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Results of Non-Selective Inbreeding in Maize*

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Summary. The results reported here indicate that selection, as practiced by maize breeders during the development of inbred lines, has markedly reduced the potential morphological variability of Corn Belt germ plasm. It is suggested that a number of traits which appear to a greater degree in "elite" lines than in those resulting from non-selective inbreeding could be the result of selection for genes or chromosomal segments derived from the introgression of maize and teosinte. Yet lines exhibiting maximum teosinte influence would not likely survive the screening imposed by visual selection.

Evidence is presented which suggests that visual selection as practiced during inbreeding has little, if any, direct influence on yield in hybrid combinations.

With respect to the inheritance of combining ability, results from these experiments support the assumption that high × high general combiners, on the average, tend to be higher yielding than any other set of combinations of high, medium, or low general combiners. It is, however, difficult to account for the relatively high yields of high × low general combiners on the basis of additive gene action alone.

It is suggested that in material as heterogeneous as open pollinated Corn Belt varieties, as much genetic diversity can come from within varieties as from between varieties, particularly if the varieties themselves have undergone extensive introgression during the course of their evolution.

Introduction

An interest in the origin and evolution of Corn Belt maize led the author, some years ago, to the assumption that a study of the comparative morphology of a typical cross section of Corn Belt inbreds might provide additional information relative to the identity of the putative parents of this most important segment of maize germ plasm. It was primarily for this reason that such a study was undertaken. It soon became apparent, however, that if the origin of Corn Belt maize even approximated that which had been postulated, many of the morphological types which should have been recovered from inbreeding Corn Belt varieties were not present in the cultures of modern corn breeders. It was assumed, therefore, that either the postulated origin of Corn Belt maize was in error, or more plausibly, that only a segment of the total phenotypic variability of Corn Belt germ plasm had survived the rigors of selection as practiced by maize breeders.

It was partly to provide answers to these questions and partly to develop a group of non-selected lines for use in experiments in quantitative inheritance that a random inbreeding scheme was started in the mid-1950's.

Materials and Methods

Seed from approximately 100 open pollinated ears of each of four varieties were selected as the original sources for inbreeding. The four varieties were Reids Yellow Dent, Krug, Lancaster and Midland. Seed from the 100 ears was bulked within each varietal source, and 600 kernels were taken at random from each variety. These were planted in blocks by variety, and at flowering, an effort was made to self each plant of each variety, irrespective of its agronomic qualities. These included lodged plants, diseased plants, and many other types which would normally be rejected by the breeder. Natural selection, of course, took its toll. A certain number of plants were lost in each generation due to the spread in time of silking and pollen shedding, and due to male sterility, insect attack, ear molds, etc.

At harvest, all ears were saved and approximately equal numbers of kernels were chosen from each ear, sufficient to make a bulk sample of 600 kernels.

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

This was done for each of the four varieties, and provided seed for the succeeding generation.

Following six generations of selfing in the manner just described, ear to row progenies of all ears which in the S_6 generation produced sufficient seed to plant a ten hill nursery row, were grown out for morphological studies. These consisted of 336 ear rows of Krug, 302 of Reids, 231 of Lancaster, and 291 of Midland. In addition to the non-selected lines derived from the four varieties, 200 selected lines from various sources, which were a part of a normal breeding program, were also grown out in ear rows for comparison with the lines developed in the absence of selection. These latter lines were representative of the kinds of inbreds being utilized by corn breeders in their regular breeding programs in the U.S. Corn Belt. A number of these lines were also in use in commercial hybrids at that time.

Following anthesis, measurements were made on each plant as follows:

1. Glume Length.
2. Number of Leaves Above Ear.
3. Number of Primary Tassel Branches.
4. Number of Secondary Tassel Branches.
5. Plant Height.
6. Tassel Exsertion.

At harvest, all ears and their associated peduncles were saved and the following traits were either measured or scored:

1. Degree of Denting.
2. Ear Length.
3. Kernel Length.
4. Row Number.
5. Shank Diameter.
6. Shank Length.

Results

Before considering comparisons of specific characteristics of selected *vs.* non-selected lines, brief comment on certain general aspects of morphology is in order. In the first place, lines whose morphology clearly approximated the putative parents of Corn Belt maize, i.e., the Northern Flints and the many rowed Southern Dents, were obtained in three varieties — Krug, Lancaster, and Midland. Furthermore, flint lines were obtained from all four varieties, although those from Reids Yellow Dent had ten to twelve kernel rows rather than eight. From the variety Krug, a number of lines were obtained which, except for endosperm color, were typical of lines derived from the Mexican race, Pepitilla. This suggests that in U.S. Corn Belt varieties, there is still present not only the Northern and Southern U.S. germ plasm from which Corn Belt maize evolved, but also even the more remote ancestral races from Mexico. That these could have survived a century or more of selection is of considerable interest. Even more surprising, however, is the occurrence in a few lines of a tendency towards single spikelets, a character which distinguishes maize from its closest relatives, teosinte and *Tripsacum*.

Now let us examine some of the comparisons of individual characteristics of selected and non-selected lines.

In Table 1 are shown the means and standard deviations for twelve plant and ear characters of the selected and non-selected lines. It will be noted that the mean value for denting in the two groups of lines is quite similar, with the selected inbreds exhibiting a slightly higher degree of denting than the unselected ones. Despite the similarity of means, however, the range in denting scores in the two groups is quite different. As was mentioned previously, several flint lines were present among the non-selected group, while no flints occurred among the elite lines.

Table 1. *Comparison of morphological traits of selected and non-selected lines.*

Trait	Selected		Non-Selected	
	Mean	S.D.	Mean	S.D.
Denting*	2.65	±0.90	2.24	±1.09
Ear Length (cm)	16.79	±2.77	15.26	±2.84
Kernel L. (mm)	9.59	±1.12	10.26	±1.00
Glume L. (mm)	10.42	±1.32	11.32	±1.48
Leaves above Ear	5.6	±0.94	6.00	±1.09
No. I Branches	12.4	±5.48	17.00	±6.70
No. II Branches	1.9	±2.17	2.90	±3.00
Plant Height	19.0	±2.36	21.30	±2.45
Row Number	15.0	±2.22	14.40	±2.36
Shank Diam. (mm)	11.7	±2.93	10.40	±2.56
Shank Length (cm)	13.3	±5.32	10.10	±4.17
Tassel Exsertion	52.5	±8.21	39.20	±5.84

* 1 = flint, 5 = extreme dent

The mean value for ear length of the selected lines is one and one-half centimeters greater than that of the random group, indicating that considerable selection pressure for ear length has been applied by breeders.

For some reason, which I do not understand, breeders seem to have selected against maximum possible kernel length in Corn Belt maize. The mean kernel length of the selected lines is less than that of the non-selected, but more striking were the differences in range of kernel lengths in the two groups. The longest kernels among the non-selected lines were almost 3 mm. longer than the longest among the elite lines.

It will also be noted that the length of the glumes of the non-selected lines exceed those of the select inbreds on the average. I would suppose the difference here, however, is not likely to be the direct result of intentional selection.

The number of leaves above the ear is greater, on the average, in the non-selected lines than in those which have undergone normal selection as practiced by breeders. Here again the differences in range in leaf number above the ear was particularly striking. For the select group the number varied from 3 to 9 as contrasted to a range of 3 to 16 among the non-selected lines. There, undoubtedly, are good reasons why breeders might reject lines with 16 leaves above the ear, yet, at the same time, it might be of interest to have them in the gene pool for special purposes.

Among the most marked differences in the two classes of lines here being compared were certain characteristics of the tassel. It would seem that lines which are the products of regular breeding programs have a much narrower range of primary and secondary branches than do those developed in the absence of selection. The maximum number of primary branches encountered in select lines was 30 as compared to 46 in the randomly developed group. Likewise, the maximum number of secondary tassel branches found among the 200 elite lines was 19 as compared to 33 in the non-selected inbreds.

These data indicate also that breeders have practiced effective selection for reduction in plant height as well as for some increase in the number of kernel rows beyond that which might occur with inbreeding in the absence of selection. Likewise, both shank diameter and shank length were, on the average, greater in the select lines than in the non-selected group.

Among the various morphological traits considered, the most striking difference between the two groups is that of tassel exsertion. This is a measure of the extent to which the terminal internode is enclosed within or exserted beyond the uppermost leaf sheath. Whether intentional or not, it seems perfectly obvious that breeders have selected strongly and successfully for well exserted tassels. The mean values, it will be noted, are 52.5 mm. for the select lines as compared with 39.2 mm. for the non-selected ones. The differences in range in the two groups are −77 to 178 mm. for the select inbreds as compared with −179 to 242 mm. for the random lines.

To summarize the morphological comparisons, it is apparent that the select lines differ from the non-selected in possessing:

1. Fewer Primary Tassel Branches.
2. Greater Tassel Exsertion.
3. Shanks of Greater Diameter.
4. Shorter Plants.
5. Longer Shanks.
6. Fewer Secondary Tassel Branches.
7. Higher Number of Rows.
8. Fewer Leaves above Ear.
9. Higher Degree of Denting.
10. Shorter Kernels.
11. Longer Ears.
12. Shorter Glumes.

Of some interest from the standpoint of evolution is the observation that for at least half of the phenotypic characters studied, the selected lines differ from the non-selected in a direction which could logically have resulted from previous admixture of maize with teosinte. These differences are a decrease in the number of primary tassel branches, greater tassel exsertion, increased shank length, fewer secondary tassel branches, shorter kernels and longer ears. Most of these are traits which have been demonstrated by SEHGAL (1963), and BROWN and MANGELSDORF (1951) to be the products of introgression of teosinte into maize.

The role played by teosinte in the evolution of maize under domestication is of particular significance to students of evolution and should be, in my opinion, of equal significance to breeders. There is considerable evidence, WELLHAUSEN et al. (1952) which suggests that each of the major kinds of maize of outstanding productivity which has been studied contains some amount of teosinte in its genetic make-up. As a consequence a number of "tripsacoid" lines should be expected to be recovered from inbreeding varieties of Corn Belt maize. Furthermore, these will likely be far from the breeders ideal of a desirable maize plant. As a result, few, if any, such lines will likely survive the screening imposed by visual selection. Yet the effects of blocks of genes from teosinte, when present in maize, can be vastly different, depending upon whether they are in the homozygous or heterozygous condition (MANGELSDORF, 1952). Thus the "appearance" of lines containing teosinte can be quite misleading in terms of their eventual usefulness and the true value of such lines can be determined only on the basis of performance in hybrid combinations.

Relation of Visual Selection and Yield

In developing inbred lines of maize, most, if not all breeders, regularly practice visual selection for a number of highly heritable traits of agronomic importance. This practice has been quite successful, particularly when applied to the improvement of such traits as root strength, resistance to stalk rot and leaf blight and resistance to various insects. Some breeders also believe that it is possible to effectively practice visual selection for yield, but despite this there remains considerable difference of opinion concerning the effectiveness of phenotypic selection in modifying hybrid performance.

In an attempt to shed further light on this problem four experienced breeders were asked to evaluate visually each of the 1160 non-selected lines the year in which they were grown as ear to row progenies, Each of the lines was scored on a scale of 1 to 5, with 5 representing the most desirable phenotypes, and 1 the poorest. This, it seems, is a normal selection procedure, and one practiced by many breeders. Following visual evaluation of the lines, a set of 20 was chosen at random from among those which had received average scores of 4 or more, and a second set of 20 was likewise taken at random from the group which had been given average scores of 2 or less. Each of the 40 lines was subsequently crossed onto a synthetic tester, and evaluated in performance trials for grain yield and other traits of agronomic value. The tests were grown two years in two locations with four replications per location. The summarized results for yield and lodging are shown in Table 2. Yields, it will be noted, are identical in the two groups. Therefore, while it cannot be said that the type of selection practiced had any adverse effect upon yield, neither did it contribute to any improvement in yield. Topcrosses of the 20 selected lines were, however, superior to the crosses involving non-selected lines, both in stalk and root lodging resistance. This, of course, is to be expected since both these traits are highly heritable.

Table 2. *Topcross performance of selected and non-selected random lines. 20 of each. 2 year average.*

Class	Bu/Ac	% Stalks Stand.	% Non-Root Lodg.
Selected	86.66	88.1	94.8
Non-selected	86.64	84.4	90.7

Combining Ability

Since many of the studies on the inheritance of combining ability have utilized inbreds which had previously undergone a considerable amount of selection, it was felt that a test of combining ability involving lines developed in the absence of intentional selection might be of interest. Consequently, 100 of the non-selected lines were taken at random from the entire group and evaluated for general combining ability on the basis of yields of topcrosses with a broad base synthetic tester. The topcross yield trial consisted of six replications at each of two

Table 3. *Topcross yield distribution of lines of high, intermediate, and low general combining ability.*

High	Bu/Ac	Inter.	Bu/Ac	Low	Bu/Ac
L-161	102.6	L-147	81.6	M-435	62.5
L-24	100.7	K-444	80.5	L-80	62.6
K-352	96.2	M-78	80.3	K-439	66.5
M-126	93.1	K-291	81.8	M-241	69.4
Mean	98.1		81.0		65.2

locations, and on the basis of the yield results, the lines were classified as high, intermediate, or low with respect to their general combining ability. From among the 100 lines, twelve were subsequently chosen, consisting of four each of high, intermediate and low general combining ability. Yields of the three classes of lines are given in Table 3. The mean yield of the high general combiners was 98.1 bushels per acre, the intermediates 81.0 bushels, and the low group 65.2 bushels per acre. Thus, the average difference between the high and intermediate group is 17 bushels; between the intermediate and low, 15.8 bushels, while the average difference between the high and low general combiners was more than 30 bushels per acre. The letter preceding the numerals used to designate the individual lines (Table 3) refers to the varietal sources Lancaster, Krug and Midland.

All possible F_1 crosses were made between these twelve lines and the resulting 66 singles were grown in yield trials in two successive years. The trials were conducted at two locations, Iowa and Illinois, and included six replications at each location.

Table 4. *Yield summary of all possible crosses of 12 non-selected lines classified with respect to general combining ability (2 year data combined).*

Type of cross	Yield
High × High	115.9 Bu/Ac
High × Intermediate	111.0 Bu/Ac
High × Low	103.6 Bu/Ac
Intermediate × Intermediate	103.0 Bu/Ac
Intermediate × Low	87.2 Bu/Ac
Low × Low	71.3 Bu/Ac

The combined average yields for the two years for each of the six classes of crosses are summarized in Table 4. As an average, the High × High crosses exceed slightly the other classes. The High × Intermediate, although on the average slightly lower than the High × High, are not significantly lower. The High × Low yields were identical with crosses between Intermediates, whereas the Low × Intermediate, and Low × Low groups were significantly poorer than anything else in the test.

An analysis of variance of these data (Table 5) indicate highly significant differences between varieties as well as a significant variety × location interaction.

Table 5. *Analysis of variance of yields (Bu/Ac) presented in Table 4.*

Source	D.F.	M.Sq.	F.
Total	791	543.24	
Between Loc.	1	166,361.76	
Reps.	10	1,973.52	
Varieties	65	2,880.36	49.09**
Var. × Loc.	65	280.44	4.78**
Error	650	58.68	

There were, of course, only six crosses each in the intra-class groups, as compared to 16 in each of the inter-class combinations. For this reason, it is difficult to make direct comparisons between the various classes of crosses. However, with this restriction and with respect to the inheritance of combining ability, these data tend to confirm the results of a number of previous investigators, including JOHNSON and HAYES (1940), COWAN (1943), GREEN (1948), and others, some of whom used as experimental material lines which had previously undergone considerable selection. The data also support the contention of HAYES (1963) that, "Single crosses of extremely high performance, in comparison with the average of all single crosses, could not be expected to occur very frequently, unless one of the inbred parents excelled in general combining ability."

Whereas these data represent average performance, and average performance is important, one cannot ignore the exceptions. The breeder, for strictly practical reasons, is more interested, I think, in finding the one or very few cross-combinations of truly exceptional performance than he is in finding the greatest number of above average crosses. For this reason, I should like to refer to some deviations from average results, which are not shown in the tables.

First, the highest yielding cross among the diallel set of 66 was not among the High × High combiners, but was a cross of High × Intermediate, and furthermore, the two parental lines involved were from the same varietal source. Secondly, among the top 25% of the 66 crosses, there were three hybrids made up of High × Low combiners. Also, one of the lowest yielding crosses tested was a High × High combination.

With respect to the type or types of gene action which might logically explain these results, it seems the average yields of the High × Low combinations cannot be adequately accounted for on the basis of additive effects alone. It would appear, therefore, that some non-additive effects, probably dominance, are also involved.

Genetic Diversity and Yield

Maize breeders have long recognized the importance of genetic diversity as a factor in obtaining maximum heterosis in crosses. Not so widely recognized, however, is the fact that a high degree of genetic diversity can be obtained in lines derived from a single varietal source.

Three quarters of a century ago MCCLUER (1892) demonstrated hybrid vigor in crosses of unrelated varieties of popcorn. Since that time numerous workers, ANDRÉS and BASCIALLI (1940), ECKHARDT and BRYAN (1940), GRIFFING and LINDSTROM (1954), LONNQUIST and GARDNER (1961), and PATERNIANI and LONNQUIST (1963), to cite only a few, have shown clearly that maximum yields in crosses were associated in part with genetic diversity of the parents.

With inbreds from three varietal sources represented equally, among the twelve lines used in the studies of combining ability referred to above, it is possible to get from the data some estimates of the relationship between genetic diversity and heterosis in crosses. The three varietal sources were Lancaster, Krug, and Midland, and a comparison of the inter- *vs.* intra-varietal yields are given in Table 6.

The mean yields of crosses of non-related lines exceed slightly those possessing varietal relationship, yet the highest yielding set of crosses were Lancaster × Lancaster and the highest individual yield among the series of crosses was a Lancaster × Lancaster hybrid. This does not mean that genetic diversity is not important in contributing to heterosis. It does mean that as great a degree of diversity can come from within varieties as from between varieties. This is especially true if the varieties themselves have undergone long periods of introgression, as have many of the open pollinated corns of the U.S. Corn Belt.

Table 6. *Average performance of F_1 hybrids of non-selected inbred lines from three varietal sources, Lancaster, Midland and Krug. Comparison of inter- vs. intra-varietal crosses.*

Inter-varietal cross	Yield Bu/Ac	Intra-varietal cross	Yield Bu/Ac
L × K	105.0	L × L	107.8
L × M	101.0	K × K	96.8
K × M	96.2	M × M	84.7
Mean	100.7		96.4

The vast range of intra-varietal morphological variation encountered in the lines derived from each of the varieties used in these experiments leads one to expect a high degree of genetic diversity to be present within each varietal group. It is interesting to note that these phenotypic differences are apparently indicative of true genetic differences.

Zusammenfassung

Aus den hier berichteten Ergebnissen geht hervor, daß die Selektion, die von den Maiszüchtern bei der Entwicklung von Inzuchtlinien vorgenommen wird, die potentielle morphologische Variabilität des Genmaterials des Corn Belts beträchtlich vermindert hat. Es wird vermutet, daß eine Anzahl von Merkmalen, die in „Elite"-Linien in höherem Ausmaß als in unselektierten Inzuchtlinien auftreten, das Ergebnis der Selektion auf Gene oder Chromosomensegmente, die aus der Introgression von Mais und Teosinte stammen, sein könnten. Linien, die einen sehr starken Teosinte-Einfluß aufweisen, würden aber nur mit geringerer Wahrscheinlichkeit das Sieb der visuellen Selektion passieren.

Es werden Nachweise erbracht, die nahelegen, daß eine visuelle Selektion während der Inzucht, wenn überhaupt, nur einen geringen unmittelbaren Einfluß auf den Ertrag der Hybridkombinationen hat.

In bezug auf die Vererbung der Kombinationseignung stützen die Ergebnisse dieser Versuche die Annahme, daß im Durchschnitt die Kreuzung von zwei Partnern mit beiderseits hoher allgemeiner Kombinationseignung bessere Erträge bringt als jede andere Kombination von Partnern hoher, mittlerer oder geringer allgemeiner Kombinationseignung. Es ist jedoch schwierig, die relativ hohen Erträge von Partnern mit hoher × niedriger allgemeiner Kombinationsfähigkeit allein mit additiver Genwirkung zu erklären.

Es wird angenommen, daß ein so heterogenes Material wie die frei bestäubten Corn Belt-Sorten ebensoviel genetische Mannigfaltigkeit innerhalb wie zwischen den Sorten aufweisen kann, besonders wenn die Sorten im Verlaufe ihrer Entwicklung beträchtlicher Introgression unterworfen waren.

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