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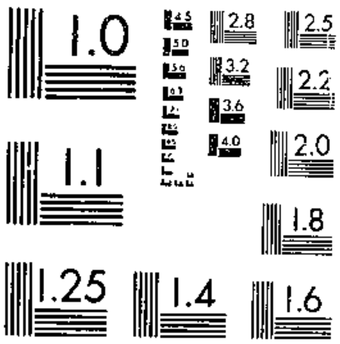

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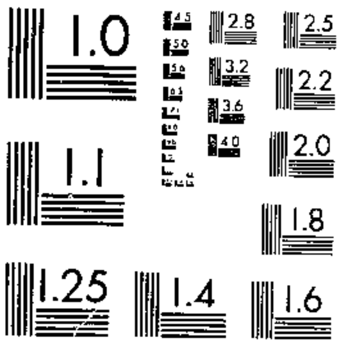

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EXPERIMENTS ON HYBRID VIGOR AND CONVERGENT IMPROVEMENT IN CORN[1]

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INTRODUCTION

The determination of the cause of hybrid vigor is a fundamental problem in practical corn breeding. The major programs of corn improvement in the United States to-day involve the isolation of more or less homozygous lines through selection and self-fertilization as the first step. At present these inbred lines must be crossed into various hybrid combinations for commercial utilization. The extent to which better inbred lines can be obtained and also the possibility of obtaining high-yielding homozygous lines depend upon just what is the cause of hybrid vigor.

There are two major hypotheses as to the cause of hybrid vigor. One of these assumes the existence of an unexplained physiologic stimulation resulting from the mere fact of heterozygosis; it holds that there is some kind of physiologic stimulation attributable to the fact that the gametes are unlike. The other hypothesis attributes hybrid vigor to the combined action of dominant favorable genes coming from the two parents.

The development of these theories and the experimental evidence upon which they are based have been reviewed so frequently and so adequately (*1, 2, 3, 5, 8*)[3] that further review here seems unnecessary.

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[1] Presented before the joint meeting of the Geneticists Interested in Agriculture and the American Society of Agronomy, Cleveland, Ohio, Dec. 29, 1930.

[2] The writers wish to express their appreciation of the valuable assistance rendered at various times during the course of these experiments by H. S. Garrison, assistant agronomist, J. M. Hammerly, senior scientific aide, and John S. Fowler, field assistant, Division of Cereal Crops and Diseases.

[3] Italic numbers in parentheses refer to Literature Cited, p. 22.

So far as the writers are aware, either hypothesis fits all of the observed facts adduced from many careful experiments on inbreeding and outbreeding. This is true because in those experiments a change in heterozygosis provided a corresponding change in the opportunity for the action of dominant favorable genes. The dominant-favorable-gene hypothesis, however, is in agreement also with the interaction of genes as observed in extensive, detailed genetic investigations. Consequently, the consensus of opinion among geneticists supports the dominant-favorable-gene hypothesis, with the reservation that physiologic stimulation from heterozygosis, too, may play some part, or at least that the existence of such stimulation has not been disproved.

A possible means of distinguishing between these two hypotheses experimentally was suggested, from theoretical considerations, in a previous paper (7). It is desired in the present paper to review briefly the theory of convergent improvement and to present such experimental data as have been accumulated.

Convergent improvement consists of a more or less definite system of crossing, back pollinating, and selfing, all accompanied by selection, in an effort to improve inbred lines of corn without interfering with their behavior in hybrid combination. It seeks to do this by bringing about the convergence of the favorable dominant genes from two or more inbred lines into a single stream of germ plasm.

Regarding yield as the measure of vigor, the theoretical basis for convergent improvement assumes that—

(1) Selfed lines that combine into a high-yielding cross carry, together, the important dominant genes necessary for increased yield, and are alike for such necessary genes as are recessive.

(2) The excess yield of a cross above that of one parent may be attributed to the dominant favorable genes received from the other parent.

(3) Back pollinating a cross, as N×R, to one of the homozygous parents, as R, in several successive generations, without selection and in the absence of linkage, will recover the genotype of the recurrent parent, R, according to the series ½, ¾, ⅞, etc.

(4) Selection of only the more vigorous, productive plants during the period of successive back pollination will retain some of the dominant favorable N genes, which will be present in the heterozygous condition, however, as long as back pollinating to R is continued.

(5) Selection within selfed lines after back pollinating will produce a line homozygous for the dominant R and some of the dominant N genes. This recovered line may be designated R (N′). It should yield more than R because of the added dominant favorable (N′) genes, and should behave the same as R in crosses with N, as only the dominant genes would be expressed in the heterozygous condition.

(6) Two reciprocally recovered lines R (N′) and N (R′) would differ in fewer dominant genes than the parental lines N and R. By repeating the breeding program, using these recovered lines as foundation stock, therefore, further increments could be added reciprocally, bringing about a gradual convergence of the dominant favorable genes from N and R into a single strain.

Briefly stated, then, convergent improvement involves the reciprocal addition to each of two homozygous selfed lines that combine to produce a high-yielding cross of those dominant favorable genes which one line lacks, but which are carried by the other, by (1) crossing the two lines, (2) back pollinating to one line through each of several generations to recover the dominant genotype of that line, (3) at the same time practicing selection to retain favorable dominant genes entering the cross from the nonrecurrent parent, (4) selecting within selfed lines to fix the added genes in the homozygous condition, (5) performing these operations in parallel with each of the original lines as the recurrent parent, and (6) repeating the operation to achieve further improvement, using the recovered lines in place of the original parent lines as foundation stocks.

Success in such a program is possible only if the interaction of dominant favorable genes is the cause of hybrid vigor. Under this hypothesis, moreover, a cross between R (N′) and N (R′) should be as productive as, or more productive than, the cross between R and N. Under the hypothesis of physiologic stimulation, on the other hand, crosses between these recovered lines would be expected to yield less than those between the original parents. This follows from the fact that the recovered lines would be more nearly like each other and crosses between them consequently would be less heterozygous. Agreement of experimental results with one of these different expectations accordingly should differentiate critically between the two theories.

Yield data are reported here bearing on the effects (1) of back pollinating to a recurrent parent for different numbers of successive generations, and (2) of crossing such lines, back pollinated for different numbers of generations, with the nonrecurrent parent or with a reciprocally back-pollinated line. Before proceeding with the data, it is desirable to discuss briefly the breeding program from which the stocks were derived.

THE BREEDING PROGRAM

Most of the inbred lines used as foundation stocks were selected from varieties adapted to Corn Belt conditions. The lines of C. I.[4] No. 227 (a strain of a Bloody Butcher type from China) and of C. I. No. 228 (Lancaster Surecrop) were selected at the Arlington Experiment Farm, in Virginia. The line of C. I. No. 540 was obtained from H. A. Wallace, Des Moines, Iowa, and the lines of C. I. No. 549 were obtained from J. R. Holbert, Bloomington, Ill. Selection of the lines of C. I. No. 201 (Delta Prolific) was begun in Arkansas and has been continued at the Arlington Experiment Farm.

It is unnecessary to give detailed yields of the F_1 crosses used. They are all two or more times as productive as the parent inbreds, thus evidencing an abundance of hybrid vigor. F_1 crosses and double crosses involving the parent inbreds also have produced high absolute yields. One double cross was second among the hybrid entries in the Ames district of the Iowa State Corn Yield Test in 1928, producing 11 bushels per acre more than the best open-pollinated variety. Another double cross was first in the same district in 1929, yielding 9 bushels per acre more than the best open-pollinated variety. Several of the foundation F_1 crosses yield practically as much as these double crosses, and the rest are only slightly less productive. It is obvious, therefore, that reasonably good germ plasm is carried by the breeding stocks.

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[4] Accession number of the Division of Cereal Crops and Diseases, formerly Office of Cereal Investigations.

SELECTION IN BACK-POLLINATED LINES

In beginning selection in back-pollinated lines, from 2 to 5 F_1 plants have been pollinated with pollen of the recurrent parent. From 40 to 100 plants have been grown from the seed so produced and the better of these have been back pollinated. The seed from what appeared at harvest to be the best of these plants then was planted in ear-to-row progenies, back pollinating and selecting being continued within and between these progenies. From 18 to 25 plants have been grown in the progeny rows, depending upon the number of progenies to be grown and the land available.

Most of the pollinating has been controlled by hand. In one season it was possible to have several isolated plots. Each of these was utilized for one recurrent parent line, the back-pollinated progenies being grown in two of every three rows and detasseled. This practice eliminates the preliminary selection ordinarily made during hand pollinating unless this selection is made a special task. In the present experiments, where the number of progenies back pollinated to any one recurrent parent was relatively small, the use of isolated plots did not add much to the efficiency of operation. If many progenies were being back pollinated to one recurrent parent, isolated plots would be helpful.

The specific crosses and the recurrent parents being used in the convergent-improvement program at the Arlington Farm are shown in Table 1. The number of progenies grown in each breeding line in each generation through 1930 is also shown. A relatively large number of lines was used in order to provide generality of experience. This fact, together with adverse seasonal conditions during three years of the experiments, has kept the possibilities of selection within the individual lines below what seems desirable.

TABLE 1.—*Pedigrees of stocks in the program of convergent improvement*

Pedigree No.	Number of progenies grown in stated generation of—						
	Back pollinating					Selfing	
	1	2	3	4	5	1	2
227-2-S4×227-1-S4	6	5	7	----	----	7	----
227-3-S4×227-1-S4	4	1	2	3	----	4	----
227-4-S4×227-1-S4	2	2	4	----	----	2	----
227-6-S4×227-1-S4	2	2	3	3	----	4	----
227-1-S4×227-2-S4	2	1	5	1	----	5	----
227-3-S4×227-2-S4	2	2	3	6	----	4	----
237-4-S4×227-2-S4	2	4	5	5	----	2	----
227-6-S4×227-2-S4	2	5	5	4	----	3	----
540-S4×227-2-S5	5	5	6	----	----	7	----
549-A-S10×227-2-S5	4	8	----	----	----	0	----
549-B-S10×227-2-S5	1	1	----	----	----	1	----
227-1-S4×227-3-S4	2	3	6	8	----	1	----
227-2-S4×227-3-S4	2	2	5	4	----	2	----
227-6-S6×227-3-S6	2	2	----	----	----	2	----
228-4-5-S7×227-3-S6	1	3	4	----	----	7	3
540-S4×227-3-S6	4	5	6	----	----	11	8
549-A-S10×227-3-S6	2	3	----	----	----	4	4
549-B-S10×227-3-S6	1	2	2	----	----	2	3
227-1-S4×227-4-S4	6	9	5	6	----	4	----
227-2-S4×227-4-S4	6	3	3	----	----	5	----
227-1-S4×227-6-S4	2	4	4	6	----	3	----
227-2-S4×227-6-S4	2	2	5	3	----	0	----
228-3-3-S5×228-1-2-S5	2	4	2	4	----	3	----

TABLE 1.—*Pedigrees of stocks in the program of convergent improvement.*—Contd.

Pedigree No.	Number of progenies grown in stated generation of—						
	Back pollinating					Selfing	
	1	2	3	4	5	1	2
228-4-8-S5×228-1-2-S5	1	2	3	-----	-----	5	-----
228-6-5-S5×228-1-2-S5	2	2	3	-----	-----	3	-----
228-1-2-S5×228-4-8-S5	3	5	2	3	-----	6	-----
228-2-2-S5×228-4-8-S5	3	6	3	5	-----	6	-----
228-3-3-S5×228-4-8-S5	2	1	2	5	-----	2	-----
228-6-5-S5×228-4-8-S5	4	40	11	5	11	8	-----
227-3-S6×228-4-8-S7	1	2	2	-----	-----	3	-----
540-S4×228-4-8-S7	2	2	5	-----	-----	10	16
540-A-S10×228-4-8-S7	2	2	6	-----	-----	4	3
549-B-S10×228-4-8-S7	3	2	7	-----	-----	9	-----
228-1-2-S5×228-6-5-S5	2	3	2	-----	-----	3	-----
228-2-2-S5×228-6-5-S5	2	6	3	-----	-----	3	-----
228-3-3-S5×228-6-5-S5	2	6	5	5	-----	1	-----
228-4-1-S5×228-6-5-S5	2	1	2	3	-----	-----	-----
228-4-8-S5×228-6-5-S5	4	19	6	6	-----	1	-----
540-S4×228-6-5-S7	5	3	6	-----	-----	4	-----
549-A-S10×228-6-5-S7	3	4	-----	-----	-----	7	-----
540-B-S10×228-6-5-S7	1	1	3	-----	-----	6	-----
201-C-S9×201-A-S7	2	2	2	-----	-----	-----	-----
201-H-S9×201-A-S7	2	12	5	-----	-----	-----	-----
201-C-S9×201-B-S6	2	6	5	-----	-----	-----	-----
201-F-S9×201-B-S6	2	1	2	-----	-----	-----	-----
201-H-S9×201-B-S6	2	3	3	-----	-----	-----	-----
201-A-S7×201-C-S9	2	5	2	-----	-----	-----	-----
201-B-S6×201-C-S9	2	3	4	-----	-----	-----	-----
201-F-S9×201-C-S9	1	6	1	4	-----	-----	-----
201-H-S9×201-C-S9	2	7	4	7	-----	-----	-----
201-H-S11×201-E-S7	2	4	-----	-----	-----	-----	-----
201-B-S6×201-F-S9	2	4	5	-----	-----	-----	-----
201-C-S9×201-F-S9	2	5	5	10	-----	-----	-----
201-H-S9×201-F-S9	2	7	23	19	-----	-----	-----
201-A-S7×201-H-S9	2	2	-----	-----	-----	-----	-----
201-B-S6×201-H-S9	4	2	-----	-----	-----	-----	-----
201-C-S9×201-H-S9	2	4	3	4	-----	-----	-----
201-E-S7×201-H-S11	2	2	-----	-----	-----	-----	-----
201-F-S9×201-H-S9	5	2	-----	-----	-----	-----	-----

GREENHOUSE SELECTION

In order to advance the breeding program as rapidly as possible, a crop has been grown in the greenhouse each winter. The greenhouse crops were restricted chiefly to material being back pollinated for the first or second time, though a few progenies further advanced were also grown. Except for minor differences, the F_1 plants would be expected to be alike genetically, providing no opportunity for selection. Genetic differences would become apparent among the plants in the lines back pollinated once and among the progenies and plants in the lines back pollinated two or more times.

Selection among plants in the greenhouse was attempted by planting 25 seeds of a progeny 2 inches apart and thinning out the poorer seedlings as they became apparent, until only the 4 or 5 best plants remained. Seed from all the pollinated ears that could be obtained from these selected plants then would be planted in the field the next season. Generally no attempt was made to select among progenies except in the field, either all or none of the ears of a certain line of breeding being carried forward in the greenhouse.

Selection was made once among progenies, however, by the following method. Seed from the available ears was planted in sand on a slowly rotating table, 17 seeds from each ear to a row. The seedlings were measured shortly after emergence and again 11 days later.

Differences in the growth increments were assumed to be due to differences in inherent vigor. An experiment planned to verify both this and the efficacy of plant selection within the progenies could not

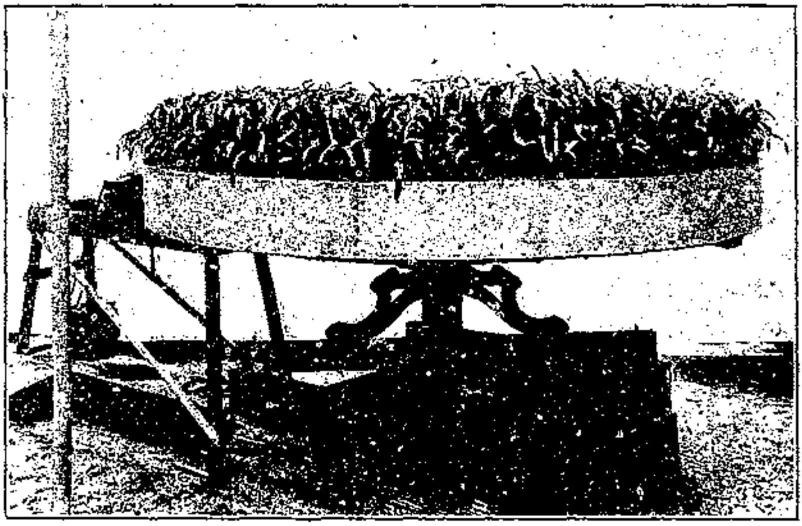

FIGURE 1.—Motor-driven rotating table for growing corn seedlings under conditions of uniform light and temperature

be completed because of failure to obtain the necessary seed. Observation of the mature plants, however, showed that the seedling differences persisted through the immediate generation. Kyle's *(6)*

FIGURE 2.—Appearance of seedlings grown on rotating table, showing arrangement

results, moreover, have shown that similar differences found in the field carried into the next filial generation. The appearance of the seedlings on the rotating table is shown in Figures 1 and 2, and that of the greenhouse crop of 1929–30 is shown in Figure 3.

EXPERIMENTS ON BACK POLLINATING AND RECROSSING

In the original discussion of convergent improvement (7), it was estimated that six generations of back pollinating might be adequate for recovering that part of the recurrent parent genotype important for practical corn improvement. It was recognized, however, that any reliable estimate of the number of generations necessary would have to wait on the accumulation of experimental data. Experiments were conducted in 1929 and 1930 to provide evidence on this question and on the question of how long back pollinating could be continued without losing too many of the favorable genes coming in from the nonrecurrent parent. The concepts back of these experiments were (1) that back pollinating could be continued as long as the plants were

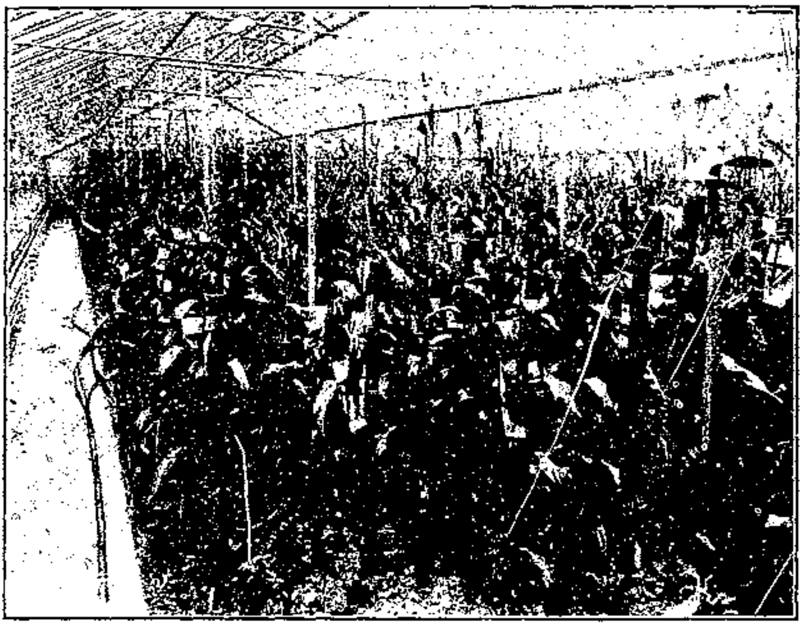

FIGURE 3.—Corn breeding stocks produced in the greenhouse during the winter of 1929–30

appreciably superior to the recurrent parent, and (2) that back pollinating must be continued until the cross between a back-pollinated line and the nonrecurrent parent yielded approximately equally with the cross between the original recurrent and nonrecurrent parents. Equality of the original cross with a cross between recovered lines obtained by back pollinating to both parents would be equivalent evidence of sufficiency of back pollination.

The system of pedigrees used in the breeding program is illustrated in Table 2. The foundation F_1 cross is in parentheses, with the recurrent parent last, regardless of the direction in which the cross was made. The numerals following and separated by dashes indicate generations of back pollinating to the recurrent parent. Crosses recorded without parentheses are shown as made, the pistillate parent being written first. Where the particular pedigree is unimportant, a generalized pedigree is used. The exponent of the recurrent parent shows the number of times that parent has been used. Thus, $(6\text{–}5\times 4\text{–}8^2)$ is the cross $(6\text{–}5\times 4\text{–}8)$ back pollinated once to parent line 4–8, whereas $(6\text{–}5\times 4\text{–}8^4)$ is the same cross back pollinated three times to 4–8. A more generalized form of the same system is used to indicate the generation of operation where the particular cross is of no importance. Here the letters N and R indicate the nonrecurrent and the recurrent parent. The letter S indicates the beginning of selfing, or, with a subscript, the number of selfed generations.

TABLE 2.—*Designations used in convergent improvement experiments*

Generation	Operation	Pedigree	
		General	Specific examples
N×R, R×N, or F_1	6–5×4–8, or 4–8×6–5	Actual	
$(N\times R^2)$	(6–5×4–8)×4–8	$(6\text{–}5\times 4\text{–}8^2)$	(6–5×4–8)–1.
$(N\times R^3)$	(6–5×4–8)×4–8; ×4–8	$(6\text{–}5\times 4\text{–}8^3)$	(6–5×4–8)–1–1. (6–5×4–8)–1–2.
$(N\times R^4)$	(6–5×4–8)×4–8; ×4–8; ×4–8	$(6\text{–}5\times 4\text{–}8^4)$	(6–5×4–8)–1–1–1. (6–5×4–8)–1–1–2. (6–5×4–8)–1–2–1.
$(N\times R^4)S$	(6–5×4–8)×4–8; ×4–8; ×4–8; ×S	$(6\text{–}5\times 4\text{–}8^4)S$	(6–5×4–8)–1–1–1–S1. (6–5×4–8)–1–2–1–S1.
$(N\times R^4)S_2$	(6–5×4–8)×4–8; ×4–8; ×4–8; ×S, ×S	$(6\text{–}5\times 4\text{–}8^4)S_2$	(6–5×4–8)–1–2–1–S1–1.

GROWING SEED FOR THE EXPERIMENTS

In preparation for yield comparisons in 1930, seed was grown in 1929 to represent the various generations completed. Eight back-pollinated lines were chosen for which remnant seed of the preceding generations was available. Each generation of each line was planted between rows of the recurrent and of the nonrecurrent parent. The recurrent parent was pollinated with pollen of the different generations of the back-pollinated line. This advanced each lot one generation and provided seed representing successive generations of back pollinating. As all this seed was produced on plants of the inbred recurrent parent, any material systematic variation in seed size was avoided. Similarly, the nonrecurrent parent was pollinated by the different generations of the back-pollinated line to obtain seed representing crossing with the nonrecurrent parent after successive generations of back pollinating to the recurrent parent. Here, all of the seed was produced on plants of the inbred nonrecurrent parent. Where reciprocally back-pollinated lines were available, crosses were made between them in the various generations. The following diagram shows the plan of planting for producing seed of 4–8×6–5 back pollinated to 4–8 and to 6–5, and seed of the crosses between the reciprocally back-pollinated lines.

4–8 × 4–8×6–5, F_1 × 6–5	×	6–5 × 4–8×6–5, F_1 × 4–8
4–8 × (6–5×4–8)–2[5] × 6–5	×	6–5 × (4–8×6–5)–2[5] × 4–8
4–8 × (6–5×4–8)–1–1 × 6–5	×	6–5 × (4–8×6–5)–1–3 × 4–8
4–8 × (6–5×4–8)–1–1–3 × 6–5	×	6–5 × (4–8×6–5)–1–3–2 × 4–8
4–8 × (6–5×4–8)–1–1–3–1 × 6–5	×	6–5 × (4–8×6–5)–1–3–2–1 × 4–8
4–8 × (6–5×4–8)–1–1–3–1–1 × 6–5		

METHODS OF COMPARING YIELDS

Weather conditions were exceedingly unfavorable following emergence of the seedlings in 1929. Growth was slow, and the stand, originally good, was decimated by the southern corn rootworm. Heavy rain on June 21 flooded the field and caused further damage. As a result of these conditions it was impossible to obtain seed of all the combinations or as much seed as was desired.

Seed was obtained in quantities for what seemed adequate replication in several different lines of breeding. This was planted in 1930, and the plants emerged to a good stand only to meet the serious drought of that summer. Where the soil was not too sandy, reasonable growth was made in spite of the drought. The corn on the sandy spots was a total loss. As these spots occurred at more or less frequent intervals over the field used for the comparisons, they eliminated some of the experiments entirely and some of the replications in other experiments. Inasmuch as the individual replications were small and each was a unit in itself, however, it was possible to obtain results for several comparisons that seem reliable within the limits of their errors. The present discussion is confined to these.

The plan of planting to compare the effects of successive generations of back pollinating is shown in Table 3. Each pedigree represents a 13-hill single-row plot of the kind stated. Excess seeds were planted and the plot was thinned to a final stand of three plants per hill. The arrangement was such that, beginning with the most vigorous material, the F_1 cross, the inbreeding of the successive plots increased to that represented by the selfed recurrent parent and then decreased again to the F_1. In the second series of 13-hill rows the order was the

[5] Used in place of (6–5×4–8)–1 and (6–5×4–8)–1, of which no seed was available.

reverse of this, and the third series was similar to the first. For the particular experiment shown in Figure 5 there were eight replications, but for most of the comparisons seed was available for only six.

TABLE 3.—*Planting arrangement in three series of 18-hill rows of corn with three plants per hill, for comparison of successive generations of back pollinating*

Series 1	Series 2	Series 3
6-5×540 F_1	6-5 S_9	6-5×540 F_1.
6-5×(540×6-5)	6-5×(540×6-5^4)	6-5×(540×6-5).
6-5×(540×6-5^2)	6-5×(540×6-5^3)	6-5×(540×6-5^2).
6-5×(540×6-5^3)	6-5×(540×6-5^2)	6-5×(540×6-5^3).
6-5×(540×6-5^4)	6-5×(540×6-5)	6-5×(540×6-5^4).
6-5 S_9	6-5×540 F_1	6-5 S_9.
6-5 S_9	6-5×540 F_1	6-5 S_9.
6-5×(540×6-5^4)	6-5×(540×6-5)	6-5×(540×6-5^4).
6-5×(540×6-5^3)	6-5×(540×6-5^2)	6-5×(540×6-5^3).
6-5×(540×6-5^2)	6-5×(540×6-5^3)	6-5×(540×6-5^2).
6-5×(540×6-5)	6-5×(540×6-5^4)	6-5×(540×6-5).
6-5×540 F_1	6-5 S_9	6-5×540 F_1.
6-5×540 F_1	6-5 S_9	
6-5×(540×6-5)	6-5×(540×6-5^4)	
6-5×(540×6-5^2)	6-5×(540×6-5^3)	
6-5×(540×6-5^3)	6-5×(540×6-5^2)	
6-5×(540×6-5^4)	6-5×(540×6-5)	
6-5 S_9	6-5×540 F_1	

The plan of planting for comparing crosses of the nonrecurrent parent with the successively back-pollinated lines was entirely similar. Both of these arrangements minimized competition by placing together the generations most nearly alike. Guard rows of the F_1 crosses or of the selfed parents bordered similar rows where these occurred on the outside. Stands were nearly perfect. The writers do not believe that competition influenced the yields materially in these experiments, either when inequalities occurred because of the differences in the vigor of adjacent plots or because of the very minor differences in stand which existed.

EXPERIMENTAL DATA

The yields presented are the mean air-dry weights of ear corn from the number of replications stated. Except for the two cases noted, they are based only on complete replications. The product of three or more replications of each experiment was dried in a steam-heated room, the percentages of shrinkage calculated, and the yields of the other replications computed to air-dry weights from these data.

The probable errors for the individual experiments were determined through the analysis of variance as suggested by Fisher (*4*). The net variance for any generation, however, was maintained in the same ratio to the net variance for the experiment as the total variance for that generation bore to the total variance for the experiment. This was done because of the large differences in yield and variability of the different generations. The probable errors reported for the means of the corresponding generations in similar experiments are based on weighted averages of the variances in those experiments. That is, the different experiments are not treated as replications, but their yields and errors are averaged only to provide a more convenient basis for discussing the experiments as a whole. It is believed that the results in the different experiments are enough alike to warrant this simplified consideration.

The yields of the F_1 crosses successively back pollinated for different numbers of generations to one parent and the yield of that parent are shown in Table 4. The number of replications ranged from four to seven. The two cases in which one generation was not represented in all replications are indicated by references to footnotes 1 and 2. The probable errors in the different experiments and generations probably differ no more than should be expected. Their averages for the different generations range from about 4 to about 5 per cent.

TABLE 4.—*Plot yields of F_1 corn crosses successively back pollinated to one parent for different numbers of generations, and of that parent*

Parent stocks (N and R), number	Replications	Yields for designated generation and for parent							
		R×N, F_1	R×(N×R)	R×(N×R^2)	R×(N×R^3)	R×(N×R^4)	R×(N×R^5)	R×(N×R^6)	R (selfed)
	Number	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*
549-A and 4-8	4	23.2±0.60	12.4±0.99	7.4±0.61	6.5±0.14	4.9±0.49			
549-B and 4-8	6	17.7± .83	10.6± .57	8.3± .42	8.8± .32	8.5± .37			[1]4.3±0.13
540 and 4-8	6	20.2± .42	13.7± .44	10.6± .33	8.8± .35	8.3± .24			6.5± .22
6-5 and 4-8	4	19.0± .34	9.8± .44	7.5± .20	5.0± .28	4.5± .19	2.8±0.09	3.1±0.20	2.4± .18
4-8 and 6-5	6	16.6± .41	10.3± .23	[2]6.8± .21	7.7± .10	3.9± .12	3.9± .21		2.8± .13
540 and 6-5	7	21.5± .78	13.6± .53	8.9± .34	6.8± .31	6.8± .31			2.9± .13
Mean		19.7± .66	11.7± .54	8.2± .37	7.2± .30	5.8± .31	[3]4.5± .19	[3]4.6± .20	3.0± .16

[1] Only 4 replications. [2] Only 5 replications. [3] In same ratio to 3.6 as to own parents.

The product of each generation in each experiment is illustrated in Figure 4. Each lot shown represents the mean weight for all replications. The smaller size and poorer filling of the ears of the more inbred generations are typical and perfectly familiar to those who have carried on inbreeding with corn. The heights of the columns of ears afford a fair picture of the actual mean yields. This is shown more clearly, however, in Figure 5.

The excess yield of an F_1 cross, A×B, above that of one of its parents, B, may be attributed to genes brought in from the other parent, A. The cross will be heterozygous for these genes, and successive generations of back pollination to the parent B, without selection, will decrease the percentage of heterozygosis in accordance with the series ½, ¾, ⅞, etc.

Similarly, if the excess yield occurs because the genes from A are dominant and favorable, the number of such genes in each generation, without selection, would be halved. Under either hypothesis, then, the yield of a cross back pollinated to one parent without selection should approach the yield of that parent as a limit approximately in accordance with the same series. Effective selection of the more vigorous plants during back pollinating would retain the more heterozygous individuals, or those carrying the larger numbers of dominant favorable A genes, and so maintain yield above the theoretical.

The lower limit of each graph in Figure 5 represents the yield of the recurrent parent as 0 per cent, and the upper limit represents the yield of the F_1 cross as 100 per cent. The series ½, ¾, ⅞, etc., is shown by the solid lines as the theoretical behavior of strains back pollinated without selection. The observed behavior of the strains back pollinated with selection is shown by the broken lines. For the experiment with stock (549A×4-8) no yield of the recurrent parent is available, and the theoretical decrease in the later generations is plotted as ½, ¾, etc., of the decrease from the F_1 generation to the F_1 generation back pollinated once.

The data from the different experiments are in excellent major agreement. The lines back pollinated once range closely around the mid-point between the F_1 cross and the recurrent parent. At this stage theory and observation should be most likely to agree, as there

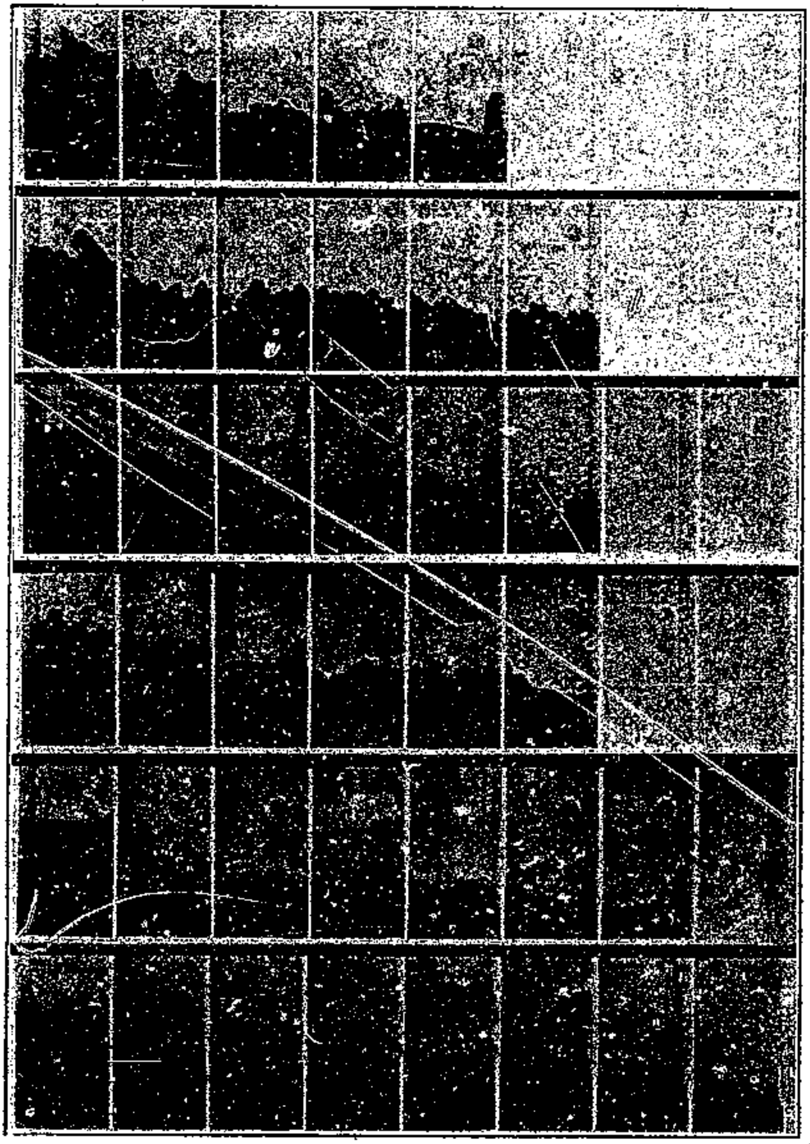

FIGURE 4.—Ears harvested from one replication each of an F_1 cross (left), of that cross back pollinated for 1, 2, 3, etc., generations to one of the inbred parents, and (right) of that inbred parent, for each of the six experiments

could be practically no selection among the F_1 plants first back pollinated. After this generation selection could be effective, and all of the yields but one are in excess of the theoretical no-selection yields based on a series ½, ¾, ⅞, etc. There is considerable variation in the amount of the excess, but probably no more than reasonably might be expected from the random sampling of different breeding stocks plus the experimental variation.

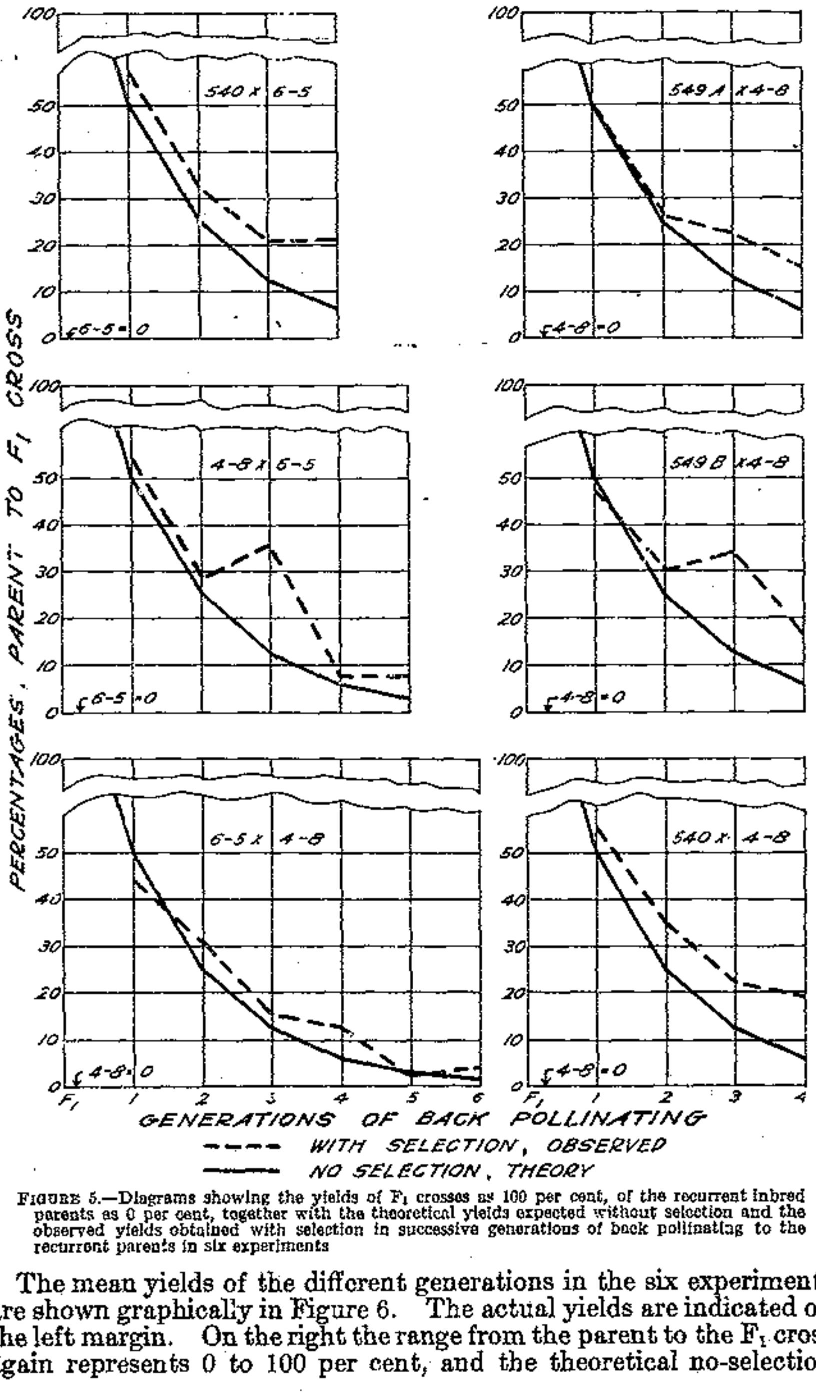

FIGURE 5.—Diagrams showing the yields of F_1 crosses as 100 per cent, of the recurrent inbred parents as 0 per cent, together with the theoretical yields expected without selection and the observed yields obtained with selection in successive generations of back pollinating to the recurrent parents in six experiments

The mean yields of the different generations in the six experiments are shown graphically in Figure 6. The actual yields are indicated on the left margin. On the right the range from the parent to the F_1 cross again represents 0 to 100 per cent, and the theoretical no-selection curve is shown by the solid line. The excess yields of the lines back pollinated three and four times above the theoretical appear to afford ample evidence that selection has been effective in retaining some additional favorable dominant factors entering the cross from the nonrecurrent parent, or else in retaining plants more heterozygous than the expectancy. In either case, and to this extent, then, the lines at these stages are more nearly like the nonrecurrent parents than would be theoretical unselected back-pollinated lines.

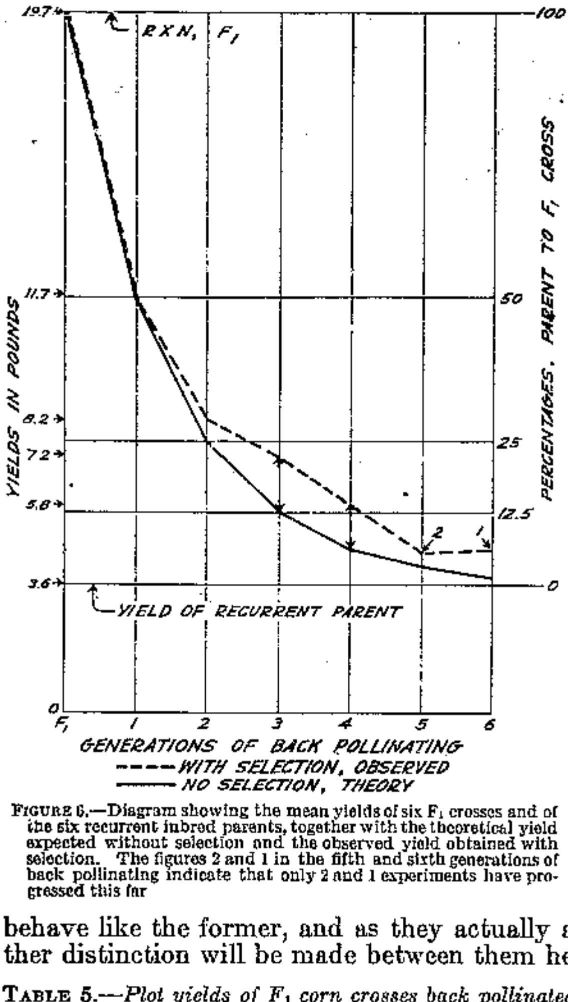

FIGURE 6.—Diagram showing the mean yields of six F_1 crosses and of the six recurrent inbred parents, together with the theoretical yield expected without selection and the observed yield obtained with selection. The figures 2 and 1 in the fifth and sixth generations of back pollinating indicate that only 2 and 1 experiments have progressed this far

Leaving the results of back pollinating for the moment, the yields of F_1 crosses between the nonrecurrent parent and the lines recovered after successive generations of back pollinating with the recurrent parent are shown in Table 5. These data include for two stocks the yields of F_1 crosses between two lines derived by back pollinating a cross to each of its parents. As the latter theoretically should behave like the former, and as they actually appear to do so, no further distinction will be made between them here.

TABLE 5.—*Plot yields of F_1 corn crosses back pollinated to one parent for different numbers of generations and then crossed with the nonrecurrent parent*

Parent stocks (N and R), number	Replications	Yields for designated generation[1]						
		N×R F_2	N×(N×R^2)	N×(N×R^3)	N×(N×R^4)	N×(N×R^5)	N×(N×R^6)	N×R, F_1
	Number	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*
540-A and 4-8	6	----------	18.5±0.19	20.1±0.23	21.1±0.24	----------	----------	21.1±0.55
540-B and 4-8	6	----------	16.3± .23	17.6± .31	19.0± .30	----------	----------	17.8± .20
6-5 and 4-8	6	----------	12.2± .22	14.9± .17	13.9± .26	14.4±0.29	15.0±0.22	16.4± .31
4-8 and 6-5	6	----------	11.5± .37	14.7± .33	16.4± .29	----------	----------	17.5± .24
4-8×6-5 and 6-5×4-8	6	11.3±0.54	13.8± .29	15.6± .17	16.4± .23	18.6± .16	----------	17.7± .37
3×2 and 2×3	4	7.3± .27	9.0± .40	11.4±1.05	18.0± .92	18.8± .79	----------	17.5±1.32
Mean[2]	------	9.4± .55	13.5± .20	15.7± .30	17.5± .35	18.3± .38	17.4± .22	17.8± .45

[1] For (4-8×6-5)×(6-5×4-8) and for (3×2)×(2×3), both parents were back pollinated the same number of generations before crossing.

[2] Mean values not based on all crosses are computed to same ratio to the mean of the F_1's as to their own F_1's.

The more uniform soil occupied by these experiments is reflected in the fact that all six replications could be used in all of the experiments but one, in which four were available. Moreover, the probable errors are slightly smaller than in the experiments on back pollinating.

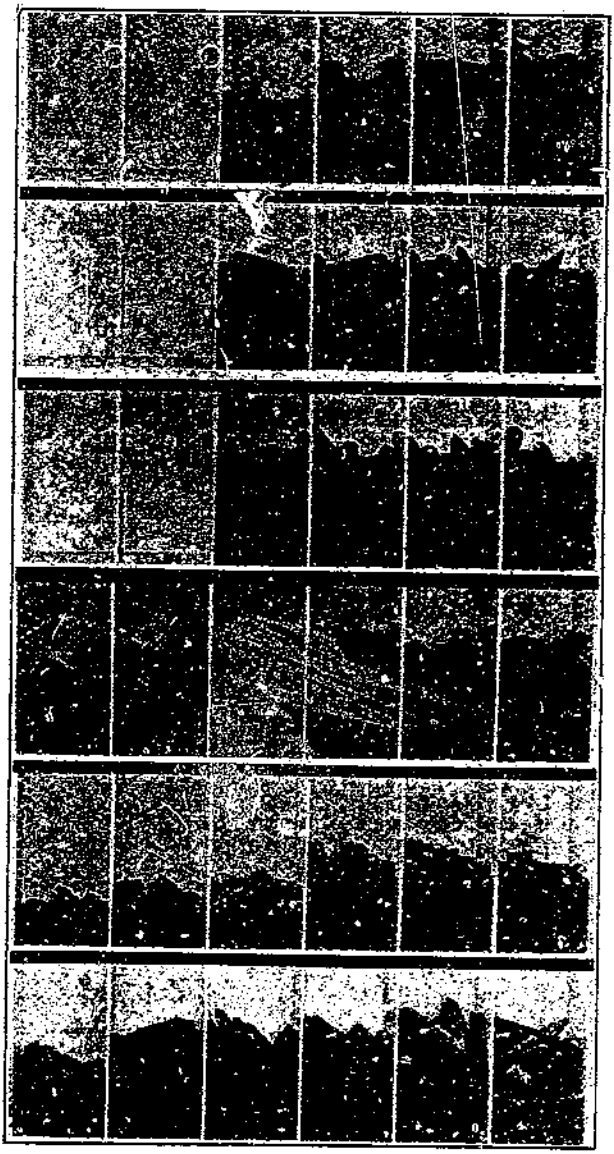

FIGURE 7.—Ears harvested from one replication of each generation in the six experiments on recrossing after back pollinating

The appearance of the crop from each of the different generations is shown in Figure 7. Here, too, each lot represents the mean weight of ears for each generation.

Just as the yields under continuous back pollination without selection should approach the yield of the recurrent parent, so the yields of crosses between unselected back-pollinated lines and the nonrecurrent parents should approach the yields of the original F_1 crosses as a limit, according to the series ½, ¾, etc. The solid lines in Figure 8 show this theoretical behavior for crossing following back pollinating without

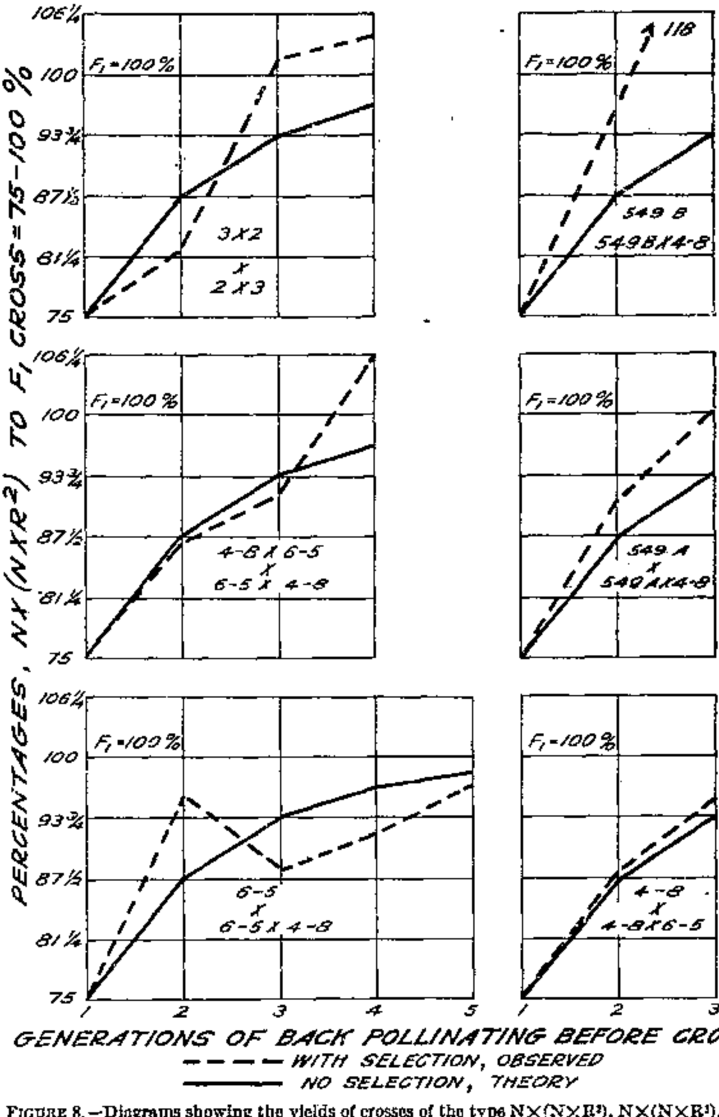

FIGURE 8.—Diagrams showing the yields of crosses of the type N×(N×R²), N×(N×R³), etc., and of the original N×R, F_1 for comparison, in the six experiments on recrossing after back pollinating

selection. The broken lines show the observed yields of crosses made following back pollinating with selection.

No data on the N×(N×R) generation are available for the crossing experiments. In the experiments on back pollinating the mean yield of this generation, i. e., the F_1 crosses which had been back pollinated once, was almost exactly 50 per cent of the range from the parents to the F_1 crosses. On the basis of numerical relationships, the yield of the cross following one generation of back pollinating, $N\times(N\times R^2)$, would be halfway farther toward the original F_1, or 75 per cent of the total range. Accordingly, the percentages shown on the graphs are on a scale of from 75 per-cent for the $N\times(N\times R^2)$ generation to 100 per cent for the original cross. The theoretical points for the succeeding generations represent increments of one-half of the remaining range.

The results in the different experiments again seem sufficiently uniform to warrant discussion on the basis of the average tendencies. The mean yields of the corresponding generations are shown graphically in Figure 9. Here, as in the back-pollinating experiments, the observed yields obtained with selection are in excess of the theoretical values for no selection. In fact, the mean yield of the 6 crosses made following 3 generations of back pollinating is almost equal to that of the original crosses, and the mean yield of the 3 crosses made following 4 generations of back pollinating is in slight excess of that of the original crosses. On the basis of these data, it required only three or four generations of back pollinating to the recurrent parent to produce recovered lines which behaved like that parent in crosses with the nonrecurrent parent. This answers the second question, namely, how long must back pollinating be continued.

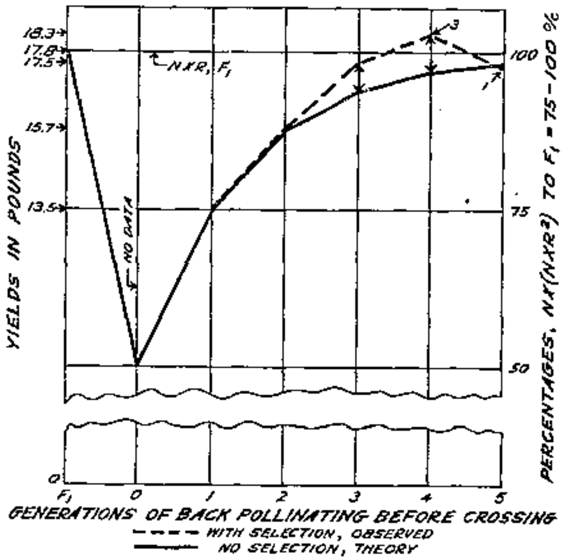

FIGURE 9.—Diagram showing the mean yields for six experiments of crosses of the type $N\times(N\times R^2)$, $N\times(N\times R^3)$, etc., and the original $N\times R$, F_1

DISCUSSION

The data for the experiments on back pollinating and crossing are shown graphically in Figure 10. Because of the losses of some of the experiments undertaken, two of the six lines in the back-pollinating experiments are not represented in the crossing comparisons. Similarly, data are not available on the back-pollinated lines used in one of the six crossing experiments. This lack of strict comparability is unfortunate, but does not appear seriously to limit the value of the results obtained. As plotted in Figure 10, the mean yield of the recurrent parents is 0 per cent and that of the foundation F_1 crosses is 100 per cent. The data on crossing have been displaced one generation to the left so as to bring those for crossing following x generations of back pollinating on the same ordinates as those for the parents back pollinated x times.

RELATION TO THE THEORY OF HYBRID VIGOR

The average yield of the six F_1 crosses back pollinated once to their recurrent parents was almost exactly midway between the average yield of the F_1 crosses and that of the recurrent parents. In these experiments, then, regardless of their method of action, one-half of the original number of genes from the nonrecurrent parent was one-half as effective as the original number. This same relation may be expected to hold on the average for the smaller fractions of the nonrecurrent-parent genes that would be present after additional generations of back pollinating to the recurrent parent. As a matter of fact, the yields of lines back pollinated, with selection, for three and four generations were consistently and significantly in excess of the theoretical no-selection values.

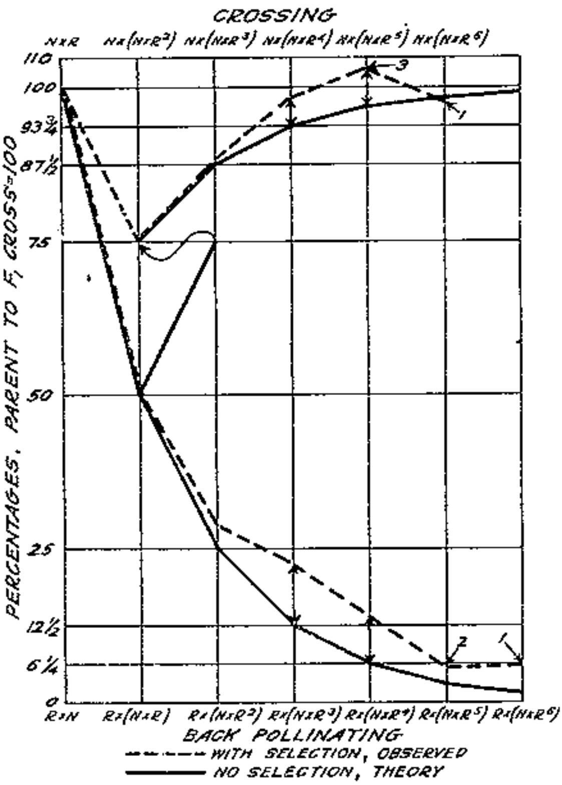

FIGURE 10.—Diagram of the mean yields in the back pollinating and the recrossing experiments

It is reasonable to conclude that this excess yield was due to genes from the nonrecurrent parent retained by selection during back pollinating, in excess of those that would be expected from the mere process of halving. These selected back-pollinated lines, therefore, were more nearly like the nonrecurrent parents than would be unselected back-pollinated lines. It follows immediately that crosses between the nonrecurrent parents and the selected back-pollinated lines would be less heterozygous than would analogous crosses involving unselected back-pollinated lines. If heterozygosis, as such, were the cause of hybrid vigor, these less heterozygous crosses should yield less than the theoretically expected yields of crosses involving unselected back-pollinated lines. The actual crosses involving selected lines yielded significantly more than the theoretical values, however, and the results accordingly are in direct negation of the hypothesis that heterozygosis, as such, is the cause of hybrid vigor.

This last conclusion is based on deviations from expected theoretical values. It is supported and strengthened by other facts in the crossing experiments. The F_1 crosses $(3\times2^4)\times(2\times3^4)$ and $(3\times2^5)\times(2\times3^5)$ yielded more than the actual parental F_1 cross 2×3. (Table 4 and fig. 8.) Data are not available in these experiments to show that (3×2^4) and (3×2^5) are superior to 2 and that (2×3^4) and (2×3^5) are superior to 3. It may be stated from a knowledge of the stocks, however, that such is the case. This superiority can be the result only of genes from the other lines not yet lost through back pollinating. The F_1 crosses between these partly recovered lines, accordingly, are less heterozygous but more productive than the parental F_1 cross.

A similar situation occurs for the cross $(4\text{–}8\times6\text{–}5^5)\times(6\text{–}5\times4\text{–}8^5)$ in comparison with the parental F_1 cross 6–5×4–8. (Table 4 and fig. 8.) Here, however, data on the back-pollinated lines (Table 3 and fig. 5) show them after four generations of back pollinating $(N\times R^5)$ to have been significantly more productive than their selfed parents. Finally, the cross of $549\text{–}B\times(549\text{–}B\times4\text{–}8^4)$ was much more productive than 549–B×4–8. In all of these cases, then, the less heterozygous crosses were more productive than were comparable, more heterozygous crosses. This appears to constitute crucial evidence that heterozygosis, as such, has not been the cause of hybrid vigor within the limits of the differences in yield between the parent lines and the selected back-pollinated lines in these experiments.

Heterozygosis, however, is not excluded completely as a possible partial cause of hybrid vigor. There was a tendency for the selected lines and their crosses to approximate, with consistent departures, the theoretical curves for back pollination without selection. The general approximation might result from either (1) a decrease in heterozygosis, or (2) a lack of effective selection during back pollination. Such a lack of effective selection might be due to the fact that many genes of small individual effect precluded it or to the conduct of this particular experiment.

The lines recovered by back pollinating in these experiments now have been self-pollinated for two additional generations. They are more nearly like the nonrecurrent parents than were the foundation stocks. If these recovered lines produce results in a second cycle of convergent improvement comparable to those reported here, the probability that dominant genes are the sole cause of hybrid vigor will have been further increased. Thus, with each repetition, the possible importance of heterozygosis as such should be shown to be less and less, or otherwise, depending upon the results. The possibility that heterozygosis has some effect can not be excluded completely, however, unless high-yielding lines can be obtained which do not decrease in vigor with inbreeding.

RELATION TO CORN BREEDING

Since they concern the cause of hybrid vigor, the results of these experiments naturally bear on the theory of present-day corn breeding. They have, however, far more concrete relations. Any progress made is progress in an actual experimental program of corn improvement involving breeding stocks of demonstrated productiveness in hybrid combination. Furthermore, the results provide reasonably definite evidence on methods that may be followed in similar programs of corn breeding.

Three of the six crosses between the nonrecurrent parent and the lines back pollinated to the recurrent parent for three generations were more productive than the F_1 crosses between the foundation parents. An additional cross between recovered lines after four generations of back pollinating was more productive than the foundation cross. The actual lines used in these experiments were chosen from the breeding program as a whole, more or less at random, largely on the basis of remnant seed available in the different generations. Accordingly, it seems reasonable to conclude that three or four generations of back pollinating are adequate to recover the important part of the recurrent parent genotype, that is, the part necessary for the recovered line to behave like the recurrent parent in crosses.

This does not mean that every line after three or four generations of back pollinating will behave in crosses like the recurrent parent, but that some among every few that are tested are very likely to do so. This substitutes perhaps three or four generations of back pollinating for the six postulated as possibly necessary in the original publication (7). Experience also indicates that only two or three generations of selfing after back pollinating will be required to fix the recovered lines sufficiently for a second cycle of convergent improvement. If this latter indication is supported in future experiments, some 5 to 7 generations for a cycle will be substituted for the possible 12 originally suggested. This would materially shorten the time required.

It seems sufficiently clear that back pollinating must be continued three or four generations. How much advantage can be retained at this stage? Of the six back-pollinated lines compared in these experiments, all yielded more than would be expected from theoretical unselected lines. The average excess above the theoretical was 30 per cent of the yield of the recurrent parents after three generations and 27 per cent after four generations of back pollinating.

Inasmuch as this excess presumably is due to the retention of additional dominant genes from the nonrecurrent parent by selection during back pollinating, the recovered lines are heterozygous for these genes. Accordingly, with self-fertilization and without selection, only half of these would be retained, becoming homozygous, whereas the recessive allelomorphs of the other half would become homozygous.

On this basis, one-half of the excess at the termination of back pollinating should be retained after continued selfing without selection. It seems reasonable to assume, therefore, pending further evidence, that at least one-half of this gain can be retained. This would be a permanent improvement of some 13 to 15 per cent in the productiveness of the inbred stocks. Considering the fact that opportunity for selection in these stocks has been materially less than is desirable for such a program, as already noted, this seems to constitute a real gain.

This gain is in vigor as measured by productiveness. There are other objectives in corn breeding. Thus, for some of the recurrent parents used, resistance to lodging was one of the very important characters sought. Much improvement has been accomplished in this direction. Again, all of the lines of C. I. No. 227 have a red pericarp, which is undesirable, and some have white endosperm for which it was desired to substitute yellow. Both of these desiderata have been accomplished wholly or in part. Finally, 227–6 has such scanty pollen that it is difficult to maintain. After four generations of back pollinating, lines have been recovered which strongly resemble 227–6 but which have ample pollen. Some of the recovered lines in which miscellaneous improvement has been accomplished are not represented in the experiments for which data have been reported but remain to be tested. They appear, however, to be more productive than the recurrent parents, in addition to their superiority in the specific character sought. There also seems no reason to suppose that some of the several lines represented in each stock should not behave much like the recurrent parents in crosses with the nonrecurrent parents.

One further condition remains to be noted. Convergent improvement was suggested as a means of increasing the productiveness of inbred lines without interfering with their behavior in hybrid combination. In the six comparisons of crossing after back pollinating reported here, at least three of the crosses between recovered lines yielded more than the foundation crosses. These results suggest, therefore, that convergent improvement may be utilized not only to improve the inbred parents but also to increase the productiveness of the crosses in which these parents are used. This may provide a method by which the yields of our present crosses can be brought to an even higher level.

SUMMARY

The yields of F_1 crosses between selfed lines of corn back pollinated once to one parent were, in accordance with theory, almost exactly intermediate between the yields of the parents and those of the F_1 crosses. The yields of progeny lines derived by successive generations of back pollinating to the same recurrent parent, with selection of the more vigorous plants in each generation, were somewhat above the theoretical yields for back pollinating without selection.

The yields of F_1 crosses between these selected back-pollinated lines and the nonrecurrent parents also were in excess of the theoretical values for similar crosses with unselected back-pollinated lines.

The excess yields of the selected back-pollinated lines may be attributed to dominant favorable genes retained by selection during the back pollinating. The fact that the yields of the crosses involving these lines also are in excess of the theoretical values for back pollinating without selection supports the hypothesis of dominant genes as the cause of hybrid vigor and is in contravention of the physiologic-stimulation hypothesis.

The yields of the crosses made following three and four generations of back pollinating were approximately equal to the yields of the F_1 crosses between the foundation parent lines. Three or four generations of back pollinating to a recurrent parent, then, was enough to recover lines which behaved like that parent in crosses with the nonrecurrent parent. In these generations there was an indicated permanent improvement of 13 to 15 per cent over the recurrent parent, allowing for differences in the degree of inbreeding.

In addition to the larger yields of the recovered lines, improvement has been achieved in ability to resist lodging and in the amount of pollen shed. Yellow endosperm has been substituted for white and clear pericarp for red, all without changing significantly the behavior of the lines in crosses.

Convergent improvement, suggested originally from theoretical considerations as a means of improving selfed lines of corn without interfering with their behavior in hybrid combination, so far has been found successful. Furthermore, the results suggest that this method also may provide a means by which the yields of F_1 crosses between selfed lines can be raised to an even higher level.

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