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GENOTYPIC AND PHENOTYPIC CORRELATIONS IN CORN

AND THEIR IMPLICATIONS IN SELECTION

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The report to follow concludes the project as originally written and is a manuscript prepared for publication in the Agronomy Journal.

The variations occurring in segregating populations of corn are attributable to three main sources; namely, additive genetic effects, non-additive effects due to dominance and interaction of non-allelic genes, and environmental effects. The term genotypic variation is used throughout with reference only to the additive genetic or heritable variation which is the portion of the variation responsible for progress resulting from selection. Phenotypic fluctuations may result from combinations of all of these types of variations. Since the breeder is concerned with selecting superior genotypes, but of necessity must choose individuals from their phenotypic expressions, estimates of the genotypic and phenotypic variances for various characters are needed. Furthermore, since most of the characters of economic importance, such as yield, are complex in inheritance and may involve several related characters, the degree of genotypic and phenotypic correlation of the characters is also important. To obtain these correlations it is necessary to have estimates of the genotypic and phenotypic covariances in addition to the variances for the various characters. These correlations are not only of interest from a theoritical consideration of the quantitative inheritance of the characters, but of practical value since selection is usually concerned with changing two or more traits simultaneously.

The experienced breeder has certain desired plant characteristics in mind when selecting for particular genotypes and thus must apply various weights to different traits as he makes his decisions. This suggests the use of a selection index which gives proper weight to each of the two or more characters to be considered. Hazel and Lush [3] showed that selection based on such an index is more efficient than selecting individually for the various characters. The basis for the development of the selection indexes has been provided by Hazel [2] with an example in animals and by Smith [7] who illustrates its use in plants. Simulate [6] , applying this technique, concluded that tiller number and grain weight should be the basis for selection of higher yield in certain _durum_ wheats in India.

The optimum weights to be assigned the characters in selection will depend upon the following factors:

(1) phenotypic variances and covariances between each of the characters to be involved.

(2) the genotypic variances and covariances

(3) the relative economic values of the several characters or a proper evaluation of the ultimate product.

The purposes of this paper are: (1) to present estimates of additive genetic variance and covariance for eight characters of prolific corn; (2) to show how phenotypic variances and covariances, appropriate for a particular situation, can be constructed from the estimates of additive genetic, dominance deviations and environmental variances and covariances; and (3) to demonstrate the construction of a selection index. Indexes are presented involving various combinations of several of the characters using yield of ear corn as the ultimately desired product.

These selection indexes are not to be taken as the best available or even applicable for corn in general. They are presented to illustrate the type of information possible from such data. The conditions determining the usefullness of

an appropriate selection index may vary with individual plant breeders. Comparable gains may be possible following other procedures with less cost per unit of progress.

Furthermore, yield by itself is probably not an adequate criterion of economic worth. Selection based on that premise could easily lead to the development of unsatisfactory plant types. A completely satisfactory criterion would need to include such characters as plant and ear types, lodging and disease resistance in addition to yield.

Materials and Methods

Biparental crosses were made within each of the following F_2 populations of prolific corn: CI 21 X NC 7, NC 16 X NC 18 and NC 34 X NC 45. Each of the plants used as male parents was crossed on three to four plants used as female parents. The progeny of these biparental crosses were grown in duplicate plots in 1947. Details of the design of the experiment, estimates of heritability and degree of dominance for eight characters were reported by Robinson et.al. [5]. The characters studied were plant height, ear height, husk extension, husk score (length + tightness), ears per plant, ear length, ear diameter and yield of ear corn.

An example of the Analyses of Variance computed from the data is presented in Table 1 for ears per plant and yield. These results are for the combined analyses of the three populations. The components of variance describing each of the mean squares are symbolized in the last column to the right of the table. The pooled error mean squares for "males in blocks X replications in blocks" and "females in males in blocks X replications in blocks" are the result of the plot-to-plot environmental variability, Ep, and the plant-to-plant variability within plots, Ew + A, the latter being divided by k (number of plants per plot) to obtain a comparable expression with the other items shown. The non-environmental portion of the intra-plot component of variance, symbolized by "A", contains 1/2 of the additive genetic

Table 1. Analyses of Variance and Covariance of Ears per Plant and Yield from Three Populations of Prolific Corn.

Source of Variation	Degrees of freedom	Ears per plant M.S.	Yield M.S.	Ears per plant x yield M.P.	Components of variance a/
Blocks	39	.1968	.0220	.0781	
Replications in blocks	45	.0289	.00553	.00641	
Males in blocks	146	.1873	.0214	.0466	$\frac{E_w + A}{k} + E_p + k'F + k''M$
Females in males in blocks	518	.0745	.0112	.0188	$\frac{E_w + A}{k} + E_p + k'F$
Males in blocks x replications in blocks / Females in males in blocks x replications in blocks	618	.0395	.00472	.00767	$\frac{E_w + A}{k} + E_p$

a/ E_w = Environmental variance between plants in the same plot
E_p = Environmental variance between plots in a block
A = Genotypic variance among full sibs = $1/2\ V_g + 3/4\ V_d$
F = Additional variance among paternal half sibs due to female differences = $1/4\ V_g + 1/4\ V_d$
M = Additional variance among random progeny due to male differences = $1/4\ V_g$
k = Harmonic mean of the plants per plot
k' = Plots per female = 2
k'' = Females per male x k' = 7.3972

variance and 3/4 of the variance resulting from dominance deviations. The remaining 1/2 of the additive genetic variance, V_g, is equally divided between the "males in blocks" and "females in males in blocks" items of the analyses, the latter containing also the remaining 1/4 of the variance due to dominance deviations, V_d. The derivation of these components of variance in such populations was given by Comstock and Robinson [1] .

Covariance analyses between all pairs of the eight characters, similar to that illustrated in the mean product column for ears per plant X yield in Table 1, were computed. The symbols and content of the components of covariance for mean products are completely analogous to those for the mean squares and components of variance.

Experimental Results

Estimates of the Components of Variance and Covariance.

As mentioned previously, phenotypic variation includes intra- and inter-plot variance, variance due to dominance deviations and additive genetic variance. To construct phenotypic variances and covariances for a particular situation it is necessary to have estimates of the various components of variance and covariance.

The plot variances and covariances from each of the analyses are presented in Table 2. These values are the mean squares and mean products for the pooled error for each character and pair of characters. For example, the error mean squares, .0395 and .00472 for ears per plant and yield, respectively, and their mean product, .00767, given in the bottom line of the analyses of table 1, are listed in the Table 2.

Table 2. Estimates of the Plot Variance and Covariance for Eight Characters in Three Populations of Prolific Corn. (Components of Variance in Parentheses)

	Plant height	Ear height	Husk length	Husk score	Ears per plant	Ear length	Ear diameter	Yield
Plant height	(9.9833)	5.0625	0.0448	-0.0121	0.0681	0.1848	0.00133	0.0407
Ear height		(9.7700)	-0.0747	-0.2280	0.1178	0.0256	0.0212	0.00455
Husk length			(0.1942)	0.1769	0.00614	-0.0334	-0.00326	-0.00406
Husk score				(0.3058)	0.00779	-0.0426	-0.00215	-0.00276
Ears per plant					(0.0395)	0.00472	0.00013	0.00767
Ear length						(0.1046)	0.00815	0.00830
Ear diameter							(0.00408)	0.00158
Yield								(0.00472)

The variances and covariances due to female differences, F, estimating $1/4 \, V_g + 1/4 \, V_d$, are given in Table 3. Each of the values was obtained in the following manner, using the yield mean squares for illustration. An estimate of F for yield results from subtracting the pooled error from the "females in males in blocks" and dividing by $k' = 2$, the number of plots per female. Thus from Table 1, F for yield is $\frac{.0112 - .00472}{2} = .00324$. Similiar computations were performed with each analyses to obtain the remaining values.

Table 3. Estimates of the Components of Variance and Covariance Containing 1/4 Vg + 1/4 Vd for Eight Characters in Three Populations of Prolific Corn. (Components of Variance in Parentheses)

	Plant height	Ear height	Husk length	Husk score	Ears per plant	Ear length	Ear diameter	Yield
Plant height	(12.3049)	6.4387	0.1574	0.0894	0.0710	-0.0186	0.0168	-0.0282
Ear height		(4.9637)	0.0939	0.0390	0.0739	-0.1126	-0.00655	0.0421
Husk length			(0.1999)	0.2252	-0.00787	-0.0416	-0.00367	-0.0115
Husk score				(0.2140)	-0.0162	-0.0378	-0.00216	-0.0130
Ears per plant					(0.0175)	-0.00009	-0.00182	0.00556
Ear length						(0.0446)	0.00288	0.00640
Ear diameter							(0.00194)	0.00076
Yield								(0.00324)

The estimates of the variances and covariances resulting from male differences, M, which contain 1/4 Vg are listed in Table 4. These estimates are obtained by subtracting the "females in males in blocks" mean square from "males in blocks" and dividing by k", the average number of plots per male. For example, the estimate of M for yield, using values in Table 1, is $\frac{.0214 - .0112}{7.3972} = .00138.$

Table 4. Estimates of the Component of Variance and Covariance Containing 1/4 Vg for Eight Characters in Three populations of Prolific Corn. (Components of Variance in Parentheses)

	Plant height	Ear height	Husk length	Husk score	Ears per plant	Ear length	Ear diameter	Yield
Plant height	(11.6033)	7.3831	0.3773	0.2666	0.1263	0.0312	-0.00756	0.0482
Ear height		(6.6524)	0.1372	0.0333	0.0654	0.0137	-0.00598	0.0458
Husk length			(0.1370)	0.1482	0.00675	-0.00258	-0.00510	-0.00154
Husk score				(0.1629)	0.00105	-0.00627	-0.00481	-0.00346
Ears per plant					(0.0152)	-0.00069	-0.00031	0.00376
Ear length						(0.0353)	0.00116	0.00131
Ear diameter							(0.00112)	0.00022
Yield								(0.00138)

Phenotypic and Genotypic Correlations.

Phenotypic variances and covariances depend upon the nature of the selection units and in the following example were constructed for the means of two replications of biparental progenies. The formula for these values is $\frac{\sigma^2_{pl}}{2} + F + M$, where σ^2_{pl} is the estimated plot variance or covariance given in Table 2 and F and M estimates, defined above, appear in Tables 3 and 4. The phenotypic variance for ears per plant is $\frac{.0395}{2} + .0175 + .0152 = .0526$. Similiar calculations, using components of variance for yield and covariance components for ears per plant X yield, give .00694 and .0132, respectively. The phenotypic correlation between these characters

$$= \frac{.0132}{\sqrt{(.0526)(.00694)}} = .691.$$ Genetic correlations were computed from the additive

genetic variances and covariances given in Table 4. The genotypic correlation for

cars per·plant and yield is $\frac{.00376}{\sqrt{(.0152)(.00138)}} = .819.$ The twenty-eight possible

genotypic and phenotypic correlations between the eight characters are presented

in Table 5.

Table 5. Genotypic and Phenotypic Correlations Between Characters in the Combined
Populations of Biparental Progenies. (Phenotypic Correlations in
Parentheses)

	Plant height	Ear height	Husk length	Husk score	Ears per plant	Ear length	Ear diameter	Yield
Plant height		.840 (.749)	.299 (.157)	.194 (.089)	.300 (.188)	.049 (.054)	-.066 (.025)	.381 (.216)
Ear height			.144 (.072)	.032 (-.014)	.205 (.213)	.028 (-.058)	-.069 (-.007)	.478 (.266)
Husk length				.992 (.963)	.148 (.013)	-.037 (-.254)	-.412 (-.221)	-.112 (-.275)
Husk Score					.021 (-.068)	-.083 (-.247)	-.356 (-.155)	-.231 (.295)
Ears per plant						-.030 (.021)	-.075 (-.126)	.819 (.691)
Ear length							.184 (.313)	.188 (.393)
Ear diameter								.174 (.298)
Yield								

It should be noted that the phenotypic and genotypic correlations may differ in

magnitude. In some cases, e·g., cars per plant and plant height and cars per plant

and yield, selection for one of the characters would result in greater changes in

the other character than would be expected from the phenotypic correlations. The

opposite is the case with husk score and yield. This, of course, is based on the assumption that the differences indicated between genotypic and phenotypic correlations are true differences and not due to sampling variation alone.

Ear length and ear diameter have very low positive or negative correlations with all other characters. In no instance is there a wide discrepancy in the genotypic and phenotypic correlations between either of these and any of the other six characters.

The genetic correlations of the seven characters with yield may be grouped in the following three classifications:

(1) ears per plant having a high correlation

(2) plant and ear height with medium positive genetic correlations

(3) husk length, husk score, ear length and ear diameter having little or no inherited relationship with yield.

Construction of Selection Indexes.

The correlation coefficients are of interest but of little value unless some application is made of the various relationships. The phenotypic and genotypic variances and covariances used to compute the correlations provide the basis for constructing a selection index.

The selection index, of the form $b_1X_1 + b_2X_2 + \cdots + b_nX_n$, is so constructed as to have the estimated b values give the best available weights to each of the various characters considered in selection. The symbols used in the general formula for the selection index are X_1, X_2, ..., X_n, the phenotypic values of the traits; and b_1, b_2, ..., b_n, the relative weights to be applied to each character.

The general formulae for the set of simultaneous equations, the solution of which yields the b values required in the selection index, is shown here:

$$b_1 p_{11} + b_2 p_{12} + \ldots + b_n p_{1n} = g_{1y}$$

$$b_1 p_{12} + b_2 p_{22} + \ldots + b_n p_{2n} = g_{2y}$$

$$\begin{array}{cccc} \bullet & \bullet & \bullet & \bullet \\ \bullet & \bullet & \bullet & \bullet \\ \bullet & \bullet & \bullet & \bullet \end{array}$$

$$b_1 p_{1n} + b_2 p_{2n} + \ldots + b_n p_{nn} = g_{ny} \; .$$

The p symbols refer to phenotypic variances and covariances and the g symbols on the right side of the equations refer to genotypic variances and covariances. To be more specific:

p_{11} is an estimate of the phenotypic variance of X_1

p_{12} is an estimate of the phenotypic covariance of X_1 and X_2

etc.

g_{1y} is an estimate of the genotypic covariance of X_1 and Y

g_{2y} is an estimate of the genotypic covariance of X_2 and Y

etc.

Should one be setting up a selection index for yield and yield was also to be one of the characters in the index, then both the phenotypic and genotypic variances of yield would occur in the set of equations; the phenotypic on the left and genotypic on the right-hand side.

The solution of the set of equations given below will yield the desired b values in the selection index for yield when selection is based on the

following observable characters: X_1 = plant height, X_2 = ears per plant and X_3 = yield.

$$b_1\ 28.8796 + b_2\ 0.2313 + b_3\ 0.0968 = 0.09640$$

$$b_1\ 0.2313 + b_2\ 0.0526 + b_3\ 0.0132 = 0.00752$$

$$b_1\ 0.0968 + b_2\ 0.0132 + b_3\ 0.00694 = 0.00276$$

Three equations are necessary since there are three unknown b values. The following phenotypic and genotypic values have been substituted into each equation:

First equation:

p_{11} = 28.8796 = estimate of phenotypic variance of plant height

p_{12} = 0.2313 = estimate of phenotypic covariance of plant height and ears/ plant

p_{13} = 0.0968 = estimate of phenotypic covariance of plant height and yield

g_{1y} = 0.0964 = estimate of genotypic covariance of plant height and yield.

Second equation:

p_{21} = 0.2312 = estimate of phenotypic covariance of ears/plant and plant height

p_{22} = 0.0526 = estimate of phenotypic variance of ears/plant

p_{23} = 0.0132 = estimate of phenotypic covariance of ears/plant and yield

g_{2y} = 0.00752 = estimate of genotypic covariance of ears/plant and yield.

Third equation:

p_{31} = 0.0968 = estimate of phenotypic covariance of yield and plant height

p_{32} = 0.0132 = estimate of phenotypic covariance of yield and ears/plant

p_{33} = 0.00694 = estimate of phenotypic variance of yield

g_{3y} = 0.00276 = estimate of genotypic variance of yield.

The phenotypic variances and covariances were computed as illustrated previously for two replications of the biparental progenies. The genotypic variances and covariances, used in computing the selection index, are twice the appropriate values listed in Table 4. This is necessary since values in Table 4 contain an estimate of 1/4 Vg, whereas the genotypic variance among biparental progenies contains 1/2 Vg.

When the equations are solved the selection index becomes:

$$.02X_1 + .08X_2 + .22X_3.$$

It is now possible to put this index to use. Suppose, that from the population from which the index was computed, it is desired to select the superior progenies on the basis of the selection index. For example, one progeny had the following mean values: 110 inches in height, 2.0 ears per plant, and yielded .50 pounds per plant. Applying the weights in the selection index, .02(110) + .08(2.0) + .22(.50) = 2.5, the selection score. Another progeny was 90 inches in height, had 1.6 ears per plant and yielded .65 pounds per plant. This progeny has a selection score of .02(90) + .08(1.6) + .22(.65) = 2.1. Thus, in this example, the entry with the highest yield does not get the highest score resulting from use of the selection index.

<u>Expected Genetic Advance and Relative Efficiency from Use of Selection Index.</u>

The formula for computing the expected genetic advance is

$$\frac{z}{p} \sqrt{b_1 g_{1y} + b_2 g_{2y} + \ldots + b_n g_{ny}}$$

where $\frac{z}{p}$ is the selection differential in standard units.[1] The terms beneath the radical have already been defined; the b values being the weights in the selection index and g_{1y}, g_{2y}, etc. the genotypic covariances of the observed characters with the character being selected.

For example, the expected genetic advance in yield from selecting the superior 5% of the progeny when selection is based on the selection index for plant height, ears per plant and yield can be calculated. The expected genetic advance would be

$$2.06 \sqrt{(.02)(.0964) + (.08)(.00752) + (.22)(.00276)} = .0768.$$

The values used are defined as:

(1) 2.06 = the selection differential in standard units for 5% selected

(2) .02 = b value for plant height

(3) .0964 = estimate of genotypic covariance for plant height and yield

(4) .08 = b value for ears per plant

(5) .00752 = estimate of genotypic covariance for ears/plant and yield

(6) .22 = b value for yield

(7) .00276 = estimate of genotypic variance for yield.

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[1] z is the value of the ordinate of a normal curve above which lies the area corresponding to the percentage of the population to be selected and p is that percentage to be saved. In otherwords $\frac{z}{p}$ is the mean phenotypic difference between the selected material and all material available for selection in units of the standard deviation. Lush [4] lists the values for $\frac{z}{p}$ for various percentages of the population selected or they may be computed from values of the ordinate found in mathematical tables listing values of the normal curve.

Converting the .0768 to bushels per acre by multiplying by 118.3, the factor

appropriate for the plant spacing used in the study, gives the expected genetic

advance to be 9.1 bushels per acre.

A number of different indexes were constructed and the estimated genetic

superiority from the use of each was calculated. In each case it is assumed that

the top 5% of the progeny would be saved. The results are reported in Table 6.

Table 6. Expected Genetic Advance in Yield from the Use of Various Selection
Indexes and Their Relative Efficiency.

Index number	Content of index	Bushels per acre	Relative efficiency
	Yield	7.0	100%
(1)	Ears/plant	8.0	114
(2)	Ears/plant and yield	8.7	124
(3)	Plant height and ears/plant	8.5	121
(4)	Plant height, ears/plant and yield	9.1	130
(5)	Plant height, ears/plant, ear diameter and ear length	8.9	127
(6)	Plant height, ears/plant, ear diameter, ear length and yield	9.1	130

The top line gives the expected genetic progress when selection is based on

yield alone. This predicted advance, 7.0 bushels per acre, is used as a basis for

comparison of the relative efficiency from use of the various selection indexes.

The results showing 14% more expected genetic progress in yield when selection is

based entirely on ears per plant compared with selecting for yield alone may at

first not appear feasible. However, since yield is a complex character and highly

influenced by environmental variations, related characters with higher heritabilities, when properly weighted, may well serve as better indicators of the genetic yield potentialities of a progeny.

Discussion

A theoretical evaluation of various selection procedures such as mass selection, ear-to-row breeding, use of biparental progenies, top-cross testing, etc. requires the characterization of the variability between the units used in the breeding procedure. These values can always be worked out in terms of additive genetic variance, variance due to domance deviation and the environmental variance between and within plots. As an example the progress expected from selection among biparental progenies has been estimated. The estimates of the variances and covariances presented in Tables 2, 3, and 4 may be used in the evaluation of other selection procedures.

The positive genetic correlation between height and yield might be questioned since the correlation, if present at all, is very low among varieties involving different plant types. However, the correlations reported were computed within populations and might logically be expected as a result of both height and yield being positively correlated with general vigor.

As pointed out earlier yield by itself is probably not a satisfactory measure of economic value in corn, since such plant characters as lodging, ear height, and husk characters have economic importance. The problem is further emphasized by the positive genetic correlations of yield with ear number and ear height. Attaching no economic importance to ear number and ear height we find that giving positive weight to both these characters will contribute to rate of genetic improvement for yield. However, such selection would eventually result in the

development of material taller than desirable and which produced ears objectionably small in size. To make proper use of such characters in selection, their importance must be appropriately considered in the definition of economic worth. It should be emphasized, however, that when this is done the progress measured in terms of yield alone will almost certainly be less than when the economic importance of plant type is ignored.

SUMMARY

The twenty-eight possible genotypic and phenotypic correlations were computed from the combined analyses of three populations of prolific corn for the following characters: plant height, ear height, husk extension, husk score, ears per plant, ear length, ear diameter and yield. Ear length and ear diameter had relatively low positive or negative correlations with each of the other characters. Ears per plant had the highest positive genetic correlation with yield of all characters. The only other characters found to have an appreciable genetic association with yield were plant and ear height.

The genotypic and phenotypic variances and covariances entering into the computation of the correlations were used to illustrate the construction of selection indexes in corn. Various selection indexes were constructed and the expected genetic advance from the use of each was determined. The relative efficiency from the use of the various selection indexes, compared with selection for yield alone, is given for the material contained in this study. The limitations of these specific results are emphasized.

LITERATURE CITED

1. Comstock, R. E. and Robinson, H. F. The Components of Genetic Variance in a Population of Biparental Progenies and Their Use in Estimating the Average Degree of Dominance. Biometrics, 4:254-266. 1948.

2. Hazel, L. N. The Genetic Basis for Constructing Selection Indexes. Genetics 28: 476-490. 1943.

3. Hazel, L. N. and Lush, J. L. The Efficiency of Three Methods of Selection. J. Hered. 33: 393-399. 1943.

4. Lush, J. L. Animal Breeding Plans. Ames, Iowa: The Collegiate Press. Ed. 3. 1949.

5. Robinson, H. F., Comstock, R. E. and Harvey, P. H. Estimates of Heritability and the Degree of Dominance in Corn. Agron. Jour. 41: 353-359. 1949.

6. Simlate, K. M. An Application of Discriminant Function for Selection in Durum Wheats. Indian Jour. Agr. Sci. 17: 269-280. 1947.

7. Smith, H. F. A Discriminant Function for Plant Selection. Ann. Eug. 7: 240-250. 1936.