FURTHER STUDIES ON CONVERGENT IMPROVEMENT IN CORN¹

G. F. SPRAGUE, W. A. RUSSELL AND L. H. PENNY²

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THE breeding practices and production technics in the utilization of hybrid corn have developed much more rapidly than our complete understanding of the genetic mechanism of the heterosis involved. The procedures in general use would be expected to have a rather high degree of efficiency if dominance were the primary type of gene action involved. On the other hand, if overdominance were the primary type of gene action, some of the procedures used would be of limited effectiveness and others would be essentially worthless. For example, new inbred lines are customarily given a preliminary evaluation in top-cross trials (inbred $\times$ open-pollinated variety) to measure average combining ability. Information on average combining ability is meaningful if partial or complete dominance is of importance. However, information on average combining ability would have limited predictive value if overdominance were of major importance. Other procedures used may exhibit similar but less extreme variation in efficiency under the two contrasting assumptions regarding the types of gene action involved in heterosis. Thus, from the standpoint of either plant breeding or genetic theory, it would be desirable to have a more complete understanding of the relative importance of the various types of gene action which may be involved in yield heterosis.

The present paper is concerned with studies on convergent improvement. Convergent improvement is one of the procedures that has been suggested as offering promise of providing critical information on the relative importance of various degrees of dominance.

The method assumes that all longtime inbred lines are lacking in important attributes that combine to produce maximum yield. A high yielding single cross is chosen and crossed to one of the parental lines through several successive generations. During the backcrossing selection is practiced for general vigor and for the desirable attributes contributed by the nonrecurrent parent. After n generations of backcrossing the sublines are heterozygous at all loci where selection has been effective in retaining desirable characteristics of the nonrecurrent parent. Self-pollination is then practiced for two or more generations to fix as many as possible of these desirable alleles in a homozygous condition. If the process is done reciprocally, the new lines A(B) and B(A) will differ from the original

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² Principal Agronomist, U. S. Dept. Agr., Assoc. Prof., Iowa State College, and Agronomist, U. S. Dept. Agr.

parents A and B by certain gene substitutions. If selection has been effective, the new lines A(B) and B(A) should be superior to the original parents in yielding ability.

The recovered lines A(B) and B(A) may then be used as parental material for a repetition of the entire procedure. If successful gene transfers can again be accomplished, one would expect the eventual convergence of all of the desirable attributes of the two original lines into a single inbred strain.

Critical evidence on the type of gene action involved is provided by comparisons of the lines in single cross combinations after each cycle of reciprocal back crossing or convergent improvement. Obviously a range in yield is to be expected at both the inbred and hybrid level. However, if any of the substrains of the recovered lines A(B) and B(A) are superior to the original lines A and B, and if single crosses between such superior substrains are equal or superior to the original single cross $A \times B$, then complete or partial dominance is indicated. However, if the substrains of A(B) and B(A) which are superior to the original line produce hybrids $A(B) \times B(A)$ which are significantly lower in yield than the parental cross, then overdominance may be indicated. Such results could be obtained, however, by certain types of gene substitutions even in the absence of overdominance. The present paper is concerned with evidence obtained from two cycles of the convergent improvement process.

Review of literature

The method of convergent improvement and some of the theoretical considerations were reported by RICHEY (1927). At a later date RICHEY and SPRAGUE (1931) presented data obtained from one cycle of convergent improvement. It was found that the yield of the recovered lines was increased by 13 to 15 percent. The F_1 crosses between recovered lines following three and four generations of backcrossing were equal or superior to the yields of the parental single crosses.

Murphy (1942) reported data indicating superiority of recovered lines after two and three generations of backcrossing. Some of the single crosses between recovered lines yielded significantly more than the original F_1 cross. The data from the studies reported by RICHEY and SPRAGUE and by MURPHY were interpreted as being in agreement with expectations under the dominance hypothesis and in contradiction to expectations under the physiological stimulation or overdominance hypothesis.

The tests conducted by the workers cited above involved only a single cycle of convergent improvement. The results, therefore, are critical for only that portion of the F_1 vigor that was retained in the recovered lines. Proof that dominance is of major importance in the heterosis unaccounted for after a single cycle of convergent improvement may be obtained only by successive successful repetitions of the process.

MATERIAL AND METHODS

The recovered lines resulting from the studies reported by RICHEY and SPRAGUE (1931) were grown at Missouri in 1934 to 1936 as potential parental material for a second cycle of convergent improvement. The material was poorly adapted and two new lines, B2 and K4, were chosen as parental material. The F_1 hybrid was backcrossed reciprocally to the two parental inbreds for three successive generations using standard pedigree culture procedures. The various sublines were then self-pollinated for three generations to fix the desirable genes retained by selection during the backcross generations. The recovered lines were then evaluated in single cross combinations. The results obtained from this first cycle of convergent improvement were similar to the results presented earlier by RICHEY and SPRAGUE (1931) and by MURPHY (1942), and the details will not be presented here. The best of the B2 and K4 recovered lines were designated B2a and K4a, respectively.

The lines B2a and K4a were used as parental material for the second cycle of convergent improvement. Reciprocal backcrossing was practiced for three generations, selecting in each generation for attributes contributed by the nonrecurrent parent. Following the backcrossing procedure, each of the sublines was selfed for two generations and then combined into single crosses. The single crosses and the inbred parents were grown in replicated yield trials. The tests were planted at three locations in each of three years. Due to unfavorable conditions at some locations in each of the three years, one or more of the tests were discarded because of drought damage. Four repetitions of the inbred yield trials and five repetitions of the single cross yield trials were available for summarization.

EXPERIMENTAL RESULTS

The yields of the original and the first and second cycle lines derived by the convergent improvement process are presented in Table 1. The first cycle lines were higher in yield than the original lines. The increase for B2a was 22.4 percent and for K4a, 6.3 percent. Among the second cycle B2b lines, yields ranged from less than that for the original B2 to an increase of approximately 21 percent above the first cycle line B2a. In the K4b series all of the sublines were equal or superior to the original line K4. The second cycle lines having the highest mean yield, K4b-5 and K4b-6, exceeded that yield of the original and first cycle lines by 19 and 12 percent, respectively. These results suggest that the visual selection practiced during the backcrossing and selfing procedures was, on the average, reasonably effective.

The yields of single crosses among the second cycle lines (Table 2) ranged from 53.7 to 92.0 bushels per acre. The constant parent test cross means and the parental line means were significantly associated, the r value being 0.52. The highest yielding single crosses all involved the highest yielding of the B2b lines,

TABLE 1

Yield in bushels per acre for two original and first cycle lines and a series of second cycle lines derived by convergent improvement

Pedigree	Yield bu. acre	Pedigree	Yield bu. acre
B2	28.6	K4	36.5
B2a	35.0	K4a	38.8
B2b-1	22.1	K4b-1	37.2
-2	29.7	-2	39.7
-3	30.3	-3	41.6
-4	31.1	-4	42.7
-5	32.4	-5	43.5
-6	34.4	-6	43.5
-7	35.2		
-8	40.0		
-9	42.3		

Difference necessary for significance at five percent level = 5.5 bu.

TABLE 2

Yield in bushels per acre of single crosses between two original lines and first and second cycle lines derived from convergent improvement

	B2	B2a	B2b-1	B2b-2	B2b-3	B2b-4	B2b-5	B2b-6	B2b-7	B2b-8	B2b-9	Av.
K4	94.4	...	...	...	...	...	...	...	...	...	...	...
K4a	...	91.6	...	...	...	...	...	...	...	...	...	...
K4b-1	...	...	63.4	65.1	75.3	65.0	74.2	82.0	61.8	84.7	79.9	72.4
K4b-2	...	...	71.5	68.6	68.7	65.4	72.4	66.7	74.6	83.6	92.0	73.7
K4b-3	...	...	63.8	71.6	58.0	65.3	66.1	74.9	66.1	78.3	75.5	68.9
K4b-4	...	...	68.9	65.2	53.7	57.9	72.6	60.8	66.6	72.8	89.7	67.6
K4b-5	...	...	67.6	59.6	69.4	61.2	73.4	62.4	75.0	83.7	87.1	71.0
K4b-6	...	...	75.2	67.7	68.1	72.5	74.8	76.4	73.2	88.0	87.3	75.9
Av.	...	...	68.8	65.3	65.5	64.6	72.3	70.5	69.6	81.9	85.4	...

Difference necessary for significance at five percent level = 9.2 bu.

B2b-8 and B2b-9. The K4b parental lines involved in the highest yielding single crosses ranged from the second lowest yielding line K4b-2 to the highest yielding lines K4b-4, K4b-5 and K4b-6. However, it will be recalled that there was no significant difference in yield among this group of lines.

Parent-progeny regressions were calculated for each constant parent group. In the K4 series all of the regressions were positive and nearly equal to 1.0. In the B2 series both positive and negative regressions were obtained ranging in magnitude from +1.24 to -1.87. Both of these extremes are suggestive of overdominance. However, the range in yield among the inbred parents was slight and the number so limited as to make all of these estimates of questionable significance. The b2 values obtained for both series were essentially zero, one being positive and the other negative in sign. b2 values of this magnitude have been interpreted

by HULL (1947, 1952) as indicating either negative or partial dominance rather than overdominance.

DISCUSSION

It was stated in an earlier section that convergent improvement provides a method for making desired gene substitutions, thus improving the performance of an inbred line, without serious modification of hybrid performance. In actual fact single gene substitutions rarely if ever occur. Rather the substitutions involve blocks of chromosomes of varying length. In spite of the intensity of selection practiced during inbreeding, each inbred line so far developed contains many alleles having less than maximum efficiency. The net effect of chromosome block substitutions could be either favorable or unfavorable depending upon the relative number of favorable alleles within the substituted segment.

It would appear that the net effect of the total substitutions involved in the line B2b-1 was unfavorable since the line yielded significantly less than the original parent B2 or the first cycle recovered line B2a. In the lines B2b-2 through B2b-6 the net effect of the chromosome segment substitutions was to reduce the yield level of the inbred below that of the recurrent parent, B2a. In only two of these lines, B2b-8 and B2b-9, did the net effect of the substitutions lead to a significant increase in yield at the inbred level. In the K4b series, in no case did the substitutions lead to significant yield increases.

HENDERSON (1949), using a somewhat restricted definition of dominance, has postulated that certain favorable alleles may have an effect on vigor but show an absence of dominance. The transfer to and accumulation of such alleles in the recovered lines would then lead to increased yields at both the inbred and hybrid level because of homozygosity. This argument would appear to have little validity. Even in those cases in which the gene substitution values for $AA \rightarrow Aa$ and $Aa \rightarrow aa$ are exactly equal, any single heterozygous locus or the sum of all such loci would contribute to heterosis. However, the less favored alleles having such attributes would be expected to be in rather low frequency since such alleles would be most amenable to elimination as a result of the selection practiced during the development of open pollinated varieties.

The results presented here appear to lend some support to the dominance hypothesis as an explanation for yield heterosis. Significant increases in yield were obtained at the inbred level for some of the recovered strains. The single crosses among the best of the recovered lines were slightly lower in yield than the original or first cycle hybrids. However, most of the crosses involving the higher yielding lines were not significantly lower in yield than the parental hybrids. It appears reasonable to assume that, had this study been conducted on a more extensive scale, higher yielding lines and single crosses might well have been obtained.

Additional evidence supporting the dominance hypothesis was the significant correlation between the yields of the recovered lines and the average of their test cross progeny. Furthermore, the parent-offspring regressions for the constant

parent groups indicated either dominance of low yield or partial dominance of high yield rather than overdominance.

SUMMARY

Data are reported on inbred and single cross yields of corn at the completion of two cycles of convergent improvement.

The best of the recovered lines exhibited significant increases in yield amounting to 21 percent in the B2 series and 12 percent in the K4 series.

The yields of single crosses among the recovered lines were less than comparable hybrids between the original parental lines. However, the F_1 crosses between certain of the best recovered lines were not significantly lower in yield than single crosses involving the original parents.

The results are interpreted as providing some support for the dominance theory of heterosis. Additional evidence suggesting the importance of dominance was obtained from the parent and test cross progeny relationships.

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