jarvis, Weekley and Indian Chief varieties as described for the study reported by ROBINSON *et al.* (1949). Each plant used as a male or staminate parent was crossed with four plants used as female or pistillate parents. Sixty-four such male groups or a total of 256 crosses were made within each of the Jarvis and Weekley varieties in 1949 which constituted the first of two samples of biparental matings made in these varieties. Four male groups, four progenies per male, were randomly chosen to form a block of 16 progenies and were tested with two replications, giving a block of 32 plots. A total of 16 such blocks of material were used within each of the two populations, making a total of 512 plots in each population. The same progenies tested in 1950 were tested in 1951, a new randomization within blocks being used the second year. The same type of biparental matings were made again in the Jarvis and Weekley varieties in 1951 to give a second sample of 256 crosses in each of these varieties. At the same time 512 such biparental crosses were made within the Indian Chief variety. These crosses were tested in 1952 and retested in 1953 with an arrangement of the progenies within each population similar to that described for the 1950 and 1951 tests. The studies were conducted in Wake County, North Carolina, and on the same farm in 1953 as in 1951 but on a different farm in each of the other two years. Plots were two rows wide and 10 hills long with three feet between rows and plants spaced 18 inches within rows.

Data were taken on date of flowering, plant height, ear height, kernel row number, number of ears, ear length, ear diameter and yield of ear corn in the Jarvis and Weekley populations. Five of the same characters were measured in the Indian Chief progenies, omitting kernel row number, ear length and ear diameter. Date of flowering was recorded by plots at the time when approximately 50% of the plants were shedding pollen. The data on all other characters were based on 10 competitive plants in each plot wherever possible. Plant and ear height were measured in inches

from ground level to the tip of the tassel and uppermost ear bearing node, respectively. Data on kernel row number, ear length and ear diameter were taken on only the topmost ear of the plant and the measurements taken to the nearest one-tenth inch. Data on number of ears and yield were based on all ears. Yield was measured on ear corn and recorded in pounds.

Plot values were obtained by dividing the total for a plot by the number of competitive plants that contributed to the total. Individual plant data (except in the case of date of flowering) on approximately every 12th plot were used for estimation of plant-to-plant variability within the plots.

Data for each of the characters of each sample of progenies in a population were analyzed by individual blocks and the results pooled to give the combined analysis for two years. The form of the analysis is given in table 1.

Under assumptions listed by COMSTOCK and ROBINSON (1952), the variance of

TABLE 1

Form of the analysis of variance computed for data for each sample of biparental progenies in three open-pollinated varieties of prolific corn

Source of variation	D. F.	M. S.	M. S. Expectations
Years	$t - 1$		
Blocks	$b - 1$		
Years x blocks	$(t - 1)(b - 1)$		
Reps in blocks in years	$bt(r - 1)$		
Males in blocks	$b(m - 1)$	M_1	$\sigma_w^2/k + \sigma_e^2 + r\sigma_{fy}^2 + r\sigma_f^2 + rn\sigma_{my}^2 + r\ln\sigma_m^2$
Females in males in blocks	$bm(n - 1)$	M_2	$\sigma_w^2/k + \sigma_e^2 + r\sigma_{fy}^2 + r\sigma_f^2$
Years x males in blocks	$b(m - 1)(t - 1)$	M_3	$\sigma_w^2/k + \sigma_e^2 + r\sigma_{fy}^2 + rn\sigma_{my}^2$
Years x females in males	$bm(n - 1)(t - 1)$	M_4	$\sigma_w^2/k + \sigma_e^2 + r\sigma_{fy}^2$
Pooled error	$bt(mn - 1)(r - 1)$	M_5	$\sigma_w^2/k + \sigma_e^2$
Total	$btmnr - 1$		
Plants in plots	$\sum_i (k'_i - 1)$	M_6	σ_w^2

KEY TO TABLE 1

- t = years = 2
 b = blocks per year = 16, except 32 for Indian Chief
 r = replications per block = 2
 m = male groups in a block = 4
 n = females per male = 4
 k'_i = number of plants in i^{th} plot on which individual plant data were taken
 k = harmonic mean of the number of plants per plot
 σ_w^2 = the sum of intra-plot environmental variance and the genetic variance among individuals of the same progeny
 σ_e^2 = the variance of plot effects
 σ_{fy}^2 = variance due to interaction between female effects and environment as it varied between years.
 σ_{my}^2 = the interaction variance between male effects and environments
 σ_f^2 = the variance of female effects
 σ_m^2 = the variance of male effects

male effects (σ_m^2) equals one-fourth of the additive genetic variance (σ_g^2), and the variance of female effects (σ_f^2) equals one-fourth the additive genetic variance plus one-fourth the dominance variance (σ_d^2). Symbolically,

$$\begin{aligned}\sigma_m^2 &= \frac{1}{4}\sigma_g^2 \\ \sigma_f^2 &= \frac{1}{4}\sigma_g^2 + \frac{1}{4}\sigma_d^2\end{aligned}$$

so that $\sigma_g^2 = 4\sigma_m^2$. The dominance variance, σ_d^2 , is equal to $4(\sigma_f^2 - \sigma_m^2)$ and the ratio of σ_d^2 to σ_g^2 , the quantity of primary interest in this study, is

$$\frac{\sigma_d^2}{\sigma_g^2} = \frac{\sigma_f^2 - \sigma_m^2}{\sigma_m^2} = \frac{\sigma_f^2}{\sigma_m^2} - 1.$$

Procedure in estimation was to estimate σ_m^2 and σ_f^2 , and then to substitute estimates of these quantities in the above expressions to obtain estimates of σ_g^2 , σ_d^2 , and σ_d^2/σ_g^2 . Estimates of σ_m^2 and σ_f^2 were computed as follows

$$\begin{aligned}\sigma_m^2 &= (M_1 - M_2)/rln \\ \sigma_f^2 &= (M_2 - M_3)/rl\end{aligned}$$

These are not unbiased estimates. Instead their expectations (value that would be approached in the long run if successive estimates were averaged) are, from expectations of the separate mean squares

$$\begin{aligned}E(\hat{\sigma}_m^2) &= \sigma_m^2 + \sigma_{my}^2/l \\ E(\hat{\sigma}_f^2) &= \sigma_f^2 + \sigma_{fy}^2/t.\end{aligned}$$

However, if it is assumed that the variance from interaction of genotype with environment will on the average be proportional to the variance of the genetic effects involved; in this case that

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

Then

$$\frac{\sigma_f^2 + \sigma_{fy}^2/t}{\sigma_m^2 + \sigma_{my}^2/l} = \frac{\sigma_f^2}{\sigma_m^2}$$

and the biased estimates of σ_f^2 and σ_m^2 are as useful as unbiased estimates would be for our purposes. This assumption of proportionality between interaction variance and variance due to direct effects of genotypic variation involved is reasonable on the argument that all kinds of genetic effects (additive or non-additive) must operate through the same sorts of physiological paths and hence may be expected to be equally sensitive to variation in environment. On the other hand it might be argued that σ_{fy}^2/σ_f^2 would be larger than σ_{my}^2/σ_m^2 whenever σ_f^2 was larger than σ_m^2 which would be the case when dominance variance was present. The rationale of this argument would rest on the premise that as variation in genotypic effects increases the general magnitude of interaction effects would increase by a greater than proportional

amount. Intuitively, this seems possible, whereas deviation from proportionality in the opposite direction does not. If this argument is correct, then

$$\frac{\sigma_f^2 + \sigma_{fu}^2/t}{\sigma_m^2 + \sigma_{mu}^2/t} > \frac{\sigma_f^2}{\sigma_m^2}.$$

As will be seen later, the possibility of this sort of bias in the ratio between estimates of σ_f^2 and σ_m^2 will have no important bearing on the interpretation of results.

It should be noted that $E[(M_1 - M_2 - M_3 + M_4)/rtn] = \sigma_m^2$
and $E[(M_2 - M_4)/rt] = \sigma_f^2$

and hence these functions of the mean squares would have provided unbiased estimates of σ_m^2 and σ_f^2 , respectively. However, though it is not immediately obvious,

TABLE 2
Estimates of additive genetic variance (σ_a^2) obtained with biparental progenies in three open-pollinated varieties of corn

Character	Jarvis			Weekley			Indian Chief
	Sample		Combined	Sample		Combined	
	I	II		I	II		
Date of flowering	3.26	5.36	4.31	3.56	11.45	7.51	4.14
Plant height	35.48	37.28	36.37	26.40	35.24	30.84	33.84
Ear height	21.88	10.92	16.40	28.20	31.00	29.60	26.60
Kernel row number	1.5756	1.4056	1.4908	0.9928	0.8220	0.9072	—
Ears per plant	0.0656	0.0263	0.0460	0.0836	0.0350	0.0593	0.0335
Ear length	0.1448	0.1720	0.1585	0.2580	0.3645	0.3113	—
Ear diameter	0.0066	0.0028	0.0047	0.0058	0.0086	0.0072	—
Yield	0.0044	0.0036	0.0040	0.0032	0.0036	0.0033	0.0024

TABLE 3
Estimates of dominance variance (σ_d^2) obtained with biparental progenies in three open-pollinated varieties of corn

Character	Jarvis			Weekley			Indian Chief
	Sample		Combined	Sample		Combined	
	I	II		I	II		
Date of flowering	1.67	(-1.51)	0.08	0.95	(-6.47)	(-2.76)	(-1.33)
Plant height	6.68	9.64	8.18	4.92	9.68	7.28	(-1.64)
Ear height	6.56	12.92	9.73	8.96	(-0.76)	4.08	(-8.16)
Kernel row number	(-0.2044)	0.3348	0.0648	(-0.0764)	0.0620	(-0.0072)	—
Ears per plant	0.0048	(-0.0030)	0.0008	(-0.0556)	0.0	(-0.0277)	0.0160
Ear length	0.0772	(-0.0408)	0.0181	0.0368	(-0.0611)	(-0.0122)	—
Ear diameter	0.0001	0.0031	0.0015	0.0058	(-0.0010)	0.0024	—
Yield	0.0004	(-0.0012)	(-0.0003)	0.0024	0.0008	0.0017	0.0008

TABLE 4

Ratios of estimates of dominance variance and additive genetic variance, σ_d^2/σ_g^2

Character	Variety		
	Jarvis*	Weekley*	Indian Chief
Date of flowering	.02	**	**
Plant height	.22	.24	**
Ear height	.59	.14	**
Kernel row number	.04	**	—
Ears per plant	.02	**	.48
Ear length	.11	**	—
Ear diameter	.32	.34	—
Yield	**	.52	.33

* Ratios of estimates from sample I and II combined.

** Estimate of σ_d^2 was either zero or negative.

the coefficients of variation of estimates so obtained would have been considerably greater than of the estimates actually made. For this reason the biased estimates were considered preferable, particularly since the effect (if any) on estimate of σ_d^2/σ_g^2 is most likely of a nature that does not affect the primary conclusions from the study.

RESULTS

Estimates of additive genetic variance and dominance variance for the various characters measured in the three varieties are listed in tables 2 and 3. The combined estimates for Jarvis and Weekley were computed from the pooled results of the two samples of progenies in each of these varieties and will be used in subsequent discussion of the estimates for these varieties.

Considering sampling errors to which the estimates are subject, the pattern of results is remarkably similar for different samples of material from the same variety and for the three different varieties. As the experiment was conducted, estimates of σ_d^2 have considerably greater sampling variance than estimates of σ_g^2 . The negative estimates of σ_d^2 are well within the range possible through sampling error assuming the true variances to be positive but small. In fact since variances, by definition, are never negative it is most reasonable to conclude that true values of these negative variances are small positive quantities and that the negative estimates resulted from sampling error.

Ratios of estimates of dominance and additive genetic variance are listed in table 4.

DISCUSSION

Comparative magnitudes of additive genetic and dominance variance

Without exception, the estimate of additive genetic variance used in computing the ratios in table 4 was larger than that of dominance variance in the same character. Thus the *a priori* possibility that observation of considerably more dominance than additive genetic variance would provide strong support to the case for importance of overdominance was not realized. The conclusion seems obvious that,

though there may be overdominance at some loci, overdominance loci at which gene frequencies are such that much more dominance than additive genetic variance is produced *are not* the single important source of genetic variation in the varieties studied. This raises the question of possible alternatives, with respect to the genetic situation in these varieties, that are consistent with results of the experiment.

Following symbolism² employed by COMSTOCK and ROBINSON, (1948) and (1952), the additive genetic and dominance variances in a randomly breeding diploid population are

$$\sigma_g^2 = \sum_i 2q_i(1 - q_i)[1 + (1 - 2q_i)a_i]^2 u_i^2 \quad (1)$$

and

$$\sigma_d^2 = \sum_i 4q_i^2(1 - q_i)^2 a_i^2 u_i^2 \quad (2)$$

if only two alleles are involved at each segregating locus. The subscript, i , identifies the locus so that summation in the above expressions is over all loci. When the frequencies of all segregating genes are one-half,

$$\sigma_g^2 = \frac{1}{2} \sum_i u_i^2 \quad \text{and} \quad \sigma_d^2 = \frac{1}{4} \sum_i a_i^2 u_i^2$$

and $2\sigma_d^2/\sigma_g^2$ becomes a weighted average of the (a_i^2) 's weighting being relative to the (u_i^2) 's. With this in mind COMSTOCK and ROBINSON (op. cit.) noted that, in the case of populations in which $q = 1/2$ could be assumed for all segregating loci, the ratio $\bar{a}^2 = 2\sigma_d^2/\sigma_g^2$ constitutes a meaningful estimate of the average dominance of genes affecting the character in question. It is obvious, on the other hand, that this ratio does not provide a basis for inference concerning level of dominance unless there are satisfactory grounds for assumptions concerning gene frequencies.

The following discussion will have reference to the single character, grain yield, though it will apply in varying part to the other characters on which data were reported. Reasons for this restriction are (a) it is with respect to yield inheritance that importance of overdominance has been postulated by HULL (1945), CROW (1948) and BRIEGER (1950); (b) yield is the one character in corn for which there is any body of experimental evidence that is suggestive of overdominance (see ROBINSON *et al.* (1949), HULL (1952) and GARDNER *et al.* (1953)) and (c) a history of unidirectional selection (for high yield) can probably be assumed. The significance of the third point is that it provides a basis for assumptions concerning gene frequencies. We take the stand that in view of past selection it is reasonable to postulate that in adapted open-pollinated varieties favorable genes are present in higher frequencies than are their less favorable alleles.

Assume as a starting point for discussion that multiple alleles were not present in the varieties studied. Then using equations (1) and (2) the ratio σ_d^2/σ_g^2 for genetic

² Let B symbolize the more favorable of two alleles at the i -th locus. Then definition of a_i and u_i is such that the average effects of genotypes classified according to whether they are BB , Bb , or bb at the i -th locus may be represented as $z + 2u_i$, $z + u_i + a_i u_i$, and z , respectively. Clearly, the effect of the heterozygote relative to those of the homozygotes, i.e. the nature of dominance present, is reflected in the value of a_i . q_i is the population frequency of the more favorable allele.

TABLE 5
Values of σ_a^2/σ_g^2 for a single locus, and for various values of a and q

a	q				
	.5	.6	.75	.9	.99
.8	.32	.44	.66	.89	.27
1.0	.50	.75	1.50	4.50	49.50
1.5	1.12	2.20	13.50	10.12	.20
2.0	2.00	5.33	∞^*	2.00	.08

* When $q = \frac{1+a}{2a}$, $\sigma_g^2 = 0$ and σ_a^2/σ_g^2 becomes infinite. $(1+a)/2a$ takes a value in the range, 0.5 to 1.0, whenever $a > 1.0$, i.e. when overdominance exists. In such cases it may be called the equilibrium gene frequency since it is the value (or very nearly so) toward which q gravitates in response to intrapopulation selection (unless selection is based on outcross progeny performance).

variance from any single locus can be computed as a function of a and q . A series of values³ are listed in table 5.

A specific example will help to clarify how the information in table 5 applies. Consider a segregating locus where dominance is complete ($a = 1.0$) and the population frequency of the more favorable allele is 0.9. In terms of genetic variance arising at this single locus, σ_a^2 would be 4.5 times as large as σ_g^2 . Thus if the same situation ($a = 1.0$ and $q = 0.9$) prevailed at all loci affecting yield, the value of σ_a^2/σ_g^2 would be 4.5 as compared to the low estimates actually obtained (table 4).

Arguing solely from table 5, three proposals can be advanced in explanation of the experimental results.

(a) That there is no overdominance, i.e. $a < 1.0$ at all loci. There is an obvious variety of combinations of $q > .5$ and $a \leq 1.0$ for which the expectation of σ_a^2/σ_g^2 would conform with estimates obtained.

(b) That there is both partial and overdominance, gene frequencies at the overdominant loci being close to "equilibrium" so that these loci are the source of much more dominance than additive genetic variance. The situation visualized is one in which some loci (the ones showing partial dominance) are the source of much more additive genetic variance than dominance variance while others (those showing overdominance) are producing mostly dominance variance, the net result when measured in terms of total σ_g^2 and σ_a^2 from both classes of loci being ratios of the order observed. This is in accord with arguments by Crow (1952).

³ Only positive values of a are considered. It is reasonable to question whether this is justified. a would be negative in value if the average effect of the Bb genotypes were less than the mean for average effects of the BB and bb genotypes, i.e. in the case of what we shall here refer to as negative dominance. The possibility of negative dominance is ignored for the following reasons:

1. The invariable expression of heterosis in crosses of inbred lines in corn is evidence that, at least at the vast majority of loci, dominance is positive.
2. Overdominance has unique implications with regard to the genetic situation in corn only if it is of the positive type. It is selective advantage of the heterozygote that reconciles segregation (intermediate gene frequencies) and ineffectiveness of selection for variety improvement. With negative overdominance the heterozygote is at a selective disadvantage and continued selection should result in a gradual approach to elimination of one of the two alleles from the population.

(c) That there is only overdominance, gene frequencies being close to 1.0 (see lower right corner of table 5).

Of these proposals, the third must be rejected on the grounds that gene frequencies in the necessary range are unlikely in the face of past selection. On the other hand neither general considerations nor the experimental results themselves provide firm grounds for choice between the first two proposals. The situation then is that these results, taken by themselves, are explainable in terms of only partial dominance but are equally compatible with presence of both partial and overdominance.

The foregoing discussion is premised on the assumptions (a) that the estimates of σ_d^2/σ_a^2 were unbiased and (b) that multiple alleles were not present. These issues deserve further comment.

Multiple alleles

FISHER (1918) noted that the definitions of σ_a^2 and σ_d^2 (τ^2 and ϵ^2 in his notation) can be generalized to apply without restriction concerning the number of segregating alleles per locus, and that the way in which σ_a^2 and σ_d^2 contribute to parent offspring and fraternal correlations in random breeding populations is then independent of the length of allelic series. The importance of this generalization is that it gives meaning to σ_a^2 and σ_d^2 that remains consistent whether multiple alleles are or are not present without in any way changing the definitions as they apply in the two allele case.

Speaking now in terms of this broader concept of additive genetic and dominance variance the following can be shown to hold as in the two allele situation.

(a) Assuming equilibrium with respect to linkage relations among loci, no epistasis, and random mating, the variances referred to herein as σ_m^2 and σ_f^2 have the composition

$$\sigma_m^2 = \frac{1}{4} \sigma_a^2 \text{ and } \sigma_f^2 = \frac{1}{4} \sigma_a^2 + \frac{1}{4} \sigma_d^2.$$

Thus $\frac{\sigma_f^2}{\sigma_m^2} - 1$ remains an appropriate estimate of σ_d^2/σ_a^2 .

(b) Effectiveness of intra-variety selection depends on presence of additive genetic variance. Thus observation of considerable additive genetic variance raises the same question relative to possibilities of variety improvement whether or not multiple alleles are considered an important element in the genetic system.

Given two alleles and heterozygote superiority, i.e. overdominance, selection should eventually bring gene frequencies to near equilibrium at intermediate values. This is the base of the argument of those who emphasize overdominance in explanation of the genetic situation in corn varieties. The same sort of equilibrium is possible starting with multiple alleles and, depending on relative values of the homozygous and heterozygous genotypes possible at the locus, the equilibrium state could involve non-trivial frequencies of three or more alleles (see WRIGHT and DOBZHANSKY 1946). However, in any event, loci at such an equilibrium would produce dominance variance but no additive genetic variance. Thus multiple allelism by itself requires no essential change in the interpretation of our estimates of σ_d^2/σ_a^2 .

Possible sources of bias in estimates of σ_d^2/σ_g^2

The estimate of σ_d^2/σ_g^2 was computed in terms of the estimates of σ_m^2 and σ_f^2 as $(\sigma_f^2/\sigma_m^2) - 1$, see *Material and Methods*. It was noted that variance due to interaction of genotype with environment is a probable source of bias in $\hat{\sigma}_f^2$ and $\hat{\sigma}_m^2$ but that if the magnitude of bias is proportional to that of the variance estimated there is no net effect on the estimate of σ_d^2/σ_g^2 . It was further noted that if biases in σ_f^2 and σ_m^2 from genotype-environment interaction variance were not proportional, there is reason to suspect that, expressed percentage-wise, bias would be greatest in σ_f^2 . The effect of this would have been to cause upward bias in the estimates of σ_d^2/σ_g^2 .

Another possible source of bias is in the assumed relations:

$$\sigma_m^2 = \frac{1}{4} \sigma_g^2 \text{ and } \sigma_f^2 = \frac{1}{4} \sigma_g^2 + \frac{1}{4} \sigma_d^2$$

COMSTOCK and ROBINSON (1953) list assumptions on which derivation of these relations rests. Multiple allelism has been considered above. Of the remaining, the most suspect are those of no epistasis and no effect of linkage on the relative frequencies of genotypes. Demonstration of possible consequences of epistasis and linkage requires a great deal of space and will be presented elsewhere. It will suffice to state here that when linkage effects are present⁴ they operate to make the quantity $\frac{\sigma_f^2}{\sigma_m^2} - 1$ greater than σ_d^2/σ_g^2 , and that, with possible rare exceptions, the same seems true for effects of all types of epistasis at least when multiple alleles are absent.⁵

Note that all these possible sources of bias in estimates of σ_d^2/σ_g^2 lead to upward bias. Hence to the extent that any one or more of them is considered of probable importance, the evidence from the experiment becomes less favorable to the overdominance hypothesis.

Relation to other experimental evidence

Estimates of the average dominance of genes affecting grain yield reported by ROBINSON *et al.* (1949) and GARDNER *et al.* (1953) were in the overdominance range (values of $\hat{a}$ ranged from 1.31 to 2.14). However, as noted at the beginning of this article, the authors in both instances warned that their estimates were subject to bias from both linkage and epistasis and hence would be considered as indications of an upper limit for average dominance. HORNER (1952) has evaluated the amounts of bias that would result from some specified types of epistasis. His findings are not easily summarized in a few sentences nor, in view of possible linkage effects, is it considered vital to do so here except to state that in the estimates referred to above, linkage is considered of greater immediate concern as a source of bias than is epistasis. COMSTOCK and ROBINSON (1952) demonstrated that upward linkage bias is probable in estimates by the method used by GARDNER *et al.* (1953). Later they also

⁴ It was noted earlier that there is reason to believe linkage effects to be minimal in long established varieties.

⁵ The consequences of epistasis in multiple allelic systems have not been investigated. While there would appear no special reason to suspect they would differ in pattern between multiple and two allele systems, the issue merits investigation.

showed (1951) that if the number of loci involved in yield inheritance is as great as often assumed, linkage bias in the procedure used by ROBINSON *et al.* (1949) as well as in that used by Gardner and his coworkers would be sufficient so that estimates as large as those reported by these groups of workers are to be anticipated in the presence of no more than partial or complete dominance. Thus the suggestion here that overdominance may not play an important role in corn yield inheritance is not incompatible with other results reported from this station and in a sense receives support therefrom. On the other hand it must be emphasized that the totality of our evidence does not exclude overdominance as a factor of major consequence.

HULL (1952) presents the results of regression analyses of data on yields of inbred lines and the F_1 hybrids obtained from crosses among them, and shows the basis for inference (about level of dominance) from these analyses. Results from 16 of 25 independent sets of data are in accord with the overdominance hypothesis, while those from the other 9 sets are not. HULL points out that sampling errors are large and states that "more comprehensive and precise data" are needed.

ROJAS and SPRAGUE (1952) report estimates of variance components from field comparisons of the possible F_1 hybrids among inbred lines within each of two groups of lines. The lines of a group probably were not derived from the same variety but might be considered a sample from some population having wider boundaries than those of a single variety. Ignoring possible effects of epistasis,⁶ what the authors call variance in general combining ability would be equal to half the additive genetic variance of the parent population and their variance of specific combining ability would be the dominance variance of the parent population. Thus their estimates of these two variances⁷ provide estimates of σ_d^2/σ_g^2 . From their table 3, the estimate from data on group 1 (unweighted analysis) is $1.20/2(1.56) = .38$ and from data on group 2 is .59. SPRAGUE and TATUM (1942) pointed out that if the inbred lines involved in data of this kind have been selected on the basis of previous estimates of general combining ability, the general combining ability variance among them will tend to be depressed. ROJAS and SPRAGUE (1952) indicate that their lines had been subjected to preliminary selection of this kind, which suggests the possibility of an upward bias in the above estimates of σ_d^2/σ_g^2 derived from their results. SPRAGUE and TATUM (1942) give results (see footnote 7) for two sets of lines that were unselected in terms of general combining ability from which derived estimates of σ_d^2/σ_g^2 are .24 and .32, respectively. Admittedly the sampling variances of these and our own estimates of σ_d^2/σ_g^2 are large, and there may be reason to argue that the ratio need not be of the same order for single varieties as for populations of the kind to which estimates derived from the data of ROJAS and SPRAGUE and SPRAGUE and TATUM must be referred. Nevertheless, the general concordance among the several estimates of σ_d^2/σ_g^2 is striking.

⁶ Linkage goes unmentioned because its effect here is to increase the sampling error of the specific and general combining ability variances rather than to introduce bias.

⁷ The ROJAS and SPRAGUE estimates were so computed as to be free from bias from genotype-environment interaction effects. This was not the case for the SPRAGUE and TATUM estimates.

It is most likely that the effect of epistasis in this kind of data is to contribute proportionately more to the variance in specific combining ability than to the variance in general combining ability and hence to cause upward bias in the derived estimates of σ_d^2/σ_g^2 .

The magnitude of additive genetic variance

If overdominance loci with gene frequencies at or near to equilibrium values were the primary source of genetic segregation in these varieties there should be little additive genetic variance. The data indicate, however, that σ_a^2 is of moderate size; large enough in fact so that intra-variety selection should be rather effective. Suppose one selfed a series of plants from one of these varieties and at the same time outcrossed each of these plants to a random sample of other plants of the variety (the sample being a different one for each pollen parent). The result would be a series of half-sib test progenies, one for each pollen parent. Assume further that selection among pollen parents is based on performance of the test progenies in field comparison and that a new population is produced by interbreeding the inbred progenies of selected pollen parents. This is the type of procedure reported by LONNQUIST (1949). It can be shown that, in terms of symbolism of this paper, the expected improvement per generation from such selection is

$$\frac{s\sigma_a^2/2}{\sqrt{\sigma_m^2 + \sigma_{my}^2 + \frac{\sigma_f^2 + \sigma_{fy}^2}{n} + \frac{\sigma_e^2}{r} + \frac{\sigma_w^2}{rk}}}$$

where s is the selection differential expressed as a multiple of the standard deviation of progeny means and n is the number of plants to which each pollen parent was outcrossed (on the basis that each seed parent contributes the same number of offspring to the progeny). The formula as given assumes selection is based on comparison of the progenies in r replications in a single year and location. Substituting variances estimated from our data and setting $r = 6$, $k = 10$, $n = 20$, and $s = 1.3$ (values of n and r are those used by LONNQUIST and $s = 1.3$ is approximately the selection differential to be expected on the average when the best 8 of 36 are selected as in LONNQUIST's experiment), the predicted improvement in yield from selection based on test progeny performance is found to be .054, .045 and .039 pounds per plant for the Jarvis, Weekley and Indian Chief varieties, respectively. Expressed in percent of observed mean yields these become 15%, 12% and 13%.

These represent considerable increments of improvement and presumably improvement could be extended further by selection in recurrent cycles. Actually our estimates of σ_a^2 are subject to upward bias from genotype-environment interaction effects (as noted earlier) and hence the above estimates of effect of selection would be subject to corresponding bias. At the same time it is worth emphasis that in LONNQUIST's selection experiment with the variety Krug the improvement from selection as measured in field comparison of descendants of the inter-bred selected material with the Krug variety was 18% (actually larger than any of the figures given above).

While our estimates of additive genetic variance and LONNQUIST's results both indicate that varieties are susceptible to significant improvement through selection, the long held tenet of corn men to the contrary reflects too much experience by too many capable workers to be ignored. In the opinion of these authors the published evidence falls short of conclusive proof that no further improvement of adapted

varieties is possible.⁸ It is recognized, however, that this belief probably rests on much more experience than that actually recorded in the literature. Without insisting that significant varietal improvement is definitely possible, we believe the issue should be re-examined and we have initiated selection programs with the Jarvis, Weekley and Indian Chief varieties to check whether predictions based on data herein reported can be attained.

If selection is indeed ineffective in these varieties a way must then be found to reconcile that fact with the apparent presence of significant amounts of additive genetic variance. Two quite different possibilities will be discussed.

LERNER and DEMPSTER (1951) reported that selection for long shanks in White Leghorn chickens was effective through five or six generations but that further increase in length was not obtained by continuing selection in another five generations. At the same time their data suggested that additive genetic variance in shank length was of the same order of magnitude in late as in early generations of their experiment. A similar picture is reflected in a report by REEVE and ROBERTSON (1953) on results of selection for long wings in *D. melanogaster*. The principal difference is in time relations; wing length increased intermittently through about 46 generations, then remained roughly constant through 30 generations of continued selection, though considerable additive genetic variance in wing length was judged to be present. Though interpretations advanced in the two cases differ in detail, they are similar in essence. Stated briefly and perhaps therefore inadequately, the substance of hypotheses advanced by the two pairs of authors is that if there is negative genetic covariance between a desired trait and fitness (net reproductive rate), selection for the trait may be ineffective even though additive genetic variance exists. The crux of the situation postulated is that the positive force of selection is counterbalanced by lower reproduction on the part of the individuals that are genetically most desirable with respect to the trait under selection. In neither case do the authors claim quantitative fit of observations to hypothesis. Nevertheless their proposal appears entirely reasonable. So long as wing or shank length were subjected to only natural selection it would be expected that genes (or chromosome blocks) that would increase length but decrease reproductive rate would remain rare and be the source of little genetic variance in length. But under direct selection for length the population frequencies of such genes would be increased to the point where they might account for the sort of situations observed. Other genes with effects only on length presumably provided most of the original additive genetic variance, i.e. the basis for early gains from selection. These genes would gradually approach homozygosity as a consequence of selection and the additive genetic variance associated with them would gradually be replaced by variance due to segregation of the originally rare genes (those having positive effects on length but negative effects on reproduction). If so, absence of noticeable change in amount of additive genetic variance would be quite possible.

This same situation may conceivably be present in corn and would account for ineffectiveness of selection even though additive genetic variance in yield is present. However, other things being equal there should be a high correlation between grain

⁸ This view was advanced by COMSTOCK and ROBINSON in a paper read at the 1950 Annual Meeting of the American Society of Agronomy.

yield and reproductive rate since each kernel produced represents a potential member of the next generation. (FISHER (1949) suggests as reasonable the equating of chance of survival to yield in grain crops and CROW (1948) and (1952) postulated that an increment in grain yield is associated with a proportional increment in survival value.) Therefore, to make the argument apply in this case it is necessary to distinguish components of reproductive capacity and to point out that certain genes favorable to yield may be unfavorable to such other components of reproductive rate as germination rate and seedling survival. The same argument has, in fact, been presented in these terms by BRIEGER (1950). It is not necessary that the same genes which supply the bulk of the additive genetic variance present also be those primarily responsible for heterosis in crosses of inbred lines (this was implied earlier when we postulated that the additive genetic and dominance variance observed may have been supplied for the most part by two different classes of loci, and is emphasized by CROW, 1952). However, such could be the case if for a locus with dual effects as outlined, a degree of dominance of favorable effects on yield were associated with recessiveness of unfavorable effects on one or more other components of reproductive rate.

Another possibility for reconciling presence of additive genetic variance with ineffectiveness of selection is that gene frequencies at loci providing most of the additive genetic variance are already at equilibrium between the forces of mutation and selection. In this case continued selection would have no net observable effect on mean yield but would operate only to maintain the equilibrium. If such loci had effects only in yield, no single locus would provide very much genetic variance but, if one is willing to assume enough of them, one can account for the amount of additive genetic variance observed. An obvious question is "how many loci must be assumed?" The answer depends upon the level of dominance, magnitudes of gene effects and natural mutation rates. For example, suppose that all additive variance is produced by loci at which gene action is completely additive, that the deleterious effect of the mutant allele at such loci is great enough so that any plant homozygous for the mutant at but one locus is barren even though the plant is homozygous for the favorable allele at all other loci, and that the mutation rate is 1.0 in 100,000. It can be shown that in such a situation the additive genetic variance would be of the order observed in these varieties if the number of loci were about 14 or 15 thousand. Thus an equilibrium of the sort outlined may be either part or all of the explanation for ineffectiveness of selection even though a moderate amount of additive genetic variance is present. Further speculation here concerning the probability that this is the complete explanation is hardly to the point since so very little is known concerning number of loci, natural mutation rates, or the average magnitude of effect of deleterious mutant genes.

SUMMARY

Estimates of the additive genetic and dominance variances in various quantitative characters are reported for three open-pollinated varieties of corn. These were based on data from 512 biparental progenies in each of the varieties. All progenies were grown with two replications in each of two years making a total of 2048 plots

of material from each of the three varieties. Principal features of the findings are (a) the fact that in all characters of the three varieties the estimate of dominance variance was less, and in most instances considerably less, than the estimate of additive genetic variance and (b) the considerable amount of additive genetic variance in grain yield that appears to exist. Implications of the estimates are discussed with primary reference to the character, grain yield.

In view of the smallness (less than 0.6) of estimates of the ratio of dominance to additive genetic variance, it must be concluded that overdominant loci are not the single important source of genetic variability in the varieties studied. The results are explainable in terms of either partial to complete dominance at all loci or a mixture of partial and overdominant loci. Epistasis, linkage, and genotype-environment interaction are potential sources of bias but it appears most likely that all would operate to increase the estimate of dominance variance proportionately more than that of additive genetic variance. Hence if the estimates of σ_d^2/σ_g^2 are biased, the bias is probably upward rather than downward.

While it appears that overdominant loci cannot be admitted as the only important source of segregation for grain yield in corn varieties, this does not imply that overdominance is necessarily insignificant in the genetics of yield. Present evidence must be considered inconclusive in this regard.

Two possibilities are advanced for reconciling presence of additive genetic variance with ineffectiveness of intra-variety selection. The first rests on negative genetic correlation between grain yield and other components of net reproductive capacity. The second envisages the additive genetic variance as arising from loci at which gene action is largely additive and gene frequency is at equilibrium between the forces of mutation and selection. At the same time it is suggested that effectiveness of intra-variety selection should be thoroughly re-examined.

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