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A COMPARISON OF MAIZE-BREEDING METHODS

By G. N. Collins, *Senior Botanist in Charge of Office of Biophysical Investigations, Bureau of Plant Industry*

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INTRODUCTION

Methods of breeding for the improvement of agricultural plants are undergoing many changes as a result of rapid progress in the science of genetics. In self-pollinated species methods of selection, although conducted with more insight, have not been modified greatly. The principal change has been the increasing use of hybridization. In maize and other cross-fertilized species, however, entirely new methods of selection are being tried.

The change from the old method of mass selection or of selection by progeny performance followed the work of Shull, who in 1908 pointed out the diversity in selfed lines and suggested the improvement of maize by combining selected selfed strains.

The experiments here reported were begun in 1918 to determine the possible advantage of a method of close breeding in which inferior lines were eliminated through selfing and the surviving strains recombined to restore the vigor lost by selfing.

It seemed clear that increases in yield resulting from the ear-to-row method of crossbreeding were due almost entirely to an increased uniformity of performance. In other words, the maximum yield of the individual corn plant was not increased, though the general average might be raised through a reduction in the number of unproductive or sterile plants. Many forms of sterility were known to be simple Mendelian recessives, and the most expeditious and certain way of eliminating these undesirable types was to bring them into expression by selfing and reject all lines showing undesirable characters.

The early advocates of the isolation of pure lines by intensive inbreeding planned to utilize this method as a means of discovering the best strains. Vigor was to be restored by crossing two of the selected strains or at most by combining two F_1 hybrids. To confine the reconstructed variety to such narrow limits seemed a serious defect, precluding the realization of maximum adaptability, which could be obtained only by maintaining a greater diversity of ancestral lines. In this experiment, therefore, an attempt was made to resolve a variety of maize into a number of selfed lines and eliminate the least desirable. The original variety was to be reconstituted by allowing the remaining lines to interbreed. The plan was to reject the poorest rather than to select the best. The results of this method were to be compared with those of ear-to-row crossbreeding based on the same foundation stock.

An early objection to selfing as a preliminary to selection was that the reduced vigor of selfed strains is an abnormal condition, and therefore the results might be inapplicable to vigorous crossbred stocks.

Much progress has been made toward an understanding of the nature of the reduction of vigor that follows selfing; but recent experiments, including those here reported, show that the original objection is not without foundation. It has been demonstrated that high performance in a selfed strain is no assurance that superior progenies will result when normal vigor is restored by crossing. Notwithstanding this fact, the idea still persists that homozygous strains represent the orginal building materials of which normal varieties are composed rather than the mistakes which nature has made.

DESCRIPTION OF THE EXPERIMENTS

The experiments were conducted at Sacaton, Ariz., and Sacaton June corn was chosen as the variety. This variety was derived from "Laguna," a strain of Mexican June corn. The variety had been subjected to careful plant and ear selection for a number of years, first by E. W. Hudson and later by S. H. Hastings. The same method of ear selection has been continued to the present time, thus providing a base from which to measure progress.

The variety has proved to be well adapted to Arizona conditions and is as uniform and free from abnormalities as most well-bred varieties.

Since 1920 the planting, harvesting, and note taking have been under the direction of C. J. King, superintendent of the United States Field Station at Sacaton.

The procedure may be described best by transcribing the original directions.

Foundation stock.—Select 20 of the best ears available, shell each separately, and divide the seed from each ear into two equal parts.

Plant two identical blocks, an ear to the row, rows of 50 plants each. One block is to form the foundation of the "crossed experiment," the other to form the foundation of the "selfed experiment."

Label the rows in the crossed experiment C 1 to C 20 and those of the selfed experiment S 1 to S 20.

Crossed experiment.—At flowering time, number the plants C 1–1 to C 1–50, C 2–1 to C 2–50, etc., select the 10 best-appearing rows, and secure at least two ears representing each possible combination of these 10 rows, using best-appearing plants. Make note on tag of pollen plant used. This will mean at least 90 ears. (9+8 . . . . .+1)×2. Superior plants to be used as many times as possible, avoiding reciprocals.

Determine row yields based on length of ear. Arrange the five highest yielding rows in order of the yield and select the ears representing crosses 1×2, 1×3, 1×4, 1×5, 2×3, 2×4, 2×5, 3×4, 3×5, and 4×5 and 10 additional hand-pollinated ears representing the highest yielding parent plants without regard to row, thus obtaining 20 selected ears for next season's crossed experiment.

Selfed experiment.—Obtain at least 5 selfed ears from each of the rows, making 100 ears. Determine the row yields based on length of ear. From the 100 ears select a selfed ear from each of the two highest yielding plants of the 5 highest yielding or otherwise desirable rows, freedom from diseased or abnormal plants being given due consideration, and from the remaining selfed ears select 10 from the highest yielding plants, regardless of row, not more than one from each row, making 20 selected ears for next season's selfed experiment.

PRELIMINARY COMPARISONS

The first planting was made in 1918, and the procedure described above was followed in subsequent years. Beginning in 1920, in addition to providing the seed for continuing the experiment, crosses were made between selfed lines for preliminary comparisons with the crossed experiment. In 1921 F_2, or compound F_1 hybrids, were made by crossing the first-generation hybrids made in 1920, and these compound hybrids were crossed again in 1922, making F_3, or double compound hybrids.

The results of these preliminary comparisons are set forth in Table 1. There is little uniformity in the relative behavior of the various seed stocks in the three seasons. The diversity may be due to genetic differences, since different selfed lines are represented in the F_1 hybrids of the different seasons. On the other hand, although many of the differences appear statistically significant, it is not at all impossible that the variations are due to errors of sampling. The probable errors were calculated from the array of progeny means, taking N = the number of progenies. This gives a large probable error, but the seed stocks compared were not always adjacent in the field, and even these large probable errors should not be interpreted too literally.

TABLE 1.—*Comparison of the average ear length of maize in crossbred and selfed experiments*

Year and experiment	Number of crosses	Number of plants	Mean length of ear (cm.)
1921:			
Crossed block	20	933	25.6±0.5
Selfed block F_1	4	179	34.1±1.1
1922:			
Crossed block	20	496	23.3± .8
Selfed block F_1	9	205	27.1±1.0
F_2	5	124	36.2± .7
1923:			
Crossed block	20	454	30.4± .6
Selfed block F_1	16	301	33.9± .8
F_2	12	243	26.3± .8
F_3	16	298	31.0± .7

ABNORMALITIES IN SACATON JUNE CORN

When plants of Sacaton June corn are examined carefully, minor abnormalities or departures from type may be detected in something like 25 per cent of the individuals. This may seem to many a very high percentage, but to those accustomed to a critical examination of commercial varieties of maize the proportion will be recognized as not unusual. The number recorded as abnormal depends, of course, on the rigor with which the standard of uniformity is applied. In the first season when the open-pollinated ears were planted as the foundation stocks of the two breeding blocks, 35 types of abnormalities were recognized in the 1,936 plants involved. In 1919, following the first year of selfing, this number was increased to 60. The nature of these abnormalities is indicated by the following list of brief designations taken from our early notes:

Weak stalk, twisted stalk, stalk bent above ear, rolled leaves, contorted main stalk, ear replacing main stalk, main stalk missing, shortened internodes, upper leaf blades erect, monostichous blades, tubular leaf sheaths, light-colored broad blades, variegation, small light-green spots, blades striped light green, yellow blotches, dead stripes, dead blotches, dead leaves, dead with no ear, bullate blades, crumpled blades, longitudinally folded blades, eroded blades, concave blades, narrow blades, short stiff blades, leaves failing to unroll, dead tissue between the veins, blades broadly streaked with dark red, tassel branches erect, bract at base of tassel, bladeless sheath, seed in tassel, staminate tip to ear, interrupted ear, no ear, deformed ear, aborted tassel, sterile anthers, dwarf plant, aborted husks, ear crossing main stalk, second ear silking first, silk in tassel, ear exceeding husk, bear's-foot ear, central spike thickened.

Subsequent studies have shown that many of these aberrations appear not to be inherited, and others are different manifestations of the same genetic variation. Most of the abnormalities were of such a minor nature as to make it seem improbable that they would influence yield.

The results in the 1919 selfed experiment, however, showed a rather high negative correlation between yield and the prevalence of abnormalities. This planting comprised 20 progenies and 764 plants, and on these a total of 545 abnormalities was recorded, an average of 0. 7 abnormalities per plant. In the individual progenies the average ranged from 0. 20 to 1. 91. Arranged in their order of freedom from abnormalities the series agrees very closely with their order when arranged by total ear length. The product movement correlation of percentage of abnormalities and length of ear is -0.48 ± 0.12. These results seem to indicate that minor detectable abnormalities have a measurable influence on yield.

PARENT-OFFSPRING CORRELATIONS IN THE SELFED EXPERIMENT

The four seasons from 1919 to 1923 provide 76 parent-offspring comparisons. At the end of each season the progenies were arranged in order of the average total ear length, and the relation between the rank of the progeny from which the parent ear was selected and the rank of the resulting progeny affords a measure of the inheritance. The method of selection whereby two plants were selected from each of the five rows having the highest average ear length results in most of the parents being chosen from the higher yielding rows. During the entire experiment approximately one-half of the parent ears were taken from progenies of ranks 1 to 4. The average rank of the progenies resulting from this group of ears was 8. 3, while the average rank of the progenies from parents of ranks 5 to 20 was 12. 2.

The interannual parent-offspring correlation of rank for the six seasons was as follows:

Year	Correlation of rank[1]	Year	Correlation of rank[1]
1918–19	0.41±0.16	1921–22	0.87±0.06
1919–20	.76± .10	1922–23	.18± .20
1920–21	.56± .15	1923–24	.30± .20

All correlations are positive in sign, and for the early years the coefficients are significant.

PLANTS FROM HIGH-YIELDING ROWS COMPARED WITH HIGH-YIELDING PLANTS SELECTED WITHOUT REGARD TO THE PROGENY PERFORMANCE

In each year's experiments one half of the progenies represented selections from the highest performing progenies of the preceding year. The other half represented selections from high-yielding individuals without regard to the behavior of the progeny in which they occurred.

Table 2 shows that, in the crossed blocks, over a period of six years there was no significant difference between the progenies descended from high-yielding progenies and those descended from high-yielding plants. In four of the six years the "high-row" progenies outyielded the "high-plant" progenies, but in no single year is the difference significant, and in the total for the six years the yields are practically equal.

TABLE 2.—*Mean length of ears of maize progenies descended from high-yielding progenies and from high-yielding individuals*

Year	Crossed block (cm.)			Selfed block (cm.)			Selfed as percentage of crossed
	High row	High plant	Total	High row	High plant	Total	
1919	25.5	22.7	24.10	20.2	19.2	19.7	81.7
1920	37.86	42.23	40.04	36.22	28.34	32.28	80.6
1921	25.77	25.15	25.46	22.70	19.70	21.2	83.3
1922	34.19	32.42	33.31	29.10	25.35	27.23	81.7
1923	30.55	31.14	30.84	29.23	23.47	26.35	85.4
1924	31.00	29.90	30.45	27.10	22.60	24.85	81.6
Average	30.81	30.60	30.70	27.43	23.11	25.27	82.3

In the selfed blocks, on the contrary, the high-row blocks outyield the high-plant blocks in all of the six years. The mean difference is 4.48±0.57 per cent, a departure from zero of 7.9 times the probable error.

The comparisons are based on small plantings, and the yields vary from year to year. The effects of annual fluctuations are eliminated by confining the comparisons to the differences instead of the absolute yields. That the small size of the blocks does not vitiate the results is indicated by the regularity of the results. This regularity is most apparent in the percentage difference between the selfed and crossed blocks. In the six years the maximum range of

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[1] Calculated by Spearman's formula $\rho=1-\frac{6\Sigma d^2}{N(N^2-1)}$, where d=difference in rank and N=number.

the selfed block expressed as a percentage of the crossed blocks was from 80.6 to 85.4 per cent.

These results indicate that in the crossed blocks there is as much genetic diversity in the plants of a row as among plants from different rows and taken at its face value would suggest the futility of ear-to-row breeding as compared with plant selection in a cross-pollinated stock. In the selfed blocks the progenies have become more nearly homozygous and the individual differences are largely environmental.

In both the crossed and selfed blocks the high plant selections have been descriminated against in that the high row selections were made first and the high plant selections were restricted to what was left.

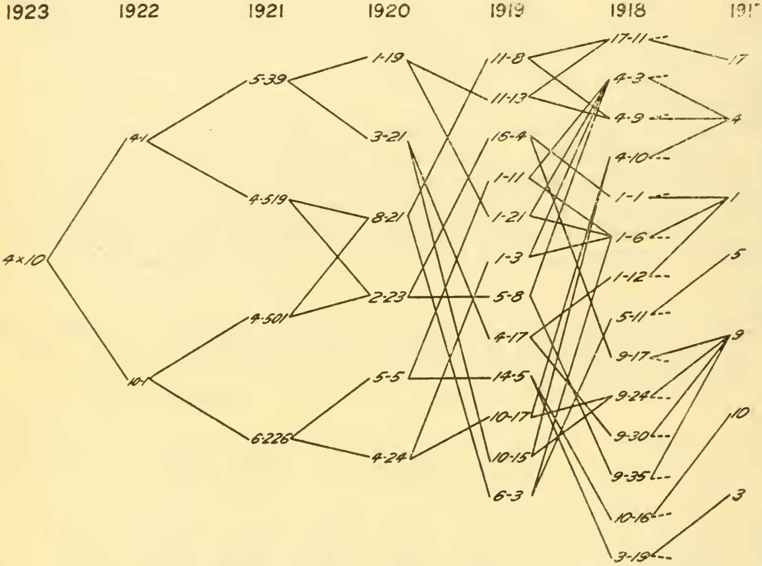

FIG. 1.—Representative pedigree of progenies in the crossbred seed stock of maize tested in 1923. Numbers in the pedigree indicate individual plants. The numbers in 1917 are those assigned to the original ears first planted in 1918. F=11.2

The pronounced superiority of the selections from high-yielding progenies compared with selections from high-yielding plants taken with the parent-offspring correlations in the selfed experiment demonstrates that substantial progress was made in the isolation of high-yielding lines in that experiment.

YIELD COMPARISONS OF THE TWO BREEDING METHODS IN 1923

After selecting the ears for continuing the experiments in 1923, the remaining hand-pollinated ears from the 1922 crossed block were shelled into a mixed sample designated CB and the yield compared with that of a mixed sample of F_2 seed of hybrids between selfed lines. The selfed lines were crossed originally in 1921, and in 1922 crosses were made among the several F_1 progenies. The mixture of these F_2 progenies was taken as representing tentatively the end result of the selfed method.

The comparison was made by planting the seed stocks in alternate rows. There were twelve 400-foot rows, and in harvesting each row was subdivided into four sections, making 24 comparisons.

There was a slight positive correlation between the number of plants per section and the yield per plant, indicating that conditions favorable to germination were likewise favorable to growth. Yield per plant therefore seems a more suitable measure of production than yield per section.

The 12 rows occupied one irrigation border and part of another. There were thus three outside rows. Two of these were planted with F_2 seed; the other with seed from the crossed block. It is further necessary to consider the possibility of a general trend in the fertility of the field that would favor one or the other kind when taken in pairs. The uncorrected mean difference ($CB-F_2$) of the entire 24 pairs was 0.22 ±0.02 pound per plant. Excluding all pairs involving outside rows, the mean difference was 0.205 ± 0.029. Dropping the first row and subtracting the yield per plant of the F_2 from the preceding instead of the following adjacent section, to disclose the effect of a possible trend in the field, the mean difference was 0.24 ± 0.025. All of these measurements are in substantial agreement, and the difference is from 7 to 10 times the probable error.

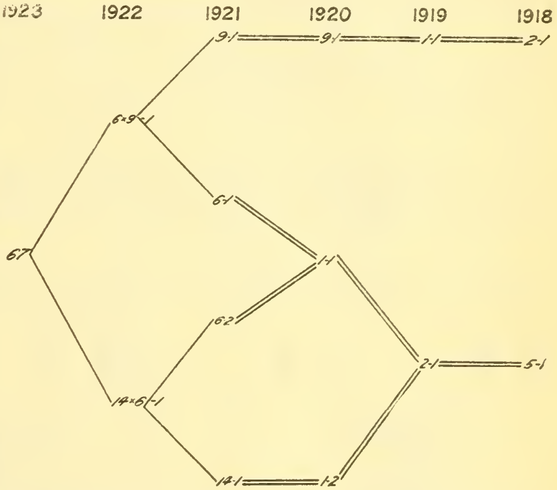

FIG. 2.—Representative pedigree of progenies in the F_2 seed stock of maize tested in 1923. The numbers indicate individual plants. Selfed generations are shown by double lines. F=40.6

The mixed sample of F_2 seed that was compared with crossed seed in 1923 comprised 10 ears. These were derived from five F_1 hybrids grown in 1922. These five F_1 hybrids came from six selfed lines grown in 1921; five of these selfed lines were sister progenies descending from selfed plants in a single line in 1920. The sixth selfed line was unrelated, having descended from a different original ear.

Sample pedigrees of the crossbred and F_2 seed stocks grown in the 1923 yield test are shown in Figures 1 and 2.

YIELD COMPARISONS OF THE TWO BREEDING METHODS IN 1924

In the season of 1924 a more thorough trial was conducted. The yields of five seed stocks were compared. These were: (1) Seed from the crossbred experiment designated CB, (2) composite sample of F_1 crosses between selfed lines designated F_1, (3) composite sample of crosses between F_1 lines designated F_2, (4) composite sample of crosses between F_3 lines designated F_4, and (5) crib-selected seed of Sacaton June corn. In all instances the seed was from the 1923 plantings. Comparisons were made by grouping the seed stocks into pairs and planting the members of each pair in alternate rows, repeating as often as the quantity of seed would permit. Sample pedigrees of the various seed stocks grown in 1924 are shown in Figures 3 to 6.

The field in which the yield test was made is divided into irrigation borders 400 feet long by 25 feet wide. The borders are separated by ridges of soil, but within each border the ground is kept as level as may be except for the slight and uniform drop along the length of the border. The plantings were made in rows running the long way of the border and 3½ feet apart. The plants in the row were about 2 feet apart, making approximately 200 plants to the row. Each border of seven rows and with an area of one-fourth acre was considered an independent experiment in which the yields of two seed stocks were compared.

The arrangement of the comparisons made in 1924 is shown in Table 3. There was a pronounced and rather uniform decline in fertility in passing from border 1 to border 8, as shown in the yield of crib-selected seed which was planted in all borders as outside rows.

For this reason the actual yields in different parts of the field may not be compared, and it will be best to consider the individual comparisons as separate experiments. Five seed stocks are involved, and there are six of the comparisons.

TABLE 3.—*Arrangement of seed stocks of maize in comparisons of yield in 1924*

Border No.	Row No.	Seed stock	Border No.	Row No.	Seed stock
1	1	Crib selected.	5	29	Crib selected.
	2	Crossbred.		30	Crossbred.
	3	Self F_2.		31	Self F_1.
	4	Crossbred.		32	Crossbred.
	5	Self F_2.		33	Self F_1.
	6	Crossbred.		34	Crossbred.
	7	Crib selected.		35	Crib selected.
2	8	Crib selected.	6	36	Crib selected.
	9	Crossbred.		37	Crossbred.
	10	Self F_4.		38	Self F_1.
	11	Crossbred.		39	Crossbred.
	12	Self F_4.		40	Self F_1.
	13	Crossbred.		41	Crossbred.
	14	Crib selected.		42	Crib selected.
3	15	Crib selected.	7	43	Crib selected.
	16	Crossbred.		44	Self F_1.
	17	Crib selected.		45	Self F_2.
	18	Crossbred.		46	Self F_1.
	19	Crib selected.		47	Self F_2.
	20	Crossbred.		48	Self F_1.
	21	Crib selected.		49	Crib selected.
4	22	Crib selected.	8	50	Crib selected.
	23	Do.		51	Self F_1.
	24	Crossbred.		52	Crib selected.
	25	Crib selected.		53	Self F_1.
	26	Crossbred.		54	Crib selected.
	27	Crib selected.		55	Self F_1.
	28	Do.		56	Crib selected.

At harvest the borders were divided transversely into eight sections of equal length, and the number of plants and the weight of good ears in each row of each section were recorded. Omitting the outside rows, there are in each border three rows of one kind of seed, occupying the second, fourth, and sixth rows of the border, compared with two rows of another kind, occupying the third and fifth rows. A series of differences for each of the sections was determined as follows: (1) The difference between row 3 and the mean of the two adjacent rows 2 and 4 and (2) the difference between row 5 and the mean of the two adjacent rows 4 and 6. There were thus 16 separate comparisons in each border. The 16 differences were treated as an array and the mean with its probable error determined. Borders 3 and 4 and borders 5 and 6 were duplicates, so that in these two instances there were 32 differences to be averaged. By treating differences between adjacent sections instead of absolute yields the disturbing effect of soil diversity is very largely eliminated. By this system the middle row of the border figures in the comparison with the rows on either side and is thus given a double weight. There was no evidence that the middle row yielded either more or less than rows 2 and 4, and the only error this practice would involve would be a very slight spurious reduction in the probable error. The method has the advantage of eliminating any error due to a trend in fertility across the field.

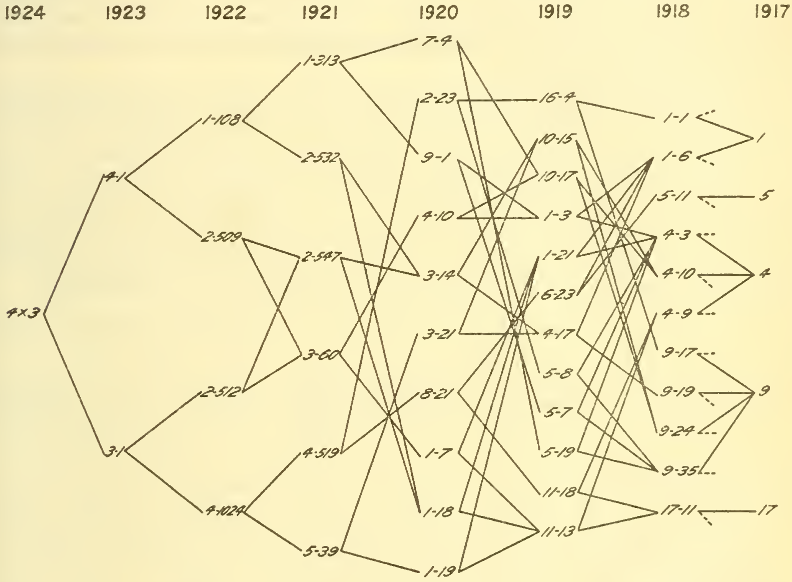

FIG. 3.—Representative pedigree of progenies in the crossbred seed stock of maize tested in 1924. Numbers in the pedigree indicate individual plants. The numbers in 1917 are those assigned to the original ears, first planted in 1918. F=16.8

The distance between the outside rows of adjacent borders was slightly greater than that between the rows inside the borders, and there is a general belief that the outside rows receive a little less water than the other rows. For these reasons the two outside rows of each border were excluded from the comparisons and were planted with crib-selected seed. The same stock of crib-selected seed was used as one of the members compared in blocks 3, 4, and 8, thus affording an opportunity to compare the effect of outside rows on yield.

The yield of the bulk seed of inside rows exceeded that of outside rows 1.02 ± 0.28 pounds per section—D ÷ E = 3.6. The difference in yield per plant is slightly less significant, being 0.028 ± 0.01 pound—D ÷ E = 2.8. Although not certainly significant, the results justify the rejection of the outside rows.

The possible influence on yield of position in the border, other than outside rows, was tested by averaging the differences between the mean yield per plant of the second and sixth rows and that of row 4, the center row. Rows 2, 4, and 6 were always planted with the same kind of seed. The eight sections in each of the eight borders afforded 64 comparisons. The result showed the mean difference to be 0.0176 ± 0.0067 pound per plant, the mean of rows 2 and 6 being the higher.

The difference is 2.6 times the error; but, since it is in the opposite direction from that of the comparison of the outside rows with rows 3 and 5, this difference is probably the result of chance.

The results of the 1924 yield test are set forth in Table 4. The comparisons are arranged in the order in which they were placed in the field. In each comparison the two seed stocks compared are designated as first and second members. Thus in column 2 crossbred seed (first member) is compared with F_2 seed (second member).

TABLE 4.—*Comparison of yields of crossbred and recombined selfed strains of maize*

Items of comparison	Crossbred and F_2	Crossbred and F_4	Crossbred and crib selected	Crossbred and F_1	F_1 and F_2	F_1 and crib selected
Yield per acre (bushels):						
First member	42.1	41.4	38.1	33.3	32.7	34.5
Second member	42.6	28.7	33.2	35.7	31.5	23.6
First member minus yield of second member	−.70±1.68	13.00±1.02	4.70±.56	−2.82±.88	.17±.8	10.86±.86
Difference ÷ probable error difference	.42	12.4	8.4	3.2	.2	12.6
Yield per plant (pounds):						
First member minus second member	.006±.021	.094±.012	.022±.003	−.039±.009	.013±.009	.134±.012
Difference ÷ probable error difference	.28	7.8	7.3	4.3	1.4	11.1

It will be seen that seed from the crossed experiment was compared with each of the four other kinds, and in addition there were two borders in which F_1 seed was compared with crib-selected and F_2 seed.

The results show that the five seed types fall into two groups with respect to yield, a high-yielding group comprising the F_1, F_2, and the crossbred. All the members of this group show significantly higher yields than either the F_4 or the crib selected, the difference ranging from 15 to 45 per cent and each of them over eight times the probable error of the difference.

In the higher yielding group the F_1 seed stock resulting from the selfed experiment outyielded the crossbred block by 8 per cent in both yield per section and yield per plant, but these differences are but three or four times the probable error.

The yields of crossbred and F_2 were practically the same. The crossbred exceeded the F_2 slightly in yield per plant but occupied the reverse position in yield per acre. The F_4 and crib selected were not directly compared, but both were compared with the crossed block, and judged by this indirect comparison the crib selected exceeded the F_4 in both yield per plant and yield per acre by an amount that is more than six times the probable error of the difference. Arranged in a descending order the standing of the five seed stocks was as follows: F_1, F_2 and crossed block, crib selected, F_4.

A check on the direct comparison is possible in the cases where both seed stocks of an experiment are elsewhere compared with a third kind. The results are consistent within the limits of errors of sampling.

CORRELATION OF NUMBER OF PLANTS WITH YIELD PER PLANT

In comparing the yields of the various seed stocks, both the yield per row and the yield per plant have been considered. If the space afforded by missing plants is utilized by those remaining to increase their yield, the yield per plant would favor progenies with a low germination and would vitiate conclusions based on this measurement. On the other hand, if poor stands result from unfavorable soil conditions, the same factors that result in failure to germinate or the death of plants might be expected to reduce the yield of the surviving plants. If the former is the correct explanation, there should be a negative correlation between the number of plants and the yield per plant. In the latter case the correlation should be reversed, and the sections with the fewest plants should have the lowest yield per plant.

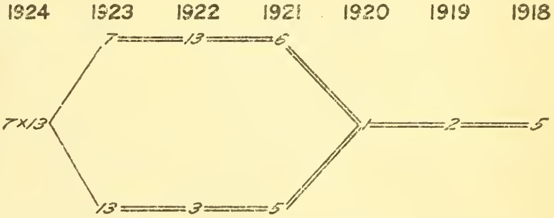

FIG. 4.—Representative pedigree of progenies in the F_1 seed stock of maize tested in 1924. The numbers indicate individual plants. Selfed generations are shown by double lines. F=87.5

In calculating the correlation coefficient of number of plants with yield per plant, differences in the yield of the various stocks were allowed for by using the departures of the sections from the mean of the row for both yield and number of plants. The result was a coefficient of 0.063 ± 0.037, not a significant correlation. From the probable error it would appear that no correlation greater than 0.1 is to be expected, and with a relation of this order the effect of the number of plants on the yield per plant would be negligible.

MEASURES OF INBREEDING

It is obvious that in both the crossed and the selfed breeding methods followed in the present experiments the portion of the foundation stock from which the seed has descended will become reduced as the selection proceeds. In the crossed experiment, restricting the pollinations to the 10 best-appearing rows narrows the foundation stock to 10 ears the first season. In succeeding years the rejecting of 10 of the 20 rows before making pollinations will eliminate the blood of still other foundation ears. Eventually, however, the intermingling of blood through cross-pollination will bring about a condition in which at least a trace of the blood of all the remaining foundation ears will be present in each of the progenies. When this condition is reached no further eliminations can take place.

An analysis of the pedigrees shows that in this experiment seven of the foundation ears were represented in the selections of 1924. The total contribution by the individual ears varied from 1.6 to 21.8 per cent.

In the selfed method as planned in this experiment a maximum of 15 foundation ears might be retained the first season, but as selfing continues additional ears would be dropped. In this experiment but two foundation ears were represented in the 1923 plantings, and in 1924 all progenies were descended from a single foundation ear.

The number of foundation ears retained in a pedigree is a very imperfect indication of the degree of inbreeding. For the maize breeder the most valuable measure of inbreeding would be one that expressed the degree of heterosis. Fortunately, such a measure is now available in the coefficient of inbreeding of Wright (*6, 7, 8*)[2]. Beginning at any generation in the ancestry of an individual or strain, this coefficient gives the percentage of the characters or factors heterozygous at the beginning of the pedigree that have become homozygous through consanguineous matings. The generally accepted theory of heterosis, or hybrid vigor, assumes this increased vigor to be due to the increased number of dominant factors. The larger number of dominant factors in a hybrid as compared with the mean of the inbred lines of which it is composed is due entirely to the increase of heterozygous factors and the phenomenon of dominance. Since the coefficient of inbreeding determines the degree of heterozygosity, it should be a direct measure of heterosis.

Any method of breeding except the continued use of F_1 hybrids involves some reduction in heterosis, and it is therefore of importance to know to what extent selection may overcome or offset the ill effects of inbreeding.

The theory of the coefficient of inbreeding assumes a relatively large number of factors heterozygous in the foundation stock. As a result of consanguineous matings a portion of this number will become homozygous. The coefficient expresses this portion as a percentage of the total number of factors heterozygous in the foundation stock. It represents an average condition and is only applicable to any particular individual within the limits of random sampling. It further assumes the absence of selection. In the absence of selection the homozygous factors would be dominant and recessive in equal numbers. Where the selection of vigorous lines and individuals is practiced there would be a tendency to retain lines and individuals with an excess of dominant factors and also those with a larger number of heterozygous factors. If selection were without effect we should expect a close negative correlation

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[2] The serial numbers (*italic*) in parentheses refer to "Literature cited," at the end of this bulletin.

between the degree of inbreeding and vigor. This is true especially where the combination of a number of lines approximates an average condition, as in the yield tests of 1923 and 1924.

Table 5 gives the average coefficient of inbreeding of the seed stocks compared in 1923 and 1924 and affords a striking illustration of the extent to which the effects of inbreeding may be overcome by selection. The F_1 progenies of 1924 exceeded all other seed stocks in yield, yet the average coefficient of inbreeding of these progenies was 78.91, the highest coefficient of the series. A coefficient of 78 indicates a degree of inbreeding slightly in excess of that resulting from two generations of selfing. If uninfluenced by the selection of heterozygous individuals, more than three-fourths of the factors heterozygous in the foundation stock would have become homozygous.

Table 5.—*Coefficient of inbreeding of the seed stocks of maize compared in 1923 and 1924*

Year and seed stock	Coefficient of inbreeding	
	Average	Range of individual progenies
1923:		
Crossbred	11.9	7.9 to 15.7
F_2	42.2	31.3 to 78.1
1924:		
Crossbred	13.6	8.7 to 18.3
F_1	78.9	0 to 96.9
F_2	51.6	25.0 to 78.3
F_4	27.1	23.3 to 28.5

Some explanation is needed of the diversity in the behavior of the various seed stocks representing combinations of selfed lines. The 1923 F_2 and 1924 F_4 seed stocks proved to be decidedly inferior to the crossbred seed, while the 1924 F_1 and F_2 equaled or exceeded the crossbred stock. It is of course expected that individual combinations will differ widely in yield and vigor, but it was thought that in each seed stock a sufficient number of combinations were lumped to represent an average condition, and the difficulty of making accurate field comparisons makes it impracticable to test a large number of individual combinations.

The disparity is not to be explained by differences in heterosis, for the coefficients of inbreeding show the 1923 F_2 and the 1924 F_4 to be less inbred than the other seed stocks from the selfed experiment.

The selfed lines from which the 1923 F_2 and 1924 F_4 were derived were combined in 1920 and 1921. The lines comprising the F_1 and F_2 of 1924 were not combined until 1922 and 1923. In the latter stocks there had been, therefore, more opportunity for selection. An examination of the pedigrees shows that the descendants of a single row in 1921, No. 1, contributed 45 per cent of the blood of the F_1 progenies and 35 per cent of the blood of the F_2 progenies tested in 1924. This particular 1921 row was not represented in the ancestry of either the 1923 F_2 or the 1924 F_4. The original crosses from which the 1924 F_4 descended were made in 1920.

The selfed descendants of row 1, 1921, stood higher than the descendants of any other 1921 row in 1922, 1923, and 1924, and it seems probable that the prepotency of this strain is the explanation of the high performance of the F_1 and F_2 in 1924.

Figure 7 shows the descent of the progenies in the selfed experiment up to and including the plantings in 1924. The progenies are numbered each year in the order of their standing with respect to ear length. The portion of the diagram within the dotted line shows the descendants of progeny No. 1, 1921.

DISCUSSION

In the light of the modern knowledge of inheritance, theories of maize improvement fall rather naturally into three groups, depending on whether departures from the maximum vigor are assumed to be due to (1) mutation, (2) the segregation of simple Mendelian characters, or (3) the segregation of multiple-factor characters.

MUTATIONS

Attempts to apply the findings of genetics to the improvement of maize have been directed almost exclusively to the elimination of existing variations. Indeed, if mutations are of sufficiently frequent occurrence to be the important factor, existing knowledge of the laws of genetics can be of little aid to breeding. The proper procedure would be that which reduces the occurrence of mutations to a minimum, and at present practically nothing is known regarding the causes of mutation.

The selfing of maize varieties brought to light such large numbers of existing recessive characters that the appearance of new variations by mutation has been disregarded to a large extent. If deleterious mutations are taking place with any great frequency the improvement of varieties by the combination of inbred strains may afford relief so temporary as to be economically impracticable. It should be kept in mind also that mutations may be more frequent in homozygous than in heterozygous strains. There is no direct evidence on this point, and if the findings of Emerson (*2*) with respect to somatic mutations of the variegated character in the pericarp are any index of gametic mutations, no increase in the rate of mutations need be expected to follow selfing.

SEGREGATION OF SIMPLE MENDELIAN CHARACTERS

The hope that maize may be improved by intensive inbreeding is based very largely on two facts: (1) The continuous appearance of unproductive off-type plants even in carefully selected crossbred stocks, and the behavior of these variations as Mendelian characters; and (2) heterosis, or the vigor of F_1 hybrids.

The generally accepted view of heterosis that followed the work of Bruce (*1*), Keeble and Pellew (*4*), and Jones (*3*), is that the first and second facts mentioned are essentially the same phenomenon, the only difference being one of magnitude in the effect produced by the genetic factors involved. Admitting this fundamental similarity, however, the indicated breeding methods would differ profoundly, depending on whether the object was the elimination of a comparatively few recognizable recessive characters or a multitude of recessive characters too small to be detected individually.

The hope of improvement through the elimination of recognizable variations by selfing is based on the idea that these unproductive variations appear in commercial varieties with sufficient frequency to depress the yield materially. Although seed from the unproductive variations is not planted, the characters persist in the heterozygous state and by means of the pollen from the unproductive plants. Careful detasseling would, of course, eliminate the last source of infection; but so long as the plants are cross-pollinated, heterozygous individuals can not be distinguished from homozygous dominants, and recessive characters will persist.

On the other hand, selfing brings simple heterozygous characters into expression, and failure to appear in even a small population makes it reasonably certain that the line carries only dominant factors.

So far as simple characters are concerned there would seem to be no value in selfing for more than one generation, for with a population of only 50 F_2 individuals the chance of a simple heterozygous character not coming into expression is less than one in a million.

It probably is safe to conclude that the great majority of the conspicuous variations of maize are less productive than the normal type. The question is: Do these appear in commercial varieties in sufficient numbers to reduce the yield appreciably?

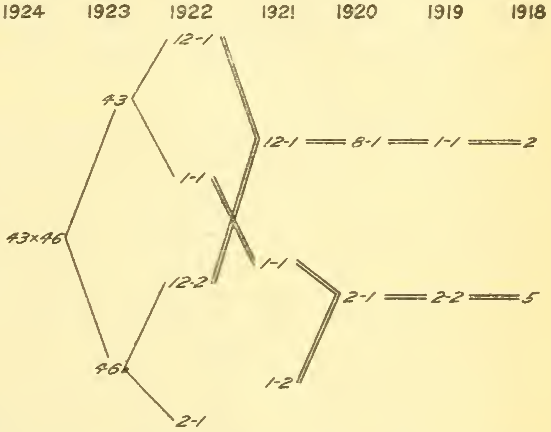

FIG. 5.—Representative pedigree of progenies in the F_2 seed stock of maize tested in 1924. Numbers indicate individual plants. Selfed generations are shown by double lines. F=45.3

In the course of these experiments 400 selfed lines have been grown and the characters of the individuals noted. These lines exhibit the usual diversity, including numerous minor chlorophyll disorders, but only three conspicuous variations of a clearly deleterious nature have been observed. These are "golden," "silkless," and "zigzag" stalks. In a careful examination of the commercial plantings of Sacaton June corn, golden and silkless plants were found, but with a frequency something less than one in a thousand, and no zigzag plants were observed.

It is obvious that in this variety at least the elimination of conspicuous variations can not be expected to effect any material improvement in yield.

Breeding with simple characters, the individual effects of which are too insignificant to be recognized, is the essence of the dominant growth-factor idea. When this theory was formulated, it was assumed that although the individual characters were not recognizable, the stocks most desirable in combination might be selected from their behavior as selfed lines. The work of Richey (*5*) has shown that this requirement is not always fulfilled. In a careful and comprehensive comparison of the value of 10 selfed lines as the parents of F_1 hybrids the most desirable selfed line was one of the weakest.

If the selfed lines must be tested in combination before selection is practicable the problem is greatly complicated, and it may not be out of place to discuss briefly what is to be expected under these circumstances. The object is to obtain the maximum number of dominant characters.

An F_1 cross between two varieties or two individuals of the same variety falls short of producing the minimum number of homozygous recessive characters to be derived from the cross only to the extent that factors heterozygous in both parents have united to produce one in four homozygous recessive individuals.

If the number of common heterozygous characters is small in comparison with the number of homozygous characters which are dominant in one parent and recessive in the other, any combination of selfed lines from the original cross will almost certainly have a larger number of homozygous recessive characters than the original cross, because of the characters which were DD in one parent and RR in the other that will reappear as RR. Thus, if the parental plants are distantly related it would be hopeless to attempt an increase over the vigor of the F_1.

The other extreme in which the parents have a maximum number of heterozygous characters in common would be represented by two F_1 plants in a hybrid between two unrelated stocks. The question then would be to decide whether it is possible to obtain a stock by combining selfed lines that would exceed the F_2 in the number of dominant characters. This should be possible, for even a random combination of selfed lines would equal a random F_2 population in dominant factors. The conditions imposed, however, are not likely to be met with in practical breeding. The nearest approach that would occur is in the attempt to improve a commercial variety without introducing foreign blood, as in the experiment here reported. The marked decline in vigor that follows the first generation of selfing indicates that commercial varieties are far from representing the extreme condition assumed above and that very different sets of characters are heterozygous in different individuals.

The most practicable method of obtaining a large proportion of simple dominant characters would seem to be to make a series of hybrids between plants of unrelated strains and compare their vigor, retaining remnants with which to continue either selfed or crossbred stocks of the most desirable parents.

SEGREGATION OF MULTIPLE-FACTOR CHARACTERS

If the deleterious characters that are to be eliminated from maize varieties are largely multiple-factor characters, the problem takes on a very different aspect.

Most of the conspicuous abnormalities that have been observed in maize require for their expression more than one homozygous recessive factor. Many of these characters appear in one-quarter of the individuals of a progeny, indicating a single factor difference; but when the abnormal individuals are outcrossed to unrelated strains it develops that the mutation or segregation bringing the character into expression was the last of a series. The stock in which the abnormality appeared already was homozygous recessive for one or more factors that produced no visible effect by themselves.

If most recognizable characters are multiple-factor characters is it not probable that many of the less conspicuous characters that are assumed to make up the phenomenon of heterosis also are equally complex? Observed multiple-factor characters represent varying degrees of departure from normal, small departures being more frequent than large, and it seems a logical assumption that expressed variations too small to be recognized individually also are of a compound nature.

Multiple-factor characters will come into expression in large numbers in generations later than F_2, and if they are of a nature to be recognized continued selfing would assist in their elimination. But if the characters must be treated en masse and the choice of strains be governed by behavior in crosses the value of continued selfing may be questioned. If selfing were continued to complete homozygosity, most of the characters would still be represented by homozygous recessive factors in some line, and the characters would reappear when the lines were combined.

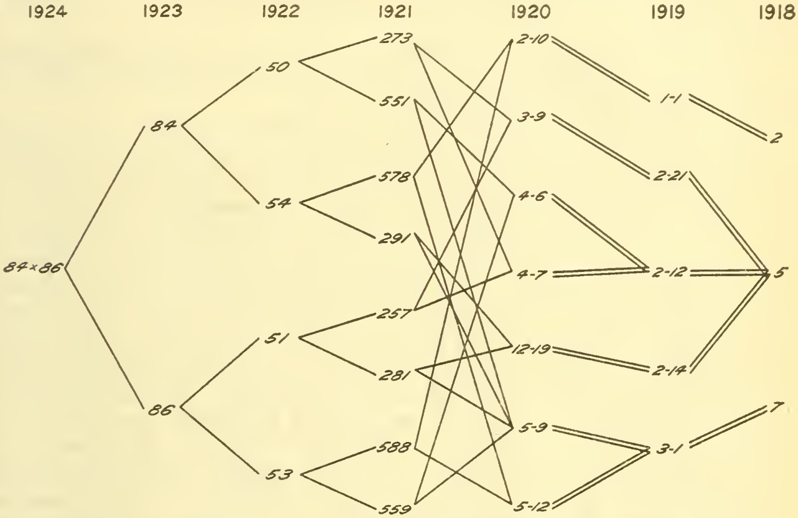

FIG. 6.—Representative pedigree of progenies in the F_4 seed stock of maize tested in 1924. Numbers indicate individual plants. Selfed generations are shown by double lines. F=27.1

Our problem here is to free a commercial variety or a cross from multiple-factor characters that come into expression from time to time through recombination.

Confining the discussion to dihybrid characters and with selfing continued until complete homozygosity is obtained, one-quarter of the characters will be brought into expression, and of these more would appear following the second generation of selfing than in any other generation. A corresponding quarter would be represented entirely by dominant allelomorphs. The remaining half would again become heterozygous when the lines were recombined. Assuming that most of the characters would cause a deviation from normal too slight to be recognized as individual characters, a choice of lines or crosses would have to be made on the comparative vigor in combination. Uncertainties thus introduced would lessen the percentage of recessive characters eliminated to something less than one-quarter. The crossing and reselection necessary to eliminate multiple-factor characters is a very laborious operation; and unless methods are devised that will greatly increase the number of comparisons that can be made the elimination of multiple-factor characters as an object in breeding appears very unpromising.

Crosses of inbred strains that are outstanding in vigor may owe their vigor to a small number of relatively important factors rather than to the chance conjunction of a large number of insignificant factors. If this is the case, the chances are better for finding any desired character among crosses of the original stocks than among a similar number of crosses of inbred lines, and in addition there is a saving of time.

This line of reasoning assumes that we are seeking exceptional, favorable, and dominant variations rather than the elimination of recessive and deleterious variations.

In the present experiments the failure to obtain significant increases by the elimination through selfing of the poorest yielding strains, together with the numerous instances in which individual crosses of selfed lines have shown exceptional vigor, suggests the greater importance of dominant variations. Against this view is the failure of high-performing selfed lines to show themselves uniformly superior as the parents of crosses. This failure may be due to the fact that in most of the reported experiments the parents of the crosses were closely related. There would be the liability for a favorable dominant variation to carry with it deleterious recessive characters. Or, to put it another way, the deleterious recessive characters would survive when offset by some accompanying favorable character.

If the parents of a cross are unrelated, most of the deleterious recessive characters will be kept out of expression. We may gain the advantage of the favorable factors and suppress the accompanying recessive characters by crossing unrelated high-yielding selfed strains. But there is great need for more information regarding the value as parents of high and low performing selfed lines in intervarietal and intravarietal crosses.

CONCLUSIONS

From a practical standpoint it appears that both the selfed and the crossbred breeding methods gave substantial increases over the original variety. Excepting the 1924 F_4, which had but two-years' selection before the crosses were made and was represented in the test by a rather small number of crosses, all seed stocks were significantly more productive than the crib-selected Sacaton June corn which was taken to represent the original variety.

The 1924 F_1 progenies outyielded the crossbred seed by an amount that is statistically significant, but it scarcely can be said that the superiority is agriculturally important. The other seed stocks representing the selfed experiment and more nearly corresponding to an improved open-pollinated variety were not superior to the crossbred seed.

The experiment was planned to test the possible value of eliminating inferior strains from a commercial variety by means of selfing; and the answer, so far as it is given by this experiment, is that the method is of doubtful value.

There is strong though rather indirect evidence that, in the course of the selfed experiment, a single superior strain was isolated that produces high-yielding progenies when combined with other strains. Whether this strain can be made agriculturally useful remains to be determined. The unique behavior of this progeny makes it unwise to attempt generalizations. There is no way of telling from the present experiment with what frequency the occurrence of similar superior strains is to be expected.

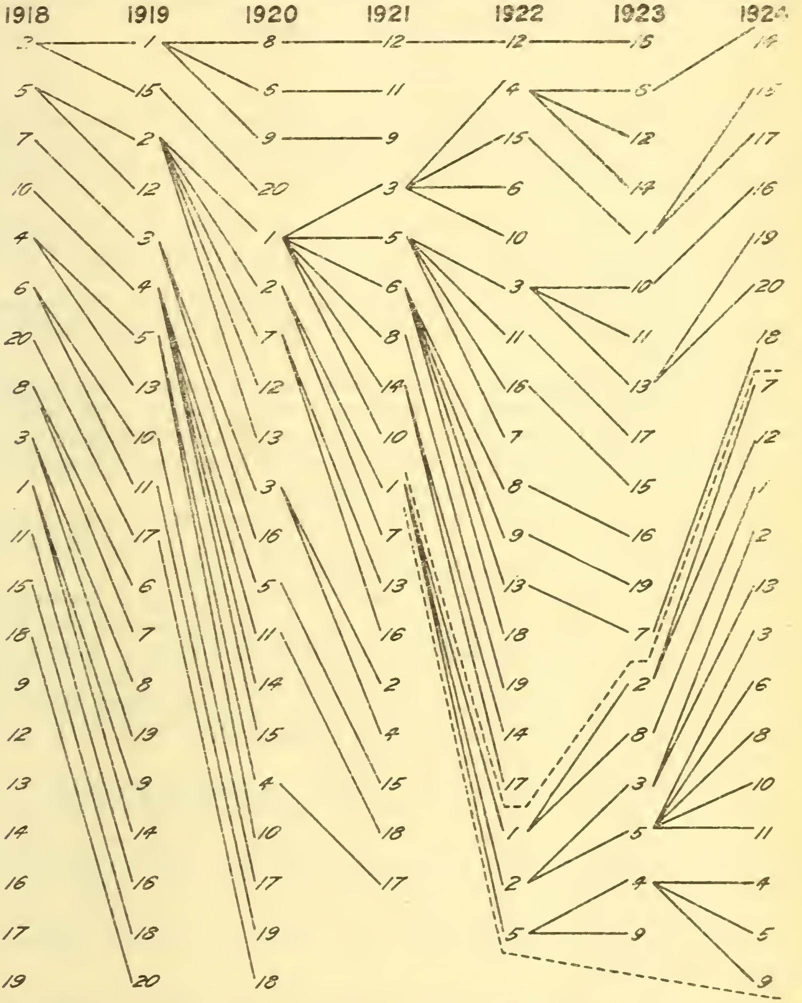

FIG. 7.—Descent of progenies of maize in the selfed experiment. Each year the progenies are numbered according to their standing as determined by the average length of ear. The dotted line incloses the descendants of progeny No. 1, 1921

The experiment in eliminating inferior strains by selfing was planned to test the practicability of increasing the yield without necessitating the making of first-generation crosses each year. The results indicate that for such a demonstration it will be necessary to start with a much larger foundation stock or with two stocks maintained separately. The time and labor involved are excessive and would appear necessary only as a concession to the reluctance of seed-corn producers to utilize first-generation crosses.

SUMMARY

A series of experiments is reported that compares the "ear-to-row" breeding method with a method of close breeding in which inferior strains were eliminated through selfing and the surviving strains recombined.

Sacaton June corn, a variety derived from Mexican June corn and adapted to the irrigated regions of the Southwest, was chosen for the experiments, which were made at Sacaton, Ariz.

Twenty ears were selected as the foundation stock. The experiments were started in 1918 with two identical ear-to-row plantings from these ears.

In the crossed experiment, crosses were made between the highest yielding rows and between the highest yielding plants regardless of row. In the selfed experiment, plants in each row were selfed, and selections for the following season were made from the highest yielding rows and the highest yielding individual plants.

Following three years of selfing, crosses were made between the selfed strains with the idea of reestablishing the vigor of the stock, the undesirable lines having been eliminated.

Numerous abnormalities were observed in the course of the experiments. Few of these appeared to be definitely associated with decreased yield, but in the selfed experiment there was a close negative correlation between yield of the strain and the number of abnormalities observed. There is thus reason for believing that the elimination of the numerous minor abnormalities common in most varieties of maize will increase the yield.

The selection of selfed lines was effective in establishing high-yielding strains. Some of the selfed strains gave yields above the average of the crossed experiment in 1923 and 1924. There was a significant parent-offspring correlation, high-yielding progenies producing high-yielding progenies the following season. In the selfed experiment, selections from high-yielding progenies greatly outyielded selections from individual high-yielding plants chosen without regard to progeny performance.

In the crossed experiment, there was no significant difference in the yields of selections from high-yielding progenies and individual high-yielding plants.

In 1923 a comparison of the results of the two breeding methods was made by planting alternate rows to a mixed sample of hand-pollinated seed from the crossed experiment and a mixture of F_2 progenies from crosses between selfed progenies. The crossed experiment outyielded the selfed experiment by about 25 per cent. The difference is undoubtedly significant, being seven times the probable error.

In 1924 a more comprehensive yield test was made, involving the continuously crossbred seed from the crossed experiment, crosses

between selfed lines representing the first, second, and fourth generations and the original variety. The highest yield was from the first-generation cross of selfed lines. The superiorty of the first-generation cross over that of the fourth and the original variety was undoubtedly significant and amounted to 40 to 50 per cent. The difference between the first-generation seed as compared with that of both the second-generation and the crossbred seed probably was significant also. The yields of the second-generation and the crossbred seed were practically identical, and both were undoubtedly superior to either the fourth-generation or the crib-selected seed. From indirect comparison it would appear that the crib-selected seed was significantly superior to the fourth-generation cross.

A calculation of the coefficients of inbreeding showed that a narrow inbreeding was not incompatible with high yields. The F_1 crosses from which the highest yields were obtained had an average coefficient of inbreeding of 78 per cent relative to the foundation stock.

The seed stocks resulting from both breeding methods were decidedly superior to the original variety.

Although the highest yields were obtained from the selfed experiment, a single high-performing selfed line played so important a part in the final yields that it seems unsafe to consider the results as sufficiently typical of the method to warrant recommendations.

Three types of deleterious variations in maize are recognized, and the breeding methods best calculated to eliminate them are discussed.

LITERATURE CITED

(1) Bruce, A. B.
1910. The Mendelian theory of heredity and the augmentation of vigor. *In* Science, vol. 32, pp. 627–628.

(2) Emerson, R. A.
1922. The nature of bud variations as indicated by their mode of inheritance. *In* Amer. Nat., vol. 56, pp. 64–79.

(3) Jones, D. F.
1917. Dominance of linked factors as a means of accounting for heterosis. *In* Genetics, vol. 2, pp. 466–479.

(4) Keeble, F., and C. Pellew.
1910. The mode of inheritance of stature and of time of flowering in peas. *In* Jour. Genetics, vol. 1, pp. 47–56.

(5) Richey, F. D.
1924. Effects of selection on the yield of a cross between varieties of corn. U. S. Dept. Agr. Bul. 1209, 20 p., illus.

Wright, S.
(6) 1921. Systems of mating. *In* Genetics, vol. 6, pp. 111–178, illus.

(7) 1922. Coefficients of inbreeding and relationship. *In* Amer. Nat., vol. 56, pp. 330–338.

(8) 1923. Mendelian analysis of the pure breeds of livestock. *In* Jour. Heredity, vol. 14, pp. 339–348, 405–422, illus.

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