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CHARACTERIZATION OF GENETIC VARIABILITY IN AN ADAPTED
AND AN EXOTIC VARIETY OF CORN (Zea mays L.)
AND IN THE CROSS DERIVED FROM THEM

by

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PREVIEW

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INTRODUCTION

A number of early geneticists, particularly Fisher and Wright, recognized that an entirely different approach was needed to obtain the type of genetic information that would allow prediction of genetic advance in continuously distributed observations when selection is practiced under various systems of breeding. Since their pioneer studies, many purely theoretical investigations of quantitative genetics have been conducted, and the principles derived from them have been gradually tested by observation and experiment. The means of study have been experiments involving controlled mating, and the observations were made in the form of means, variances and co-variances.

Fisher (1918) recognized three components of hereditary variance: 1) an additive portion resulting from average effects of genes, 2) a dominance component arising from interactions of alleles, and 3) an epistatic part associated with interactions of non-alleles. Investigations of the magnitude and composition of these variances in the quantitative characters of populations have received more attention in the last two decades because they suggest the type of breeding procedure to be followed for the improvement of that particular population.

From the experiments of Johannsen, Nilsson-Ehle and East, it became clear that variation arises from the joint action of the genotype and environment. Theoretically, the more variable or diverse the two varieties which are crossed, the greater is the heterosis expected. There are many experimental findings reported in the literature indicating that crosses of unrelated inbred lines of corn show greater heterosis than crosses of related lines, although Gilbert (1960) has recently

expressed the opinion that increased heterozygosis is not always advantageous. Moreover, these earlier experiments in corn involved lines derived from locally adapted varieties and, thus, represented a limited range of genetic diversity. With increased interest in exotic germplasm for breeding programs in various countries, the question of the association of heterosis and genetic diversity has become particularly important.

Studies on the association of heterosis and genetic diversity in crosses from a wide range of varietal material of maize have recently been reported by Moll et al. (1962) and Paterniani and Lonnquist (1963). No reported results are as yet available on the characterization of genetic variability in open-pollinated varieties and their crosses from distinct geographical regions.

The present study was designed to estimate the magnitude of additive genetic and dominance variance^{1/} and to study the association of heterosis and genetic diversity in an adapted and an exotic corn variety and in the cross derived from them.

^{1/} The term dominance variance will be used in this thesis to include all non-additive genetic variance since the design used does not permit separation of dominance variance and epistatic variance.

REVIEW OF LITERATURE

Heterosis, the increased vigor of the F_1 over the mean of the parents, has been recognized for many years. According to East and Hays (1912), Kolreuter (1763) first studied hybrid vigor in artificial plant hybrids (Nicotiana hybrids). These were isolated observations which suggested no theory as to why these hybrids should exceed their parents in size and general vigor. Knight (1799) noted the deterioration of some of the old standard horticultural varieties and advanced a theory concerning physiological vigor and its decline. Darwin (1868) demonstrated that cross-fertilization results, in many cases, in increased size, vigor and productiveness as compared with self-fertilization or with other close inbreeding within the same species. Beal (1877-1882) reported that hybrids between different open-pollinated varieties of corn yielded as much as 40 per cent more than the parent varieties. Holden (1948) commented that the hybrid corn (as we know it today) was unknown, not even dreamed of, prior to 1900. "Controlled parentage was the dominant purpose or object of early corn improvement work."

Collins (1909) reported increased yields from variety crosses. Davenport (1908), Keeble and Pellew (1910) and Bruce (1910) suggested that the increased performance of the F_1 generation over the mean of the parents could be explained by assuming dominance for the favorable alleles. East and Hays (1912) stated, "The decrease in vigor due to inbreeding naturally cross-fertilized species and the increase in vigor due to crossing naturally self-fertilized species are manifestations of one phenomenon. This phenomenon is heterozygosis, crossing produces heterozygosis in all characters by which the parent plants differ. In-

breeding tends to produce homozygosis automatically." Shull (1914) proposed the term heterosis to replace the phrases, "stimulus of heterozygosis", "heterozygotic stimulation", etc.

Objections to the dominance hypothesis were raised on two grounds. First, it should be possible to obtain individuals homozygous for all the dominant factors. Second, the F_2 distribution curve should be skewed rather than symmetrical. Jones (1917) pointed out that many genes probably affect growth and that each chromosome would be expected to contain several of these genes. A single linkage group would be expected to include some favorable alleles at some loci and unfavorable alleles at other loci. Jones was also able to reconcile the symmetrical distributions actually observed with the hypothesis on the basis that linkage between groups of favorable and unfavorable genes would lead to theoretically symmetrical distributions. Collins (1921) pointed out that even in the absence of linkage, skewness would be difficult to detect and, moreover, the chances of recovering a completely homozygous type would be remote so long as the number of genes involved was at all large.

Richey (1922) presented a summary of 244 reported comparisons between the parental varieties and their F_1 crosses as a sample of the results obtained up to that time. His summary showed that 82.4 per cent of the crosses exceeded the parental average with 55.7 per cent exceeding the higher yielding parent. In general, the crosses that produced the largest actual yields were those between parents that were themselves high yielding and represented contrasting combinations, such as flints x dents or flour x dent. Hayes and Olson (1919) presented data showing the difference in performance of varietal hybrids, dent x dent, dent x

flour and dent x flint. The greatest increases in yield came in the dent x flour and dent x flint crosses (32.5 per cent and 27.6 per cent, respectively, over the dent parent, Minnesota 13) thus showing that crosses between parents of presumably different origins gave greater heterosis.

Lonnquist and Gardner (1961) working with twelve open-pollinated corn belt varieties or varietal composites and their F_1 intercrosse reported that crosses averaged 8.5 per cent heterosis. Average yield superiority relative to high parent was 2.8 per cent. Their results are in agreement with Richey's summary of 244 reported comparisons and Crow's computed 5 per cent expected heterosis based on the dominance hypothesis. Their findings are not in agreement with those reported by Robinson et al. (1956) where F_1 heterosis of 20 per cent in southern prolific varieties was obtained. Since no standard check was included in this study, their results can be questioned on the grounds that inbreeding might have taken place in the varieties to the extent that the F_1 showed high heterotic response.

Moll et al. (1962) reported on crosses of varieties with diverse germplasm. They used two varieties from each of three geographical regions--southeastern United States, midwestern United States and Puerto Rico. Their results indicated that greater genetic diversity of the parental varieties is associated with greater heterosis in the variety cross. Highest increased yield was shown by Puerto Rican varieties with a southwestern variety, in spite of the fact that Puerto Rican varieties were low in yield.

Paterniani and Lonnquist (1963) reported on grain yields of 12 races of corn representing a wide range of diversity with respect to origin (Brazil, Mexico, Paraguay and Argentina) and comprising flint, flour and dent types and their F_1 intercrosses. Ninety-seven per cent of the crosses exceeded the mid-parent yield and 76 per cent exceeded the high parent in yield. The average heterotic response was 33 per cent. Yields exceeded the high parent by an average of 14 per cent. They observed a high correlation of mid-parent versus F_1 cross yields. Dent x dent crosses gave highest average yields followed by dent x flour and flour x flour. They emphasized that extent of genetic diversity present in varieties or races should be determined by actual performance trials of the intercrosses rather than assumed diversity based on differences in type of endosperm.

Extensive use of exotic germplasm has been made for improvement of corn in India. Four hybrids released from the program in 1961 showed an average increase of 22 per cent to 53 per cent over the best local varieties in 33 location tests. Three of the lines of these four flint-dent hybrids are from Indian germplasm, four from South American origin and three from United States germplasm.

Timothy (1963) reported on the results of an experiment involving exotic crosses in Colombia. The cross between Cuba 325 (Cuba 325 is a collection from Cuba of the Cuban yellow flint types) and West Indian composite (West Indian composite is made up of selected collections from the West Indies and the United States) showed an increase of 49 per cent over the higher yielding parent, West Indian composite. He also reported that varietal crosses of Colombian and exotic varieties showed 17 to 52 per cent heterosis. The F_1 yields exceeded those of the higher parents by an over-all average of 22 per cent.

Robertson and Reeve (1952a) reported experiments with the Nettlebed stock of *Drosophila melanogaster*. Two lines, each of which had ceased to respond to selection for long wing and long thorax, exhibited heterosis in the F_1 . A decline in the F_2 was followed by a striking response to selection for long thorax and modest response for long wings. This response continued steadily for about six generations before falling off rather suddenly. This was followed by a period of stability during which other tests demonstrated that the line remained heterozygous. They concluded that the intercrossing of large lines enabled them to increase body size to a level considerably higher than would otherwise have been the case.

Robertson (1955) reported results of two-way selection for body size in three stocks of *Drosophila melanogaster*. Using thorax length as the measure of size, he observed an immediate and sustained response to selection in either direction in all three stocks with mass selection. Although selection for small size produced a greater change than selection for large size, the actual levels of size at which the corresponding strains stabilized were approximately the same. After about 15 generations of mass selection, a level was reached beyond which it was difficult to make progress by mass selection because additive genetic variance had been dissipated. He intercrossed the strains selected in the same direction. All crosses showed heterosis in the F_1 and a decline in the F_2 . There was a tremendous response to subsequent selection. The new lines advanced beyond the average size of the parent selected strains by about 50 per cent of the deviation of the latter from the control stock. In the normal unselected wild stocks, under favorable conditions, individual gene effects both within and between loci appear more additive with respect

to size than when inbreeding occurred. He concluded, and I quote,

"Selection generally leads to an increase in variance which appears to be largely due to the increased effect of genetic segregation and this constitutes an aid to selection progress. It is possible that linkage plays a part here, since selection may build up groups of linked genes which tend to segregate as a unit. Although selection may depend in the earlier stages, on more or less additive effects, continued progress is likely to rely to increasing extent on the rejection of epistatic genes or gene combinations which are brought into greater prominence and there is no reason why the process should not continue until fixation is reached."

Shull (1908) and East (1908) independently proposed that there are loci at which the heterozygote is superior to either homozygote and that vigor increases in proportion to the amount of heterozygosis. East (1936) elaborated the idea further by proposing a series of alleles a_1, a_2, a_3, a_4 --- of gradually increasing divergence of function. He postulated heterozygotes to become increasingly more efficient as their component alleles diverged more and more in function. Thus $a_1a_2 < a_1a_3 < a_1a_4$, etc. Hull (1945) also advanced the idea of heterozygote superiority and proposed the term "over-dominance" for the condition in which heterozygote effect exceeds that of either homozygote.

Crow (1948) and Brieger (1950) have applied principles of population genetics to the problem of heterosis. Crow postulated that if all recessives in a variety at equilibrium were replaced by their dominant alleles, the vigor of the population would be increased by no more than 5 per cent. Crow concluded that dominance hypothesis cannot account for more than a small increase in the vigor of hybrids whose parents are from populations which are at equilibrium. He also pointed out that a high proportion of loci in which the heterozygote is superior are not necessary for over-dominance to be the most important factor in the genetic variance of the population.

Comstock and Robinson (1948) outlined procedures for estimating degree of dominance using data on biparental progenies. Using their Design I mating scheme, they separated the variance among full sibs within half-sib families into two fractions, σ_m^2 (variance among males) which estimates $\frac{1}{4}$ of the additive genetic variance and σ_f^2 (variance among females within males), which measures $\frac{1}{4}$ of the additive genetic variance and $\frac{1}{4}$ of the dominance variance. They used estimates of σ_m^2 and σ_f^2 to determine "a", the average degree of dominance. When dominance is complete, $a = 1$; values over 1.0 are associated with over-dominance and values less than 1.0 with partial dominance.

Robinson et al. (1949) reported estimates of average degree of dominance for genes controlling eight quantitative characters in corn hybrids. Their data indicated little or no dominance for genes determining plant height and ear height, partial dominance for ear number, approximately complete dominance for husk extension and ear diameter, and over-dominance of genes for yield. The authors pointed out that due to tight linkages of certain genes in the repulsion phase, it is theoretically possible to obtain estimates in the over-dominance range even though individual genes have no more than partial dominance with material such as used in their study. Gardner et al. (1953) using a more efficient design (Design III) for estimating "a" in the same type of material, also reported estimates of "a" to be in the over-dominance range for yield. They concluded that linkage may be an important factor, particularly for those estimates which are in the over-dominance range, but over-dominance at at least some loci cannot be ruled out.

Gardner and Lonnquist (1959) presented evidence of shift in estimate of "a" for yield toward a partial to completely dominant range as

the hybrid population approaches equilibrium. They pointed out that in the F_2 generation linkage would limit recombinations, and there will be an increase in the range of genotypic differences as generations are advanced by random mating.

Robinson et al. (1959) pointed out that if there is preponderance of repulsion linkage, the additive genetic variance would increase as the generations are advanced and if the linkage phase is preponderantly coupling, additive genetic variance would decrease. They reported a downward trend in additive genetic variance indicating that coupling linkage is predominant in the earlier generations. Gardner and Lonnquist (1959) and Moll et al. (1964) noted an upward trend in additive genetic variance in later generations, thus indicating a preponderance of repulsion phase linkages in earlier generations.

Lonnquist (1953), working with single cross combinations among a group of five high- and four low-combining inbred lines, reported the existence of both favorably dominant or partially dominant and over-dominant gene action for yield in corn, with favorable growth factors being more important in determining yielding ability in that study.

Stringfield (1950) observed higher yields in backcrosses as compared with F_2 's and in single crosses and three-way crosses as compared with double crosses. He indicated that the observed manifestations of hybrid vigor in corn are too great to be explained by the accumulation of small dominant effects only slightly greater than that of their recessives or hypostatic alleles if the alleles contribute some positive effects. He found that the addition of heterozygous pairs was perfectly and positively correlated with the addition of new dominant genes. He stated that signi-

ficant disparity in vigor between the F_2 and the backcross population could occur as a consequence of normal dominant gene action, but he concluded that he could see no reasonable basis for it if heterozygosis per se is primarily responsible for hybrid vigor.

Sentz et al. (1954) observed a curvilinear relationship between heterozygosis and performance of quantitatively inherited characters in corn. They indicated that, theoretically, a linear relationship is expected where loci effects are independent, where as a curvilinear relationship is evidence in support of non-additive accumulation of loci effects. They interpreted their observance of curvilinear relationship between heterozygosis and performance as suggesting the presence of interaction among non-allelic genes. They could not distinguish between different kinds of epistasis in corn due to the narrow base of material involved in their study.

Pollak et al. (1957), studying crosses between three open-pollinated varieties of maize, found F_2 performance intermediate between parents and F_1 . They reported the possibility of existence of different kinds of non-allelic interactions (epistasis), but their effect is so completely equalized as to lead to intermediate F_2 observed.

Bauman (1959) and Sprague et al. (1962) presented data to indicate that epistatic gene action may be of some importance in yield potential of commercial hybrids.

Eberhart* (1961) reported little evidence of epistasis in eight characters studied in two open-pollinated varieties of corn. However,

*Eberhart, S. A. 1961. Epistatic and other genetic variances in two varieties of corn (Zea mays L.). Unpublished Ph.D. thesis, North Carolina State College, Raleigh, North Carolina.

he also noted a rather substantial amount of epistasis x environmental interactions, which suggest that testing should be done over a series of environments.

Robinson et al. (1955) reported estimates of genetic variances in three open-pollinated varieties of southern prolific corn. They reported the existence of considerable amounts of additive genetic variance for grain yield. The most important feature of their findings was the fact that in all characters of the three varieties, the estimates of dominance variance were less than the estimates of additive genetic variance. They concluded that over-dominant loci are not the single important source of genetic variability in the varieties studied. Eight out of their twenty-one estimates of dominance variance were negative. They pointed out that variances by definition are never negative, so they concluded that negative estimates of dominance variance could be the result of sampling error.

Lindsey et al. (1962), working with two open-pollinated varieties (Hays Golden and Krug Yellow Dent), adapted to the Cornbelt, also reported negative estimates of dominance variance. They proposed that these negative estimates could be due to the lack of random mating in making the half-sib family groups. In their study, the estimates of additive genetic variance exceeded the estimates of dominance variance for most of the characters.

Robison^{*} (1963) used a modification of Design II mating system to eliminate possible bias resulting from assortive mating with respect to date of flowering. His estimates of additive genetic variance were greater

^{*}Robison, N. G. 1963. Estimates of additive genetic and dominance variance in an open-pollinated variety of corn (Zea mays L.). Unpublished Master's thesis, University of Nebraska.

than the estimates of dominance variance. Use of Design II eliminates the problem of assortive mating. The plants to be tested are self-pollinated and the S_1 lines are then intercrossed. It is seldom that a cross cannot be made because of differential flowering dates, since the earlier line can be used as the seed parent and the later line as the pollen parent. He concluded that better estimates of genetic variances can be obtained through the use of the Design II mating system, since the estimates do not appear to be biased by assortive mating.

Lindsey et al. (op. cited) tried to reduce assortive mating. They designated the females for each male at the time of planting and also delayed the planting of male plants by approximately one week. This insured a more random choice of females, and delay in planting of males made it possible to cross each male with all designated females in most cases. This attempt to reduce assortive mating resulted in a decrease in additive genetic variance and an increase in dominance variance for all characters measured with the exception of dominance variance for number of ears.

Compton et al. (1964) reported higher estimates of additive genetic variance in the varietal cross than the varieties and higher estimates of dominance variances in the varieties than in the varietal cross.

Moll et al. (1960) reported that an advanced generation of the variety cross contains more additive genetic variance than the varieties or the varietal cross F_1 .

Rumbaugh and Lonnquist (1959) studied a set of diallel crosses advanced from F_1 to F_5 by inbreeding. Although their data showed some indication of over-dominance, partial dominance for genes for yield prevailed. They

concluded that breeding schemes assuming additive gene action with partial dominance would give favorable results.

Robinson et al. (1951) computed genetic correlations of the eight characters in three populations of prolific corn. They reported that yield showed high correlations with ears per plant, medium positive genetic correlation with plant and ear height and little or no relationship with husk length, husk score, ear length and ear diameter.

Lindsey et al. (1962) observed high genetic correlation between date of flowering and grain yield for Hays Golden and positive but low genetic correlation for these characters for Krug Yellow Dent. Compton et al. (op. cited), working with two open-pollinated varieties (Golden Republic and Barbara Reid), adapted to the corn belt, reported that yield shows a high positive additive correlation with ear number, medium to low positive relationship with days to flower and ear height and little or no correlation with root lodging score.

Wellhausen et al. (1952) made an attempt to estimate the amount of teosinte introgression in the races of maize in Mexico. They studied 25 races and recognized teosinte introgression in 22. Their method for recognizing teosinte introgression was highly subjective and was based upon approximate scores of 0 to 4 for the induration of the rachis and the lower glumes of the ears. They reported that Tuxpeno might have been the source of germplasm of the southern dents of the United States.

Mangelsdorf (1952) has presented limited data which indicate that introduced teosinte chromosomal segments in maize in heterozygous conditions do sometimes confer a selective advantage. He also showed that when hybridization occurs, the resultant hybrid vigor may persist for an