Early Testing and Recurrent Selection

It appears desirable to review the history of corn breeding very briefly in order that early testing and recurrent selection may be placed in their proper perspective. The first breeding method used in corn was undoubtedly mass selection. The fact that the corn ear is large, and that harvesting for a long period of time was essentially a hand operation, provided excellent opportunities for selection to be practiced on ear length, diameter, and kernel characteristics. This type of selection undoubtedly was practiced from the beginning of the domestication of the corn plant until well into the twentieth century. This type of selection was quite effective in modifying ear and kernel characters even though it provided no opportunity for parentage control. Variation in ear size, etc., due to soil fertility were assumed to be genetic.

Varietal hybridization was the next breeding procedure tried. The results obtained in some cases were very promising, but no extensive use was made of the method. Varietal hybrids, however, did provide source material from which many of the widely grown varieties were isolated.

The ear-to-row method of breeding was suggested by C. G. Hopkins of the Illinois Station in 1896. This procedure, as the name implies, involved selecting a group of ears, planting these ear-to-row and obtaining information on performance. In such tests, marked differences in yield were obtained among the ears tested. This method was tried rather extensively, but was finally abandoned when it became apparent the cumulative improvement in yielding ability was not realized.

The ear-to-row breeding method provided for selection on the basis of the visual characters of the original parent ears and some measure of performance based on the progeny of the selected ears. Opportunities for genetic control were limited, and the original high yielding progenies were hybrids of unknown ancestry which could not be duplicated. The ear-to-row method of breeding was quite effective in modifying chemical composition, plant and
EARLY TESTING AND RECURRENT SELECTION

ear height, and leaf area. These characters, for which selection was effective, differ from yield in that the genetic basis is undoubtedly much less complex and environmental variability less likely to lead to mistaken classifications. We now know that the plot technics used in these ear-to-row trials were quite inadequate, and some of the failure to achieve improvements in yields must certainly be ascribed to this cause. Many of the modifications of the ear-to-row method of breeding which were introduced to minimize inbreeding probably had an opposite effect, and the rate of inbreeding was actually increased. On the basis of data now available, it is impossible to fully assess the relative importance of various causes resulting in the ineffectiveness of this method in increasing yields.

SELECTION WITHIN AND AMONG INBRED PROGENIES

The next method tried, and the one still used most extensively, involved selection within and among inbred lines and the evaluation of the lines retained in hybrid combinations. Some of the early work which served as a foundation for this breeding method has been reviewed in other chapters of this book. Extensive breeding programs were established at the various stations in the early 1920's, and a large percentage of the lines now used in the production of commercial hybrids had their origin in this early work.

In the earlier days of these programs any inbred line which could be maintained was considered to have potential value. As the work progressed it became apparent that inbred lines must meet certain minimum standards of performance as lines in order to merit testing in hybrid combinations. Studies were undertaken by Jenkins (1929) and somewhat later by Hayes and Johnson (1939) to determine which, if any, characters of the inbred lines were correlated with yield in hybrid combinations. In the studies reported by Jenkins correlations were used to measure the relationship between (1) various characters of the parental inbreds and the same character in their F1 hybrids, and (2) between characters of the parental inbreds and the means of the same characters for all of their crossbred progeny. The results obtained under 1 and 2 were somewhat different. In the first case, none of the characters of the parental inbreds were closely related to the yield of their F1 hybrids. The correlations reported ranged from -.10 to +.24. The correlations between yield of the parents and yield of their F1 hybrids were .14 and .20. Multiple correlations considering various grouping of characters of the inbreds and the yield of their hybrids ranged from .20 to .42.

In the second series which involved characters of the parental lines and the means of the same characters for all crossbred progeny, the correlations obtained were materially larger. With different groups of material the correlations involving yield ranged from .25 to .67. In some cases the degrees of freedom were few and the relationship therefore poorly determined. A weighted r calculated for the entire series was .45. The difference between these two
series can be readily accounted for by the assumption of epistasis, though no claim is made that this is the only or even the correct explanation. Where the correlations involve some character of the inbred parent and the same character in their F_1 crosses, epistatic effects would be expected to be at a maximum. When a character of the parent is correlated with the mean of all crossbred progeny opportunity would be provided for a considerable degree of cancellation of the epistatic effects.

The results reported by Hayes and Johnson are more directly comparable with Jenkins’ group 2. Various characters of the inbred parent were correlated with the yield of their topcross progeny. The correlations for individual characters ranged from .19 to .54, and the multiple r for 12 characters of the inbred parent and yield of the topcross progeny was .67.

As a result of these studies some investigators have decided that the correlations were too low to provide a wholly satisfactory basis for prediction, and the only safe measure of the worth of an inbred line was to evaluate it in hybrid combinations.

**EARLY TESTING**

Since the characteristics of the inbred lines did not provide an adequate index as to the value of a line, and since this value must be determined by crossbred progeny tests, it seemed advisable to determine whether crossbred performance could be evaluated at an earlier stage of inbreeding. Several lines of reasoning suggested that this might be feasible and desirable. First the ear-to-row tests with all of their limitations suggested that there were marked differences in yielding ability between individual carefully selected open-pollinated ears. The genotype of such high yielding ears was modified or diluted in ear-to-row testing procedure, but the identity of these individual ears could readily be maintained by self-pollination. Second, it appeared logical to assume that a potential ceiling was established for any derived line at the time of the selfing of the S_0 or F_2 parent plant. This ceiling is established by the genotype of the parent plant and the most desirable combination of genes which can be isolated from this gene sample.

The small population commonly grown from each selfed ear, the hindrance of linkage in preventing random recombination of genes, and the limited efficiency of visual selection would all operate to render the probability of isolating this most desirable gene combination very unlikely. The effort expended in growing and continued inbreeding and selection of strains having the less desirable genotype might represent a considerable waste. Third, if facilities were limited, as they always are, greater progress might be achieved by the early discarding of the less desirable genotypes and the growing of larger progenies of the more desirable genotypes in the early generations of selfing when variability and the efficiency of visual selection would be expected to be at a maximum.

Before these ideas could be put to a test, data were presented by Jenkins
(1935) which seemed to lend considerable support to the general ideas mentioned above. Remnant seed of 14 lines from the variety Lancaster and 14 lines from the variety Iodent representing eight generations of selfing were chosen in Jenkins’ study. These 28 lines represented a random sample of the lines from these two varieties which had survived the eight generations of inbreeding. Two sibs were chosen to represent each generation, one representing a selected ear in the direct line of descent and the second a discarded sib. These 56 ears were grown ear-to-row, and pollen from 10-12 plants of each line were mixed and applied to ten ear shoots of the tester variety Krug.

Due to variation in stands and the unfavorable season neither the sampling of plants within a strain nor the topcross parent was as adequate as planned. Only 12 of the lines originally chosen were represented in each of the eight generations of selfing. The yield trials of the topcrossed progeny were grown in 1932. Information on several important problems is presented in this paper, but the items of most importance in the present discussion deal with the performance of the lines after successive generations of selfing. In the Iodent series, represented by seven lines, the mean square associated with generations was not significant. In the Lancaster series, represented by five lines, the variation associated with generations was significant but there was no indication of a consistent trend.

On the basis of these results Jenkins concluded that, “The inbred lines acquired their individuality as parents of top crosses very early in the inbreeding process and remained relatively stable thereafter.” Since this paper was published, several people have assumed that the stability mentioned by Jenkins was synonymous with homozygosity, and therefore experiments demonstrating segregation in F2 or F3 were disproof of this stability. However Jenkins took particular pains to point out that the stability he was assuming did not arise from homozygosity, but was a sampling phenomenon. This sampling stability, if confirmed, makes the early testing procedure even more attractive, but stability is neither assumed nor required as a prerequisite for early testing.

Results from Early Testing

Experiments on early testing were started in Missouri in 1935. However due to unfavorable seasons, no critical data were obtained until 1938. The experiments were continued in Iowa in 1939 and subsequent years. The results of these studies were summarized in 1946 (Sprague, 1946). Some 167 selected S0 plants from a strain known as Stiff Stalk Synthetic were self pollinated and outcrossed to the double cross tester parent Iowa 13. The yields of the test crosses ranged from 61.8 to 100.8 bushels per acre. Four of the test crosses were significantly lower yielding than the synthetic parent, and two were significantly higher yielding than the tester parent. The plants chosen for selfing represented a carefully selected group on the basis of
phenotypic desirability. The wide range in topcross yields obtained is evidence of the poor relation between phenotype and performance in hybrid combinations.

The frequency distribution of topcross performance was subjected to two types of samplings. In one sample the S₁ lines representing the best 10 percent of the population were grown, and individual plants again self pollinated and outcrossed to the tester parent, Iowa 13. The distribution of the S₀ and S₁ topcrosses are illustrated in Figure 26.1. (The S₀ topcross yields have been adjusted to the S₀ topcross level on the basis of the performance of the tester parent, Iowa 13.) The distribution of the S₁ topcross yields clearly indicate that the S₀ plants exhibiting high combining ability transmitted this characteristic to their S₁ progeny. Segregation within progenies was quite apparent, indicating that opportunities for additional selection existed.

A group of twelve lines was chosen which provided a seriated sampling of the frequency distribution of S₀ topcross yields. These were grown in 100 plant progenies, and an attempt was made to self pollinate 25 of the better plants in each progeny and to outcross these to the tester parent. Because of differences in time of pollen shedding only 6 of the 12 lines chosen were finally used (Table 26.1).

Significant differences in yielding ability were obtained within each of the six S₁ families. The range in yield was of about the same magnitude in each family, suggesting that the S₀ plants having the highest test cross perform-
ance were no more heterozygous than the $S_0$ plants having poor test cross performance. The distributions arising from the four highest yielding families were not significantly different, but were significantly different from the distributions arising from the two lowest yielding families. These same general types of results were obtained when stalk breaking was considered.

Finally, three of the lines arising from selected sample when in the $S_3$ generation of inbreeding were compared with five standard lines. These eight lines were crossed in all possible combinations and compared in replicated yield trials (Table 26.2). The $S_3$ lines, as a group, were superior to the stan-

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**TABLE 26.1**

FREQUENCY DISTRIBUTION OF ACRE YIELDS IN BUSHELS FOR 20 $S_1$ TOPCROSSED PROGENIES DERIVED FROM 6 $S_0$ LINES (SPRAGUE, 1946)

<table>
<thead>
<tr>
<th>Family No.</th>
<th>Yield 1940</th>
<th>Yield 1942</th>
<th>Distribution of 1942 Acre Yields in Bushels</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1940</td>
<td>1942</td>
<td>87.5</td>
</tr>
<tr>
<td>SSS 278</td>
<td>100.8</td>
<td>105.9</td>
<td></td>
</tr>
<tr>
<td>SSS 295</td>
<td>92.9</td>
<td>104.6</td>
<td></td>
</tr>
<tr>
<td>SSS 393</td>
<td>92.9</td>
<td>102.2</td>
<td></td>
</tr>
<tr>
<td>SSS 130</td>
<td>82.5</td>
<td>103.3</td>
<td></td>
</tr>
<tr>
<td>SSS 227</td>
<td>73.5</td>
<td>94.1</td>
<td></td>
</tr>
<tr>
<td>SSS 407</td>
<td>64.9</td>
<td>97.3</td>
<td></td>
</tr>
</tbody>
</table>

**TABLE 26.2**

RELATIVE AVERAGE PERFORMANCE OF STANDARD AND NEW $S_3$ INBRED LINES OF CORN BASED ON SINGLE CROSS YIELD TRIALS (SPRAGUE, 1946)

<table>
<thead>
<tr>
<th>Inbred Designation</th>
<th>Relative Performance as Measured by</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Yield in Bu. per Acre</td>
</tr>
<tr>
<td>L317</td>
<td>78.4</td>
</tr>
<tr>
<td>187-2</td>
<td>79.2</td>
</tr>
<tr>
<td>WF9</td>
<td>87.5</td>
</tr>
<tr>
<td>38-11</td>
<td>78.8</td>
</tr>
<tr>
<td>Oh67A</td>
<td>72.7</td>
</tr>
<tr>
<td>Average</td>
<td>79.3</td>
</tr>
<tr>
<td>SSS 211-300</td>
<td>86.7</td>
</tr>
<tr>
<td>SSS 278-161</td>
<td>81.0</td>
</tr>
<tr>
<td>SSS 507-193</td>
<td>89.1</td>
</tr>
<tr>
<td>Average</td>
<td>85.6</td>
</tr>
</tbody>
</table>
ard lines in yield, and in resistance to root lodging and stalk breaking. On the basis of these results it was suggested that early testing might be a valuable tool in a breeding program. However it was pointed out that the method might be of limited value under some conditions. This warning has to some extent been ignored and some have assumed that the early testing procedure is useful at any stage of the breeding program and with any parental material.

Additional trials of the early testing procedure have been conducted by Dr. John Lonnquist (1950) of the Nebraska Station. In this experiment a series of selected plants from a strain of Krug were self pollinated and outcrossed to a series of plants of the same variety. When test cross performance data were available two samplings were made. One consisted of the group of lines exhibiting the highest topcross yields and the second group those exhibiting the lowest topcross yields.

In each group in subsequent generations selection was practiced in both directions. In the high group the phenotypically most desirable and least desirable plants were self pollinated and outcrossed to the tester. In the low group again the most and least desirable plants were selfed and outcrossed. This plan had to be modified somewhat as inbreeding progressed, since seed was not always obtained on the least desirable plants. The group actually used were the least desirable plants which could be propagated. After each test cross generation the selection of lines to be continued was based on combining ability. The single cross WF9XM14 was substituted for Krug as the tester parent after the original series of test crosses.

The results obtained during the first four selfed generations clearly indicate that topcross combining ability can be readily modified by a combination of selection and testing (Fig. 26.2). In the high group selected for high combining ability, the average topcross yields of all lines increased from 98.6 to 107.5 bushels. In the high group selected for low combining ability after the S1 yields decreased from 98.6 bushels to 93.3 bushels. In the low group selected for high combining ability after the S1 generation yield increased from 85.9 to 94.0. Where selection was practiced for low combining ability in each generation, yields decreased from 85.9 to 77.9 bushels.

Thus selecting for high combining ability for three additional generations when the original lines exhibited poor combining ability produced S4 lines which were not significantly different in combining ability from those of the high group selected for a similar period for poor combining ability. Selection in the low group therefore would be largely wasted effort. Continued selection and testing after the S1 would be most profitable for only those lines exhibiting the highest S1 topcross combining ability.

Limitations of Early Testing

Three papers have been published which are somewhat critical of the value of early testing. These will be reviewed briefly. Payne and Hayes (1949)
have presented data on a comparison of combining ability in F₂ and F₃ lines of corn. On the basis of these comparisons they concluded that early testing was of doubtful practical value. The material used in this study was 30 selfed ears from early segregates from the single cross A116×L317. Each of the 30 selfed ears was grown ear-to-row and pollen from approximately 30

![Diagram](image)

**Fig. 26.2**—The effects of visual selection and testing for combining ability during four generations of selfing in the variety Krug.

plants in each progeny was bulked and applied to the four inbreds chosen as testers; A334, A357, A340, and A392.

In addition, five individual plants selected at random were also out-crossed to the same four testers. The test crosses arising from the bulked pollinations were considered as representing a random sample of the gametic production of the individual F₂ plants and the five individual test crosses as samples of the F₃ progenies. Adequate seed was obtained from 26 of the original 30 families. Within the different tester groups correlations between F₂ and F₃ test cross means ranged from .51 to .76.
Payne and Hayes stated that:

The extent of relationship between the performance of $F_2$ test crosses and of the performance of their $F_2$ progenies in test crosses leads the writers to conclude that in these studies there was some doubt of the practical value of early testing for combining ability as a means of selecting desirable sources of $F_2$ lines. By a test however of relatively few $F_2$ lines it was possible to select $F_2$ lines that seemed to be a desirable source for improving, or substitution for certain inbred lines in Minhybrid 608.

It may be well to emphasize again that the only claim made for early testing was that it enables the separation of a population into two groups on the basis of combining ability. Also, continued selection in the more desirable group will yield a larger number of high combining lines than will the less desirable group or a random sample of lines selected solely on the basis of phenotype. The frequency distributions of test cross combining ability for $F_2$ and $F_2$ progenies seem to fulfill this claim very nicely. In the table that follows, each $F_2$ distribution has been divided into the higher yielding 50 per cent and the lower yielding 50 per cent. The distribution of $F_3$ test crosses for each of these subgroups was taken from their paper. The results are presented in Table 26.3.

The writer would conclude from these distributions that the testing of $F_2$ would have been a desirable practice. Within each test cross series it would have permitted of the discarding of a considerable number of lines. If the number of $F_3$'s to be tested had been held constant and all of the lines to be tested derived from the higher yielding $F_2$ subgroup, even greater progress might well have been expected.

The results obtained in this study are exactly those to be expected under the postulates of early testing. Early testing obviously cannot be used as a

**TABLE 26.3**

FREQUENCY DISTRIBUTIONS OF YIELD IN BUSHELS PER ACRE FOR 1 TO 3 $F_2$ PROGENIES DERIVED FROM $F_2$ LINES OF A116 X L317 CROSSED WITH 4 DIFFERENT TESTERS (AFTER PAYNE AND HAYES, 1949)

<table>
<thead>
<tr>
<th>Tester Parent</th>
<th>Distribution of $F_2$ Test Cross Yields in Bu. per Acre</th>
<th>Number of Test Crosses Yielding 60.0 Bu. or More</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>47.5</td>
<td>52.5</td>
</tr>
<tr>
<td>A334</td>
<td>Higher 50%</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lower 50%</td>
<td></td>
</tr>
<tr>
<td>A340</td>
<td>Higher 50%</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lower 50%</td>
<td></td>
</tr>
<tr>
<td>A357</td>
<td>Higher 50%</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lower 50%</td>
<td></td>
</tr>
<tr>
<td>A392</td>
<td>Higher 50%</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lower 50%</td>
<td></td>
</tr>
</tbody>
</table>
substitute for the more refined tests possible when the lines are more nearly homozygous. This limitation was clearly outlined in the 1946 paper (Sprague, 1946).

Data have also been presented by Singleton and Nelson (1945) which they interpret as demonstrating the ineffectiveness of early testing. In the study reported, forty-eight ears were chosen from the variety Whipple early yellow. These were grown ear-to-row and one self made within each lot. The selfed plants were also outcrossed to the inbred line P39. Selfing was continued for three generations. In each generation the plants chosen for selfing were outcrossed to P39. At the end of this period of selfing and testing, ten lines were chosen for this special study. By using remnant seed, test crosses were produced involving \( S_0, S_1, S_2, \) and \( S_3 \) generations. No data are given in the publication but an analysis of variance for the two-year test period is presented in Table 26.4.

At least two points concerning the analysis are worthy of mention. First there were no significant differences among the ten lines studied. In view of the extensive testing back of the group of lines chosen, and because they were selected to be very similar in yield, it is not surprising that the early testing procedure failed to disclose differences. The early testing procedure is certainly not suited to the measurement of very small differences. However the degree of genetic uniformity with respect to combining ability would normally not be expected in sampling with open-pollinated or \( F_2 \) populations.

The second comment bears on their interpretation of improvement in combining ability during the course of inbreeding. The appropriate test of significance in this case depends upon the specific question the data are asked to answer. If conclusions are to be confined to the particular lines used,
then the variation associated with generations is correctly judged significant. If, however, the experimental material is assumed to represent a random sample of lines and therefore typical of lines in general, the appropriate test indicates generations to be non-significant. Since no yield data were presented, no test of significance can be calculated for the linear component of generations. Their results, as presented, have little bearing on either early testing or the effectiveness of visual selection in modifying combining ability during the course of inbreeding.

Richey (1945, 1947) has presented a re-analysis of Jenkins’ (1935) data on combining ability after successive generations of inbreeding and reached conclusions differing from those presented by Jenkins. He questions the stability of combining ability and the effectiveness of early testing in providing a satisfactory criterion of combining ability when the lines approach homozygosity. He also presents some information on tester parents and their effectiveness in revealing segregation. This latter is a very important problem but will not be discussed here.

We return to the first criticism raised by Richey, namely that lines do not reach stability early in the course of inbreeding. To demonstrate his ideas, Richey has combined the eight generations into pairs, thus providing four groups. Then by selecting certain inbreds he has shown by graphs that, visually, quite different slopes are obtained over the period under study. Other groupings than those used by Richey may be selected with equal validity. These different groupings show quite an array of slopes upon visual inspection. However if one extends the original analysis of variance presented by Jenkins separating generations into a linear and remainder component, the linear component is not significant. This, of course, does not prove that trends are absent. It does indicate that such trends as may exist are small in comparison with the random variation.

Richey’s second criticism deals with the effectiveness of early testing as a measure of combining ability as the lines approach homozygosity. He concludes that early testing would have been quite ineffective. The real basis for the evaluation of any breeding or testing system depends upon the lines which are produced or revealed which have sufficient value for use in commercial hybrids. Of the twenty-seven lines on which Jenkins presented data, two lines of the Lancaster series have been of sufficient value to be used extensively. These are L289 and L317. These two ranked in the upper half of the lines tested and would have saved under an early testing procedure.

Two other lines have been used to a limited extent. One of these, I224, exhibited the highest yields in the Iodent S1 test cross series and would certainly have been saved. The other line L304A was in the upper 50 per cent of the S1 Lancaster series. If early testing had been used with this material, saving the upper 50 per cent of each frequency distribution, no commercially useful lines would have been discarded. The early discarding of the remain-
ing lines would have resulted in a very great saving of time and money as compared with testing at a more advanced stage of inbreeding.

**RECURRENT SELECTION**

Superficially recurrent selection has a considerable resemblance to the ear-to-row method of breeding. However, recurrent selection differs in several important respects. It provides for a much more accurate genetic control, and the plot technic can be modified to give any desired degree of accuracy. Our use of the recurrent selection technic was a direct outgrowth of the work on early testing. It appeared logical to assume that if the individual S₀ plants selected on the basis of test cross performance were a superior group, intercrosses among this group to provide source material for a new cycle of selection would minimize certain of the limitations arising from continued selfing. Accordingly a group of the best lines from the early testing series were intercrossed to provide material for the evaluation of this method.

Somewhat earlier, studies were started to compare the relative efficiency of recurrent selection and inbreeding in isolating material having a high oil percentage. At the time the work was started we were of the opinion that this was a new idea. It was some time later that we discovered that essentially the same ideas had been published independently by East and Jones (1920) and by Hayes and Garber (1919). In neither of these cases was any extensive use made of the method and no critical data were published. The first detailed description of recurrent selection was made by Jenkins (1940). The breeding procedure did not receive a name however until Hull (1945) published his article dealing with recurrent selection for specific combining ability.

Because of the shorter time period required per cycle we have much more information on recurrent selection as a method for modifying chemical composition than we have for the modification of combining ability (Sprague and Brimhall, 1949). We shall report in some detail only one study—that contrasting recurrent selection and inbreeding in modifying oil percentage in corn. The source material for this study was obtained from S₁ ears from reciprocal backcrosses involving the single cross wxOs420×Ill. High Oil. Individual plants were self-pollinated in each backcross population and analyzed individually for oil percentage in the grain. The five ears having the highest oil percentage in each population were planted ear-to-row the following season and all possible intercrosses made among the ten progenies. Equal quantities of seed from each cross were bulked and used as source material for a new cycle of selfing, analyzing, and intercrossing.

A duplicate planting of the ten ears mentioned above was made in 25 plant, ear-row progenies. The phenotypically most desirable plants in each progeny were self-pollinated. At harvest time approximately five ears were saved and analyzed individually for oil content of the grain. The two ears
of each family having the highest oil percentage were again grown in progeny rows for continued inbreeding and selection. When the analyses were available the sibling progeny having the lowest average oil percentage was discarded. The two selfed ears having the highest oil percentage in the selected sibling were used to propagate the family. This process was continued through five generations. The general procedures used in selection, with the exception of the chemical analyses, are essentially those commonly employed in the development of inbred lines by the standard method.

It should be emphasized that the time requirement, number of pollinations and analyses, land requirements, and selection differentials were essentially the same for the recurrent and the selfing series. The relative efficiencies of the two methods therefore should be directly comparable.

**RECURRENT SERIES**

The results from the recurrent series will be presented first. The material from the Ill. High Oil × wxOs420 series has been carried through two cycles after the original selfings. The frequency distributions are shown in Figure 26.3. The distribution presented for the original population is a composite for the two backcrossed populations. The solid vertical line represents the population mean and the dotted vertical line the mean of the selected sample. These selected ears were grown in ear-row progenies the following year and all possible intercrosses made by hand. Bulked seed from these intercrosses provided the source material for the next cycle of selfing and selection. The mean of the first cycle population was essentially the same as the mean of the selected parents—the full selective advantage of the parents had been retained. In the second cycle population the mean was further shifted to the right by an amount equal to 2.1 class intervals, but still failed to equal the mean of the selected parents by an amount equal to 1.1 class intervals. The mean of the original population was 7.2 per cent of oil. The mean of the second cycle population was 10.5 with the extreme deviate at 13.5.

The ranges and standard deviations of these three populations are of some interest in indicating any changes in genetic variability. Considering first the range: in the original population the range was from 4.5 to 10.5, in the first cycle 5.5 to 12.5, and in the second cycle 7.5 to 13.5—a difference of 6, 7, and 6 class intervals respectively. The first cycle had the greatest, the original population intermediate, and the second cycle the smallest standard deviations. The fact that the second cycle exhibited the smallest standard deviation may indicate some loss in genetic variability. However 65 per cent of the selective advantage of the parents was retained indicating that a considerable amount of genetic variability exists.

**SELFING SERIES**

The selfing series presents a strikingly different picture. The results are presented graphically in Figure 26.4. The values plotted for the S1 generation
represent the oil percentages of the original selfed ears. Two lines were lost during the course of inbreeding because of failure to produce any phenotypically desirable plants. The eight lines remaining however represent eight of the ten lines comprising the recurrent selection series. The values presented for the $S_2$ generation represent the mean of all ears of a particular family which were analyzed. In $S_3$ to $S_5$ the value plotted represents the

mean for the sibling population in the direct line of descent. If the highest values in each generation had been plotted instead of the means, the picture would have been essentially the same except that the fluctuation from generation to generation would have been increased. The eight lines exhibited somewhat different patterns during the course of inbreeding. Six of the eight lines exhibited an increase, and two a decrease in oil percentage. There does not appear to be any consistent trend within the families from generation to generation. It would appear that chance has played a very important role in spite of the intensive selection practiced.

Fig. 26.3—A comparison of the frequency distributions of oil percentage in the corn kernel, in the original population, Illinois High Oil $\times$ wxOs420, and after one and two cycles of recurrent selection.
Comparisons between the two systems of breeding may be made in a number of ways. Selection during inbreeding is normally practiced within and among families. If only the two families having the highest oil percentage were retained and these compared with the mean of the second cycle population, the differences are very slight but in favor of the selfing series. If these two lines are compared with the extreme deviate of the recurrent series the lines are lower in oil by nearly three per cent. If the comparison is made between the mean of the $S_5$ lines and the mean of the second cycle population the lines are again lower, the contrast being 7.5 and 10.5 per cent of oil respectively.

Any comparison involving these two series must also take into account the time at which the comparisons were made. In the selfing series, genetic
variability, and therefore opportunity for selection, would be largely ex­hausted after five generations of selfing. For reasons mentioned earlier, it is assumed that a considerable degree of genetic variability remains in the re­current series. The disparity between the two systems would therefore be expected to increase with additional generations of selfing and cycles of selection.

Recurrent selection has been practiced for oil percentage in two additional populations. One series had its origin in an $F_2$ population of the single cross I198×Hy. This population started with a much lower average oil percentage, but the effectiveness of selection was essentially the same as in the Ill. High Oil×wxOs420 series.

In a third series a strain known as Stiff Stalk Synthetic served as parental material. This material also has been divided into a selfing and a recurrent series to supplement the material already presented. This experiment has not yet been completed. The difference between the two series, in so far as data are available, closely parallels the wxOs420×Ill. High Oil series already dis­cussed.

Data on the effectiveness of recurrent selection in modifying combining ability are still quite limited. One such comparison is shown in Figure 26.5. The original stock used was the Stiff Stalk Synthetic, and the double cross Iowa 13 was used as the tester parent. The yields for the two years were not greatly different, but to facilitate a direct comparison the lower frequency distribution has been displaced to the right so that the yield of Iowa 13 for the two years falls on the same ordinate. Stands were somewhat variable in the test crosses comprising the first cycle. The effect of this variation was minimized by adjusting all yields to an average stand by means of a covari­ance analysis. This adjustment reduced the range in yields so that the con­trast between the two frequency distributions does not necessarily present a true picture of the relative variation in the two populations.

**RECIPROCAL RECURRENT SELECTION**

A modification of the recurrent selection scheme has been suggested by Comstock et al. They have designated this procedure reciprocal recurrent selection. Under this modification two diverse foundation sources, $A$ and $B$, are to be used. Individual selected plants in $A$ are self-pollinated and out­crossed to source $B$ as a tester parent. Similarly selected plants from source $B$ are self-pollinated and outcrossed to source $A$ as a tester. When test cross data become available, a group of selfed ears from source $A$ having the best test cross performance are recombined to produce $A^1$. $AB^1$ population is formed in a similar manner. $A^1$ and $B^1$ then serve as source material for a new cycle of selfing and test cross evaluation followed by the intercrossing of the most desirable plants. No data are yet available from either their experiments or ours using this method.
In the original paper by Comstock et al. (1949) a comparison is presented of improvement limits of three definite breeding procedures. These were (1) selection based on general combining ability using at least two single crosses as testers, (2) recurrent selection for specific combining ability as proposed by Hull (1945), and (3) reciprocal recurrent selections. The assumptions on which these comparisons were based were stated by Comstock et al. and will not be repeated here. The conclusions reached are briefly as follows:

1. When dominance is incomplete methods 1 and 3 are essentially equal and superior to method 2.
2. If over-dominance is of major importance methods 2 and 3 will be essentially the same and superior to method 1.
3. When dominance is complete all three methods would be rather similar.

Thus method 3, reciprocal recurrent selection, would appear to be the
safest and most efficient method to use with our present lack of knowledge concerning the relative importance of partial dominance, dominance, and over-dominance in determining combining ability.

In the discussion presented so far no emphasis has been placed upon choice of testers. It is obvious that either early testing or recurrent selection can be carried out giving special emphasis to either general or specific combining ability depending upon the tester parent chosen. In the experiments involving oil percentage of the grain this problem does not arise. In the experiments involving test crosses for yield evaluation, double crosses or open-pollinated varieties have been used as tester parents thus giving special emphasis to general combining ability.

**SUMMARY**

In the data which have been presented bearing on early testing, the method has demonstrated all of the characteristics which have been claimed for it. This is not to be interpreted as meaning early testing is the ideal corn breeding method and equally applicable under all circumstances. It is useful under some conditions. The ideal method of corn breeding probably is still to be devised.

Recurrent selection has been found to be quite effective in modifying the chemical composition of the corn grain. Tests of this method in modifying combining ability have been less extensive. Here again this method may not be equally valuable under all conditions and circumstances, but on the basis of results to date it is certainly deserving of more extensive use.