Quantitative Genetic Investigations of Yield of Maize*

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Summary. Numerous quantitative genetic studies of yield of maize, conducted at North Carolina State University, are reviewed in order to provide a joint interpretation of the various kinds of evidence found. Estimates of variance components and the comparison of observed and expected response to selection have led to the following conclusions:

1. Sufficient additive genetic variance for yield exists within many locally adapted maize populations to permit improvement by selection.
2. Average dominance for genes affecting yield of ear corn is in the range of partial to complete.
3. Overdominance is not a prevalent source of genetic variation for yield.
4. Linkage disequilibrium can result in effects which mimic overdominance. These effects diminish with random mating.
5. Epistatic variance (i. e., genetic variance not accounted for by additive and dominance variances) is negligible in the varieties, Jarvis and Indian Chief, and in the F_1 hybrid.
6. Short term predictions of response to full-sib and to reciprocal selection, based on genetic theory and computed from reasonably precise estimates of variances, are reasonably reliable.

Investigations of quantiative genetics of maize have been underway at North Carolina State University since 1946. The overall objective has been to develop an understanding of the genetic nature of hybrid vigor and to characterize variability in various maize populations. The results of many of the individual studies have been published as separate research reports. It is the purpose of this paper to focus attention upon the central theme of the program and to summarize the total results relevant to this theme. This report will be limited to a discussion of data for yield of ear corn, expressed as mean pounds per plant.

Essentially two approaches have been employed in these investigations; viz., estimation of means and variances, and response to selection. In the interpretation of variances, additive and dominance genetic variances and corresponding genetic-environmental interaction variances have been taken into consideration. However, in certain studies, epistatic variances were also considered. The interpretation of selection studies depends primarily upon the comparison of expected and observed response. Since expected selection response is computed from estimates of variances, comparison with the response actually obtained reflects back upon the interpretation of the variance estimates.

Variance estimation

Estimation of level of dominance

One of the major issues that has been investigated concerns the level of dominance of genes affecting yield. The inability of maize breeders of the 1920's and 1930's to improve yield of varieties by selection and the phenomenal success of hybrids which followed led to the idea that heterozygote superiority (overdominance) at individual loci may be a major source of variation in maize populations.

The details of the experimental approach used and the genetic interpretation are published elsewhere (COMSTOCK and ROBINSON, 1952, GARDNER et al., 1953, and MOLL et al., 1964). The studies involved F_2 and advanced generations which were derived by random mating within certain single cross populations so that the segregating populations have an expected gene frequency of 1/2. The advanced generations were developed by random plant-to-plant cross pollinations in a planting of 200 plants of each generation. The progeny evaluated in yield trials were produced by backcrossing random plants of a given generation (used as male parents) to the two parental inbred lines. Nine progeny pairs of a given generation were randomly assigned to a set, and each set was planted in 3 replications to form a block of 54 plots. Fifteen such blocks (a total of 135 progeny pairs) were planted for the F_2 and for an advanced generation. The 30 blocks were randomly assigned to locations in the field, so that each experiment included a total of 1620 plots. The analysis of variance of each block was computed individually, and the resulting analyses pooled to give an overall analysis for each generation.

The analysis of variance gives an estimate of a component of variance due to average differences among male parents (σ^2_m), and a component due to the interaction of male parents and inbred lines (σ^2_{ml}). It has been shown that with linkage equilibrium and no epistasis, σ^2_m is equivalent to $(1/4)\,\sigma^2_A$ and σ^2_{ml} is equivalent to σ^2_D, where σ^2_A and σ^2_D are additive and dominance variances, respectively. When linkage disequilibrium exists, $\sigma^2_m = (1/4)\,\sigma^2_A + B_1$ and $\sigma^2_{ml} = \sigma^2_D + B_2$, where B_1 and B_2 are terms due to linkage effects. The term B_1 can be positive or negative depending upon the relative importance of coupling or repulsion linkages. The term B_2 is always positive. Linkage disequilibrium is reduced by random mating, so that experiments involving advanced generations are expected to give estimates of σ^2_{ml} that are smaller than corresponding estimates in the F_2. Estimates of σ^2_m from advanced generations could be either larger or smaller than the F_2 estimates depending upon whether coupling or repulsion linkages predominate.

The average level of dominance is given by $\sqrt{2\,\sigma^2_D/\sigma^2_A}$, which is estimated by $\sqrt{\sigma^2_{ml}/2\,\sigma^2_m}$. When linkage disequilibrium exists, the estimate of average dominance will probably be biased. This bias should be less in advanced generations following random

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mating than in corresponding F_2 generations because of genetic recombination and approach to linkage equilibrium.

Experiments to estimate average dominance have been conducted in populations derived from three single crosses; NC33 × K64, NC7 × CI21, and NC34 × NC45. These will be referred to as populations I, II and III. Each experiment included progeny of the F_2 generation in comparison with progeny of an advanced generation.

Estimates of σ^2_{ml} (Table 1) are consistently smaller for advanced generations than for corresponding F_2 generations, which is clear evidence for linkage effects in the early generations that are partially dissipated with random mating.

Table 1. *Estimates of variance components* ($\times 10^4$) *and average level of dominance* ($\bar{a}$) *for yield in the* F_2 *and advanced generations of three single cross populations.*

Population	Generation	σ^2_m [1]	σ^2_{ml} [2]	$\bar{a}$
I	F_2	8	16	1.03
	F_8	3*	3**	0.70
I	F_2	10	22	1.08
	F_{12}	7*	8**	0.77
II	F_2	4	19	1.49
	F_8	3	9**	1.24
II	F_2	8	43	1.69
	F_{13}	7	17**	1.09
III	F_2	36	101	1.19
	F_7	9**	24**	1.15

[1] Component of variance due to male parents.

[2] Component of variance due to the interaction of male parents and inbred lines.

*, ** Significantly different from the corresponding F_2 estimate at the 5% and 1% level, respectively.

Estimates of σ^2_m in advanced generations are only slightly smaller than estimates in corresponding F_2 generations in populations I and II. In population III, the estimate of σ^2_m for the F_7 generation is much smaller than for the F_2. These results are suggestive of a preponderance of coupling phase linkages, particularly in population III.

Estimates of average dominance for each of the F_2 generations are greater than 1.0, or in the overdominant range. In populations I and II, estimates of average dominance are smaller for advanced generations than for the corresponding F_2. The smaller estimates obtained following random mating are interpreted to be a reflection of genetic recombination and approach to linkage equilibrium. Since the estimates appear to be approaching values of 1.0 or less with successive generations of random mating, there is no strong evidence for the existence of overdominance in populations I and II, i. e., the results are compatible with linkage of partially or completely dominant genes.

Fewer data have been accumulated for population III. The results available so far give estimates of average dominance that are greater than one, and there appears to have been little or no change after 5 generations of random mating. Interpretation of these results must be considered tentative, and even though the evidence might be indicative of overdominance in this population, the authors consider the data too inconclusive to be convincing. Further work is planned with this population in order to obtain definitive answers.

Genetic variance estimates in varietal populations

The experimental approach to the characterization of variability in varietal populations has been through the estimation of components of variance from analyses of variance of results of yield trials comprised of full-sib and half-sib families. The families were developed from mating schemes described as designs I and II by Comstock and Robinson (1948 and 1952).

Early investigations to estimate genetic variances in maize populations derived from single cross hybrids, open-pollinated varieties, and a variety hybrid have been reported (Robinson et al., 1949, 1955, 1958). Additional experiments have been conducted in the varieties and the variety hybrid involved in the earlier report, so the analyses of data of the earlier studies have been pooled with the analyses of data obtained subsequently to provide the overall estimates given here.

At the time of the initial experiments, large quantities of seed of the original varieties were placed in cold storage (below 0 °C) for subsequent experimentation. In order to conserve the supply of original seed, samples of original lot were increased periodically to provide seed for large scale investigations. Such increases were produced by random plant-to-plant crosses in a planting of 200 plants. The estimates presented represent samples of the varieties that were no more than 3 generations removed from the original source.

The design I progenies were formed by designating a random sample of plants as male parents, and crossing each of these to 4 randomly chosen plants used as females. The field design used to evaluate the families was formed by randomly assigning each group of male progenies (with 4 progenies per male group) to sets of 4 to make a total of 16 progenies. These 16 progenies were planted together in a randomized complete block. Most of the experiments to be reported were comprised of 16 such blocks, or a total of 256 progeny, and were grown in two environments; i. e., either two locations in the same year, or at the same location for two years.

An analysis of variance was computed for each block of 16 progenies separately. The overall analysis was obtained by pooling the analyses of the individual blocks. In the same manner, analyses of variance of data of separate experiments (which involved different samples of the same population grown in different environments) were combined into an overall analysis by pooling sums of squares and degrees of freedom.

Appropriate functions of mean squares from the analysis of variance of design I experiments provide estimates of $\sigma^2_{m_1}$ (variance component due to male parents) and $\sigma^2_{f_1}$ (variance component due to female parents) together with the corresponding environmental interaction components. If it is assumed that the populations studied are random mating populations in linkage equilibrium, with normal diploid segregation and no extra-nuclear inheritance, the interpretation of variance components estimated from the design I studies are as follows:

$$\sigma^2_{m_1} = (1/4)\,\sigma^2_A + (1/16)\,\sigma^2_{AA} + \cdots$$

$$\sigma^2_{f_1} = (1/4)\,\sigma^2_A + (1/4)\,\sigma^2_D + (3/16)\,\sigma^2_{AA} + \\ + (1/8)\,\sigma^2_{AD} + (1/16)\,\sigma^2_{DD} + \cdots$$

Table 2. *Components of variance* ($X10^5$) *estimated from Design I studies in several populations.*

Population	No. of Experiments	σ^2_m	σ^2_{me}	σ^2_f	σ^2_{fe}
Jarvis	6	51 ± 12	26 ± 10	84 ± 21	59 ± 16
Indian Chief	5	27 ± 10	28 ± 11	33 ± 22	71 ± 17
Weekley	3	54 ± 21	65 ± 37	108 ± 19	34 ± 23
(Jarvis × Indian Chief) F_1	4	35 ± 13	40 ± 14	58 ± 14	25 ± 19
(Indian Chief × Jarvis) F_1	4	34 ± 14	25 ± 11	108 ± 18	46 ± 11
(Jarvis × Indian Chief) F_3	1	116 ± 43	59 ± 25	110 ± 27	31 ± 82
(Jarvis × Indian Chief) F_6	1	67 ± 30	17 ± 14	162 ± 28	25 ± 23

in which σ^2_A, σ^2_D, σ^2_{AA}, etc. represent the additive, dominance, additive × additive, etc. genetic variance components. The genetic-environmental interaction components, $\sigma^2_{me_1}$ and $\sigma^2_{fe_1}$, are interpreted as variation due to interaction between the respective genetic effects and environmental effects. If epistatic variability is negligible, then $4\,\sigma^2_{m_1}$ provides an estimate of σ^2_A, and $4\,(\sigma^2_{f_1} - \sigma^2_{m_1})$ is an estimate of σ^2_D.

Variance component estimates from design I studies are shown for three varieties, reciprocal F_1 varietal hybrids and two generations of a varietal composite (Table 2). Significant additive genetic variance is indicated in all of the populations. The magnitudes of σ^2_m, as well as the relative magnitudes of σ^2_m and σ^2_{me}, vary among populations. For example, for the variety Indian Chief estimates of σ^2_m and σ^2_{me} are small and appear to be of equal magnitude. On the other hand, the variety, Jarvis, has a larger estimate of σ^2_m, with the interaction component only of 1/2 as large. The magnitude of σ^2_u in the F_1 varietal hybrid is estimated to be almost midway between the estimates for the two parental varieties. The genetic variance in both generations of the varietal composite appears to be considerably higher than that of either variety or the F_1 hybrid. The rather marked decrease in the estimate of σ^2_m from the F_3 to the F_5 generation might be due to recombination of linked genes with random mating, but it must be recognized that these estimates have rather large standard errors and the difference between them is not statistically significant.

Design II matings were made by utilization of random inbred lines developed by self-pollination (with no intentional selection) from the two varieties, Jarvis and Indian Chief. Sets of four randomly chosen inbred lines were designated as male parents, and each was crossed to sets of four other randomly chosen lines used as females. The 16 progeny resulting from each set of crosses were planted together in a replicated block.

Combined analyses of variance were computed in the manner indicated for design I. The components of variance estimated from functions of mean squares are given below together with their genetic expectations:

$$\sigma^2_{m_2} = \sigma^2_{f_2} = (1/2)\,\sigma^2_A + (1/4)\,\sigma^2_{AA} + (1/8)\,\sigma^2_{AAA} + \cdots$$

$$\sigma^2_{mf_2} = \sigma^2_D + (1/2)\,\sigma^2_{AA} + \sigma^2_{AD} + \sigma^2_{DD} + (3/4)\,\sigma^2_{AAA} + \cdots$$

in which the genetic components of variance are as defined previously. The assumptions underlying these expectations are the same as those for design I, but in addition it is assumed that the inbred lines used as parents are a random sample of the possible homozygous genotypes of the variety.

Experiments involving both design I and design II progenies have been conducted in order to estimate variation due to epistatic gene action. A comparison of the genetic expectations of design I and design II experiments reveals that the coefficients of the epistatic terms are nonproportional, so it is possible to estimate certain fractions of the epistatic variability from functions of variance components estimated from progenies of the two mating designs.

Results of extensive experiments to estimate epistatic variability in Jarvis, Indian Chief, and their F_1 varietal hybrid have been published in detail (EBERHART et al., 1966, and STUBER et al., 1966). For the purpose of this report, attention is focused upon a brief summary of the results (Table 3). Half of the estimates of epistatic variances are positive, and half are negative. None of the estimates appears to be statistically significant. This evidence suggests that most of the genetic variability in these populations can be accounted for by additive and dominance variances, and that very little variation is attributable to epistasis.

Table 3. *Estimates of epistatic components*[1] *of variance in two varieties and their* F_1 *hybrid.*

Population	$\sigma^2_{I_a}$	$\sigma^2_{I_d}$	$\sigma^2_{I_g}$
Jarvis	.0006	−.0021	−.0015
Indian Chief	.0004	.0005	.0008
Jarvis × Indian Chief	−.0003	−.0045	−.0024

[1] $\sigma^2_{I_a} = 1/4\,\sigma^2_{AA} + 3/16\,\sigma^2_{AAA} + 7/64\,\sigma^2_{AAAA} + \ldots$ within varieties,

$\sigma^2_{Id} = 1/2\,\sigma^2_{AD} + 3/4\,\sigma^2_{DD} + 3/8\,\sigma^2_{AAA} + \ldots$ within varieties,

$\sigma^2_{I_g} = 1/4\,\sigma^2_{AA} + 1/2\,\sigma^2_{AD} + 3/4\,\sigma^2_{DD} + \ldots$ within varieties,

$\sigma^2_{I_A}$, $\sigma^2_{I_d}$, $\sigma^2_{I_g}$ correspond to I_2, I_3, I_1, respectively, as defined by STUBER et al. (1966) for the variety cross, and are functions of the gene frequencies in the two varieties. Nevertheless, in the crossbred populations:

$\sigma^2_{I_a}$ = predominately additive × additive types,

$\sigma^2_{I_d}$ = predominately dominance × dominance,

$\sigma^2_{I_g}$ = includes all types.

The number of environments sampled in individual design I studies is limited by the amount of seed produced by the lowest yielding parental plants, which frequently produce enough seed for only two environments. The question arises as to whether one should sample two locations in the same year or two years with a single location in each.

Three experiments have been conducted which provide a basis for decision. One study was composed of 4 sets of single crosses made among random inbred lines of the Jarvis variety according to the design II mating scheme. The 64 single crosses were grown in 2 replications at 4 locations for 3 years. Another study was composed of 60 half-sib families of the Jarvis variety, which were grown in 2 replications at 5 locations for 5 years. A third experiment included 15 F_1 crosses among 6 locally adapted varieties, and was grown at 3 locations for 2 years. Estimates of genotype-environmental interaction components are summarized in Table 4 in terms of percent of the genetic variance. The important feature is that the second order interaction estimate

Table 4. *Estimates of genotype-environmental interaction variances expressed as a percent of the genetic variance in three experiments repeated over locations and years.*

Kind of Interaction	Jarvis Variety Single Crosses	Jarvis Variety Half-sib Families	Variety Crosses
Genotype × Locations	6	−11	−12
Genotype × Years	9	−11	−17
Genotype × Locations × Years	119	70	47

is relatively large and statistically significant in each experiment, whereas the first order interaction estimates involving genotypes × years or genotypes × locations were small and statistically nonsignificant.

These results have been interpreted to mean that differential response of genotypes to different environments does not appear to be associated with particular locations or years.

The most extensive study, which involved half-sib families grown at 5 locations for 5 years, provides data which apply only to the additive portion of the genetic variance (Robinson and Moll, 1959). The study involving the 64 single crosses provides estimates which may be partitioned into both additive and dominance variances and the corresponding interaction variances. The estimates, which are summarized in Table 5, show a consistent pattern of genetic-environmental interactions for both the additive and dominance partitions.

Table 5. *Genetic and genetic-environmental interaction variances of Jarvis single crosses at four locations for three years.*

$\sigma^2_A = .0013$	$\sigma^2_D = .0008$
$\sigma^2_{AL} = .0003$	$\sigma^2_{DL} = -.0002$
$\sigma^2_{AY} = -.0001$	$\sigma^2_{DY} = .0003$
$\sigma^2_{ALY} = .0015$	$\sigma^2_{DLY} = .0010$
$(\sigma^2_{AE}/\sigma^2_A) = 1.31$	$(\sigma^2_{DE}/\sigma^2_D) = 1.38$

It appears that the environmental differences which affect genotype × environmental interactions (within the region where these studies are being conducted) occur at random with respect to locations and years. On the basis of these results, it has become the practice to regard year-location combinations as random elements of the population of environments, and to ignore the year-location classification in the interpretation of estimates of genotype × environmental interaction variances.

Different agricultural regions will likely have a different pattern of genetic-environmental interaction variances as manifested by the contrast between the data above and reports by Rojas and Sprague (1952) and Matzinger et al. (1959). In both of these reports, the variance component due to genotype × year interactions was larger than either the genotype × location or the genotype × location × year component. There was also an indication that the pattern of genetic-environmental interaction variances corresponding to the additive and dominance partitions may differ among different kinds of genetic materials.

Selection experiments

Two kinds of selection experiments are being conducted with particular emphasis upon the comparison of observed response and the response expected on the basis of variance estimates and quantitative genetic theory.

Full-sib family selection is being conducted in the following populations:

I (NC7 × CI21) F_2	– a hybrid population
II Jarvis	– open-pollinated variety
III Indian Chief	– open-pollinated variety
IV (Jarvis × Indian Chief) F_4	– varietal composite

Reciprocal recurrent selection (Comstock et al., 1949) is being conducted in the crossbred of Jarvis × Indian Chief.

The details of experimental procedure are given by Moll and Robinson (1966). The mating design for the full-sib family selection studies was the same as for design I described on preceding pages. Remnant seed of superior families was planted and the progeny intermated to complete the selection cycle. The mating design for reciprocal recurrent selection was similar to that of design I, except that the seed of the females mated to a common male was bulked to provide a single entry, and each male parent was self-fertilized. Males of one population were crossed onto females of the other population, so that the progeny tested were crossbred progeny. Since this was done reciprocally, two sets of crossbred progeny were evaluated; i. e., one set in which plants of one population were used as male parents, and another set which involved males from the other population. The self-pollinated seed of males of each variety which gave superior crossbred progeny were planted and the plants were intermated.

The expected response for full-sib family selection is:

$$\Delta_{FS} = 2\,k\,\sigma^2_{m_{11}}/\sigma_{p_{11}}\,,$$

and for reciprocal selection is:

$$\Delta_{RS} = k\,[(\sigma^2_{m_{12}}/\sigma_{p_{12}}) + (\sigma^2_{m_{21}}/\sigma_{p_{21}})]\,,$$

in which k is the selection differential in standard units, $\sigma^2_{m_{ij}}$ is the variance component for males of the i^{th} variety when crossed to the j^{th} variety, and $\sigma_{p_{ij}}$ is the corresponding phenotypic standard deviation.

Accumulative expected progress for each experiment has been computed from estimates of genetic variance in the initial population except for the (NC7 × CI21) F_2 population. In the latter case, estimates were computed by pooling analyses of the second and third cycle yield tests. The estimates used to compute expected progress were obtained by pooling analyses of 6 experiments for the Jarvis variety, 5 experiments for the Indian Chief variety, 1 experiment for the varietal composite (Jarvis × Indian Chief) F_4, and 4 experiments for the varietal crossbred, Jarvis × Indian Chief. In order to obtain an estimate of the error associated with estimates of expected progress, the variance of the ratio of σ^2_m/σ_p was computed from estimates of individual experiments within each population, and then pooled to provide a single estimate of the variance of σ^2_m/σ_p with 12 degrees of freedom. The variance of expected progress estimates was then

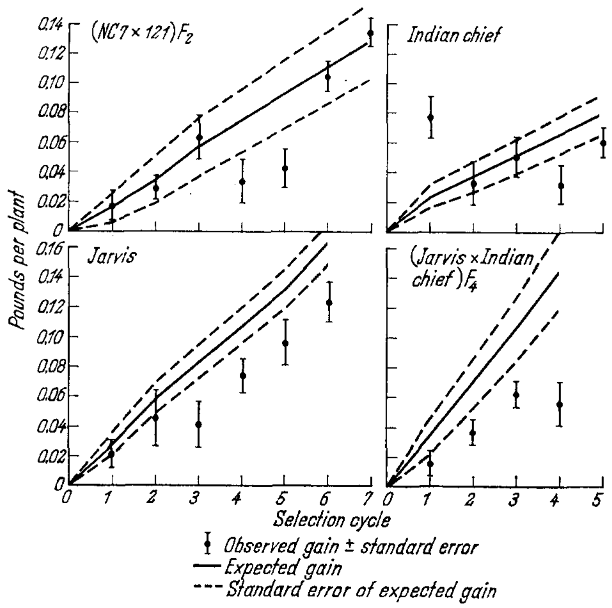

Fig. 1. Observed and expected response to full-sib family selection in four maize populations.

computed as

$$\sigma_{\varDelta}^2 = 4\, k^2\, [\mathrm{Var}\,(\sigma_m^2/\sigma_p)]\,(1/n)$$

in which n is the number of individual studies pooled to provide estimates of the variance components.

Results of the selection studies, summarized in Figures 1 and 2, show that agreement between observed and expected response is in general quite satisfactory.

In the (NC7 × CI21) F_2 and Jarvis populations, there are no significant differences between the observations and expectations. In the Indian Chief population, the gain observed after the first selection cycle appears to be unreasonably high, but otherwise the observed progress agrees fairly well with the expected. Expected progress for the (Jarvis × Indian Chief) F_4 population has been computed from estimates from a single experiment, and therefore is not as reliable as the others. There appears to be very good agreement between the observed and expected response in the reciprocal recurrent selection study.

These studies provide the opportunity to compare the effectiveness of full-sib selection (for purebred performance) with reciprocal recurrent selection (for crossbred performance). The populations resulting from 3 cycles of selection by each method were evaluated for both purebred and crossbred performance in replicated yield trials at three locations for two years. The results (Table 6) suggest that full-sib selection resulted in greater purebred performance than populations improved by reciprocal recurrent selection. It appears that full-sib selection also resulted in slightly superior crossbred performance relative to that attained by reciprocal recurrent selection.

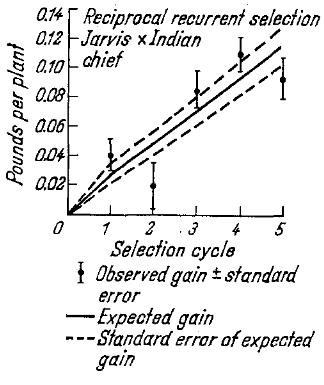

Fig. 2. Observed and expected response to reciprocal recurrent selection.

Table 6. *Comparison of intra- and inter-population improvement by full-sib selection and reciprocal recurrent selection.*

Population		Mean Yield
Varieties:		
Original Jarvis	J_0	·454
Jarvis after 3 cycles of Full-sib Selection	J_{F3}	·514
Jarvis after 3 cycles of Reciprocal Selection	J_{R3}	·512
Original Indian Chief	I_0	·478
Indian Chief after 3 cycles of Full-sib Selection	I_{F3}	·539
Indian Chief after 3 cycles of Reciprocal Selection	I_{R3}	·502
Varietal Hybrids:		
	$J_0 \times I_0$	·544
	$J_{F3} \times I_{F3}$	.604
	$J_{R3} \times I_{R3}$	·557

Discussion

The results of the two experimental approaches provide evidence concerning the nature of variability in maize populations which appears to be mutually compatible. The results of variance estimation studies have been interpreted as evidence that overdominance is not prevalent, that epistatic variability is negligible and that sufficient additive genetic variance exists to permit improvement by selection.

Evidence that overdominance is not prevalent is found in the results of the studies reported above, and in the results of similar studies reported by Gardner (1963). The results of convergent improvement experiments reported by Richey and Sprague (1931) and by Murphy (1942) are also compatible with the hypothesis of partially dominant genes. The reports of Robinson et al. (1955) and (1958) demonstrated that the relative magnitude of the additive and dominance variances found in the varieties Jarvis, Indian Chief and Weekley, and in the variety hybrid, Jarvis × Indian Chief, are compatible with a level of dominance in the range of partial to complete. It must be recognized, however, that even though the weight of the evidence favors the conclusion that overdominance is rare, the possibility of occasional overdominant loci cannot be ruled out, and may be revealed in particular hybrid combinations. Whether or not this is the case for Population III discussed earlier in this report may be established with further experimentation.

The results of the investigations reported here indicate that the additive genetic variance is at least as large or larger than the dominance variance in the varieties, the variety hybrid and in the varietal composite. Although this report deals directly with a very limited sample of maize populations, the results of the variance estimation studies are, in general, similar to published estimates involving various locally adapted populations (Table 7). In view of the magnitude of standard errors of variance component estimates presented earlier in this report, the similarity among the estimates for most of the populations is quite remarkable. While it is reasonable to expect differences in genetic variances among locally adapted varieties, the data summarized here suggest that these differences are not large. With

Table 7. *A summary of genetic variance estimates*[1] *for varieties, varietal hybrids and composite populations.*

Population	Reference	σ_A^2	σ_D^2	Number of Experiments	Number of Environments per Experiment
		(pounds/plant)			
Varieties:					
Jarvis	Moll et al., 1966	.0020	.0013	6	2
Indian Chief	Moll et al., 1966	.0011	.0002	5	2
Weekley	Robinson et al., 1955	.0033	.0017	2	2
Hayes Golden	Lindsey et al., 1961	.0046	.0002	2	2
Krug Yellow Dent	Lindsey et al., 1961	.0080	.0042	2	2
Golden Republic	Compton et al., 1965	.0089	.0035	1	2
Barber Reid	Compton et al., 1965	.0056	.0041	1	2
Midland	Sprague, 1964	.0009	.0047	1	1
Hickory King	Sprague, 1964	.0012	.0012	1	1
Reid's Yellow Dent	Williams et al., 1965	.0017	.0003	1	2
Varietal Hybrids:					
Jarvis × Indian Chief	Moll et al., 1966	.0010	.0009	2	2
Barber Reid × Golden Republic	Compton et al., 1965	.0096	.0029	1	2
Composite Populations:					
(Jarvis × Indian Chief) F_3	Moll et al., 1960	.0046	−.0002	1	2
(Jarvis × Indian Chief) F_5		.0027	.0038	1	2
Corn Belt Composite	Goodman, 1965	.0059	−.0013	1	1 (in Iowa)
		.0017	.0036	1	1 (in N. C.)
West Indian Composite	Goodman, 1965	.0138	.0000	1	1 (in Iowa)
		.0040	.0022	1	1 (in N. C.)

[1] In some of the reports cited, estimates given were in terms of σ_m^2 and σ_f^2. In order to make all estimates comparable, σ_A^2 has been estimated as $4\,\sigma_m^2$ and σ_D^2 as $4\,(\sigma_f^2 - \sigma_m^2)$. When necessary, estimates were converted from the units of measurement given to pounds per plant.

only two exceptions, the estimate of additive genetic variance exceeds the estimate of dominance variance; and these two exceptions involve estimates obtained from limited data.

The report by Goodman (1965) provides a comparison between a composite of midwestern maize and a composite made up of both midwestern and West Indian maize. Both composites had been intermated in Iowa for several generations prior to this study, which was conducted in both Iowa and North Carolina. Therefore, the study provides not only a comparison between composites containing material of widely different degrees of divergence, but also a comparison of estimates obtained in the region of adaptation (Iowa) with those obtained in an environment that is somewhat foreign. The estimates presented suggest that the composite of the more divergent parentage has greater genetic variance. It also appears that the genetic variance was considerably larger in Iowa where the composites were developed than in North Carolina where they were expected to be less well adapted. It is noteworthy that the estimate of additive genetic variance for the West Indian Composite obtained in Iowa was considerably larger than those reported for varieties, variety hybrids or composites of less divergent material.

The interpretations discussed above concerning the level of dominance in maize and the relative magnitude of additive and dominance genetic variances are based upon the assumption that non-allelic gene interactions (epistasis) are unimportant. Therefore, the data presented here which indicates that variances attributable to epistasis are small and not statistically significant adds support to the foregoing interpretations.

There is published evidence that significant epistatic effects are detectable in certain maize crosses (Sprague et al., 1962; Gamble, 1962, and Bauman, 1959), which may appear to be in contrast with the findings discussed here. The techniques used in these earlier studies merely indicated the presence of the effect in specific inbred line combinations. The magnitude of the effect detected could not be estimated, nor is it realistic to extrapolate to a random mating population with arbitrary gene frequencies. At the same time, the failure of variance experiments to detect epistatic variance does not rule out the possibility that epistatic effects exist. Rather, the results suggest that if epistatic effects do exist, they do not contribute significantly to variation beyond that accounted for by additive and dominances variances.

The results of the selection studies show reasonably good agreement between observed and expected response. Even though short term selection response is probably not a critical test of the genetic model, the results appear to be consistent with the evidence gathered from variance studies. Furthermore, it appears that the short term effects of inter- and intrapopulation selection are very similar, which is interpreted as an additional indication that genetic variation in these populations can be largely attributed to an additive genetic model with partial to complete dominance.

The agreement between observed and expected response also indicates that the population sizes involved in the selection experiments were large enough so that drift and inbreeding do not obscure the effects of selection. The population size employed for full-sib selection was 256 families, out of which 25 families were selected in each cycle. In the reciprocal recurrent selection experiment, the goal has been 150 families tested of each reciprocal in each cycle. Although the number actually tested was fewer in some cycles, 20 parents of the families tested were selected in each reciprocal in each cycle. It should also be mentioned that when the selected families were intermated to provide the population for the next selection cycle, the matings were chosen in such a way as to reduce the inbreeding below that expected from matings chosen at random. While the population sizes may have been adequate for the purposes of the experiments, larger population sizes would be expected to result in smaller fluctuations from cycle to cycle. In view of the fluctuations seen in the data presented, the population sizes used here should be viewed as minimal for a practical selection program.

Two possible ways that estimates of expected response to selection might be useful are in the choices among populations and among selection procedures in a practical plant improvement program. In the studies reported in Figure 1, the expected response estimates might have led one to choose the Jarvis variety and the (Jarvis × Indian Chief) F_5 composite as the more promising populations for the initiation of selection. Of these two, the varietal composite appears to be the most promising on the basis of expected progress estimates, but it must be recognized that this is based upon rather limited data. The observed results suggest that there may be little difference between these two populations with respect to short term selection response, but both of them show greater response than the (NC7 × CI21) F_2 or the Indian Chief variety. In these studies, then, the observed response tends to support the rate of progress indicated by predictions based on variance estimates. The rather large discrepancies between observed and expected progress for the varietal composite indicate a need for caution in interpreting predictions based upon limited data. When one considers the amount of information that would usually be available on specific populations prior to the initiation of selection, it becomes evident that estimates of expected progress will serve best if used as a guide to the choice among *kinds* of populations that are expected to have widely different variances; e. g. adapted vs. unadapted, varieties vs. composites, etc., rather than to attempt to distinguish among similar populations with genetic variances of the same order of magnitude.

Estimates of genetic variances are being accumulated in the literature for various kinds of populations, and as suggested by the data in Table 7, populations of a similar historical development may have similar patterns of variability. Accumulated information of this kind may be extremely valuable in designing efficient selection programs to meet specific needs. Consider, for example, the comparative merits of mass selection and full-sib family selection. In order to define systems that are comparable, consider 250 full-sib families grown in 2 replications with 10 plants per plot. This will require the accommodation of 5000 plants. With a 10% selection intensity, 25 families would be selected representing progeny of 50 parents. A comparable mass selection system might be 5000 individual plants with a 1% selection intensity.

Expected progress for full-sib selection will be $\Delta_{FS} = (1.75)\ 2\,\sigma^2_m/\sigma_{pf}$, and for mass selection will be $\Delta_{MS} = (2.66)\ 2\,\sigma^2_m/\sigma_{pi}$, in which σ_{pf} and σ_{pi} refer to the phenotypic standard error for full-sib family means and for individual measurements, respectively. It follows that:

$$\sigma_{pf} = \sqrt{\sigma^2_{m'} + \sigma^2_{f'} + \sigma^2_p/2 + \sigma^2_w/20}$$

and

$$\sigma_{pi} = \sqrt{\sigma^2_{m'} + \sigma^2_{f'} + \sigma^2_p + \sigma^2_w}$$

in which $\sigma^2_{m'} = \sigma^2_m + \sigma^2_{me}$, $\sigma^2_{f'} = \sigma^2_f + \sigma^2_{fe}$, σ^2_p is plot error and σ^2_w is plant to plant variance within plots, which includes both genetic and environmental components. It can be shown that, in this example, if $\sigma^2_{m'} + \sigma^2_{f'} + .12\,\sigma^2_p - .68\,\sigma^2_w > 0$, mass selection will result in greater expected gain than full-sib selection. If the inequality is reversed, full-sib selection will be favored. A rather high magnitude of the genetic variance relative to the environmental variance will be necessary to allow a greater rate of gain by mass selection.

In the Jarvis variety, for example $\hat{\sigma}^2_p = .00287$ and $\hat{\sigma}^2_w = .02626$, which give estimates of expected gain of .025 pounds per plant for full-sib family selection and .015 pounds per plant for mass selection. The full-sib matings would require an additional generation per cycle, so that mass selection appears to have a greater expected gain per generation. However, if the full-sib matings can be made in an off-season nursery so that a cycle can be completed in a year, then full-sib family selection would appear to have an advantage.

Data which bear upon the relative effectiveness of purebred and crossbred selection in the improvement of hybrid performance has important implications in practical maize breeding programs. The issue is whether one should initiate a hybrid program by purebred selection or by crossbred selection. If genetic considerations are ignored, economic considerations would favor purebred selection (mass or full-sib selection) over reciprocal recurrent selection. The very limited results presented here suggests that there may be little or no difference in hybrid improvement for the first few selection cycles. It is essential to know whether or not the kind of results observed here can be repeated with other populations and in different environments before practical conclusions can be drawn. The results so far bear only upon short term response and the relative rates of progress in later selection cycles is open to question. In a long term selection program, there are at least three basic alternative procedures: (1) purebred selection throughout the program, (2) purebred selection at the outset with a change to reciprocal selection in later cycles, and (3) reciprocal selection throughout. There is no published experimental data which bears upon the relative rates of improvement by these three alternatives in later selection cycles.

Critical evaluations of alternative selection procedures in maize are urgently needed. Too often, data reported in the literature which bear upon this issue are obtained from experiments with other primary objectives and evaluation of selection technique appears to be an afterthought rather than one of the planned objectives. In other reports, the primary objective is the evaluation of a selection procedure, but in some cases the selection practiced involves both subjective and objective selection criteria, and in other cases the selection practiced is radically modified during the course of the study such that the interpretations cannot be definitive. Comparable evaluation of selection procedures is a long term undertaking, and merits painstaking consideration in the development of clear objectives and rigorous experimental design and techniques. The authors are aware that several workers have undertaken such studies, but information with sufficient generality to be practically useful to maize breeding projects will require the accumulated efforts of a number of workers in order to sample a wide range of materials, environments, and experimental procedures.

Zusammenfassung

An der North Carolina State University wurde in zahlreichen Untersuchungen die quantitative Genetik des Maisertrages erforscht, über die mit dem Ziel berichtet wird, die verschiedenen Ergebnisse zusammen auszuwerten. Die Schätzung der Varianzkomponenten und der Vergleich der tatsächlichen und erwarteten Ergebnisse der Selektion haben zu folgenden Schlüssen geführt:

1. Zahlreiche lokale Maispopulationen verfügen bezüglich der Ertragsfähigkeit über eine genügend große additiv-genetische Varianz, um eine Verbesserung durch Selektion möglich zu machen.
2. Der durchschnittliche Dominanzgrad der Gene, die den Kolbenkornertrag beeinflussen, liegt im Bereich zwischen partiell bis vollständig.
3. Überdominanz ist nicht als vorherrschende Ursache der genetischen Variation des Ertrags anzusehen.
4. Kopplungsungleichgewicht kann Wirkungen ergeben, die Überdominanz vortäuschen. Zufallspaarung vermindert diese Wirkungen.
5. In den Sorten 'Jarvis' und 'Indian Chief' sowie der F_1-Hybride ist die Interaktionsvarianz (d. h. die genetische Varianz, die nicht als additive oder Dominanz-Varianz zu erklären ist) unbedeutend.
6. Kurzfristige Vorhersagen auf Ergebnisse einer Vollgeschwister- und reziproken Selektion, die auf der genetischen Theorie beruhen und aus verhältnismäßig genauen Varianzschätzungen errechnet wurden, sind ziemlich zuverlässig.

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Genetic Advance from Inter-Line Selection in Poultry*[1]

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Summary. This study was based on 5 years of random sample performance test data on commercial varieties of chickens bred for egg production collected in Iowa from 1958 to 1962. In each year, 15 or 16 varieties were compared on 15 to 20 farms for differences in egg production and other economically important traits. Varieties were tested in duplicate pens in both randomized blocks and lattice designs. The data were analyzed into variance components to determine the relative importance of variety and variety × farm interaction variance. The ratio of the variety variance to the total, on a pen mean basis, was .33, .22, .26 and .42 for egg rate, laying house mortality, adult body weight and egg size, respectively. The estimated genetic advance in egg production was 11.5 eggs by choosing the best producing variety in a test on 16. If the selected variety is based on a performance index determined from a multiple regression equation of expected income on the same four traits the estimated correlated responses are expected to increase egg number by 11.7, decrease mortality by 1.8 percent, decrease body weight by 0.6 pounds and increase egg weight by .23 ounces per dozen.

A study of the optimum use of test resources for maximum genetic advance showed that, if 160 test pens were available, then 40 to 80 varieties should be tested on two to four farms in single pen replicates.

The problem of chicken breeding for improved egg production closely parallels that for corn breeding. In each case, the primary trait for which improvement is sought is yield (eggs or grain). Corn breeders early recognized that mass selection and ear-row testing gave slow progress in improving yield; hence, corn production today mainly depends on inter-population selection procedures.

Evidence that selection for egg production by conventional intra-population procedures is also not effective has been presented by DICKERSON (1955, 1961 and 1962), GOWE and STRAIN (1963) and MORRIS (1963). More recently, NORDSKOG, FESTING and VERGHESE (1967) found no increase in rate of egg production from 8 generations of selection for early record percentage egg production in 2 breeds of chickens (Leghorns and Fayoumis).

Commercial corn breeding in the U.S. today almost exclusively employs inbreeding and hybridization which has also been applied successfully to poultry. Yet, the large majority of commercial varieties of chickens are not inbred hybrids but strain crosses. These are produced from crossing distinct, but not highly inbred, strains. Some of the larger producers of strain crosses, as well as inbred-hybrids, follow a field testing program similar to that used in the development of hybrid corn. Thus, poultry breeders use statistically designed experiments to assess environmental effects and interactions with test varieties. Moreover, random sample poultry tests have been used in the U.S. for almost 20 years to evaluate commercial varieties in a manner similar to corn yield tests familiar to plant breeders.

It seems fitting, therefore, for poultry breeders to recognize Dr. G. F. SPRAGUE, who through his important contributions to corn breeding, also has contributed, although indirectly, to the advances in modern methods of commercial poultry breeding.

This paper considers some of the possibilities for genetic improvement of egg yield and other important economic traits in poultry, by inter-line selection procedures as applied to corn by FEDERER (1951) and SPRAGUE and FEDERER (1951). Optimum allocation of testing resources for maximum genetic advance will also be considered from further application of procedures used by these workers.

The Data

This study is based on results from the Iowa Official Multiple Unit Poultry Test, a random sample egg laying test. Its main purpose is to provide poultrymen with performance data on commercial varieties of egg-laying chickens offered for sale in the U.S. Also, the test has provided research data bearing on factors influencing the reliability of test results.

Data collected over a 5-year period from 1958 to 1962 on over 65,000 adult chickens were analyzed. In each year, commercial varieties were tested on several farms. At each farm, varieties were tested in duplicate pens (the experimental units) by using a randomized blocks design in 1958, a partially balanced lattice design in 1959 and 1960, and a completely balanced lattice design in 1961 and 1962 (see Table 1). Further details on the test design and procedure are given by NORDSKOG and KEMPTHORNE (1960) and NORDSKOG (1966).

Table 1. *Nature of data from the Iowa Multiple Unit Random Sample Poultry Performance Test.*

Year	1958	1959	1960	1961	1962
No. of varieties entered	15	16	16	16	16
Av. no. chicks/ variety	942	840	950	1578	1314
Total adult birds tested	10,768	12,600	11,570	15,015	15,493
No. cage farm units	6	4	0	0	0
No. floor farm units	9	12	16	20	20
Total no. of test pens	150	128	128	160	160

Test designs: 1958 — 15 entries tested on 15 farms in three 5 × 5 randomized blocks with a common control entry for each farm. — 1959, 1960 — 16 entries tested on 16 farms in 4 replications of 4 × 4 blocks in a partially balanced lattice design. — 1961, 1962 — 16 entries tested on 20 farms in 5 replications of 4 × 4 blocks in a balanced lattice design.

The data included egg number, egg size, body size, flock mortality and age at 50 percent egg production (a measure of sexual maturity). In addition, a performance index was constructed from information on the most important economic traits. The index is,

$$I = 2.59\,D + 1.19\,E - 32.4\,W - 2.88\,M - 66$$

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* Dedicated to Dr. GEORGE F. SPRAGUE on the occasion of his 65th birthday.

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where,

D = Hen-day egg production in number of eggs
E = Percent of eggs laid larger than 2 ounces
W = Body weight in pounds at end of test
M = Percent laying house mortality.

The Performance Index, in units of dollars, was based on a multiple regression analysis of these traits on actual income in an earlier study (NORDSKOG, 1960). In this study, the four traits accounted for about 90 percent of the variance in income over feed costs of entries in random sample egg laying tests.

Statistical

Analysis of Variance

Data from the 1958 test was subjected to an analysis of variance assuming a linear model appropriate for randomized blocks. The model for the lattice test designs used in the years 1959—1962 is

$$Y_{hijk} = u + r_h + f_{hi} + s_j + (fs)_{hij} + e_{hijk}$$

where,

Y_{hijk} = the observation of the k^{th} pen of the j^{th} strain tested on the i^{th} farm in the h^{th} replicate
μ = general mean
r_h = effect common to pens in the h^{th} replicate
f_{hi} = effect common to pens on the i^{th} farm in the h^{th} replicate
s_j = effect common to pens of the j^{th} strain
$(fs)_{hij}$ = effect common to pens of the j^{th} strain tested on the i^{th} farm in the h^{th} replicate
e_{hijk} = effect peculiar to the k^{th} pen of the j^{th} strain tested on the i^{th} farm in the h^{th} replicate.

The terms f_{hi}, s_j, $(fs)_{hij}$ and e_{hijk} are assumed uncorrelated random variables with variances σ_f^2, σ_s^2, σ_{sf}^2 and σ_p^2, respectively.

The form of the analyses of variance and the expectation of the mean squares in terms of variance components are given in Table 2.

Table 2. *Analysis of variance and variance components.*

	Range in Degrees of freedom per Test	Expected mean squares
Block replications	2— 4	
Varieties	11—15	$\sigma_p^2 + 2\,\sigma_{vf}^2 + k_1\sigma_v^2$
Farms	12—15	$\sigma_p^2 + 2\,\sigma_{vf}^2 + k_2\sigma_2^f$
Var. × Farms	33—45	$\sigma_2^p + 2\,\sigma_{vf}^2$
Pens	64—78	σ_2^p

Computing Genetic Advance

Genetic advance from selection (ΔG) is predicted from the degree of heritability of trait (H) and the amount of selection practiced (δ) measured in standard deviation units. Thus, $\Delta G = H\,\delta$.

This basic formula is strictly appropriate to intraline selection where H is the fraction of additive genetic variance among individual differences and selections are made on the individual phenotypes. The formula can be modified to account for selection among groups such as families or lines with different amounts of inbreeding. For inter-line selection, SPRAGUE and FEDERER (1951) used formulas of the following type:

$$G = \frac{\bar{d}\,\bar{X}\,m}{\sqrt{\frac{1}{r\,p} + \frac{\bar{b}}{p} + \bar{d}}}$$

where G is the average genetic advance in positive standard deviation units due to selection of the highest-yielding variety, rather than a randomly selected one in a corn yield test, $\bar{d}$ is the average unbiased estimate of the ratio of variety variance to error variance, r is the number of replicates, p is the number of test places, and $\bar{b}$ is the average unbiased estimate of the ratio of interaction variance to error variance. The quantity $\bar{x}_m$ is the average value of the largest normal deviate from the sample m varieties tested (obtained from FISHER and YATES, 1957, Statistical Tables, Table XX).

SPRAGUE and FEDERER (1951) further showed that the unbiased estimate of the ratio of the variety × farm variance to the error variance component is

$$b = \frac{f_e - 2}{f_e}\left[\frac{\sigma_{vf}^2}{\sigma_e^2} - \frac{2}{r\,(f_e - 2)}\right]$$

and that of the variety variance to the error variance component is

$$\hat{d} = \frac{f_e - 2}{f_e}\left[\frac{\sigma_v^2}{\sigma_e^2}\right].$$

When the degrees of freedom for error (f_e) are large the unbiased estimates are not far different from the variance ratios taken directly. Thus, if we ignore the small correction for bias when degrees of freedom are large, it is easy to show that the formula for genetic advance takes a form more familiar, at least, to animal breeders,

$$\Delta G = \sqrt{H}\,\delta_s\,\sigma_v\,.$$

Here, H is the ratio, $\sigma_v^2/(\sigma_v^2 + \sigma_e^2)$, and δ_s is equivalent to $\bar{x}_m$ in SPRAGUE and FEDERER's formula, the average selection differential expected by selecting the elite variety of s tested.

In essence, H represents the "heritability" of the observed mean differences between test varieties. No assumptions are made, however, concerning the additive and non-additive composition of H, since we are selecting between varieties.

By increasing the number of experimental units per variety tested, H can be made larger, but for any fixed amount of testing facility, this reduces the number of varieties that can be tested, which therefore lowers δ. Recognizing this, SPRAGUE and FEDERER (1951) showed that ΔG can be maximized for some optimum number of varieties and test replications.

Results

Variance Components

A summary of the variance component analysis by years is given in Table 3 for three traits only: egg production rate, mortality, and the performance index. However, the average values of the variance components for other traits, from the four years when the lattice design was used, are presented in Table 4. The main effects for both the variety and farm mean squares were statistically significant for each of the traits in each year. The variety × farm interaction effects were statistically significant in about half the cases.

Table 3. *Variance components by years for egg production rate, laying house mortality and the performance index.*

		Varieties	Farms	Varieties × Farms	Pens
Degrees of Freedom	1958	11	12	44	70
	1959	15	12	33	64
	1960	15	12	33	64
	1961	15	15	44	78
	1962	15	15	45	76
		Var. Comp.			
Egg prod. rate	1958	15.55**	50.34**	13.85**	7.88
	1959	7.15**	27.92**	3.76*	5.64
	1960	15.37**	14.91**	3.61	8.84
	1961	3.94*	9.56**	4.62*	15.59
	1962	8.09**	26.79**	8.71**	11.46
Mortality	1958	.53	13.78**	29.2**	48.7
	1959	9.18**	11.68**	0	28.9
	1960	14.05*	42.13**	16.2*	13.4
	1961	9.16**	16.40**	0	58.7
	1962	9.27**	44.85**	13.7**	26.9
Performance Index	1958	.1329**	.1946**	.0559**	.0935
	1958	.1873**	.1947**	0	.0502
	1960	.3746**	.2304**	.1222**	.0839
	1961	.1111**	.1577**	.0161	.1159
	1962	.1167**	.1940**	.0966**	.1083

* $P < .05$. — ** $P < .01$

Table 4. *Average variance components of the test years 1959, 1960, 1961 and 1962*

Trait	σ^2_v	σ^2_i	σ^2_{vf}	σ^2_p
Egg prod. (rate)	8.64	19.80	6.30	11.36
Egg. prod. (numb.)	118.80	230.35	58.23	119.58
Mortality	10.42	28.76	14.80	33.70
Body wt.	.014	.046	.012	.028
Egg wt.	.362	.602	.056	.452
Sexual maturity	47.54	154.86	15.67	56.33
Performance index	.1974	.1942	.0695	.1016

Heritability

We define heritability as the ratio of the variety variance component to the total. The variety component includes, additive, dominance, and epistatic effects as well as possible interaction effects other than those accounted for by variety × farm interaction. The total variance is based either on individual records, variety pen means, or variety test means. Heritabilities, computed as indicated, are presented in Table 5. The results show how the heritability of variety differences varies according to the number of experimental units included in a variety mean. The values for H_i simulate, but are not equivalent to, heritability estimated for individual differences within a population. In general, the values for H_i are markedly lower. Of particular interest are the estimates for hen-day egg production. On the average, the variance between variety means is only 2.5 percent of the total variance among individual hens. When the test pen mean is the experimental unit, the heritability is 33 percent, and when the total variance is based on variety means of 2 pens at 4 farms, the heritability of variety differences is 74 percent.

Table 5. *Heritability of variety differences on the basis of individual hens (H_i), pen means (H_p) and test means (H_t).*

	H_i	Hp	H_t
Egg production rate	.025	.33	.74
Laying house mortality	.009	.22	.63
Body wt. at 154 days	.154	.75	.95
Body wt. at 486 days	.042	.26	.68
Egg wt. at 300 days	.082	.42	.84
Age at 50% egg production	.009	.40	.81
Performance Index	.021	.54	.87

$H_i = \sigma^2_v/(\sigma^2_v + \sigma^2_{vf} + \sigma^2_p + \sigma^2_i)$

$Hp = \sigma^2_v/(\sigma^2_v + \sigma^2_{vf} + \sigma^2_p + \sigma^2/n)$

$H_t = \sigma^2_v/(\sigma^2_v + \sigma^2_{vf}/m + \sigma^2_p/mp + \sigma^2_i/mpn)$

m = 4, number of test farms per variety

p = 2, number of pen replications per variety per farm

n = 90, number of birds per pen

The variance component, σ^2_i, represents differences between individual hens in a pen.

The observed variance among pen means is then, $\sigma^2_e = \sigma^2_p + \sigma^2_i/n$.

Genetic Advance

Table 6 gives the estimated genetic advance from selecting the elite variety of 16 tested for some particular trait. We assume that each variety is tested on four farms in duplicate pens of 90 birds each, corresponding to the test conditions used in the Iowa Multiple Unit Test. The results show that, if selection had been made solely for increased egg production, egg number would have been expected to increase by 17.2. If selections were based only on the performance index I, the expected increase in the index is 73 cents.

DICKERSON (1962) pointed out that the expected genetic change in a trait observed in one environment as a consequence of selection in another environment is proportional to the genetic correlation, $r'G$, of the traits measured in the two environments, as originally suggested by FALCONER (1952), and that $r'G$ can be estimated from the ratio, $\sigma^2_G/(\sigma^2_G + \sigma^2_{GE})$. In a strict sense, therefore, it is never possible to measure a direct response from selection (ΔG) because the response of the test population ($\Delta G'$) is always measured in a later generation: hence, in an environment different from the selected population. Thus,

$$\Delta G' = r'G \cdot \Delta G = \frac{\sigma^2_G}{\sigma^2_G + \sigma^2_{GE}} \cdot \Delta G .$$

In this spirit, Table 6 also gives the adjusted estimated genetic advance ($\Delta G'$). The results show that selecting the best one of 16 tested varieties under the conditions specified, is expected, for example, to advance egg production by 11.5 eggs, or lower maturity by 8.2 days, assuming all selection is based on a single trait. Likewise, if selections were based solely on the index, it is expected to increase by 54 cents.

Table 6. *Estimated genetic advance (ΔG) by selecting the elite variety of 16 tested on the basis of a single trait. Each variety is assumed to be tested on 4 farms in duplicate pens of 90 birds each.*

	δ	$\sqrt{H_t}$	σ_v	ΔG	$r'G$	$\Delta G'$
Egg production	1.76	.86	10.9	17.2 eggs	.67	11.5 eggs
Mortality	1.76	.79	3.2	−4.5 %	.41	−1.8 %
Body wt.	1.76	.97	.12	.17 lb.	.54	−.09 lb.
Egg wt.	1.76	.92	.60	.97 oz.	.87	.84 oz.
Maturity	1.76	.90	6.9	−10.9 days	.75	−8.2 days
Perform. index	1.76	.93	.44	73 cents	.74	54 cents

$\Delta G = \delta \sqrt{H_t}\, \sigma_v$. , $r'G = \sigma^2_v/(\sigma^2_v + \sigma^2_{vf})$. , $\Delta G' = (r'G)\, \Delta G$.

If selections were made solely for the index, we can predict the expected correlated responses in the individual traits. From the original data, covariances between the index and other traits were computed for each of the years corresponding to the variance components presented in Table 3. From the variety variance and covariance components, "genetic" regression coefficients were computed. Multiplying the regression coefficients by the expected genetic advance in the index ($\Delta G = 73$) of Table 6 gives the expected correlated responses, CR. Finally, correcting the correlated response by the interaction term, $r'G$, gives the corrected correlated response, CR'. These results (Table 7) show that, if selection is made solely on the performance index I, it is expected to increase the index by 54 cents, but this causes body weight to decline by .06 pounds, egg weight to increase by .23 ounces per dozen, egg production to increase by 11.7 eggs, mortality to decline by 1.8 percent and sexual maturity to decline by 5.8 days.

Table 7. *Estimated correlated responses (CR) when selection is on the Performance Index (I).*

Trait (X)	Units	Regression of X on I (b_{XI})	CR	CR'
Egg production	eggs	24.0	17.5	11.7
Mortality	%	-5.89	-4.3	-1.8
Body wt.	lb.	-.154	-.11	-.06
Egg wt.	oz./doz.	.364	.27	.23
Sexual maturity	days	10.7	-7.8	-5.8

$b_{XI} = \mathrm{Cov}\,(v)\,XI/\sigma^2_{(v)}\,I$. — $CR = b_{XI} \cdot \Delta G(I)$. — $CR' = r'G \cdot CR$.

Optimum Allocation of Test Resources

Following the procedure suggested by Sprague and Federer (1951), the optimum allocation of test resources is given in Table 8. The results assume a fixed total number of 160 test pens divided arbitrarily among farms and pen replicates at each farm. Thus, test procedure *a* in Table 8 specifies 10 varieties tested at 16 farms in single-pen replicates. The average deviation in standard deviation units of the top single variety out of 10 is $\delta = 1.54$ as found in Fisher and Yates' Table XX. Results are given for three traits, egg production (P), mortality (M), and the index (I). We find that test procedure f is expected to give maximum genetic advance for P and for M while test procedure g is optimum for the index, I. Thus, maximum genetic advance requires at least two and perhaps four or five test farms and, except for the gathering of experimental data, only one pen per strain should be used.

Table 8. *Optimum allocation of test resources for maximum genetic advance (ΔG), in a fixed number (160) of available pens assigned to number of varieties tested (s), test farms (m) and pen replication (p) and applied to egg production (P), mortality (M) and the performance index (I).*

Test Procedure	s	m	p	ΔG		
				(P) eggs	(M) %	(I) cents
a	10	16	1	16.0	-4.5	66
b	10	8	2	15.8	-4.4	65
c	16	10	1	17.9	-4.8	75
d	16	5	2	17.5	-4.7	72
e	20	8	1	18.7	-5.0	79
f	40	4	1	*20.05	*-5.1	87
g	80	2	1	20.03	-4.7	*90
h	160	1	1	18.3	-4.0	87

$\Delta G = \delta \sqrt{H_t}\, \sigma_v$. — * optimum test procedure.

Discussion

In the case of both corn yield and egg production, a theoretically large part of the genetic variance is expected to be non-additive because these traits are fitness components. As a consequence, natural selection should exhaust the additive variance in accordance with Fisher's fundamental theorem, although perhaps not in a simple manner. If so, the variance of specific combining ability should be relatively more important than general combining ability (Sprague and Tatum, 1942). For single-cross corn yield trials, Rajas and Sprague (1952) found specific combining ability variance consistently greater than general combining ability variance. Also the interaction variances of locations and years with specific combining ability were larger than the interactions with general combining ability. In the case of single crosses in chickens, however, Goto and Nordskog (1959) found general combining ability was more important than specific combining ability in both white-egg and brown-egg crosses. Logan (1959) found that, among white-egg strain crosses, specific combining ability was largest for egg production adjusted for hatch effects. Hill and Nordskog (1958) found general combining ability for hen-housed egg production largest in Leghorn and heavy-breed crosses. Strain (1960) analyzed data from 78 white-egg type single crosses and found general combining ability accounted for 13 percent of the variance in hen-housed egg production, on an individual bird basis, in the early phase of the test. By the end of the test, however this declined to 1.1 percent. At the same time, specific combining ability, which was initially lower, increased as the test progressed to 2.7 percent. Therefore, the evidence on the relative importance of additive to non-additive genetic-variance for egg production is not yet clear, although it appears that general combining ability is more important.

Extrapolation from the Iowa Multiple Unit Random Sample Performance Test to a specific breeding enterprise obviously is highly speculative. The main difficulty is in specifying the population of "varieties" represented by commercial entries in a random sample test. However, we can say that the estimated variety variance approximates that available to a breeder who establishes lines for a subsequent test cross program from commercially existing varieties. This seems not too unrealistic since it is common knowledge that commercial breeders systematically keep samples of competitors' stocks for possible use in the formation of new varieties.

Viewed superficially, the indicated genetic advance in this study from inter-line selection might seem too large; for example, that one cycle of selecting the best one of 16 tested varieties should increase egg number by 11.5. The question is what happens after the breeder selects the single elite variety. If the selected variety is a source for starting new "synthetic" strains or inbred lines, then to form the lines and to produce crosses from them again, would take considerable time. For corn breeding, such a cycle, including top-cross and single-cross testing, might require 10 to 12 years (Sprague, 1946). In the case of chickens, with less inbreeding and testing, perhaps 6 years would be a minimum time to produce a batch of single-cross varieties for test purposes. Hence, dividing the observed increase by 6 gives an average of 1.9 increase in egg production per year from inter-line selection.

It would be interesting if we could compare this estimate of genetic advance with the more conventional family selection method within a single population. If we assume (1) that the additive genetic variance for egg production is 2 1/2 percent among individuals in a population, (2) that selection is on a family basis, with an average of 5 birds per family, (3) that the best 20 percent of the families are selected, (4) that selecting cockerels on the sib-test is equal to selection of the full sisters, and (5) that the standard deviation of annual egg production among survivors is 40 eggs, then it can be shown that the estimated genetic advance per year is 1.8 eggs. This is of the same order of magnitude as the increase from inter-line selection indicated previously. Therefore, we cannot conclude from this study that progress from inter-line selection is necessarily more effective than conventional intra-line family selection procedures. At the same time, since considerable doubt yet remains as to the real effectiveness of intra-line selection for egg production as discussed by Dickerson (1961), Morris (1963), Nordskog et al. (1967) and others, there is reason to believe that future progress in the genetic advance of egg production should be greater from inter-line selection than from intra-population selection just as we find in the case of corn yield.

In estimating the optimum allocation of testing resources, the value of replicating over years was ignored. The present data were not convenient to study year interaction effects because the array of test varieties varied from year to year. Hill and Nordskog (1956) found statistically significant variety × year interactions for egg production from a study based on commercial inbred-hybrids. They found that replicating tests over years lowered the experimental error more than replicating over farms. For corn yield, Sprague and Federer (1951) deduced that the optimum allocation of 100 test plots would be obtained by planting 25 varieties at 2 locations in each of 2 years. Undoubtedly, a similar situation should prevail in the testing of chickens for egg yield and that maximum genetic advance would require testing in more than a single year.

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Zusammenfassung

Die Untersuchung beruht auf 5jährigen Leistungsprüfungen (1958—1962), ausgeführt an zufälligen Stichproben aus kommerziellen Varietäten von Hühnern, die in Iowa auf Legeleistung gezüchtet wurden. In jedem Jahr wurden 15 oder 16 Varietäten von 15—20 Farmen auf Unterschiede in Legeleistung und anderen wirtschaftlich wichtigen Merkmalen untersucht. Die Varietäten wurden in zweifacher Wiederholung sowohl in zufallsverteilten Blocks als auch in Gitteranlagen geprüft. Die Daten wurden in Varianzkomponenten zerlegt, um die relative Bedeutung der Varietäten- und die der Varietäten ×-Farm-Interaktionsvarianz zu bestimmen. Das Verhältnis der Varietäten zur Gesamtvarianz war auf der Basis der Wiederholungsmittel für Eizahl, Stallmortalität, Körpergewicht der Adulten und Eigröße jeweils 0,33, 0,22, 0,26 und 0,42. Der geschätzte genetische Fortschritt in der Legeleistung war bei Verwendung der ertragreichsten unter den 16 getesteten Varietäten 11,5 Eier. Wenn die Selektion der Rasse auf einem Ertragsindex beruht, der mit Hilfe der multiplen Regression des erwarteten Einkommens auf die vier obigen Merkmale bestimmt wird, so ist zu erwarten, daß die geschätzte korrelierte Antwort in einer Steigerung der Eizahl um 11,7, einer Verminderung der Mortalität um 1,8%, einer Abnahme des Körpergewichts um 0,27 kg und einer Zunahme des Eigewichts um 6,5 g je Dutzend besteht. Eine Analyse des optimalen Einsatzes der Prüfverfahren auf maximalen genetischen Fortschritt zeigt, daß unter der Voraussetzung, daß etwa 160 Prüfglieder zur Verfügung stehen, ca. 40—80 Varietäten auf 2 bis 4 Farmen in einfacher Wiederholung getestet werden sollten.

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The Proportion of Genetic Deviates in the Tails of a Normal Population*[1]

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Summary. If genetic and environmental effects upon a quantitative phenotype $X = G + E$ are normally and independently distributed then the probability distribution of genetic value G among individuals of fixed phenotypic value X is likewise a normal distribution. The mean of this *a posteriori* distribution of genetic values is $\bar{g} + h^2 (X - \bar{g})$ and the variance is $\sigma_g^2 (1 - h^2)$, where $\bar{g}$ is the *a priori* mean of X, h^2 is the heritability ratio, and σ_g^2 is genetic variance. For any fixed values of h^2 and σ_g^2 the *a posteriori* probability that the genetic value G associated with a given phenotype X exceeds the population mean by any specified amount can therefore be read directly from the tables of the standard normal distribution. The expected proportion of these superior genetic deviates among individuals whose phenotypic value exceeds some specified constant may also be calculated (by numerical analysis) and is presented here in graphical form.

If phenotypic selection is practiced by choosing the best out of N phenotypes then N should be large enough to assure high probability of obtaining a superior genetic deviate. The operating characteristics of this type of selection are displayed in tabular form, again based upon numerical integration.

Introduction

The phenotypic array exhibited by a segregating genetic population reflects both the genetic and the environmental variability within the population. As a consequence, an element of uncertainty attaches to selection for genetically superior individuals on the basis of their phenotypic traits. The latter may, by chance, be merely the result of an unusually favorable environment acting upon a genotype which under less favorable conditions would display only a mediocre or even undesirable phenotype. Chances for the occurrence of such phenotypic deception depend, of course, upon the magnitude of variability environmentally induced as compared to that caused by genetic differences.

Any mathematical formulation of this problem to enable the geneticist to evaluate numerically his chances for successful selection would require a detailed description of the phenotypic frequency distribution in the population. The total segregating population is a mixture of subpopulations, each of which represents the distribution of phenotypes produced by a single genotype under the existing range of environmental conditions. Each subpopulation or genotype contributes to the total population in proportion to its genotypic frequency. A mathematical description of the population consists, therefore, of specifying the relative frequency of each genotype and the exact form of its associated distribution of phenotypes.

Usually, when selection is practiced for economic purposes, a large number of both genetic and environmental factors operate at variable levels to determine the phenotypes in the population. Empirical evidence supports the belief that, in this case, the total-frequency distribution and also the component distributions for a quantitative phenotypic trait are approximately Gaussian in form. A standard population model has therefore come into use for such problems as the prediction of advancement under selection. It is Eisenhart's Model II (1947) which represents, in the simplest case, a normal mixture of normal subpopulations with constant variance. Each genotype is assumed to generate a normal distribution of phenotypes under the existing range of environmental conditions. The distribution of phenotypic means (called genotypic values) is likewise normal.

Graphs of the Proportion of Genetic Deviates

The phenotypic value X, for some quantitative trait of an individual selected at random from a genetic population, may be regarded, conceptually, as the sum of two components:

G = average phenotype for the genotype of the chosen individual

E = deviation of the particular phenotype of the chosen individual from the average phenotype (G) for the genotype of that individual $= X - G$

or

$$X = G + E\,.$$

The first component G is conventionally called the genotypic value. E is the environmental effect. If the population structure is a normal mixture of normal subpopulations having a common environmental variance, then the chance variables G and E follow independent normal distributions. G has a mean value of $\bar{g}$ and variance σ_g^2. E has a mean value of zero and variance σ_e^2. Thus X itself follows a normal distribution, with mean $\bar{g}$ and variance $\sigma_g^2 + \sigma_e^2$.

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