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GENETIC VARIANCE FOR YIELD AND ITS COMPONENTS IN A SYNTHETIC POPULATION OF MAIZE (*ZEA MAYS L.*)

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Estimates of genetic variance for yield and its components, ear number, kernel rows, kernels per row and kernel weight were obtained for a synthetic variety of maize produced from eight inbred lines. Design II mating system was used. A significant amount of additive genetic variance was present in the population for all characters and in each case the estimate of additive genetic variance exceeded that of dominance variance. The relative magnitude of the additive genetic and dominance variances for kernel rows and kernel weight suggested that the expression of these characters resulted primarily from additive gene effects. However, for the expression of ear number, kernels per row and yield, loci with partial to complete dominance were involved. Overdominance did not appear to be very important in the expression of any of these characters. These results would suggest that improvement in yield performance of the population investigated or other similar populations, is possible by selection.

INTRODUCTION

Improvement in a plant population and the choice of the means to achieve it is primarily dependent on the magnitude, nature and interaction of genetic and non-genetic variations in the various plant characters. According to Fisher (1918) and Wright (1935), total genetic variance, in a random mating population, can be divided into three components viz: (1) Additive genetic variance, (2) Dominance variance, and (3) Epistatic variance. Partitioning of the genotypic variance provides a means for the estimation of relative magnitude of the various components of variance and thus leads to a basis for selecting between a number of breeding systems available to improve genetic populations.

The primary objective of these investigations was to obtain estimates of additive genetic and dominance variance for yield and its four components viz: ear number, kernel rows, kernels per row and kernel weight in a synthetic variety of maize.

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REVIEW OF LITERATURE

Comstock and Robinson (1948, 1952) presented theoretical derivations and outlined experimental procedures for the estimation of genetic variance in random mating populations. These procedures have generally been referred to as Designs I, II and III. Sprague and Tatum (1942) described a procedure to estimate variance due to general combining ability and specific combining ability, using diallel crosses. In essence this procedure is a special case of Design II where for parents the inbreeding coefficient equals to one.

Using Design I, Robinson *et al.* (1949) reported estimates of additive and dominance variance for several characters in F2 populations of three single cross hybrids. In general the estimates for grain yield and ear diameter showed appreciable dominance variance relative to the additive genetic variance, and were mostly in the overdominance range. However, the estimates for the other characters indicated partial to complete dominance. Gardner *et al.* (1953) using design III material from two F2 populations of corn, found that in both populations the estimates of dominance variance for yield were greater than the additive genetic variance. For the remaining characters, the estimates of additive genetic variances were in general, higher than the dominance variance.

Comstock and Robinson (1952) pointed to the possible upward bias due to linkage in the estimates reported above, and suggested the use of advanced generations of hybrid populations with design III to minimize this bias.

Gardner and Lonnquist (1959) and Robinson *et al.* (1960) using design III material for F2 and F8 generations of hybrid populations obtained consistent and appreciable reduction in dominance variance in advanced generation material.

Appreciable amount of genetic variance both of the additive and non-additive type has been reported by Hull (1945), Robinson *et al.* (1955) and Lindsey *et al.* (1962) in adapted open pollinated varieties of maize. In general the estimates of additive genetic variance were larger than those for dominance variance for yield and most of the other characters. These results were interpreted to indicate that, although there may be overdominance at some loci, overdominance loci are not the single important source of genetic variation in the varieties studied.

Majority of the experimental evidence reviewed above suggests that considerable additive genetic variance is present both in hybrid populations and in open pallinated varieties so that intrapopulation selection either individual or family could be effectively employed to improve such populations and crosses among them. Gardner (1961) was able to make considerable advance in yield performance of an open pollinated variety through intra variety mass selection.

MATERIALS AND METHODS

Genetic Material

The population evaluated in this study was derived from synthetic–3, an eight line synthetic developed from the inbred lines OH5, OH43, OH51A, W22, A73, A286, A295 and A375. The eight inbred lines were first combined into four single crosses which were then crossed to make two double crosses. The two double crosses thus obtained were then crossed together to make, synthetic–3. After sib pollination for one generation an inbreeding programme was started. 510 selfed S_0 plants were retained from 600 plants self pollinated at random, with only minor selection against grossly defective agronomic traits. Of these 350 lines survived to the S_3 generation. From amongst the available lines 100 were picked at random and divided into 10 groups of 10 lines each. Within each group, 5 lines were designated as male parents and the remaining lines as the female parents. All possible matings (diallel crosses) between the two sets of parents were attempted producing a set of 25 F_1 progenies for each group of 10 lines. Synthetic–3 was included once in each set as a check resulting in a total of 260 entries for the experiment.

Field Plan

The experiment was conducted at two locations and was arranged in a randomized complete block design with two replications at each location. Within the replication, each set of 26 entries was randomly placed in a separate block and the entries within sets were assigned at random to the plots within each block. Single row plots, 15 hills long were used in all cases. Row spacing was 36" and hills were spaced 12" apart. Planting was made at the rate of two seeds per hill, and when the seedlings were 12 to 15 inches tall they were thinned to one plant per hill. Ten equally competitive plants were harvested from each plot wherever possible and data were calculated on a per plant basis for the following characters :

1. Grain yield in grams adjusted to zero per cent moisture.
2. Ear number index-grain weight for the second ears as fraction of the grain weight for the first ears plus one.
3. Kernel row number-average number for the first ears.

4. Kernels per row-average count of 3 rows on first ears.
5. 100 kernel weight-weight per 100 kernels, adjusted to zero per cent moisture, determined per a 600 kernel bulk sample to the nearest one tenth gram on a shadowgraph balance.

Statistical Methods

The genetic design employed in this study has generally been referred to as design II of Comstock and Robinson (1948, 1952) which is generally applicable to multiflowered plants. The procedure, however, can be applied to corn by establishing inbred lines in a random mating population and then using several plants from each line to make diallel crosses. Material at any level of homozygosity can be used by taking the inbreeding coefficient into consideration in the genetic expectation of the variance components.

Analyses of variance were done for all characters for individual locations and combined for the two locations, using mean values per plant for each plot. The combined analyses were based on the assumption that performance as measured in any of the character studied, corresponds to the following genetic model :

$$X_{ijks} = u + M_i + F_j + (MF)_{ij} + L_k + (FL)_{jk} + (MFL)_{ijk} + E_{ijks}$$

where X_{ijks} is the measured value for the plot specified by the subscripts

u = mean performance of all progenies
M_i = effect of the ith male parent
F_j = effect of the jth female parent
$(MF)_{ij}$ = interaction effect of the ith male with the jth female parent
L_k = effect of the kth location
$(ML)_{ik}$ = interaction effect of ith male parent with kth location
$(FL)_{jk}$ = interaction effect of the jth female parent with kth location
$(MFL)_{ijk}$ = interaction effect of the ith male, jth female and kth location
E_{ijks} = random element associated with sth observation of the ijth progeny at the kth location

The parental lines and locations were considered as random variables resulting in a random model. The data were analysed by individual sets and then the results pooled over all sets. The form of the combined analysis of variance is given in Table 1.

where,

L = Number of locations = 2
r = Replications per locations = 2
b = Blocks per replication = 10

m = Male groups in a block = 5

f = Female groups in a block = 5

s_e^2 = Random plot to plot variation and the mean variance among plants within the same plot, resulting from environmental genetic differences.

s_{mfL}^2 = Variance due to interaction between male and female interaction effects and environments as it varied between locations.

s_{fL}^2 = Variance due to interaction between female genotypes and locations.

s_{mL}^2 = Variance due to interaction between male genotypes and locations.

s_{mf}^2 = Variance due to interaction between male and female genotypes.

s_m^2 = Variance due to genetic differences among male parents.

s_f^2 = Variance due to genetic differences among female parents.

Genetic interpretations associated with s_m^2, s_f^2 and s_{mf}^2, given by Comstock and Robinson (1948, 1952) and by Cockerham (1954), permits the estimation of additive genetic variance, s_g^2 and non-additive genetic variance (designated as dominance variance) s_d^2. This interpretation is based on the following assumptions :

1. Regular diploid meiosis
2. Two alleles at each locus
3. No epistasis
4. No linkage
5. Variations in environments are random relative to the progenies.
6. Equal viability of gametes and zygotes
7. The inbred lines constitute a random sample

Granting validity of the above assumptions and assuming no non-genetic effects of the male and female parents, the three components of variance S_m^2, S_f^2 and S_{mf}^2 would be entirely genetic in origin and would have the following expectations.

$$S_m^2 = S_f^2 = \frac{(1+F)}{4} \quad S_g^2, \; S_{mf}^2 = \frac{(1+F)^2}{4} \quad S_d^2$$

Where F is the inbreeding coefficient of the effective parent plants and equals to .9375 for the material used in these studies.

TABLE 1 *General form for the combined analyses of variance*

Source of variation	Degrees of freedom	Expectations of mean squares
Locations (loc.)	L–1	
Replications (reps.) in loc.	L(r–1)	
Sets	b–1	
Sets × loc.	(b–1)(L–1)	
Sets × reps. in loc.	L(b–1) (r–1)	
Males (M) in sets	b(m–1)	$s_e^2 + rs_{mfL}^2 + rfs_{mL}^2 + rLs_{mf}^2 + rLfs_m^2$
Females (F) in sets	b(f–1)	$s_e^2 + rs_{mfL}^2 + rms_{fL}^2 + rLs_{mf}^2 + rLms_f^2$
(M × F) in sets	b(m–1) (f–1)	$s_e^2 + rs_{mfL}^2 + rLs_{mf}^2$
Males in sets × loc.	b(m–1) (L–1)	$s_e^2 + rs_{mfL}^2 + rfs_{mL}^2$
Females in sets x loc.	b(f–1) (L–1)	$s_e^2 + rs_{mfL}^2 + rms_{mfL}^2$
(M × F) in sets x loc.	b(m–1) (f–1) (L–1)	$s_e^2 + rs_{mfL}^2$
Pooled error	bL(mf–1) (r–1)	s_e^2
Total	bLrmf–1	

EXPERIMENTAL RESULTS

The mean performance for various characters of Synthetic–3 population and of the F_1 progenies among inbred lines derived from it, is given in Table 2.

TABLE 2 *Mean performance of Synthetic–3 and the F_1 progenies*

Character	Mean values	
	Synthetic–3	F_1 progenies
Yield	164.52*	164.45*
Ear number	1.04	1.03
Kernel rows	17.74	17.04
Kernels per row	41.84	42,46
Kernel weight	23.31**	23.73**

* grams per plant

** grams per 100 kernels

For all the characters measured the differences between the mean values for Synthetic-3 and those for F_1 progenies were not significant statistically.

Thus the offspring resulting from the mating system used in this study, reconstituted the original random mating population and the partition of variance among full sib and half sib families would be the same as for the original population.

Analysis of Variance

The data were analysed by individual locations and also combined over the two locations. The results for the combined analysis are presented in Table 3.

The mean squares were tested for significance using appropriate denominators. Denominators to test male and female effects were constructed using mean squares for males x females, males x locations and males x females x locations for the former and males x females, females x location and males x females x locations for the latter. Significance of male x females, male x location and female x location effects was tested against the mean square for males x

TABLE 3 *Combined analysis of variance for yield and the four components*

Source of variation	Degrees of freedom	MEAN SQUARES				
		Ear number	Kernel rows	Kernels per row	Kernel weight	Yield
Males	40	.01454**	19.067**	86.213**	64.698**	1956.285**
Females	40	.02585**	20.928**	65.810**	79.271**	1065.268*
Males x females	158	.00582**	.922**	11.947**	4.810**	441.603**
Males x locations	40	.00309	.290	5.152*	2.068	351.687**
Females x locations	40	.00599**	.500	6.527**	1.943	379.590**
Males x females x locations	157	.00240**	.349	3.224*	1.468	191.912
Pooled error	472	.00162	.292	2.401	1.310	157.487

** exceeds 1% level of significance

* exceeds 5% level of significance

females x location effects. The mean squares for males, females and males x females were found to be highly significant, thus providing evidence that, in the material investigated, significant amounts of additive genetic and dominance variance are present for all the characters. For kernel row number and kernel weight all the interaction mean squares involving locations were non-significant, indicating very little genotype-location interaction in case of these two traits. For all the other characters, interactions with locations were, in general, significant.

Estimates of Components of Variance

The importance of the components as sources of variation is indicated by their relative magnitude. Based on the expectations of mean squares listed in Table 1, the estimates of the various components of variance were computed and are presented in Table 4. For all the characters estimates of s^2_m, s^2_f and s^2_{mf}, which are assumed to be genetic in origin, are significantly different from zero. The relative magnitude of these components, in comparison with the error variances for the various characters, are of higher magnitude for kernel row number, kernels per row and kernel weight, and of lower magnitude for ear number and yield. The components of variance due to the interaction of male and female genotypes with locations were negligible for kernel row number and kernel weight, however, those for ear number and yield were significant. The negative estimate obtained in case of male x location interaction component for kernel row number is not sufficiently different from zero and could be expected due to sampling variation, the actual value being zero or a small positive value A comparison of the estimates of genetic components of variation in the various characters with the component of variation due to interaction with locations, indicates that the components involving interaction with locations were of relatively higher magnitude in yield than in the four components of yield.

Estimates of additive genetic variance, dominance variance and their interaction with locations for the combined analyses are given in Table 5, along with their standard errors and the ratios S_d/S_g^2, S_{gL}^2/S_g^2 and S_{dL}^2/S_d^2. Comparing the size of the standard error relative to the corresponding estimates, it is evident that all of the estimates of S_g^2 and S_d^2 are significantly different from zero. The estimates of additive genetic variance were greater than the estimates of dominance variance for all the characters, as indicated by the ratios S_d^2/S_g^2 which are less than one in every case. Considering the relative size of these two genetic variances, the estimates of S_g^2 for yield and ear number were approximately one and a half times that of S_d^2 whereas for kernel rows, kernels per row and kernel weight, the estimates of S_g^2, were several times

TABLE 4 *Estimates of components of variance from combined analysis*

Component of variance	Genetic expectations	Ear number	ESTIMATES			
			Kernel rows	Kernels per row	Kernel weight	yield
s_m^2	$\frac{1+F}{4} S_g^2$	.00041	.910	3.617	2.964	67.745
s_f^2	$\frac{1+F}{4} S_g^2$	.00082	.993	2.528	3.699	21.699
s_{mf}^2	$\frac{1+F}{2} S_d^2$	.00086	.143	2.181	.836	62.423
s_{ml}^2	—	.00007	—.006	.193	.060	15.978
s_{fl}^2	—	.00036	.015	.330	.948	18.768
s_{mfl}^2	—	.00039	.029	.041	.079	17.213
s_e^2	—	.00162	.292	2.401	1.310	157.487

TABLE 5 *Estimates of additive genetic and dominance variances and their interaction with locations*

	ESTIMATES OF COMPONENTS						
Character	s^2g	s^2d	s^2gl	s^2dl	s^2d/s^2g	s^2gl/sg	s^2dl/s^2d
Ear number	.00126 .00036	.00091 .00019	.00046 .00016	.00044 .00015	.722	.365	.483
Kernel rows	1.964 .327	.153 .030	.009 .013	.033 .023	.078	.005	.216
Kernel per row	6.343 1.264	2.324 .371	.557 .206	.046 .211	.366	.088	.019
Kernel weight	6.879 1.182	.891 .151	.115 .074	.090 .099	.129	.17	.101
Yield	92.433 26.979	66.513 14.438	37.024 12.754	19.543 12.767	.719	.300	.294

that of $S_{d.}^{1}$ This indicates that for the synthetic population used in this experiment, the genetic variability for the components of yield other than ear number was predominantly due to additive gene effects.

DISCUSSION

The magnitude of the estimates of genetic variability for the various characters, reported in Table 5 suggest the possibility of progress through selection. Without exception the estimate of additive genetic variance was larger than that for dominance variance for the same character. For kernel row number and kernel weight, the estimate of additive genetic variance was many times that of dominance variance suggesting that the average level of dominance in the action of genes governing these characters was very low. For yield and ear number an appreciable amount of dominance variance was present. The relative size of the dominance variance to additive genetic variance ratios does support the suggestion (Robinson et al. 1955, Gardner et al. 1953) that overdominant loci may not be important in the expression of these two traits. However, these results, like theirs, do not exclude the possible existence of overdominance at some loci. In F2 populations from a cross of two homozygous lines, Robinson et al. (1949) and Gardner et al. (1953) obtained ratios of S_d^2/S_g^2 for yield in the overdominance range. However their later estimates, obtained by using advanced generations of the same material, suggested partial to complete dominance, earlier estimates being possibly biased upward due to linkage. The results of the present studies are in general agreement with their results from the advanced generation material. Kernel row number and yield data are in good agreement with those reported by Robinson et al. (1955) in open pollinated varieties. The estimates of the ratios S_g^2/S_d^2 for ear number are much higher, but may not be critical due to the fact that this is not a multiple eared population.

The validity of several assumptions made in computing these estimates of genetic variances is questionable (Comstock and Robinson 1952), so that the results must be accepted with some degree of reservation. With several to many genes governing quantitative characters, linkages are expected to exist. Since the material used in this study was sib-mated only for one generation prior to selfing and crossing, linkages, if present, would not have dissipated or attained a state of equilibrium. Consequently, estimates of S_d^2 would be biased upward. However, since estimates of dominance variance were in all cases smaller than those of additive genetic variance, the consideration of bias will affect only the degree of interpretation of these results. Absence of epistasis is an assumption which is of questionable validity. Horner et al. (1955) showed that when non-allelic interactions are present, design II overestimates both additive genetic and dominance variances, the bias being proportionately greater in the latter case. However the information available so far (Horner 1952, 1955; Kempthorne 1957; Cockerham 1956) indicates that epistasis is not an important source of bias in such estimates. Since 7 of the 8 constituent lines used in producing synthetic–3 were of diverse origin, the assumption of not more than two alleles is of doubtful validity. Considering the chances of a different allele entering from each inbred line, a maximum of eight alleles are possible in the population. However, as noted by Robinson et al. (1955), if considerable additive genetic variance is present in the population the implications with regard to the possibilities of variety improvement through selection would not be affected by the presence of multiple alleles.

Any interpretation of these results must be conditioned by possible bias due to interaction of genotype with environment. Since this study was conducted in only one year, variance due to interaction of genotypes with years would contribute to the apparent genetic variance. By growing progenies at two locations it was possible to obtain estimates of additive genetic and dominance variance free of interaction of the genotype with the environment as they vary from one location to another. Information was also obtained on the interaction of both additive genetic effects and dominance effects with these environments. A reference to Table 4 would show that the estimates of S^2_{gl} and S^2_{dl} for kernel rows and kernel weight were not different from zero indicating consistency of these estimates over locations. If considerable genotype x year interaction variances are present the estimates of additive genetic and dominance variances obtained in these studies would be biased upward. However the ratios S^2_d/S^2_d would be affected only if the interactions are not proportionate to the variances.

As a concluding remark it may be mentioned that for initiating a selection program two points are of significance. Firstly, the mean level of performance of the population which would determine the starting point with respect to the selection and secondly the amount of genetic variability in the population. If a synthetic variety is constituted of inbred lines selected for their high combining ability, it may be expected to give a high level of performance (Hayes *et al.* 1944). The presence of any significant amount of genetic variance in such a populations would indicate the scope of further improvement over the already high base performance, by using appropriate breeding procedures. How long such a population would respond to selection will depend on the rate of dissipation of the genetic variance. With many genes influencing quantitative characters, particularly yield, one can reasonably expect that it would not be dissipated rapidly. The choice of a breeding procedure will depend on the relative magnitude of additive genetic variance and dominance variance. The estimates of these two variances reported and discussed so far may apply in a general way to other similar populations, so that if selection is based on characters like kernel rows and kernel weight, which gave a low estimate of dominance effects in the action of genes governing their expression, then mass selection, family selection or recurrent selection for general combining ability would be appropriate. Reciprocal recurrent selection would be appropriate for all situations.

Such an improvement in the synthetic can be useful from two aspects. Firstly, in places where economic and technical difficulties do not permit a regular supply of double cross hybrid seed, the synthetic can be improved as a commercial variety. Secondly, it would result in the development of a germ plasm reservoir with higher frequency of genes for yield or any other trait selected for, and thus highly suitable for extraction of superior inbred lines.

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