wobei $k = 1, 2, \ldots, p$ ist, möglich sind. Eine bestimmte Interaktionskomponente eines p^2 faktoriellen Versuchs, $(A\ B^{p-1})_g$, wobei $g = 0, 1, \ldots, p-1$ ist, wurde benutzt, um diese partiellen Wiederholungen aufzubauen, weil die Selbstungen die Elemente von $(A\ B^{p-1})_0$ sind. Eine Liste unvollständig dialleler Kreuzungsversuche (PDC) wird für verschiedene Werte von x und p gegeben. Zugleich wird ein Algorithmus für den Aufbau von PDC-Anlagen des obigen Typs mitgeteilt.

Diallele Kreuzungspläne und verwandte genetische Verfahren finden auch auf vielen Gebieten außerhalb der Genetik direkte und indirekte Anwendung. Es wird eine Anzahl spezifischer Beispiele diskutiert, um die Mannigfaltigkeit der Anwendung von CDC- und PDC-Verfahren darzulegen. Die besprochenen Beispiele umfassen die Konkurrenz zwischen Weizensorten, Berufsklassifizierungen, Mitteilungen zwischen Einzelpersonen, Drogenanwendung, Lehrmethoden, Hahnenkämpfe und Turniere.

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Genetic Variances in the Open-Pollinated Variety of Maize, Iowa Ideal[*][1]

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Summary. Iowa Ideal is a white, open-pollinated variety of corn that has been under mass selection (or individual plant selection) for the improvement of grain yield. In order to make a comparison between the observed and predicted response to selection for increased grain yield, a mating design was imposed on the original Iowa Ideal variety. Ninety-six half-sib families containing 384 full-sib families were developed and evaluated in three environments. Estimates of additive and total genetic variances were obtained for grain yield and eight other traits.

For all traits, the estimates indicated that the greatest proportion of the total genetic variance was due to additive effects; this was under the assumption of no epistasis. The estimates for yield indicated that approximate 80% of the total genetic variance was additive. This would indicate that some form of intra-population selection should be effective, initially, for increasing the frequency of favorable factors determining yield. Additive genetic, genotypic, and phenotypic correlations showed that ear length was the most important component of yield in the Iowa Ideal variety.

The initial evaluation of the original and three reconstituted populations, formed by compositing equal quantities of seed from individually selected ears, was made in 1965. The observed progress for increased grain yield was less than the predicted on the basis of the variance component estimates. For a selection intensity of 7.5% in each cycle of selection, observed progress for increased grain yield was 1.5% per cycle or year. Either the estimates of additive genetic variance were over-estimated, or the individual plant selection techniques were not precise enough to properly identify the higher-yielding genotypes in the selection program.

Introduction

The determination of genetic variability of a quantitative trait is based upon the division of the phenotypic value into genetic and environmental effects. If the observed phenotype (P) of a quantitatively inherited character is determined additively by genetic (G) and environmental (E) effects (*i.e.*, $P = G + E$), it is important to the plant breeder to know how much of the variation in the phenotypic values can be attributed to genetic and environmental forces. A knowledge of the relative contributions of the various types of genetic effects present for quantitative traits in the populations undergoing selection is also basic to all plant-breeding programs. Estimates of heritability, prediction of response to selection, and the designing of the most effective breeding sche-

mes are dependent upon the relative proportions of additive and non-additive genetic effects and environmental deviations. If the estimates of genetic variance indicate that the additive genetic variance is of major importance, heritability would be expected to be relatively high, and single plant selection (mass selection) or selection among progenies should initially be effective in improving the trait under consideration. If a major portion of the genetic variation is non-additive, an inbreeding and hybridization program may be the most effective alternative breeding scheme. In either case, the most effective breeding scheme is determined by the type of gene action present in the population under consideration; the lack of this basic information results in a breeding program that is largely empirical.

COMSTOCK and ROBINSON (1948) presented the theory and methods for study of genetic variation for quantitative characters in maize (*Zea mays* L.). Since then, studies in maize have been reported that estimated the relative portions of additive and non-additive genetic variance in F_2 and advanced generation populations from two inbred lines, open-pollinated varieties, and synthetic varieties. With the exception of the studies reported by WILLIAMS et al. (1965), CHI (1965), EL-ROUBY (1965) and COMPTON et al. (1965), these have been summarized by GARDNER (1963) and GOODMAN (1965). Generally, the mating designs used provided estimates of covariance half-sibs and full-sibs developed from non-inbred parents. Thus, only additive and dominance variances were estimable.

Additive genetic variance has been shown to exist in moderate amounts in most maize populations; although, it was acknowledged that dominance probably exists at some or a majority of the loci involved. The initial estimates were obtained in F_2 populations developed from two inbred lines (ROBINSON et al., 1949). Estimates of average degree of dominance were obtained that indicated over-dominance was operative at some loci for some traits. They emphasized, however, that linkage may have biased the estimates of additive and dominance variances. Studies on advanced generations developed by random mating the F_2 and subsequent generations (GARDNER and LONNQUIST, 1959; ROBINSON et al., 1960) have indicated that linkage was a factor in the estimates obtained in the F_2 generation of a cross of two inbred lines.

Very few data have been reported on the relative importance of epistatic variance in maize, although procedures have been presented by COCKERHAM (1956, 1961) for the estimation of epistatic variance. A study by EBERHART et al. (1966) indicated that the epistatic variance is relatively small compared with the total genetic variance in maize populations. However, qualitative evidence for the presence of epistatic effects in specific combinations of inbred lines of maize have been reported (BAUMAN, 1959; GORSLINE 1961; GAMBLE, 1962; SPRAGUE et al., 1962; EBERHART et al., 1964).

Materials and Methods

Iowa Ideal is an open-pollinated variety that has been under mass selection for the improvement of yield at Ames, Iowa. The variety is characterized by having a tall, vigorous plant type, tillers, and white seeds on long, cylindrical ears. Information was desired about the nature of the gene action involved in yield, primarily, and for eight other traits in the Iowa Ideal variety.

The Design I experiment, described in detail by COMSTOCK and ROBINSON (1948), was the mating design used to develop the experimental material. To minimize the possible effects of assortative mating, the mating procedures suggested by LINDSEY et al. (1962) were used. One hundred random plants (males) were each mated to six random plants designated as females. At harvest, ears were obtained from the first four plants for each particular male that had sufficient viable seed for testing. Ninety-six male groups (half-sib families) were obtained, and resulted in 384 full-sib families. The material was developed in 1964 by using seed from a bulk sample of the original Iowa Ideal stock used to initiate the mass selection experiment.

The seed produced in 1964 was grown at three locations (Kanawha, Ames, and Ankeny) in 1965. A randomized incomplete block design was used. Twelve male groups were randomly assigned to each set; thus, each set contained 48 full-sib families. The full-sib families were randomly assigned to each plot and replicated twice within the set to produce 96 plots for each set. Eight such sets constituted an experiment at each location. Precision of comparison among progeny means was reduced by this grouping, but the primary interest of the experiment was to obtain estimates of genetic variance for the Iowa Ideal population rather than progeny mean performance.

Each plot contained 17 hills spaced 25.4 cm apart within a single row. The distance between rows (or plots) was approximately 1 meter. Each plot was over-planted and later thinned (without selection) to one plant per hill. Final stands were excellent in each experiment.

Data were obtained for 10 competitive plants within each plot, whenever possible. The characters measured were number of tillers, plant and ear height (cm), ear length and diameter (cm), kernel row number, weight of 300 kernels (gms), and total yield (expressed as gms per plant). Average silking date was obtained for the Ames location only. Number of tillers were determined by actual count for 10 bordered plants within each plot. Plant and ear height measurements were made after anthesis at each location.

The ear measurements and yield were determined from ears harvested from 10 competitive plants and artificially dried to uniform moisture. Ear length and diameter measurements and kernel row number counts were made on the top ears before shelling. The ears (including second ears, if present) for each plot were shelled in bulk and weighed to the nearest gram. Average yield per plant for each plot was calculated by dividing the weight of shelled grain by the number of bordered plants in each plot (a maximum of 10). A random sample was obtained from the bulk shelling of each plot to make the 300-kernel measurements. The 300-kernel samples were counted by an electronic seed counter and weighed to the nearest decigram.

The analyses of variance for each trait were computed on plot means. Each set was analyzed and then pooled for all sets at each location for each trait. The form of the analysis of variance for each set was presented by Comstock and Robinson (1948), and an example was given by Robinson et al. (1949) that involved pooling for all sets in one environment. The analysis of variance for one experiment is shown in Table 1. A combined analysis of the three experiments provided estimates of the effects due to males and females by location. The general form for the combined analysis of variance over experiments was given by Lindsey et al. (1962).

Because of the mating design used, the components of variance, σ_m^2 and $\sigma_{f/m}^2$, have genetic interpretations. The component of variance, σ_m^2, arises from the genetic differences among the male parents and is the covariance of half-sibs. The component of variance, $\sigma_{f/m}^2$, is due to the genetic differences among female parents mated to the same male parent and is the covariance of full-sibs minus the covariance of half-sibs. The assumptions made in deriving the mean squares were (1) parental plants used in making the crosses are non-inbred members of the variety, (2) regular diploid behavior, (3) no maternal effects, (4) equilibrium of repulsion and coupling phase linkages, (5) no selection of parental plants, and (6) no epistasis. If the assumptions are fulfilled, the genetic interpretations are as follows:

σ_m^2 = covariance half-sibs = $(1/4)\ \sigma_A^2$; and
$\sigma_{f/m}^2$ = covariance full sibs minus covariance half-sibs = $(1/4)\ \sigma_A^2 + (1/4)\ \sigma_D^2$.

Then, $4\ \sigma_m^2$ is the additive genetic variance (σ_A^2), and $4\ \sigma_{f/m}^2$ is the total genetic variance $(\sigma_G^2 = \sigma_A^2 + \sigma_D^2)$ under the assumption of no epistasis. If an estimate of dominance variance (σ_D^2) is desired, this may be computed as $4\ \sigma_{f/m}^2 - 4\ \sigma_m^2$. Since the components of variance were estimated as linear combinations of independent mean squares, the variance of the components of variance $[V(\hat\sigma_i^2)]$ was computed as follows:

$$V(\hat\sigma_i^2) = (1/C^2)\ \sum_i V(MS_i) =$$
$$= (2/C^2)\ \sum_i [(MS_i)^2/(d.f._i + 2)] ,$$

where MS_i are the appropriate mean squares in the analysis of variance.

Additive genetic, total genetic, and phenotypic correlations were obtained for all pairs of traits except silking date. It has been shown that the expectations of the mean cross-products have the same form as the expected mean squares (Mode and Robinson, 1959). Assuming absence of epistasis, the correlations among pairs of traits in one environment were computed as follows:

additive genetic correlation $= \hat r_A = s_{m\,m'}\ /\sqrt{s_m^2 \cdot s_{m'}^2}$;

total genetic correlation $= \hat r_G = s_{f/m\,f'/m'}/\sqrt{s_{f/m}^2 \cdot s_{f'/m'}^2}$;

and phenotypic correlation =

$$\hat r_P = s_{i\,i'} + 4\ s_{f/m\,f'/m'}/\sqrt{(s_i^2 + 4\ s_{f/m}^2)\ (s_{i'}^2 + 4\ s_{f'/m'}^2)} ,$$

where $s_{m\,m'}$, $s_{f/m\,f'/m'}$, and $s_{i\,i'}$ are the estimated covariance components for males, females in males, and plot effects, respectively, for a pair of traits. The phenotypic correlations computed from the combined analysis for the three environments also included an estimate of the genotype by environment effect, $4\ s_{f/m\times1}^2$, $4\ s_{f'/m'\times1}^2$, and $4\ s_{f/m\times f'/m'\times1}$.

Results

The mean performances for each trait are shown in Table 2. Environmental conditions varied for the three locations, as evidenced by the differences in the means for each of the traits. Yield at the Ames location was depressed because of a stress period during July and August. Very poor seed set was obtained on many plants, and barrenness was common in some plots. All measurements except number of tillers and weight of 300 kernels were less than for the Kanawha

Table 1. *Form of the analysis of variance for full-sib and half-sib progenies pooled over sets tested in one environment.*

Source of variation	Degrees of freedom General Experiment[*]		Mean square	Expected mean square[**]
Sets	$s - 1$	7		
Replications in sets	$s\ (r - 1)$	8		
Males in sets	$s\ (m - 1)$	88	M_1	$\sigma^2 + 2\sigma_{f/m}^2 + 8\sigma_m^2$
Females in males in sets	$sm\ (f - 1)$	288	M_2	$\sigma^2 + 2\sigma_{f/m}^2$
Pooled error	$s\ (r - 1)\ (mf - 1)$	376	M_3	σ^2
Total	$srmf - 1$	767		

[*] s, r, m, and f refer to sets, replications, males, and females, respectively.
[**] σ_m^2 = variance due to genetic differences among males = covariance half-sibs.
$\sigma_{f/m}^2$ = variance due to genetic differences among females mated to the same male = covariance full-sibs - covariance half-sibs.
$\sigma^2 = (\sigma_{E\,W}^2 + \sigma_{G\,W}^2)/10 + \sigma_p^2$ where $\sigma_{E\,W}^2$ and $\sigma_{G\,W}^2$ are the environmental and genetic variance among plants in the same plots; σ_p^2 is the variance among plots.

Table 2. *Mean performance ($\bar x$) and standard errors (σ) for 9 traits obtained from 384 full-sib progenies grown in 3 experiments (Kanawha, Ames, and Ankeny) in Iowa, 1965.*

Experiment		Date silk	Number of tillers	Height (cm)		Ear (cm)		Kernel row no.	Wt. 300 kernels (gms)	Avg. yield per plant (gms)
				Plant	Ear	Length	Diameter			
Kanawha	$\bar x$	—	1.5	255.1	134.1	18.3	4.7	17.1	71.2	147.4
	σ	—	0.40	7.04	8.14	1.27	0.26	0.82	7.04	23.31
Ames	$\bar x$	30.4	0.9	240.2	123.8	17.0	4.5	16.8	74.5	120.6
	σ	1.89	0.36	9.38	8.07	1.70	0.28	0.84	6.79	31.49
Ankeny	$\bar x$	—	0.6	258.6	139.3	17.9	4.7	17.1	80.3	149.1
	σ	—	0.33	8.30	7.42	1.55	0.26	0.81	7.78	29.46
Combined	$\bar x$	—	1.0	251.3	132.4	17.7	4.6	17.0	75.3	139.0
	σ	—	0.36	8.30	7.88	1.51	0.27	0.82	7.21	28.29

Table 3. *Estimates of additive genetic variance* (σ^2_A), *total genetic variance* (σ^2_G), *their interactions with locations* $(\sigma^2_{A\times L}$ *and* $\sigma^2_{G\times L})$, *the ratio of additive and total genetic variance* (σ^2_A/σ^2_G) *for 9 traits of the Iowa Ideal variety obtained in 3 experiments in 1965.*

Trait	Experiment	σ^2_A	σ^2_G	σ^2_A/σ^2_G	$2\sigma^2_{A\times L}$	$\sigma^2_{G\times L}$
Tillers	Kanawha	0.44 ± 0.09	0.36 ± 0.06	1.22		
	Ames	0.32 ± 0.07	0.31 ± 0.06	1.04		
	Ankeny	0.26 ± 0.06	0.26 ± 0.04	1.00		
	Combined	0.32 ± 0.06	0.30 ± 0.03	1.07	0.0184 ± 0.0085	0.0152 ± 0.0201
Plant height	Kanawha	244 ± 48	210 ± 27	1.16		
	Ames	219 ± 45	146 ± 30	1.50		
	Ankeny	224 ± 47	207 ± 30	1.08		
	Combined	224 ± 43	190 ± 21	1.18	5.28 ± 4.60	-2.38 ± 9.84
Ear height	Kanawha	284 ± 55	209 ± 30	1.36		
	Ames	268 ± 52	192 ± 28	1.40		
	Ankeny	250 ± 50	227 ± 29	1.10		
	Combined	261 ± 48	195 ± 20	1.34	7.22 ± 4.88	14.12 ± 9.67
Ear length	Kanawha	2.14 ± 0.56	2.91 ± 0.56	0.74		
	Ames	3.81 ± 0.88	2.19 ± 0.78	1.74		
	Ankeny	3.31 ± 0.80	2.98 ± 0.73	1.11		
	Combined	2.55 ± 0.56	2.23 ± 0.34	1.14	0.53 ± 0.20	0.47 ± 0.35
Ear diameter	Kanawha	0.02 ± 0.05	0.04 ± 0.02	0.50		
	Ames	0.04 ± 0.02	0.06 ± 0.02	0.67		
	Ankeny	0.04 ± 0.01	0.06 ± 0.02	0.67		
	Combined	0.03 ± 0.01	0.04 ± 0.01	0.75	0.0068 ± 0.0054	0.0168 ± 0.0110
Kernel row number	Kanawha	2.98 ± 0.59	2.54 ± 0.34	1.17		
	Ames	2.62 ± 0.57	3.29 ± 0.40	0.80		
	Ankeny	2.85 ± 0.57	2.55 ± 0.34	1.12		
	Combined	2.72 ± 0.54	2.83 ± 0.27	0.96	0.0896 ± 0.0490	0.0336 ± 0.0980
Weight 300 kernels	Kanawha	28.4 ± 11.6	81.7 ± 16.6	0.35		
	Ames	60.7 ± 15.9	80.2 ± 15.8	0.76		
	Ankeny	75.2 ± 19.8	95.7 ± 20.0	0.79		
	Combined	41.7 ± 11.5	78.7 ± 9.9	0.53	13.05 ± 4.63	7.27 ± 7.88
Yield per plant	Kanawha	361 ± 122	599 ± 160	0.60		
	Ames	995 ± 258	782 ± 271	1.27		
	Ankeny	1057 ± 269	1207 ± 275	0.88		
	Combined	576 ± 149	670 ± 111	0.86	229 ± 76	193 ± 125
Date silk	Ames	11.4 ± 2.4	9.6 ± 1.5	1.19		

and Ankeny experiments. Because of the scattered seed set, kernel weight was not lower at Ames than at the other two locations. Except for number of tillers and kernel weight, the mean performances were similar for the Kanawha and Ankeny experiments.

The standard errors for each of the traits were similar for all locations, except yield. As expected, the standard error for yield was highest at the Ames location; Ankeny also had a large standard error, probably due to the effects of severe lodging before harvest. No trend is apparent for the relative magnitude of the standard errors for the other traits.

The estimates of additive genetic variance (σ^2_A), total genetic variance (σ^2_G), their interactions by locations $(\sigma^2_{A\times L}$ and $\sigma^2_{G\times L})$, and the ratio of additive to total genetic variance (σ^2_A/σ^2_G) are shown in Table 3. Except for ear diameter at Kanawha and Ames, the estimates of σ^2_A were larger than twice their standard errors; the estimate at Ames was equal to twice its standard error. The estimates of σ^2_G were larger than twice their standard errors for all traits at all locations except for ear diameter at Kanawha, which was equal to twice its standard error. For all traits the estimates indicate that the greatest proportion of the total genetic variance is due to additive effects; this is under the assumption of no epistasis. The ratio, σ^2_A/σ^2_G, indicates that the estimate of σ^2_A was larger than the estimate of σ^2_G in 18 of the 33 estimates. The estimate of σ^2_A was consistently larger than σ^2_G for tillers, plant and ear height, and ear length. In 2 of the 4 estimates, the estimate of σ^2_A was larger than

σ^2_G for kernel row number. Only one estimate was available for silking date, and σ^2_A was 19% larger than σ^2_G. If an estimate of dominance variance (σ^2_D) had been calculated, negative estimates would have been obtained for the ratios that are larger than unity.

Estimates of the genotype × environment $(\sigma^2_{G\times L})$ interactions indicated the genotypic effects were consistent for the three locations; there were no estimates that were larger than twice their standard errors. Four estimates of σ^2_A (tillers, ear length, kernel weight and yield) varied significantly among the three locations. Except for number of tillers, the traits were associated with yield.

Additive genetic, genotypic, and phenotypic correlations will be presented only from the combined variance and covariance analyses (Table 4). There was no indication that tillers were correlated with any of the other traits measured in these experiments. Plant height was highly correlated, as expected, with ear height. Except for the additive genetic correlations, plant height tended to have a positive correlation with ear length and yield. The largest and most consistent correlations for ear height were obtained with yield; however, these were also relatively low. Ear length tended to have a negative association with ear diameter, kernel row number, and kernel weight but a relatively large, positive association with yield. The data from this study indicate that ear length is the most important component of yield. Ear diameter had a positive association with kernel row num-

Table 4. *Additive genetic, genotypic, and phenotypic correlations among 8 traits of the variety, Iowa Ideal, obtained from the combined analysis of 3 experiments grown in Iowa, 1965.*

	Tillers	Plant height	Ear height	Ear length	Ear diameter	Kernel row no.	Wt. 300 kernels	Avg. yield per plant
Tillers	—	.1370[1]	.1550	—.0569	.0610	—.1777	—.1071	—.1058
	—	—.0693[2]	.0758	.0906	—.1237	—.0258	—.1324	.2308
	—	—.0574[3]	.0279	.1250	—.0203	—.0023	—.0754	.1561
Plant height		—	.7890	.0851	—.0267	—.0628	.1083	.0465
		—	.6870	.3890	—.0031	—.1834	—.0082	.2318
		—	.6614	.3032	.0916	—.1266	.0174	.2512
Ear height			—	.1000	—·1758	—.0372	—.1663	.1996
			—	.1665	.4043	—.0433	—.0385	.2166
			—	.1836	.2575	—.0536	—.0334	.1845
Ear length				—	—.3902	—.4613	—.1248	.6898
				—	—.3843	—.3104	—.1582	.5425
				—	.2056	—.1768	.0241	.6024
Ear diameter					—	.6004	—.0086	.2676
					—	.3519	.2005	.2751
					—	.2746	.1693	.4203
Kernel row no.						—	—.5318	—.1399
						—	—.5834	—.1135
						—	—.4439	—.0361
Wt. 300 kernels							—	—.1445
							—	—.0161
							—	.1449

1, 2, and 3 refer to the additive genetic, genotypic, and phenotypic correlations, respectively, for each pair of traits.

ber and yield; however, the correlations of yield and ear diameter were not as large as those for ear length with yield. This is not in agreement with studies in the Reid Yellow Dent variety (WILLIAMS et al., 1965; CHI, 1965); their studies indicated that the genotypic correlation between yield and ear diameter was larger than between yield and ear length. Kernel row number had a relatively large, negative association with kernel weight. This relationship may be expected because, as the number of kernel rows increased, there would be a tendency to have smaller kernels. This is in agreement with the studies in Reid Yellow Dent variety (WILLIAMS et al., 1965; CHI, 1965). Kernel row number and kernel weight had small, negative associations with yield.

Discussion

The assumptions used in the derivation and interpretation of the genetic variances derived for the mating design used in the present study have been discussed by several authors (COMSTOCK and ROBINSON, 1948; LINDSEY et al., 1962; GOODMAN, 1965; WILLIAMS et al., 1965). Because more than half of the estimates of σ_A^2 were larger than σ_G (Table 3), either the assumptions necessary to the analyses were not satisfied, or the bias due to the inclusion of genotype $\times$ environment interaction caused some of the inconsistencies.

Since the experimental material was evaluated in three environments, estimates of the additive genetic ($\sigma_{A\times L}^2$) and total genetic ($\sigma_{G\times L}^2$) interactions were available from the combined analyses. The estimate of σ_A^2 was larger than σ_G^2 for tillers, plant and ear height, and ear length. In all cases, the estimates of σ_A^2 and σ_G^2 were considerably larger than their respective interaction components, although $\sigma_{A\times L}^2$ was larger than twice its standard error for tillers and ear length. Although the dominance effects are included in the estimate of σ_G^2, the interactions of the domi-

nance effects by environment were not proportionately different than those for the additive effects; the estimates of $\sigma_{A\times L}^2$ and $\sigma_{G\times L}^2$ are similar for the four traits. The estimates of σ_A^2 were smaller than σ_G^2 in the combined analysis for ear diameter, kernel row number, kernel weight, and yield. The estimate of $\sigma_{G\times L}^2$ was larger than $\sigma_{A\times L}^2$ for only ear diameter. The effects of the environment do not appear to have caused an overestimation of σ_A^2 and/or an underestimation of σ_G^2.

In considering the assumptions used in deriving the mean squares, only the assumption of no epistasis may not be valid. Iowa Ideal is an old, open-pollinated variety that was developed in the early 1900's. Except for the possible effects of drift during the growing and maintenance of the variety, the parental plants would have been non-inbred. The exact history of the variety is unknown, but the variety should be in equilibrium for repulsion and coupling phase linkages because it has been grown in farmers' fields and maintained in the nursery for several generations. The assumptions of no maternal effects and regular diploid behavior should not present any difficulties in maize. To minimize the possible effects of assortative matings, the male plants were delayed approximately one week and mated to consecutive female plants. Precautions were taken to prevent the selection of male and female plants in the production of the full-sib progenies on the basis of silking date.

Is has been shown that epistasis is included in the male (σ_m^2) and female within male ($\sigma_{f/m}^2$) components. For a random mating population with no linkage, the expectations of the covariance half-sibs and covariance full-sibs for digenic epistasis are

covariance half-sibs = $(1/4)\,\sigma_A^2 + (1/16)\,\sigma_{AA}^2$, and
covariance full-sibs = $(1/2)\,\sigma_A^2 + (1/4)\,\sigma_D^2 + (1/4)\,\sigma_{AA}^2 +$
$+ (1/8)\,\sigma_{AD}^2 + (1/16)\,\sigma_{DD}^2$.

Only the additive types are included in the covariance half-sibs and both additive and dominance types in

the covariance full-sibs. The estimate of σ_A^2 was obtained as $4\,\sigma_m^2$, which would be $\sigma_A^2 + (1/4)\,\sigma_{AA}^2$. The estimate of σ_G^2 was calculated as $4\,\sigma_{f/m}^2$, which would be $4\,\{[(1/2)\,\sigma_A^2 + (1/4)\,\sigma_D^2 + (1/4)\,\sigma_{AA}^2 + (1/8)\,\sigma_{AD}^2 + (1/16)\,\sigma_{DD}^2] - [(1/4)\,\sigma_A^2 + (1/16)\,\sigma_{AA}^2]\}$, and this would become $\sigma_A^2 + \sigma_D^2 + (3/4)\,\sigma_{AA}^2 + (1/2)\,\sigma_{AD}^2 + (1/4)\,\sigma_{DD}^2$. Therefore, both estimates are biased by epistasis; the bias in σ_A^2 is a function of additive types, and the bias in σ_G^2 is a function of all components of epistasis. It does not appear that the epistatic effects are causing the inconsistencies in the estimates of σ_A^2 and σ_G^2 shown in Table 3. If epistasis were a serious bias in the estimates, it would have a greater effect on the estimates of σ_G^2 rather than on the estimates of σ_A^2. The dominance-type epistatic effects are not present in the estimates of σ_A^2. Also, the effects of additive-type epistasis would be greater in the estimates of σ_G^2.

LINDSEY *et al.* (1962) hypothesized that assortative mating for date of flowering could bias the estimates of genetic variances. The hypothesized effect would lead to an overestimation of σ_m^2 and an underestimation of $\sigma_{f/m}^2$. Since the genetic components of variance are obtained as $\sigma_A^2 = 4\,\sigma_m^2$, $\sigma_G^2 = 4\,\sigma_{f/m}^2$, and $\sigma_D^2 = 4\,(\sigma_{f/m}^2 - \sigma_m^2)$, this would bias the respective components of genetic variance for date of flowering. To the extent other traits are correlated with date of flowering, variance estimates for other traits would be similarly affected. LINDSEY *et al.* (1962) found that the forced mating procedures consistently reduced the relative magnitude of the estimates of σ_A^2 and increased the estimates of σ_D^2. GOODMAN (1965) and EL-ROUBY (1965) used the mating procedures suggested by LINDSEY *et al.* (1962) and obtained estimates of σ_A^2 that were larger than σ_G^2 in 41% of the estimates; although the estimates of σ_D^2 were generally within the limits of two standard errors.

Eighteen estimates of σ_A^2 were larger than σ_G^2 in the study reported herein. Although procedures were used to minimize the effects of assortative mating due to flowering date, the estimate of σ_A^2 was 19% larger than the estimate of σ_G^2. The degree of association between date silk and tillers, plant and ear height, and ear length are not known for Iowa Ideal, but the estimates of σ_A^2 are consistently larger than those for σ_G^2 (Table 3). Either the variation among males was greater because of assortative mating, or the errors in the estimation of the male component, σ_m^2, were large.

The variation among males due to genetic differences, σ_m^2, was determined by crossing each male to four different plants designated as females. This is similar to a topcross test in a maize breeding program except that the tester is the same for each male. In testcross seed production, various sample sizes have been proposed and used. Because of sampling variation, larger samples are desirable to reduce the sampling variation, but are difficult to use. Perhaps the estimates of σ_m^2, and consequently σ_A^2, were overestimated in the Iowa Ideal variety because of insufficient sampling. SPRAGUE (1939) concluded from a study of the Reid Yellow Dent variety, that for most experiments, a 10-plant sample should be adequate; GENTER and ALEXANDER (1965) concluded that there was a need for more uniform sampling when testcrossing to a heterogeneous tester; and NOBLE and RUSSELL (personal communication) con-

cluded that 5 to 7 plants were sufficient to reduce sampling variation to a satisfactory level.

Yield data for the Ankeny experiment were used to determine the relative information obtained when plants (designated as males) are crossed to a varying number of tester plants (designated as females). From the analysis of variance, the components of variance for error (σ^2), females within males $(\sigma_{f/m}^2)$, and males (σ_m^2) were calculated. These values were then used to reconstruct the analysis of variance for varying number of females (Table 5). To use this procedure, it is important to make the assumption that the values of σ^2, $\sigma_{f/m}^2$, and σ_m^2 remain unchanged, even though we change the number of females and/or replications. A constant number of males was assumed for the calculations shown in Table 5. Calculations had shown that the amount of information obtained by varying males and females and holding number of plots constant was considerably less than assuming a constant number of males.

Table 5. *Relative information of the male component of variance, σ_m^2, when a constant number of males are mated to a varying number of females. The comparisons are made relative to males mated to 4 females and compared in 2 replications.*

Number					Relative information %
Replications	Sets	Males	Females/ males	Total plots	
2	10	100	2	400	−147
2	10	100	4	800	0
2	10	100	6	1200	+28
2	10	100	8	1600	+39
2	10	100	10	2000	+46
4	10	100	2	800	−58
4	10	100	4	1600	+24
4	10	100	6	2400	+41
4	10	100	8	3200	+48
4	10	100	10	4000	+52

Information was calculated as the inverse of the variance of the male component, $1/V\sigma_m^2$. Relative information was obtained by comparing the information obtained by using four females per male (as was done in the present study) with the information obtained by using more (or less) than four females per male. It is obvious that each male should be mated to more than two females; four females per male provided 147% more information. Increasing the number of females above four provides more information, but the differences are not as great as increasing from 2 to 4. If each male is mated to six females and grown in two replications, 28% more information is obtained.

An increase in the number of replications does not appear as effective as increasing the number of females per male. If the males mated to four females are evaluated in four replications, 24% more information will be obtained relative to using two replications. However, 4% (24 compared with 28) more information can be obtained by mating each male to six females and growing in two replications; there would also be 400 less plots using this approach.

Increasing the number of tester or female plants for each male might have aided in reducing σ_A^2 in this study. This is based on the premise that the number of female plants was not sufficient to identify accurately the male plant's genotype. If the errors in

Table 6. *Performance of the original and three reconstituted populations developed by mass selection in Iowa Ideal for seven agronomic traits.*

Populations	Yield (gms per plant)		Stand	Grain moisture	Lodging		Dropped ears	Date silk
	Observed	Predicted*			Root	Stalk		
Iowa Ideal C_0	109.1	—	97.1%	24.3%	15.6%	23.7%	3.9%	33.7**
C_1	112.0	115.1	96.6	23.8	16.8	21.6	4.7	34.4
C_2	114.5	117.9	99.3	24.4	17.4	22.8	6.0	34.0
C_3	114.0	120.5	98.5	26.0	23.6	23.1	6.2	34.0

* $\Delta_g = 2 s_m^2(1.89)/\sqrt{s_m^2 + s_{f/m}^2 + 10 s^2}$ (GOODMAN, 1965).

** Number of days 50% silk from July 1.

discriminating the genetic differences among males were large, it would have inflated the male component of variance.

The estimates for grain yield per plant (Table 3) indicated that the greatest proportion of the total genetic variance was due to additive effects. This would indicate that some form of intra-population selection should be effective for increasing the frequency of factors determining yield. Three cycles of individual plant selection (mass selection) have been completed in the Iowa Ideal variety. Approximately 0.4 hectare of the variety had been grown in isolation each year. A grid system (GARDNER, 1961) was imposed upon the experimental area to reduce the confounding effects of environment on selection for yield. Each plot contained 40 competitive plants, and an equal volume of seed from the three highest yielding ears was saved and bulked to form the succeeding population. Selection intensity was 7.5% in each cycle. Approximately 100 plots were harvested each year.

The initial evaluations of the effectiveness of mass selection for yield were made in 1965. The original and three reconstituted populations were grown in 16 replications of 40 plant plots at Ames. Measurements were made for yield (adjusted to 15.5% grain moisture), grain moisture, stand, root and stalk lodging, dropped ears, and date silk (Table 6). Progress for increased yield, on the basis of this one test, has been disappointing. In each cycle, the observed yield is less than the predicted on the basis of the variance component estimates. Either the estimates of additive genetic variance have been overestimated, or the plot techniques have not been precise enough to eliminate the effects of the environment. On a percentage basis, 4.5% gain has been realized after three cycles of selection. The results are in close agreement with those reported by LONNQUIST et al. (1966). They obtained 12.7% improvement for yield after six cycles in Hays Golden variety. If the realized gains are expressed on a per-cycle basis, the rate of improvement was 1.5% in Iowa Ideal as compared to 2.1% in Hays Golden (LONNQUIST et al., 1966).

Yield was the only trait under selection in Iowa Ideal. Grain moisture showed an increasing trend. This may be expected, because high yield is generally associated with plants that are later maturing and which make maximum utilization of the growing season. There was also an increasing trend observed for root lodging and ear droppage; no significance can be attached to the trends for these two traits at the present time.

Zusammenfassung

Iowa Ideal ist eine weißkörnige, frei-abblühende Mais-Sorte, die zur Erhöhung des Kornertrages der Massen- (oder Einzelpflanzen-) Selektion unterworfen war. Um Vergleiche zwischen dem tatsächlichen und erwarteten Erfolg der Selektion auf höheren Kornertrag anstellen zu können, wurde mit der Originalsorte Iowa Ideal ein Paarungsprogramm durchgeführt. 96 Halbgeschwister-Familien mit 384 Vollgeschwister-Familien wurden hergestellt und an 3 Orten untersucht. Für Kornertrag und weitere 8 Merkmale wurden Schätzungen der additiven und totalen genetischen Varianzen erhalten.

Unter der Annahme des Fehlens von Epistasie ergab sich für alle Merkmale, daß additive Wirkungen den größten Anteil an der genetischen Gesamtvarianz hatten. Die Schätzungen für den Ertrag zeigten, daß etwa 80% der genetischen Gesamtvarianz additiv waren. Das würde bedeuten, daß jede Art von Selektion innerhalb der Populationen anfänglich wirksam sein müßte, um die Frequenz günstiger ertragsbestimmender Faktoren zu erhöhen. An Hand additiv genetischer, genotypischer und phänotypischer Korrelationen wurde gezeigt, daß die Kolbenlänge bei der Sorte Iowa Ideal die wichtigste Ertragskomponente ist.

Die erste Untersuchung der Ausgangspopulation und dreier rekonstituierter Populationen, die aus gleichen Samenmengen selektierter Einzelkolben gebildet wurden, erfolgte 1965. Die tatsächliche Erhöhung des Kornertrages war geringer als anhand der Schätzungen der Varianzkomponenten erwartet wurde. Bei einer Selektionsintensität von 7,5% in jedem Selektionszyklus betrug die tatsächliche Ertragssteigerung 1,4% je Zyklus oder Jahr. Das bedeutet, daß entweder die additive genetische Varianz überbewertet wurde oder die Technik der Einzelpflanzenselektion nicht präzis genug war, um die ertragreicheren Genotypen bei der Selektion einwandfrei herauszufinden.

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Mass Selection for Prolificacy in Maize[*][1]

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Summary. Results of 5 generations of selection for improved productivity in corn by selecting for prolificacy, a correlated trait, are reported. The regression for gain in yield per cycle of selection relative to the parental variety, Hays Golden, was 6.28%. This compares favorably with a previously reported gain from mass selection in the same variety using weight of grain per plant as the selection trait. The greater effectiveness of selection where prolificacy was the primary trait is believed due to higher selection intensity used as well as higher heritability.

Mass selection has been shown to be effective in modifying highly heritable traits in maize (SMITH 1909). In the early part of the present century, it was concluded generally not to be effective in the improvement of yield in adapted varieties although as pointed out by SPRAGUE (1955), no critical evaluation of the procedure was available from the early literature. Selection effectiveness for yield improvement in maize populations is dependent upon the presence of additive genetic variation for yield. HULL (1945) attributed the failure of mass and ear-to-row selection for yield in maize to the lack of additive genetic variation in varietal populations. He concluded that the genetic variation present was largely non-additive and therefore not subject to utilization in mass selection procedures. Subsequently, the characterizing and quantifying of relative amounts of genetic variation in open-pollinated varieties of maize became of utmost importance in providing guidelines for most efficient approaches in corn breeding.

COMSTOCK and ROBINSON (1948) outlined the use of certain mating systems in maize for the derivation of genetic variance components. A number of studies using these mating systems in maize varietal populations has been reported in recent years (ROBINSON et al. 1955, LINDSEY et al. 1962, LONNQUIST et al. 1966, WILLIAMS et al. 1965, COMPTON et al. 1965, GOODMAN 1965 and others). These studies generally revealed the presence of a considerable amount of additive genetic variation for yield. Selection based upon individual plant or among various types of cross progenies was therefore expected to be successful in improving yielding ability of maize populations. Recent reports have shown this to be so.

Improvement of maize populations through selection of parents based upon testcross progeny evaluation (recurrent selection) has shown substantial progress (LONNQUIST 1961, PENNY et al. 1963). Mass selection for yield under cultural practices providing reasonable control over environmental variation has also been successful (GARDNER 1961, JOHNSON 1963, LONNQUIST 1966, LONNQUIST et al. 1966). These results have substantiated reports of a considerable amount of additive genetic variance for yield in maize populations.

Yield improvement in maize populations undergoing various types of selection at the Nebraska Experiment Station has resulted in correlated changes including greater height, increased maturity and prolificacy. The latter observation resulted in an interest in the possibility of utilizing this trait in selection for increased productivity. RICHEY (1922) reviewed studies of early workers who had reported observations on the value of prolificacy for increasing the productive potential in maize. No reports are available however, of selection experiments carried