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Genetic Studies in an Exotic Population of Corn (*Zea mays* L.) Grown under two Plant Densities

I. Estimates of Genetic Parameters[1]

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Summary. Progenies of a Design II [Comstock and Robinson (1948)] using random S_1 lines from an exotic population of corn (*Zea mays* L.) were evaluated in a randomized incomplete block design with two replications at two plant-population densities (17,222 plants/ha and 68,888 plants/ha) in 1970 and 1971, at Lincoln, Nebraska. Five traits were studied i.e. grain weight, number of ears, days to flower, plant height and ear height.

Under both densities the estimates of additive genetic variance were much larger than those of dominance genetic variance for all traits. The ratio of dominance to additive genetic variance estimates was less than 0.5 suggesting that for the majority of loci controlling the traits, partial to complete dominance is likely.

The estimates of additive genetic × year interaction variance were high and significantly different from zero under both densities, indicating that estimates of additive genetic variance in this population obtained from experiments conducted in only one year may be seriously biased. The estimates of dominance genetic × year interaction variance were not significant and most of them were negative.

Under both densities high genetic inter-relationships were indicated between grain weight and number of ears, days to flower and plant height, days to flower and ear height, and plant height and ear height.

Even though there was a large difference between the two densities used in the study, the differences between the estimates of genetic parameters were not significant in all cases.

The sample size of S_1 plants representing each S_0 parent in the crossing nursery used in the present study (11.75) caused a small upward bias in the estimates of additive genetic variance, but it caused an upward bias in the estimates of dominance genetic variance of 6–7% of the total genetic variance.

It is suggested that a trait such as grain weight should be expressed on a unit area basis when genetic parameters (except for correlation and the ratio between two values) obtained from experiments with different plant-population densities are to be compared.

Introduction

Information on the relative levels of various components of genectic variance is of value to plant breeders as a guide in choosing a proper breeding method for a particular set of material under given circumstances. The choice of a plant-population density in which to practice selection is a problem because of possible interaction of genotypes with plant-population density and differences in heritability under different plant-population densities. Numerous published reports on the estimates of genetic variances have been based on studies conducted in only a single plant-population density. Studies of genetic variance estimates under different plant-population densities have been needed to provide breeders information about differences in genetic and phenotypic variances and genotype by density interaction in different densities.

The first objective of this study was to obtain estimates of genetic parameters involving five traits under two different plant-population densities and to investigate the effect of the latter on the estimates. A second objective was to develop information which would aid in the choice of a plant-population density in which selection is to be practiced.

This paper reports results relevant to the first objective. The results of the experiment pertinent to the second objective will be reported in a separate paper.

Material and Methods

The maize population used was Gaspé × Colombian, a cross between one Canadian variety (Gaspé) and three Colombian varieties (Eto, Nariño 330 and Peru 330). By 1967, the cross had been random mated for 6 generations in an isolated field at Lincoln, Nebraska. Except in the third generation in which ear-to-row selection was employed, only mild adaptive selection was practiced throughout the generations of random mating.

The Design II mating system (Comstock and Robinson, 1948 and 1952) was used to produce half-sib and full-sib families utilized for estimation of genetic parameters. In 1968, 240 random S_1 lines were produced and used to represent S_0 plants in the populations. Those S_1 lines were divided into 40 sets of six lines. Each set was divided into two groups of 3 lines, which were arbitrarily desig-

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nated as male and female groups, respectively. In 1969 all possible crosses between the male and the female lines within each set were made to produce full-sib families. Plants in both male and female lines were used only once, either as males or as females. In rare circumstances, due to a difference in dates of flowering or insufficient number of available plants, one S_1 plant was used more than once in the cross. In the winter of 1969–1970, additional crosses were made in Florida for those pairs with a small number of crossed ears. Because of the limited experimental area only 32 sets of cross-progenies with the highest harmonic mean of the number of S_1 plants representing S_0 plants in the pair crosses were grown in this study.

In 1970 and 1971 the thirty-two sets of nine progenies were planted in a randomized incomplete block design with two replications and two plant-population densities. Each block contained a different set of nine progenies. Two row plots of 381 cm in length with a distance of 76.2 cm between rows were used. At the low density, the hills were spaced 76.2 cm apart. Two seeds were planted in a hill and the seedlings were thinned to one plant per hill, making a plant-population density of 17,222 plants/ha. At the high density the hills were spaced 38.1 cm apart. Three seeds were planted in a hill and the seedlings were thinned to two plants per hill, leaving a plant-population density of 68,888 plants per hectare. Sweet corn was planted in the aisles. Purple marker corn was planted in the border rows and transplanted into missing hills to provide competition. Only competitive plants were harvested. The experiments were conducted according to standards of the Corn Breeding Program at the University of Nebraska.

Data were recorded for the following traits: 1. Grain weight at 15.5% moisture content (kg/plot and gram/plant); 2. number of ears per plot and per plant; 3. number of days from planting to when 50% of the plants in a plot were shedding pollen; 4. plant height (cm); 5. ear height (cm). Plant and ear height were measured from 10 competitive plants whenever possible.

To obtain within plot variation for grain weight, one plot was randomly chosen from each block, making a total of 32 plots in each year for the low density. At the high density, one plot was randomly chosen from every other block, providing a total of 16 plots in each year. Six inner hills at the low and eighteen at the high density in each of the chosen plots were harvested on an individual plant basis.

The combined analyses of variance and covariance at each density (Table 1) were performed to obtain estimates of components of variance and covariance between pairs of traits. The components of variance and covariance were estimated as linear functions of the mean squares and mean products. The assumptions for the derivation of mean square expectations and genetic interpretations of the variance components were given by Comstock and Robinson (1952). Genetic interpretation follows the formulae given by Cockerham (1956) and extended by Jones and Compton (1973) as follows:

$$\sigma^2_Z = Cov.\,HS = \frac{\left(1 + \frac{1}{2\,m_1}\right)}{4}\,\sigma^2_A$$

which allows the estimation of

$$\sigma^2_A \quad \text{as} \quad \frac{4\,\sigma^2_Z}{1 + \frac{1}{2\,m_1}}$$

$$\sigma^2_{MF} = Cov.\,FS - 2\,Cov.\,HS = \frac{1}{4}\left[\left(\frac{1}{m_2} - \frac{1}{m_1}\right)\sigma^2_A + \left(1 + \frac{5}{4\,m_2}\right)\sigma^2_D\right]$$

which enables the estimation of σ^2_D as

$$\frac{4\,\sigma^2_{MF} - \left(\frac{1}{m_2} - \frac{1}{m_1}\right)\frac{4\,\sigma^2_Z}{1 + \left(\frac{1}{2}\,m_1\right)}}{1 + \left(\frac{5}{4}\,m_2\right)}$$

where: σ^2_Z is the pooled variance due to genetic differences among males and among females within blocks; *Cov. HS* is covariance among half-sib individuals; m_1 is the harmonic mean of the numbers of S_1 plants representing each S_0 plant in the half-sib families. Assuming that each S_1 plant was used only once to represent a half-sib

Table 1. *Portion of the form of analysis of variance for data of progenies produced in a Design II mating system grown at one plant-population density in two years*

Source of variation	d.f.	M.S.	Expectation of mean squares
Males & Females (Z)/Blocks (B)	$b\,(m + f - 2)$	M_5	$\sigma^2 + r\,\sigma^2_{MFY} + r\,n\,\sigma^2_{ZY} + r\,y\,\sigma^2_{MF} + r\,n\,y\,\sigma^2_Z$
Males (M)/B	$b\,(m - 1)$	M_6	$\sigma^2 + r\,\sigma^2_{MFY} + r\,f\,\sigma^2_{MY} + r\,y\,\sigma^2_{MF} + r\,f\,y\,\sigma^2_M$
Females (F)/B	$b\,(f - 1)$	M_7	$\sigma^2 + r\,\sigma^2_{MFY} + r\,m\,\sigma^2_{FY} + r\,y\,\sigma^2_{MF} + r\,m\,y\,\sigma^2_F$
M × F/B	$b\,(m - 1)\,(f - 1)$	M_8	$\sigma^2 + r\,\sigma^2_{MFY} + r\,y\,\sigma^2_{MF}$
Z × Y (Years)/B	$b\,(m + f - 2)\,(y - 1)$	M_9	$\sigma^2 + r\,\sigma^2_{MFY} + r\,n\,\sigma^2_{ZY}$
M × Y/B	$b\,(m - 1)\,(y - 1)$	M_{10}	$\sigma^2 + r\,\sigma^2_{MFY} + r\,f\,\sigma^2_{MY}$
F × Y/B	$b\,(f - 1)\,(y - 1)$	M_{11}	$\sigma^2 + r\,\sigma^2_{MFY} + r\,m\,\sigma^2_{FY}$
M × F × Y/B	$b\,(m - 1)\,(f - 1)\,(y - 1)$	M_{12}	$\sigma^2 + r\,\sigma^2_{MFY}$
Error	$b\,y\,(m\,f - 1)\,(r - 1)$	M_{13}	σ^2
Plants within plots	$\Sigma\,(w_i - 1)$	M_{14}	σ^2_W

b, m, f, y, r = number of blocks, males per block, females per block, years, and replications, respectively. $n = m = f$ in this experiment. w_i = number of plants in the i^{th} plot in which individual plant data were taken. M_i = the value of the i^{th} mean square. σ^2_M and σ^2_F = variances due to genetic differences among males and among females within blocks, respectively. σ^2_Z = the pool of σ^2_M and σ^2_F = *Cov. HS*. σ^2_{MF} = variance due to interaction of male and female genotypes within blocks = *Cov. FS* − − 2 *Cov. HS*. σ^2_{MY} and σ^2_{FY} = variances due to interaction of males and years and of females and years, respectively. σ^2_{ZY} = the pool of σ^2_{MY} and σ^2_{FY}. σ^2_{MFY} = variance due to interaction of males, females and years. σ^2 = error variance. σ^2_W = variance among plants within plots due to genetic and environmental differences among individuals of the same family.

family, $m_1 = 35.25$ in the present experiments; σ_A^2 is the additive genetic variance; σ_{MF}^2 is the variance due to interaction of male and female genotypes within blocks; *Cov. FS* is the covariance among full-sib individuals; m_2 is the harmonic mean of the numbers of S_1 plants representing each S_0 plant in the full-sib families (in the present experiments $m_2 = 11.75$); and σ_D^2 is the dominance genetic variance.

The standard error of the estimate of σ_A^2 for each trait was computed using the following formula:

$$\frac{4}{\left(1+\frac{1}{2\,m_1}\right)k_1}\left[2\sum_i \frac{M_i^2}{f_i+2}\right]^{1/2}$$

where: M_i is the i^{th} mean square in the function associated with σ_Z^2; f_2 is the degrees of freedom associated with M_i; k_1 is the divisor of the function, which is the coefficient of σ_Z^2 in the expectations of mean squares; m_1 has already been defined. The standard error of the estimate of σ_D^2 for each trait was computed utilizing the following formula:

$$\frac{4}{\left(1+\frac{5}{4\,m_2}\right)}\left[\frac{2}{k_2^2}\sum_j \frac{M_j^2}{f_j+2}+\frac{\left(\frac{1}{m_2}-\frac{1}{m_1}\right)^2}{\left(1+\frac{1}{2\,m_1}\right)^2}\times\right.$$

$$\left.\times\,\frac{2}{k_1^2}\sum_i \frac{M_i^2}{f_i+2}+\frac{\left(\frac{1}{m_2}-\frac{1}{m_1}\right)}{\left(1+\frac{1}{2\,m_1}\right)}\cdot\frac{4}{k_1\,k_2}\sum_1 \frac{M_1^2}{f_1+2}\right]^{1/2}$$

where: M_j is the j^{th} mean square in the function associated with σ_{MF}^2; f_j is the degrees of freedom associated with M_j; k_2 is the divisor of the function, which is the coefficient of σ_{MF}^2 in the expectations of mean squares; M_i, f_i, k_1, m_1, and m_2 are already described; M_1 is the 1^{th} mean square involved in the estimation of both σ_Z^2 and σ_{MF}^2; f_1 is the degrees of freedom associated with M_1.

The same procedure was applied for the estimation of variances due to genetic × year effects and their standard errors.

The additive genetic correlation between each pair of traits was calculated according to the following relationship:

$$r_{A(pq)} = \frac{\hat{\sigma}_{Z(pq)}^2}{\sqrt{\hat{\sigma}_{Z(p)}^2\,\hat{\sigma}_{Z(q)}^2}}$$

where: $r_{A(pq)}$ is the additive genetic correlation coefficient between the p^{th} and the q^{th} traits; $\hat{\sigma}_{Z(pq)}^2$ is the pooled estimate of the male and the female components of covariance between the p^{th} and the q^{th} traits; $\hat{\sigma}_{Z(p)}^2$ and $\hat{\sigma}_{Z(q)}^2$ are the pooled estimates of the male and the female components of variance for the p^{th} and the q^{th} traits, respectively. Standard errors of the estimates of additive genetic correlation coefficients were computed following the procedure given by Mode and Robinson (1959).

An estimate of a genetic parameter is significantly different from zero at $P = .05$ or $.01$ if its confidence interval at that level of probability does not overlap zero. Two estimates of genetic parameters are considered significantly different from each other if their confidence intervals do not overlap each other at $P = 0.10$.

Experimental Results

Estimates of the components of genotypic variance and genotype × year interaction, their standard er-

Table 2. *Estimates of additive ($\hat{\sigma}_A^2$) and dominance ($\hat{\sigma}_D^2$) genetic variances, their respective interaction with year ($\hat{\sigma}_{AY}^2$ and $\hat{\sigma}_{DY}^2$) and their respective standard errors, the ratio of dominance to additive genetic variance ($\hat{\sigma}_D^2/\hat{\sigma}_A^2$), obtained from experiments in 1970 and 1971 at each density*

Trait	Density	$\hat{\sigma}_A^2$		$\hat{\sigma}_{AY}^2$		$\hat{\sigma}_D^2$		$\hat{\sigma}_{DY}^2$		$\hat{\sigma}_D^2/(\hat{\sigma}_A^2+\hat{\sigma}_D^2)$	$\hat{\sigma}_D^2/\hat{\sigma}_A^2$
Grain weight (g/plant)	Low	2932.14**	± 590.73	1243.40**	± 286.99	1276.21**	± 370.31	−70.74	± 345.86	0.30	0.43
	High	171.03**	± 39.45[1]	80.60**	± 26.97[1]	55.60	± 32.85[1]	22.63	± 41.16	0.25	0.32
Grain weight (q/ha)	Low	86.9664**	± 17.5208	36.8789**	± 8.5120	37.8520**	± 10.9832	−2.0981	± 10.2581		
	High	81.1632**	± 18.7212	38.2491**	± 12.7987	26.3852	± 15.5891	10.7391	± 19.5327		
No. of ears per plant	Low	0.3005**	± 0.0514	0.0467*	± 0.0198	0.0741*	± 0.0305	−0.0099	± 0.0338	0.20	0.24
	High	0.0124**	± 0.0026[1]	0.0043**	± 0.0016[1]	0.0036	± 0.0020[1]	−0.0009	± 0.0026	0.23	0.29
No. of ears per plot	Low	30.05**	± 5.14	4.67*	± 1.98	7.41*	± 3.05	−0.99	± 3.38		
	High	19.84**	± 4.16	6.88**	± 2.56	5.76	± 3.20	−1.44	± 4.16		
Days to flower	Low	8.50**	± 1.29	0.9530**	± 0.3140	1.38**	± 0.49	−0.3923	± 0.4939	0.14	0.16
	High	9.03**	± 1.30	0.6310**	± 0.2059	1.34**	± 0.39	0.2930	± 0.3074	0.13	0.14
Plant height (cm)	Low	424.98**	± 65.83	47.47**	± 13.67	112.17**	± 27.35	−18.17	± 20.03	0.21	0.26
	High	345.08**	± 53.52	38.52**	± 11.67	87.08**	± 22.48	−23.89	± 17.87	0.20	0.25
Ear height (cm)	Low	345.95**	± 49.82	29.61**	± 8.19	45.68**	± 14.32	−11.09	± 11.71	0.12	0.13
	High	381.62**	± 54.96	21.92**	± 8.46	59.43**	± 17.62	−0.58	± 13.94	0.13	0.15

*, ** indicate significantly different from zero at $P = .05$, and .01, respectively.
[1] indicates the two estimates are significantly different at $P = 0.10$.

rors, and the ratios of the estimates are presented in Table 2. The additive genetic variance estimates were significant for all traits at each density. The dominance genetic variance estimates were significant for all traits at the low density. They were significant for three out of five traits at the high density. Dominance genetic effects for all traits at each density contribute only 30% or less to the total genetic variance. The ratios of dominance to additive genetic variance estimates for all traits at each density were less than 0.50. It would be unlikely that the frequency of favorable genes at a segregating locus (q) ≥ 0.9 in this population since only mild adaptive selection was practiced during the development of the material. Neither is it likely that the degree of dominance is the same for all loci. Therefore, using the procedure of Robinson *et al.* (1955) the ratios of the estimates of dominance to additive genetic variance for all traits at both densities suggest that overdominance was not prevalent in causing genetic variation in the traits studied. This agrees well with the finding of many other investigators.

Estimates of additive genetic × year variance were significant for all traits at each density. None of the dominance genetic × year variance estimates were significant at either density, and, in fact, most of the estimates were negative.

The estimates at the low and the high densities were significantly different from each other only for additive genetic, additive genetic × year, and dominance genetic variances for grain weight and number of ears expressed on a per plant basis. The corresponding estimates for grain weight and number of ears expressed on a unit area basis were not significant.

Estimates of additive genetic correlation coefficients and their standard errors are presented in Table 3. Grain weight and number of ears, and pairs of traits among days to flower, plant height and ear height were highly significantly correlated at each density. The remaining genetic correlation coefficients between pairs of traits at each of the densities were low and mostly non-significant. The magnitude of the estimates at the two densities was not significantly different at $P = .10$ for any pairs of traits.

Within plot variance estimates for grain weight were computed from individual plant data collected from the sampled plots. This variance was used to calculate the plot-to-plot component of error variance. Using the estimates of genotypic components of variance and their interaction with years the within-plot variance due to environmental effects was also computed. The results (Table 4) showed that the plot-to-plot variance was a smaller portion of the error variance, particularly at the low density, and the within-plot variance was mainly due to environmental effects, especially at the high density.

Discussion

Several of the assumptions needed for the derivation of the mean square expectations and the genetic interpretations, which were not satisfied and could cause a bias in the estimates of genetic parameters studied, will be briefly discussed. With respect to random mating, even though crosses between members of paired lines were made in both ways, two different dates of planting would have better avoided any possible deviation from random crosses. The present study was conducted at a single location and the results were confounded with genotype × location interaction. Further discussion will not refer to this bias.

According to Comstock and Robinson (1952) it appears safe to assume no non-genetic maternal effect for many characters or no consequence of its presence, but F tests indicated different results for M × Ds and F × Ds associated with grain weight and number of ears and for M × Ds × Y and F × Ds × Y associated with three out of five traits [Table 2, Subandi and Compton (1973)]. These differences could partly be due to the relatively small size of the sample used. Aberration segregation during meiosis could have occurred but the frequency was possibly too low to have significant influence on the estimates. Bias in the estimates of genetic

Table 3. *Estimates of additive genetic correlation coefficients between pairs of traits obtained from combined analyses over 2 years (1970 and 1971) at each density*

	No. of ears		Days to flower		Plant height		Ear height	
Grain weight	0.834**	±0.050	0.229	±0.117	0.219	±0.117	0.226*	±0.113
	0.605**	±0.107	−0.127	±0.124	0.070	±0.130	−0.040	±0.126
No. of ears			0.168	±0.111	0.118	±0.113	0.207	±0.106
			−0.117	±0.120	−0.083	±0.127	0.084	±0.120
Days to flower					0.748**	±0.050	0.778**	±0.042
					0.765**	±0.051	0.787**	±0.040
Plant height							0.845**	±0.031
							0.815**	±0.037

[1] Upper figures are at the low and lower figures are at the high density.

Table 4. *Within-plot and plot components of error variance for grain weight (g/plant) from data combined over two years at each density*

Density	No. of plots sampled	No. of plants per plot w[a]	No. of plants sampled	Error[b] σ^2	Plot component σ^2_{pl}	Within plot component	
						Total[c] σ^2_W	Due to environment σ^2_{We}
Low	64	9.6	384	1359.90 ±84.82	179.60 ±125.88	11330.80 ±892.99	8459.79 ±1003.07
High	32	36.5	960	149.56 ± 9.32	69.58 ± 10.03	2919.05 ±135.36	2741.99 ± 139.62

[a] w = harmonic mean

[b] $\sigma^2 = \sigma^2_{pl} + \frac{\sigma^2_W}{w}$

[c] $\sigma^2_W = [0.47873\ (\sigma^2_A + \sigma^2_{AY}) + 0.72341\ (\sigma^2_D + \sigma^2_{DY})] + \sigma^2_{We}$

parameters due to linkage disequilibrium is believed to have been *extensively* reduced since the material had undergone six generations of random mating. Epistasis could be a source of upward bias, but experimental evidence accumulated so far indicates that in heterogeneous populations epistasis contributes only a minor portion of the total genetic variance for some characters including yield (Eberhart *et al.* 1966; Stuber *et al.* 1966; Stuber and Moll, 1969; Sentz, 1971).

The estimates of genetic parameters in this study have been calculated using formulae given by Jones and Compton (1973). One of several assumptions associated with their formulae is that the number of plants measured from a cross is much larger than the number of S_1 plants used to represent an S_0 parent in a particular cross. In the present study the perfect number of plants per plot was only 10 at the low density while the harmonic mean of the number of S_1 plants used to represent S_0 parents is 11.75. Thus, the experiment at the low density did not fulfill the assumption. Another assumption is that each S_1 plant is used only once in the cross. In the present study S_1 plants were used more than once in rare instances. Unfortunately, no records were kept on the number of times each S_1 plant was used in crosses so that no adjustment could be made. The bias of the estimates, however, is believed to be very small.

To determine the effect of the number of S_1 plants representing each S_0 parent in the crossing nursery, the estimates of the components of genetic variance and their interaction with years were calculated using formulae given by Cockerham (1956). For purposes of discussion, the estimates will be referred to as uncorrected estimates and those calculated with Jones and Compton's formulae as corrected estimates. The difference between the uncorrected and the corrected estimates of the components of genetic variance and their interaction with years expressed in percent of the corrected total genetic and genotypic × year interaction variances (Table 5) were in the order of 1%, 6 to 7%, 1 to 4%, and −3 to 7%, for the additive, the dominance, the additive × year, and the dominance × year interaction variances, respectively. Without correcting for the sample size the dominance genetic variance for all traits at both densities and the dominance × year interaction variance for grain weight and days to flower at the high density were highly overestimated. However, with corrected formulae, more mean squares are involved in the estimation of the dominance genetic variance and its interaction with years than is usually the case with DII. This may offset the superiority of DII over DI in the precision of estimating σ^2_D and σ^2_{DY} as already pointed out by Jones and Compton (1973).

Despite the large difference between the two density levels used in this study, significant differences between the two estimates were found only for the additive, dominance, and additive genetic × year interaction variances for grain weight and number of ears expressed on a per plant basis. However, since each plant occupies a space, and the final interest is yield per unit area, it would be meaningful to measure these two traits on a unit area basis when two density

Table 5. *Difference between uncorrected and corrected estimates of additive ($\Delta\hat{\sigma}^2_A$) and dominance genetic ($\Delta\hat{\sigma}^2_D$) variance and their interaction with years ($\Delta\hat{\sigma}^2_{AY}$ and $\Delta\hat{\sigma}^2_{DY}$) expressed in percent of the corrected total genetic ($\hat{\sigma}^2_A + \hat{\sigma}^2_D$) variance and their interaction with years ($\hat{\sigma}^2_{AY} + \hat{\sigma}^2_{DY}$)*

Traits	Density	In % of $(\hat{\sigma}^2_A + \hat{\sigma}^2_D)$		In % of $(\hat{\sigma}^2_{AY} + \hat{\sigma}^2_{DY})$	
		$\Delta\hat{\sigma}^2_A$	$\Delta\hat{\sigma}^2_D$	$\Delta\hat{\sigma}^2_{AY}$	$\Delta\hat{\sigma}^2_{DY}$
Grain weight	Low	1.0	7.2	1.5	5.4
	High	1.1	6.9	1.1	6.8
No. of ears	Low	1.1	6.7	1.9	4.1
	High	1.3	6.9	2.9	2.9
Days to flower	Low	1.2	6.4	3.6	2.0
	High	1.3	6.4	1.5	5.7
Plant height	Low	1.1	6.7	2.3	2.6
	High	1.1	6.7	3.8	−2.6
Ear height	Low	1.3	6.3	2.3	2.7
	High	1.2	6.3	1.5	5.4

Table 6. *Values of additive and dominance genetic variance estimates and their ratios for synthetic and composite populations*

Populations*	Reference	Design	Env.**	Density (plants/ha)	$\hat{\sigma}_A^2$***		$\hat{\sigma}_D^2$***	
					g/plant	q/ha	g/plant	q/ha
Corn Belt Composite	Goodman, 1965	I	1 (Iowa)	?	778		−171	
		I	1 (N.C.)	?	224		475	
West Indian Composite	Goodman, 1965	I	1 (Iowa)	?	1820		0	
		I	1 (N.C.)	?	528		290	
Minn. Synth. 3	Sentz, 1971	I	4	32,000 or 32,500	289	30.06	243	25.27
		II	3	32,500	174	18.38	132	13.94
Krug × Tabloncillo	Shauman, 1971	II	1	34,400	301	35.62	147	17.40
				51,700	233	62.28	77	20.58
Gaspé × Colombian	Present study	II	2	17,222	2932	86.96	1276	37.85
				68,888	171	81.16	56	26.58

* The populations have been random mated at least for 5 generations, and for D II by Sentz the population has been selfed for 5 generations.
In Shauman's and present study S_1 lines have been used to produce F.S. progenies.
** Environment includes years and locations.
? No plant population density was reported.
*** For estimates that were given in terms of σ_M^2 and σ_F^2 in D I, σ_A^2 and σ_D^2 have been calculated as 4 σ_M^2 and 4 $(\sigma_F^2 - \sigma_M^2)$, respectively.
Shelling percentage is assumed to be 80% for conversion of data reported for ear corn.

effects are to be compared. When the traits were measured on a unit area basis, the two estimates were not significantly different (Table 2). Thus, on a unit area basis, there was no significant difference in the magnitude of the genetic parameters measured at two densities for any of the traits studied.

Results of genetic variance studies are usually reported on a per plant basis. Several reports failed to mention plant-population densities, so no conversion to a unit area basis could be made. Whether genetic and genetic × environment interaction variance estimates are expressed on a plant or a unit area basis, there is no problem as long as only one plant-population density is concerned. Such differences in the units of measure are a matter of simple mathematical coding. However, when the magnitude of genetic variance estimates obtained from experiments with different plant-population densities are to be compared, the estimates need to be expressed on a unit area basis. This is based on the following considerations: 1. Each plant occupies a space and the ultimate interest in a trait such as yield is on a unit area rather than plant basis. 2. Results from this study indicate that differences in the magnitude of the estimates of σ_A^2, σ_D^2 and σ_{AY}^2 for grain weight and number of ears at the two densities depend on the unit of measure. 3. Plant-population densities used in various reported studies on the estimates of genetic variance range widely, possibly from about 20,000 (Lindsey *et al.* 1962) to 50,000 plants per hectare (Shauman, 1971).

To illustrate that the units of measure used in estimating genetic variances from experiments with different plant-population densities influence the interpretation of the data, results from some studies with synthetics and composite populations are presented for comparative purposes in Table 6. Such comparisons will not provide very precise information because of differences in materials, sample sizes, designs and environments from one study to another but are useful to provide a general picture of the results obtained with similar materials. In fact, similar comparisons have appeared but only with the unit of measure on a plant-to-plant basis. Note that some differences become much smaller while others are much larger as the unit of measure is changed. It is, therefore, suggested that for purposes of comparing the magnitude of genetic variance estimates obtained from different studies involving different plant-population densities, the values should be expressed on a unit area basis to reduce error in making general inferences. Reports on the estimates of genetic parameters should be accompanied by information on the plant-population density used to allow conversion of the unit of measure. Data in Table 6 indicate that the amount of σ_A^2 expressed on a unit area basis, decreases in the populations in the order of Gaspé × Colombian, Krug × Taboncillo and Minn. Synth. 3, which is reasonable since the populations could be classified as exotic, exotic × adapted variety, and adapted narrow base synthetic respectively.

Since the planting rate was not reported in Goodman's (1965) study, comparison is not possible between the estimates obtained from Gaspé × Colombian and the West Indian Composite, both of which possess wide genetic diversity.

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