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The Improvement of Naturally Cross-Pollinated Plants by Selection in Self-Fertilized Lines

II. THE TESTING AND UTILIZATION OF INBRED STRAINS OF CORN

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II. THE TESTING AND UTILIZATION OF INBRED STRAINS OF CORN*

Donald F. Jones and W. Ralph Singleton

The application of inbreeding to the improvement of corn has received an increasing amount of attention since its inception a quarter of a century ago. In 1932 more than 80,000 acres of corn were planted in this country with seed that had resulted, in one way or another, from the crossing of inbred plants. Although the production of hybrid corn seed seems to be well started in commercial practice, the development, testing and most advantageous use of inbred strains still present many problems.

The first attempt to account for the increased growth immediately resulting from cross-fertilization may be called the physiological hypothesis of hybrid stimulation. In this it was thought that the bringing together of germinally diverse elements by crossing different lines, generated the growth activity commonly referred to as hybrid vigor. Conversely, the reduced size and slower growth rate of inbred lines was considered the natural result as the germinal constitution is simplified.

It was later pointed out that hybrid vigor can be given a genetic interpretation. It was noted that many of the heritable factors which favored growth and reproduction are dominant in their expression. Therefore in heterozygous combinations it is possible to have a larger number of different factors and hence more favorable factors than in homozygous combinations. Due to linkage and other difficulties of recombination, it is extremely difficult, if not impossible, to obtain all of the growth-promoting genes that exist in a species, combined in one individual. Such a plant, if obtained in a homozygous condition, would show no benefit from crossing with other individuals and no reduction when inbred.

As a general rule, nearly every individual is benefited temporarily, in one way or another, by crossing with other specimens of the same or closely related species. This does not follow in every case since certain combinations are not compatible. Wide crosses are usually not viable and when offspring are produced they are not able to function properly. Hybrid weakness as well as hybrid vigor may result from crossing and this is more easily explained by the genetic interpretation than by the physiological hypothesis.

* Part 1, Station Bulletin 266, March, 1925.

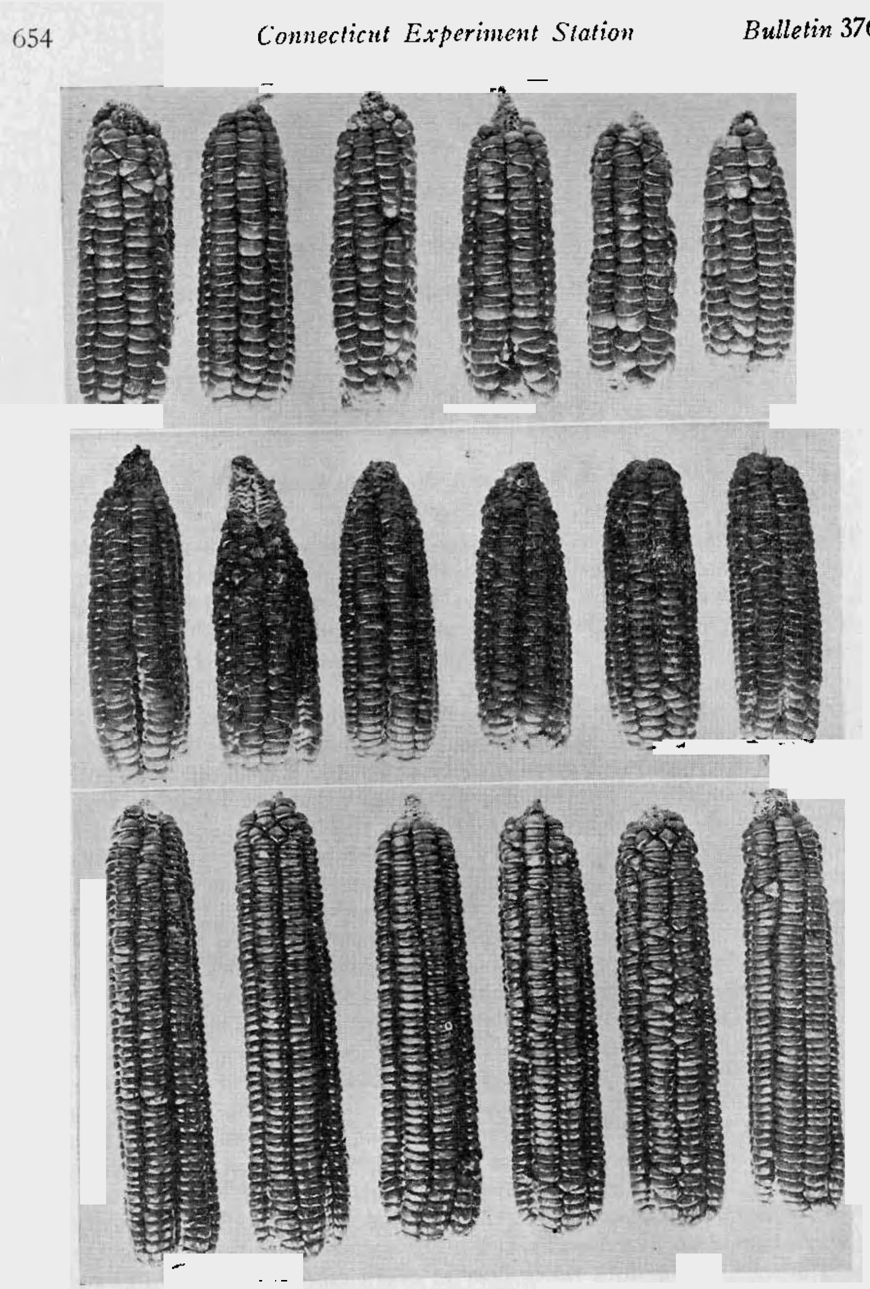

FIGURE 95. Two short-eared inbreds of Gold Nugget flint and their first generation hybrid below.

According to the dominant gene hypothesis, the effects of inbreeding are due largely, if not wholly, to the inheritance received. Species that are regularly cross-fertilized maintain a condition of heterozygosity which allows recessive factors to accumulate. Such organisms are usually reduced in size and rate of growth by inbreeding, and this condition is frequently accompanied by the production of some abnormal and undesirable individuals. Since these are generally weak and often sterile, they automatically tend to eliminate themselves. The survivors of a severe and continued process of inbreeding are usually brought to a high degree of homozygosity and are large or small, productive or non-productive, disease-resistant or not, according to the specific allotment of genes they have received.

This genetic interpretation of the effects of inbreeding and crossing has emphasized the importance of selection during and after the inbreeding process. Since the results of crossing depend upon the constitution of the inbred strains used, it is essential that the inbred material contain the qualities to be expressed in the hybrid, or in the new variety or breed sought.

The first report of this series of experiments on *Selection in Self-Fertilized Lines* was published in 1925 as Station Bulletin 266. It dealt with the production of inbred strains of corn. The possibility of obtaining vigorous inbred plants was considered, along with methods of hand-pollination, systems of selection during the inbreeding process, criteria of selection, and the correlation of characters in successive generations. The general conclusion from this study was that selection during the inbreeding period was effective in establishing specific characters.

The number of progenies grown, the number of individuals in each progeny, the number of plants self-pollinated, and the selection among the plants self-pollinated had an important bearing upon the results obtained with specific characters, such as height of plant, time of maturity, and resistance to disease. Selection during the inbreeding process for general vigor and productiveness in the inbred strain itself was of little avail. Good plants at the start gave both good and poor strains after several generations of self-fertilization. Many poor strains at the beginning were numbered among the best at the finish. Selection of the most vigorous and productive plants tended to perpetuate the heterozygous condition that existed at the start and delayed the attainment of homozygosity. The general conclusion was reached that, when productiveness is the principal objective, extensive selection within the inbred lines does not seem to be advisable.

The importance of selection lies in choosing the most useful strains after uniformity and constancy have been obtained. Most effort should be expended in producing the largest number of homozygous strains. This emphasizes the importance of starting many lines and selecting the plants for progenitors largely at random, unless the specific qualities sought are evident despite hybrid vigor.

When inbred strains have been produced, the next consideration is to test them to find which are the most useful for the purpose in mind. Having found the best strains, how can they be utilized to the greatest

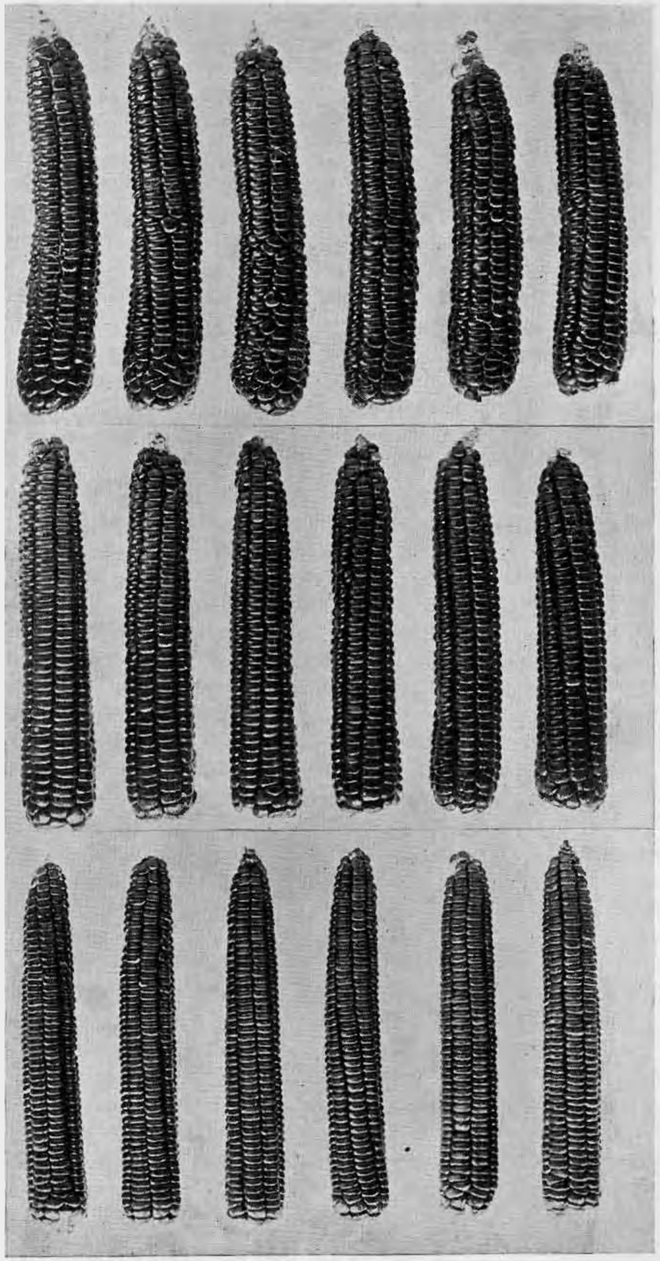

FIGURE 96. Two long-eared inbreds of Canada Yellow flint and their first generation hybrid below.

advantage? The testing and utilization of inbred strains of corn is the subject that will be considered in this part of the series.

THE PERFORMANCE OF INBRED STRAINS WHEN CROSSED

The results of self-fertilizing four varieties of corn for five generations are described in Part I of this series. These varieties are: Burwell's Flint, an early maturing type of eight-rowed Canada Yellow Flint; Gold Nugget, a late maturing, eight-rowed flint having large kernels; Century Dent, an early maturing dent corn having broad, shallow kernels; and Leaming, a local strain of this well known variety of corn that is rather late maturing in Connecticut. About 20 selected lines were started from each of these four varieties. The appearance and nature of the selected lines are described in detail in the previous publication.

From a study of the yields obtained in the first generation after crossing these inbreds in various combinations, it was at once apparent that some lines had a much more favorable effect upon productivity than others. An attempt was made to cross each strain with all of the other strains of the same variety. Not all combinations were successful in producing enough seed to grow. The yields were averaged for each series of crosses in which one strain was used as one of the parents. Averages represent from 3 to 20 crosses. All were grown in the same field under as nearly similar conditions as could be obtained and were distributed at random.

In Table 1 it will be seen that some strains produced more than twice as much grain as others when used in combination with other inbred lines out of the same variety. This is the usual result to be expected from crosses of a series of inbred lines. But is it possible to foretell the behavior of any given strain before the cross is made? If so, is it feasible to eliminate certain lines without going to the trouble of making the crosses and testing them?

TABLE 1. THE AVERAGE YIELD OF A SERIES OF CROSSES OF INBRED STRAINS CLASSIFIED AS PRODUCTIVE (P), UNPRODUCTIVE (U), OR INTERMEDIATE (I), ACCORDING TO THEIR PERFORMANCE BEFORE CROSSING.

Variety	Year Grown	Strain Class	Strain No.	Yield	Strain Class	Strain No.	Yield
Burwell Flint	1924	U	30–6	47 ± .9	P	40–7	60 ± 3.1
Burwell Flint	1925	I	40–9	27 ± 1.2	I	40–6	64 ± 4.3
Leaming Dent	1924	U	112–3	45 ± 2.3	P	112–6	61 ± 2.0
Leaming Dent	1925	I	112–8	57 ± 2.5	P	112–1	77 ± 4.7

Of the eight strains listed in Table 1, two were classified as unproductive in Bulletin 266 (Figures 53 and 57). Both of these, 30–6 and 112–3, were in the lowest yielding series of flint and of dent crosses in 1924. Three were classified as productive: 40–7, 112–1, and 112–6 (see Figures 52 and 56, Bulletin 266). The crosses in which these three strains took part as one of the parents were the most productive in three out of four cases. In no case were the highest average yields obtained from

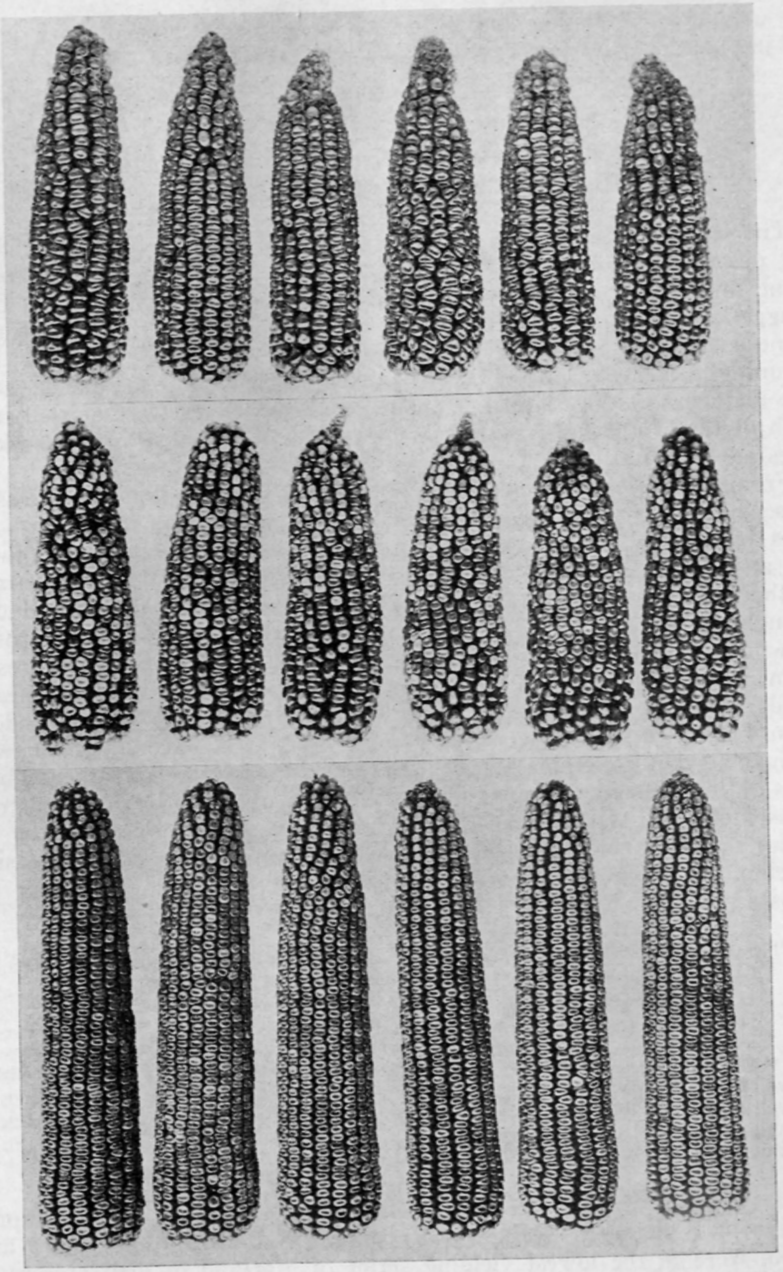

FIGURE 97. Two tapering inbreds of Leaming dent and their first generation hybrid below.

strains that were classified as unproductive. The opposite also holds true, although once in the dent, and twice in the flint, the highest or lowest average yield was made by a strain in the intermediate class.

The classification of these strains as productive or unproductive was made after they had been self-fertilized for five generations, and before any crosses had been made. Of the 15 to 20 surviving strains in the Burwell Flint and Leaming Dent, four were selected as being the most productive and four as the least productive.

Another classification was made, in which the yield of dry grain was only one criterion of selection. Others were: Size and general appearance of the plants, their freedom from disease, and the quality of the corn produced. They are listed and described in Part I on page 411. For convenience they are called "good" and "poor" lines. Some of the poor lines yielded a heavier weight of grain than any of the good lines, but were undesirable in quality and in other respects.

Jenkins (1929) made a careful statistical study of the correlation between the inbred parents and their hybrid offspring in many measurable characters. He found that yield in the crossbred progeny is correlated significantly and positively with number of days to tassel and silk, plant height, number of nodes, number of ears per plant, ear length, ear diameter, and yield of parent plants. Kiesselbach (1922) also concludes that "there appears to be some general correlation between productivity of the pure line parents and that of their hybrid offspring". The partial correlation between productiveness of the inbreds and of the crosses derived from them thus seems to be well established.

The eight lines mentioned above were crossed with one another in the three possible combinations: Good × good, good × poor or the reciprocal, and poor × poor. The results obtained are shown in Table 2. From 12 to 35 different crosses are represented in each combination. The yields are the average of all crosses grown. There is a difference of 4.2 bushels per acre between the matings of two good and of two poor strains in the flint, and 6.8 in the dent. The good by poor and reciprocal combinations give an intermediate yield as compared with the other two.

TABLE 2. THE YIELD OF FIRST GENERATION HYBRIDS IN BUSHELS PER ACRE CLASSIFIED ACCORDING TO THE GOOD OR POOR PERFORMANCE OF THE PARENTAL STRAINS.

Variety	Good × Good		Good × Poor		Poor × Poor	
	No.	Yield	No.	Yield	No.	Yield
Burwell Flint	34	52 ± 1.2	12	52 ± 1.3	23	48 ± 1.3
Leaming Dent	35	56 ± 1.4	26	52 ± 1.5	12	49 ± 2.1

There are individual crosses that stand out as good or poor in contrast to their parentage. In every case, however, the highest yielding individual cross in the good × good combination is more productive than the highest of the poor × poor combinations. Similarly the lowest of the poor × poor matings is the lowest for all the crosses. The differences are not significant.

Many of these single crosses, which combine two inbred strains, were again crossed, producing a first generation hybrid that is called, for con-

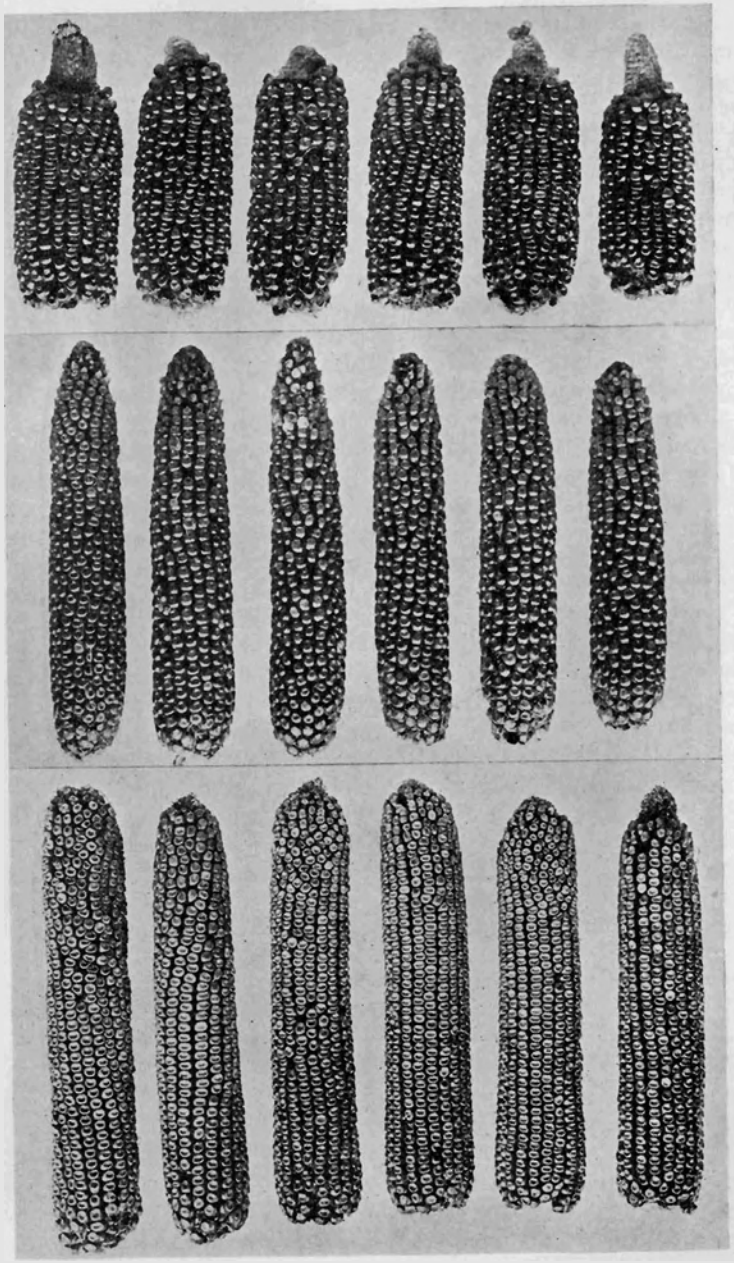

FIGURE 98. Two cylindrical inbreds of Leaming dent and their first generation hybrid below.

venience, a double cross. In Table 3 are classified the yields of 142 double crosses all made from inbred strains of one variety. The yields are grouped according to the number of strains in their pedigree that were designated as good before any of the crosses were made. The one combination that would have brought together all four of the good strains was not made, due to a failure in pollination. Each of the others had from none to three good strains in their pedigree. All of the crosses were grown in one field, in the same year, and under uniform conditions. Each was represented by several plots distributed at random throughout the field.

TABLE 3. THE DISTRIBUTION OF YIELD OF DOUBLE CROSSES BASED UPON THE NUMBER OF GOOD STRAINS USED IN MAKING THE CROSSES.

No. of Good Strains	Yield in Bushels per Acre 38	43	48	53	58	63	68	73	78	83	No. of Crosses	Average Yield
0	1	2	5	3	8	4	3	1			27	56 ± 1.1
1	1		8	14	18	7	9	3	1		61	58 ± .5
2				2	12	12	7	3		1	37	63 ± .7
3			1	4	2	4	3	2	1		17	62 ± 1.4

Difference 0 and 3 6 ± 1.8

There is a fairly consistent increase in yield from 56.2 bushels per acre, where all four of the parental strains were poor, to 62.1 bushels, where three of the parental strains were good. The difference is 6 ± 1.8 bushels per acre and is hardly significant. Yield alone does not indicate fully the superiority of crosses made from the better parental strains. There were noticeable differences in quality of grain as shown in freedom from cracking and molding. Many combinations had notable ability to stand erect throughout the season, to cover the ears well with husks, and had other outstanding qualities fully as important as the production of grain.

PARENTAL CHARACTERS IN THE HYBRIDS

The tendency of particular characters in the inbreds to be expressed in the crosses is shown in the accompanying illustrations. Two short-eared, broad-kerneled inbreds of Gold Nugget Flint, 105–18 and 105–20, give short broad ears in the first generation hybrid. In one of these strains the plant is quite short in stature, with ears starting at nodes only a few inches above the ground. The other strain is nearly twice as tall, the tip of the ears being on a level with the base of the tassels of the other strain. Both are out of the same variety and have not been selected for height. The crossed plants are taller than either parent, but not so tall as other crosses in the same material. (Figure 95.)

In contrast to this is the Burwell Flint hybrid in which two rather long, slender inbreds, 40–7 and 40–8, are brought together. The result is a long, slim ear, proportionally more slender than either of the parents. In this cross the pericarp has a tendency to crack, an undesirable feature that it not noticeable in the selfed strains themselves. (Figure 96.)

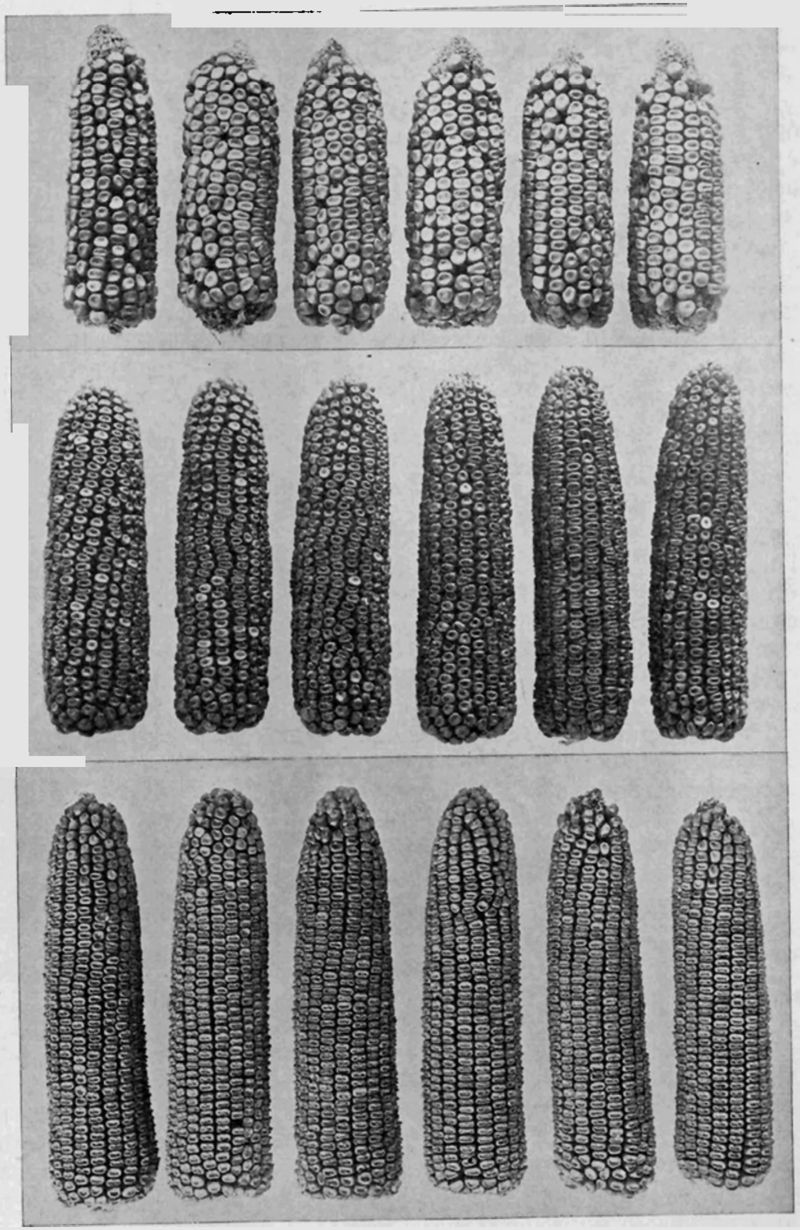

FIGURE 99. Two productive inbreds of Leaming dent and their first generation hybrid below.

The tendency of dent corn ears to be cylindrical or tapering can be fairly well foretold by the appearance of the inbreds before they are crossed. Strains 112–9 and 112–12, out of Beardsley's Leaming, each have a decided inclination to be narrower at the tip than at the butt. The first generation hybrid of these two strains has a marked tendency in this direction. (Figure 97.) This is in contrast to the cross of 112–1 × 112–4, two lines that carry their width of ear evenly throughout their length. One of these inbreds was the longest of all the selfed lines from this variety, and the hybrid is also outstanding in its length of ear. The kernels of both parental lines are small and nearly round on their exposed surface, and this feature is clearly apparent in the cross. (Figure 98.)

In the combination 14–4 by 243, both inbred strains of Leaming from a source different than the 112 lines, we see the ear and kernel characters of one of the parental inbreds directly expressed in the hybrid. The other parent has kernels that are irregular in size and shape, and the ears are poorly filled. The plant characters of this particular inbred are good. The stalks are vigorous and erect; the leaves are broad and well colored; and the plants mature early. Aside from a marked susceptibility to bacterial wilt, this is one of the best strains of dent corn we have produced. The other strain with the good ear characters also has a sturdy stalk, but is late in maturing. Their hybrid matures in satisfactory season. It is among the best of all the crosses so far obtained in productiveness, ability to stand erect and quality of grain, when grown under conditions that prevail in Connecticut. (Figure 99.)

RESULTS OF CROSSING AFTER INBREEDING AND SELECTION

White Flint Corn

Six varieties of eight-rowed white flint corn were used in an inbreeding and selection experiment. These varieties had been grown for some time in Connecticut and apparently were well adapted to local conditions. They differed considerably in length of ear, size of kernel and in uniformity of filling over the tips. They were all eight-rowed, with the typically white, corneous kernel characteristic of this class of corn.

Twenty-five or more naturally pollinated ears were chosen out of each variety. After the first generation, three progenies in each line were grown yearly. Two plants were selected for self-pollination out of about ten plants grown in each progeny. On the basis of plant characters, ear development and freedom from disease, the two best lines were noted. Whenever possible, the two selfed ears from the best and one from the next best progeny were used to continue the line the following year. Due to failure to secure sufficient seed such an arrangement was not possible in every case, but most of the lines were continued in this way for four generations.

This system was considered to be an improvement over the method of selection in self-fertilized lines first proposed. Selections were not made until the crop matured. Each line was represented by two different progenies and final elimination did not come until two of the three progenies had been grown for at least two years.

After four generations of self-fertilization and selection in this way, all lines were pollinated by a stock of yellow dent corn regularly used as

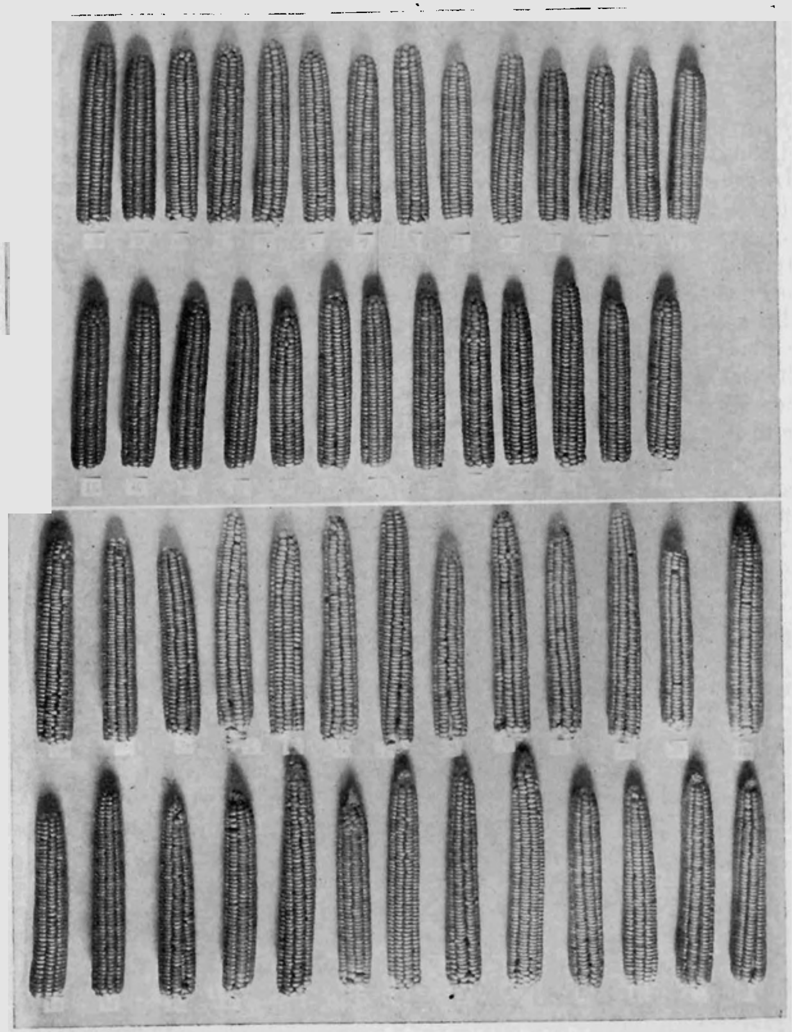

FIGURE 100. The original naturally pollinated ears of white flint from which inbred lines were derived.

the pollen parent of the Canada-Leaming hybrid, described in Station Bulletin 310. (This pollen parent is a composite of several inbred lines derived from Illinois and Connecticut strains of Leaming.) Jenkins and Brunson (1932) and Jenkins (1934) used this method of pollinating all

inbreds by a common stock to test inbreds, and found that it had advantages. St. John (1934) obtained results which indicate that inbreds used as the seed parent yield less than when used as the pollen parent in the same combinations. According to his results, a series of inbreds, all pollinated by one variety—the most convenient way to make the pollination—does not give as reliable an indication of yielding ability as when the crosses are made the other way.

In the experiment here, each of the crosses of the inbred lines × Leaming was grown in single row plots between two check rows planted with Canada-Leaming. The check plots were similar in type to the test plots. Both contained flint-dent hybrids having the same general season

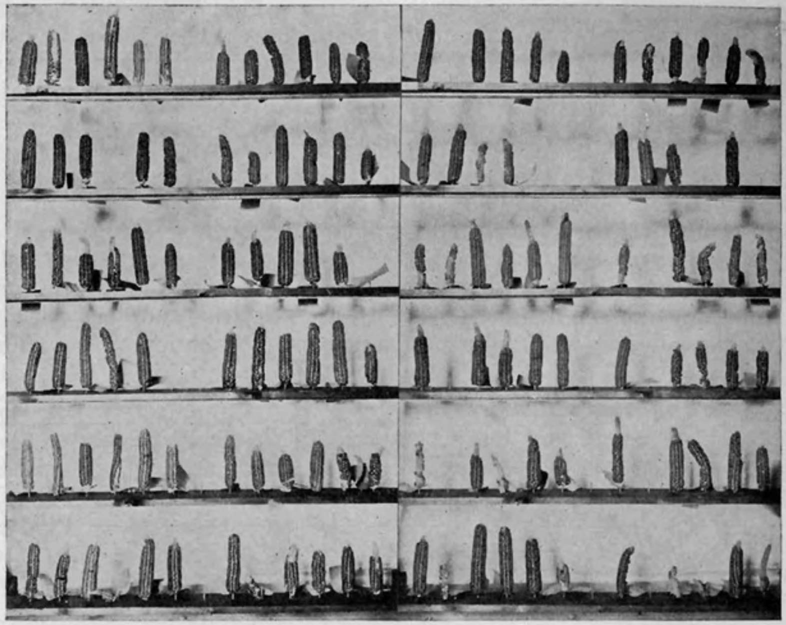

FIGURE 101. The result of pollinating two ears in three progenies of a number of lines of white flint after three generations of self-fertilization.

of ripening and about the same amount of growth. In previous tests the Canada-Leaming had proved to be a remarkably fast growing and high yielding corn, fairly uniform in type.

A photographic record was made of the original ears and the hand-pollinated ears in each generation for all self-fertilized lines. Figures 100 and 101 show the original ears of two of the six white flint varieties from which the lines were started, together with self-pollinated ears in the third generation of some of the lines that were derived from these two varieties. From their appearance, the original ears give no indication whatever as to the characters of the inbred strains derived from them. And neither the original ears nor the hand-pollinated ears in the third generation indicate clearly the results obtained when the inbreds are crossed with an unrelated variety.

Based on the appearance of the growing plants and the mature ears when harvested after three generations of self-fertilization, 51 lines out of the 153 started were noted to be promising. This selection took into consideration general vigor of the plants as judged by the stalk growth, ability to stand erect, freedom from disease, total production of grain, and quality of the grain itself. If it had been impossible to use all of the inbreds, these were the ones that would have been chosen for propagation. However, all of the surviving lines, a total of 113, were crossed, as previously stated.

For comparative purposes it is better to classify the inbreds during the same season that the crosses are grown, since one year often differs markedly from another in rainfall and temperature. The inbreds and their crosses behave differently in different seasons. In the tests, however, classification of the inbreds was made in 1925, and the yield comparison in 1927, and again in 1928.

As stated above, 113 of the original 153 lines were used in making the crosses. The rest were lost in the process of inbreeding. All of the crosses were divided into two groups according to their yield in comparison with the two adjacent check plots. In the first class were those that yielded more than the average of the two adjacent checks, and in the second those that yielded the same or less. As previously mentioned, the white flint inbreds had been classified as "selected" and "not selected." Putting these figures into a four-part frequency distribution table we have:

	Inbreds Selected	Not Selected
Number of crosses yielding more than average of checks	12	10
Number of crosses yielding less than average of checks	31	60

The coefficient of association is + .40. Of all the crosses that were above the average of the adjacent check plots in yield, 55 per cent were made with selected inbreds and 45 per cent from those not selected previously as promising. Of the crosses yielding the same or less than the check, 34 per cent were made with the selected inbreds and 66 per cent with those not selected. Stated conversely, 28 per cent of the crosses of selected inbreds were above the average in yield, while only 14 per cent of the unselected were above average. According to this there is some evidence that desirable lines can be chosen in the third generation of self-fertilization.

The lines from the six different white flint varieties were classified separately. All gave about the same result so that the figures from all are combined.

A study was made of the parentage of the exceptionally good and poor combinations. In some cases as many as four replications of each cross were grown. A classification was made including only those crosses whose replications consistently yielded more or less than either adjacent check. The four-way distribution is as follows:

	Lines Selected	Lines Not Selected
Crosses yielding more than either check	9	10
Crosses yielding less than either check	28	48

The coefficient of association is + .21, less than in the previous classification. Stating the results in general terms, we can say that a selection of one-third of the inbreds before crossing was successful in obtaining only about one-half of the higher yielding combinations, when all of the inbred lines were crossed with one distinctly different type of corn. Only one combination, replicated three times, yielded more than either check in all plots and this was not from a selected line. While there is something to be gained by making an elimination before crossing, it is questionable whether or not any normal lines can be discarded before being tested.

Evergreen Sweet Corn

In 1921, fifty-six lines of Evergreen sweet corn were started. These were selected from 200 open-pollinated ears on the basis of a germination test showing seeds free from fungous infection. The original 200 ears had been chosen because they were of desirable size and shape and the type of kernel was good for canning purposes. The 56 lines were continued by self-fertilization, three progenies being grown in each. At the time of pollination, the best-appearing of the progenies in each line was selected and five plants were self-fertilized.

In the fourth generation, six lines were chosen, on the basis of growth of stalk and ear development of the inbred plants, as the most promising of the entire lot. They were all sufficiently productive to be used as a possible seed parent in a crossing field. These six lines were used as pollinators. They were crossed on one another and on each of the other lines, with the exception of a few that were too poor to be continued.

TABLE 4. THE EFFECT OF SELF-FERTILIZED LINES OF EVERGREEN SWEET CORN UPON THE YIELD OF CROSSES IN AVERAGE WEIGHT OF GRAIN IN POUNDS PER PLOT.

Line Number	Used as seed parent and crossed by five others	Used as pollen parent and crossed on five others	Used as pollen parent and crossed on all others
5	7.6 ± .13	8.3 ± .49	8.1 ± .10
50	9.1 ± .39	8.1 ± .32	8.3 ± .12
57	8.4 ± .05	7.5 ± .43	8.0 ± .12
63	8.7 ± .26	7.8 ± .39	8.3 ± .11
188	6.4 ± .20	8.5 ± .34	8.2 ± .12
195	7.7 ± .27	7.8 ± .24	7.6 ± .09

All of these crosses were grown in single row plots in two different fields, at Mount Carmel and at Orange. The original strain of Evergreen sweet corn was used as a check in every fifth row. The total yield of air-dry ears was weighed and corrected to the check yields. These were then averaged for the six inbreds used as a seed parent and as a pollen parent in various combinations. Results are given in Table 4. The

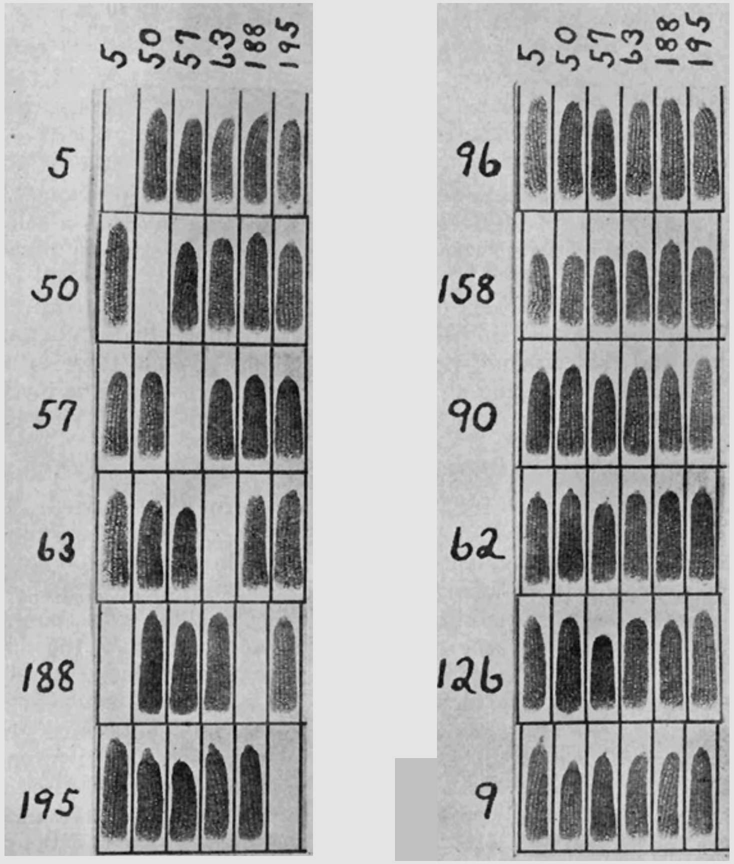

FIGURE 102. One representative ear of first generation hybrid combinations of inbred strains of Evergreen sweet corn. The pollen parents are numbered across the top and the seed parents at the left.

figures indicate that the combinations containing lines 50 and 63, either as a seed or a pollen parent, are among the highest in yield. The differences are small and significant only for the highest and lowest average yields, but they furnish some evidence that these two lines impart productiveness to their hybrid offspring.

Figure 102 shows selected ears from these various combinations. Each cross is represented by one ear. The pollen parents are shown across the top with the seed parents indicated at the sides. The combinations at the left are reciprocal crosses among the six pollinators. The ones at the right are six other lines crossed by the same pollinators. Each vertical row of ears has the same pollen parent and the horizontal rows have the same seed parent. The individual ears shown were selected in the field as the best from all of the plants grown in each plot. Most of the crosses were so uniform that the ear size and shape and the kernel characters of the specimens shown are fairly representative of the whole crop.

These various combinations show a marked influence from certain parents. Lines 50 and 63 have a tendency to produce cylindrical, well-filled ears in nearly all crosses when used either as a seed or as a pollen parent. Lines 5, 9, and 90 are exceptions in that all combinations with these as seed parents are tapering. Line 96 has a noticeable tendency to

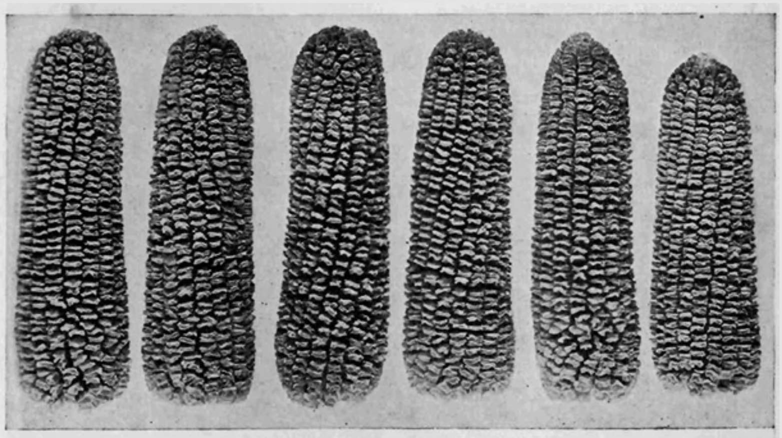

FIGURE 103. Mature ears of the first generation hybrid of C.63 × 50, Evergreen sweet corn.

produce long ears, while all of the combinations with 57, either as a seed or pollen parent, and 158 as a seed parent, are short. The cross of 57 × 158 is the shortest of the entire lot. Ears from crosses having 9, 90 and 195 are not well filled at the tips. Other differences in width and depth, color and texture of the kernels, are equally in evidence.

Before the yields were calculated, the combination of 63 × 50 had been selected as the outstanding hybrid of the entire series largely on the basis of uniformity, ear size and ear type. This selection was confirmed by repeated trials. From the first trials, 12 of the most promising combinations were grown the two following years at three different places in Connecticut.

In the second trial, the 63 × 50 combinations showed the best development but the plants had a tendency to lodge. In the third trial they displayed the same weakness. But in spite of the plants being badly down, they still maintained the best ear development. Most of the combinations with line 63 have shown root weakness, apparently associated with rootrot infection. No other combinations had the ability to produce such large, well-shaped ears. Therefore the 63 × 50 cross was selected as the most promising, and called Green Cross.

In an attempt to eliminate the root weakness, remnant seed from three progenies in the second generation of lines 50 and 63 was grown, and 61 new lines were started. These were selfed for three generations; selecting plants that were erect each time. The most promising of the new number 50 lines were crossed with the most promising of the number 63 lines, and compared with the original 63 × 50 combination. Out of 13 crosses grown in 1932, five were selected for further testing in 1933. After two years of testing, none of the new combinations were appreciably

FIGURE 104. In size of ear this Evergreen single cross, called Green Cross C63.50, is outstanding.

better than the original cross. They differed slightly in stalk growth, ear shape and time of maturity, but all had a tendency to go down and none were sufficiently better to offer much hope of improvement by reselecting a self-fertilized line from the second generation. In a case of this kind Richey's (1927) method of convergent improvement offers more promise.

The results obtained in this selection experiment emphasize the importance of subjecting the inbred lines to as many adverse conditions as possible in the hope of eliminating susceptibility. It might have been better to have used ears showing the heaviest infection on the germinating seeds in the beginning. More lines should have been started, even if it were necessary to grow fewer plants in each line and to make fewer pollinations. The hybrids should also have been tested in a wide range of seasonal and soil conditions and with as severe disease infection as possible.

It is becoming more and more apparent that these first generation hybrids of inbred strains, on account of their germinal uniformity, are lacking in adaptability to different localities and varying conditions. The very fact that they do especially well in some places and under certain seasonal and cultural conditions is an indication that they may be equally poor under other circumstances.

Whipple Yellow Sweet Corn

Ten years ago this native sweet corn was first being used extensively for market garden purposes in Connecticut. It had originated several years before as the result of natural crossing between an unnamed, large-eared, early, white, sweet corn and Golden Bantam, followed by selection in the hands of Mr. Silas S. Whipple of Norwich, Connecticut. This variety produces a large ear in a short time and is still the leading market garden corn.

In 1924 a number of naturally pollinated ears were selected and planted in an ear-row trial. Individual plants were chosen for self-fertilization in each row. In addition, two lots of bulk seed were planted and individual plants self-fertilized. Altogether 106 lines of this early yellow sweet corn were started. Two plants were selfed in each line each year and one of these was used for propagation.

After three generations of self-pollination, 32 lines had been eliminated. Of the 74 remaining, 23 were noted as promising either on the basis of stalk growth in the field or after a comparison of the mature ears. Six of these were selected as pollinators and crossed with all other lines. They were chosen largely for their ear characters with the expectation that any one of them could be used as a seed parent. It was assumed that any strain that would combine well with one of them could be used for a pollen parent if it were not satisfactory as a seed parent.

Out of the 206 first generation Whipple crosses grown in 1929, nine were selected as the most promising. The whole series, after discarding some of the poorest, were again planted in 1930 and from these, four combinations were chosen. Only one of these was included in the previously selected list.

On the basis of their behavior when crossed with the six pollinators, a number of inbreds were selected as promising and nearly all possible combinations were made among these and tested from 1931 to 1934. Each year from three to six of the most outstanding combinations were noted.

There was considerable variation in weather conditions from year to year. Also in 1932 and 1933 bacterial wilt was a serious disease and many of the best combinations were found to be quite susceptible. For these reasons no one combination is outstandingly good throughout the period of testing. Comparing all the selected crosses, we find that two inbreds, numbers 6 and 7, were represented in all six years. Two others, numbers 2 and 12, were represented by desirable crosses in four years; and five others, 5, 9, 11, 24, and 89, were used in high yielding crosses in at least two years.

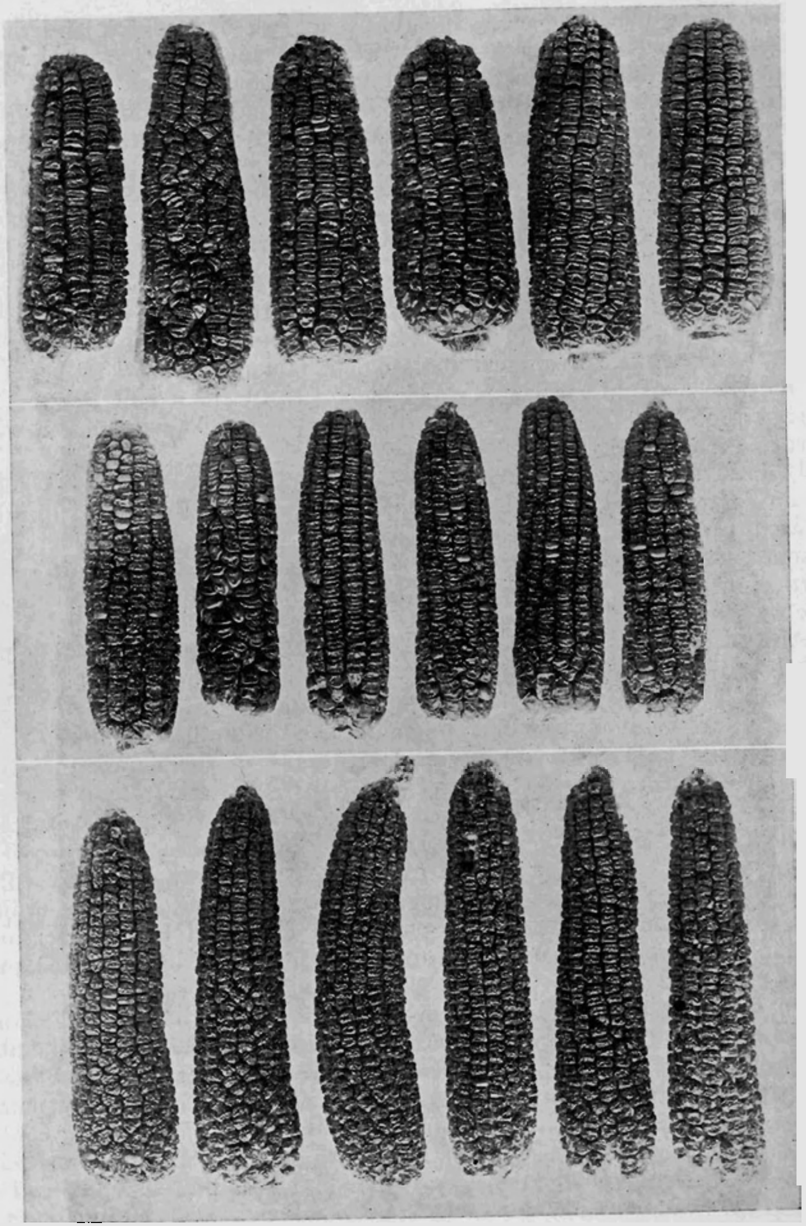

FIGURE 105. Three Whipple Yellow inbreds, numbered from top to bottom, 2, 7, 12.

Taking these nine inbreds and comparing them with the list of inbreds noted as promising after three generations of selfing, but before any crosses had been grown, we find that all the selections except one are included. In other words, if we had discarded all of the inbred lines except the 23 that were noted as desirable, we would have saved the testing of many combinations that later proved to be inferior. However, as this has not been the case in tests with other material, it cannot be relied upon as an effective method of procedure.

The combinations finally selected as the most desirable were 6.2 and 7.2. The first is more resistant to bacterial wilt and somewhat earlier in maturing. The latter usually produces a larger number of marketable ears. Both have been tested for only two years and may yet be found less desirable than other combinations in certain seasons. But all three inbreds have shown up well in some combinations in all six years and therefore should be reasonably dependable.

The influence of one inbred parent on the number and weight of ears per plant and on the amount of tillering is shown in Table 5. All crosses having one inbred in common, whether used as the seed parent or pollen parent, are grouped together. The number of crosses in each group varies considerably but in nearly every case there are from 25 to 40. The average weight and number of marketable ears are calculated for each lot. Inbred number 39 is outstanding in the average weight of mature ears. Number 5 is the highest in number of ears. The differences between the high and low averages in both weight and number of ears are significant and show clearly that inbred strains have the ability to influence the development of particular characters in a series of crosses with other strains.

TABLE 5. THE EFFECT OF ONE INBRED PARENT ON THE WEIGHT, THE NUMBER OF MARKETABLE EARS AND THE NUMBER OF TILLERS PER PLANT, IN A SERIES OF FIRST GENERATION CROSSES OF INBRED STRAINS OF WHIPPLE YELLOW SWEET CORN.

Inbred Parent	Weight of Ears per Plant	Number of Ears per Plant	Number of Tillers per Plant
39	.35 ± .004	1.13 ± .016	1.39 ± .044
82	.33 ± .004	1.14 ± .024	1.53 ± .040
7	.33 ± .004	1.19 ± .024	.84 ± .036
12	.32 ± .004	1.11 ± .020	1.10 ± .048
5	.31 ± .008	1.23 ± .032	1.49 ± .040
2	.31 ± .008	1.00 ± .016	1.07 ± .132
55	.29 ± .008	1.05 ± .024	.95 ± .044

Considerable difference also exists in the number of tillers per plant. Inbreds number 5 and 82 put nearly twice as many on their crosses as do numbers 7 and 55. Tillers are usually beneficial, especially for early sweet corn. (Jones, Singleton and Curtis, 1935). By means of tillers, corn is able to produce a large amount of foliage in a short time. Late maturing corn has enough leaf area on the main stalk to nourish a good yield of grain without the help of side branches. But nearly all early varieties of both field and sweet corn are dependent upon tillers for an adequate expanse of foliage. It might be useful to select for increased tillering, provided the tillers themselves do not produce ears. Nearly all of the best combinations of these Whipple inbreds tiller freely.

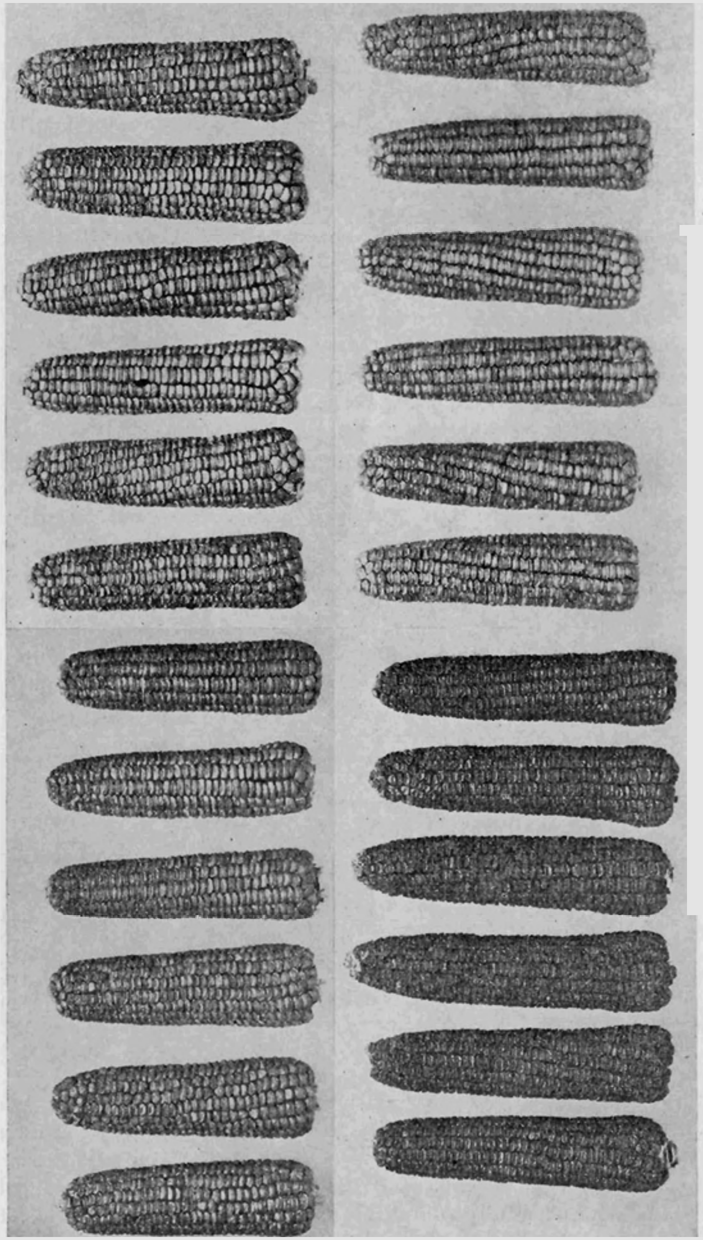

FIGURE 106. Four first-generation hybrids of Whipple inbreds. From left to right, above, C2.7 C3.7; below, C2.12, C6.7.

In Table 6, a series of inbreds is compared with their first generation hybrid offspring in height of plant, number of tillers and percentage of smut (*Ustilago Zeae*) infection. In this comparison, from one to fourteen

TABLE 6. THE RELATION BETWEEN ONE INBRED PARENT AND THE AVERAGE OF ALL OF ITS F_1 OFFSPRING IN HEIGHT OF PLANT, NUMBER OF TILLERS AND PERCENTAGE OF SMUT INFECTION IN WHIPPLE YELLOW SWEET CORN.

Inbred Parent	Height of Plant Inches		Average Number of Tillers per Plant		Percent of Plants with Smut	
	Inbred	F_1	Inbred	F_1	Inbred	F_1
2	49	75	1.7	1.7	21	4
3	39	64	.1	1.5	65	12
4	52	68	.8	1.9	7	7
7	55	75	1.3	1.6	7	9
11	44	71	.5	1.9	20	7
12	57	78	.6	1.9	5	9
19	46	68	.6	2.2	13	10
24	49	74	.02	1.1	0	2
39	47	72	2.0	2.3	23	6
89	56	72	.9	1.5	22	6
Correlation Coëf.	$+.74 \pm .10$		$+.29 \pm .20$		$+.30 \pm .19$	

crosses are used in each series having the inbred stated as one parent. Each inbred influences strongly all three characters. The tallest inbred, the one with the largest number of tillers, and the one with the least smut infection produce crosses with the same outstanding traits. The parent-offspring correlations are positive in all three characters and clearly significant in the case of height. In tillering and smut infection, certain inbreds that do not show the characters themselves have the ability to impart them to their offspring.

Ear characters are particularly important in sweet corn. A series of Whipple crosses grown in 1930 is grouped according to the inbred parents and averaged for the number of rows of grain on the ear, length of ear, breadth of ear, (average of butt and tip diameter), taper (butt diameter divided by tip diameter), kernel length and breadth. In all respects the crosses show small but noticeable differences as shown in Table 7.

TABLE 7. THE EFFECT OF ONE INBRED PARENT ON EAR AND KERNEL CHARACTERS IN A SERIES OF FIRST GENERATION CROSSES OF WHIPPLE YELLOW SWEET CORN.

EAR AND KERNEL CHARACTERS OF F_1 HYBRIDS

Inbred Parent	Ear Row Number	Ear Length mm.	Ear Breadth mm.	Ear Taper Index	Kernel Length mm.	Kernel Breadth mm.
2	14.0	172	42	1.2	10.1	8.3
3	15.8	148	45	1.3	10.6	8.9
5	12.5	160	39	1.3	10.3	9.0
7	13.6	169	40	1.3	10.0	8.4
10	16.7	158	50	1.2	10.6	8.3
11	15.8	153	46	1.3	10.3	8.6
12	13.9	174	41	1.3	9.6	8.2
39	15.4	159	46	1.3	10.3	8.5
55	14.5	155	45	1.2	10.3	8.6
82	14.3	159	44	1.3	10.5	8.8

FIGURE 107. Representative plants of Whipple inbreds, (left) number 6 and (right) number 2, with an ear of Whipcross C6.2.

In 1931 a number of crosses were badly blown down. Notes were made at the end of the season as to whether the plants were generally erect or leaning. The majority in each lot were uniform in their performance, that is, all of one combination were either erect, bent at an angle, or in some cases flat on the ground. When most of the plants were bent at an angle of more than 60°, they were classified as leaning. Table 8 shows the behavior of leaning and erect plants with respect to number of tillers, height of plants, number of marketable ears and weight of ears. In every instance the upright crosses were slightly superior, but not significantly so, except in the case of tillering, to the combinations that were not erect at the end of the growing season. The upright plants were taller, had more ears, a heavier total weight of mature ears and a significantly higher number of tillers per plant.

TABLE 8. THE RELATION OF ERECTNESS OF PLANT TO THE NUMBER OF TILLERS, HEIGHT OF PLANT, NUMBER OF EARS AND WEIGHT OF EARS PRODUCED IN A SERIES OF FIRST GENERATION CROSSES OF WHIPPLE YELLOW SWEET CORN.

Classification of Crosses	No. of Tillers per Plant	Height of Plant Inches	No. of Ears per Plot	Weight of Ears per Plot in Pounds
Upright	2.0 ± .05	74 ± .94	20.3 ± .56	7.1 ± .14
Leaning	1.8 ± .04	73 ± 1.65	18.7 ± .32	6.8 ± .11

METHOD OF TESTING INBREDS

The combination of two inbred strains, grown only the first year after crossing, is generally called a single cross. When such a cross is again cross-pollinated with a third inbred strain, it is referred to as a three-way cross, and the hybrid union of two single crosses is named a double cross. Instead of using first generation hybrids to produce a double cross, the second or later generations following a cross, have been used and such combinations have been described as advanced generation crosses.

When a number of inbred strains are combined into a true-breeding variety by continued inter-pollination, the result is a synthetic variety, or a multiple strain. And when two or more of these multiple strains are brought together to produce a first generation hybrid, the offspring is spoken of as a multiple cross.

The cross-pollination of a variety by a single inbred is called a variety-inbred, top cross, or line-variety cross. In some cases strains of corn derived from a single open-pollinated ear have been used without further inbreeding. These strains are called, for convenience, single ear, or perhaps better, single plant strains. They will probably be used in crossing, either among themselves or with inbreds. No good name seems to suggest itself for these crosses, and for the present they may be called simply single plant crosses, or single plant top crosses.

By the term inbred, it is generally understood that the plants have been self-pollinated or sib-pollinated for a sufficient number of generations to be uniform and fixed in their gross morphological characters.

Single Crosses

The greater uniformity of single crosses in comparison with the original varieties is well known. Statistical evidence for this is given in Station Bulletin 207. Arnold and Jenkins (1932) have compared the variability of single crosses with varieties, top crosses and double crosses in several measureable plant and ear characters. The mean coefficient of variability for all characters is 9.2 for single crosses, 11.2 for double crosses, 11.3 for top crosses and 13.4 for naturally pollinated varieties. The genetic diversity of different crosses of inbred strains from the same original source is shown in Table 9.

FIGURE 108. Mature plants of Whipcross C3.7 topped and husks stripped down.

Twenty inbreds of Canada Yellow Flint, selfed four years or more, were crossed in many different combinations and the hybrids grown with adjoining check rows of the original variety. Individual plot yields are placed in a frequency distribution in the accompanying table. It will be seen that the spread in yield is greater for the crosses and the variability of yield is also larger. This merely emphasizes the well known fact that some combinations are better producers than the original variety while others are poorer.

TABLE 9. THE DISTRIBUTION OF YIELD IN BUSHELS PER ACRE OF A SERIES OF FIRST GENERATION HYBRIDS COMPARED TO THE VARIETY FROM WHICH THE INBREDS WERE DERIVED.

Yield Classes	25	35	45	55	65	75	85	Total	Average	Coefficient of variability
Variety		18	63	48	12	7		148	50.1 ± .8	19.4 ± .8
Single Crosses	2	4	21	32	12	7	2	80	54.6 ± .9	21.0 ± 1.2

The similarity of the plants within a single cross in all measurable characters is also an indication of their uniform reaction to soil and seasonal conditions. Some combinations do well one year and poorly another. For the same reason, crosses that are productive in certain soils in a given latitude and under special weather conditions may be decidedly unproductive when one or more of these environmental factors are changed. Some combinations have the ability to do well in a wide range of seasons, soils and latitudes. A notable example of this is Golden Cross Bantam sweet corn. Some of the Illinois and Iowa hybrid field corns have done well in New Jersey and Connecticut. In certain years Connecticut field corn hybrids have been productive in Ohio, but they have never shown any promise in the central corn-growing states. Sweet corn single crosses, such as Redgreen and Whipcross, have yielded well in western Nevada and Idaho, in western Oregon and in western and central Washington where the temperatures during the growing season are more nearly like those of southern New England.

The adaptation of corn to climate has been discussed by Jones and Huntington, (1935). The authors propose for consideration the general rule that corn may be moved from a less favorable to a more favorable corn-growing region without loss of productiveness, and with a possible gain, provided the climate permits proper maturity. The average yields over a long period of years give some measure of the conditions necessary for the culture of corn. Very few sections are more favorable than others in all respects. Those parts of the country that are not too hot and dry during the period of maximum growth are usually too cool and wet at the beginning and end of the growing season.

Genetically diverse plants respond differently to the various factors of soil and climate. For that reason single crosses are expected to be less adaptable than the varieties from which they are derived or from other types of crosses that permit greater genetic diversity. Strains that are not reduced in size or yield to complete homozygosity produce crosses that are more adaptable. A reasonable degree of fixity of type in the characters that determine yield, and at the same time some variation in other characters are desirable from the standpoint of adaptability. Davis (1934) made crosses between inbreds that were selfed one, two, and three generations. The successive crosses gave approximately equal yields. There is the danger that inbreds which are not uniform and fixed in their type will vary from year to year and may lose their good qualities. With the object of yield alone in view, however, there seems to be little advantage in long continued inbreeding.

Reciprocal Crosses

Those who have tested many crosses know that reciprocal crosses of uniform inbred strains are closely similar in structural detail and in the time of flowering and maturing. Ashby (1932) found a difference in reciprocal crosses in the total amount of growth up to 40 days after planting. The inbreds differed in embryo size and the dry weight of the reciprocal crosses varied according to the initial weight of the embryo from which the plants started. When the plants are grown to full maturity these early variations usually disappear. St. John (1934) demonstrated that there is a difference in reciprocal top crosses.

Two inbred strains of Leaming corn, numbers 237 and 243, each self-fertilized for more than 30 generations, differ significantly in total yield of mature grain. Over a period of years, 243 is about twice as productive as 237. The plants and seeds are larger and the ears are better filled. The embryos are more nearly alike but here also 243 is distinctly larger. No determinations of embryo weights have been made.

FIGURE 109. Whipcross C2.12.

Reciprocal crosses of these inbreds were made and grown in nine alternating rows. The average yields in bushels per acre were as follows: $243 \times 237 = 69.0 \pm .11$; and $237 \times 243 = 67.4 \pm 1.62$. The difference in yield is less than the probable error of the difference. The yield of grain sums up the plant's ability to grow better than any other one measureable character.

Similarly two inbred Whipple sweet corn strains, numbers 2 and 7, are quite different in plant growth and seed size. Reciprocal crosses compare as follows:

	Days to Average Tassel	Ear Length Inches	Ear Row Number	Av. Weight Mktbl. Ears	Yield Lbs. per Plot	Thousand ears per acre Not Mktble.	Mktble.
Whipcross C2.7	56	7.5	14–16	.34	6.7	3	10
Whipcross C7.2	57	7.5	12–16	.31	7.2	3	12

These figures are based on single plots of 25 plants each, grown under similar conditions. They show that reciprocal crosses of inbred strains are sufficiently alike that they may be considered the same for practical purposes.

Although these crosses give similar results, usually the hybrid is made more conveniently one way than the other. Inbred strains differ in productiveness, in size and quality of seed and in time of flowering. Naturally the inbred that produces the larger yield and the better quality of seed is used for the seed parent, whenever possible. If practicable, the seed and pollen parents should silk and tassel at the same time, when planted on the same day. This is not always feasible but it is highly desirable.

Double Crosses

Double crosses and three-way crosses have considerable advantage from the seed production standpoint. With double crosses, both the seed parent and pollen parent are vigorous and productive. Only one row of the pollen parent need be planted to four or more rows of the seed parent. With three-way crosses, the seed parent is productive provided the inbred pollen parent supplies sufficient pollen. Combinations of this kind are genetically more variable than single crosses and for that reason somewhat more adaptable and less susceptible to injury by adverse growing conditions at critical periods. The maintenance of three or four inbred lines is a serious problem. If the single crosses are in commercial production, then the production of other types of crosses with them is a simple matter.

Advanced Generation Crosses

Production of seed would be simplified if the second or later generations of a single cross could be used. Theoretically a random sample of F_2 plants has the same proportion and composition of gametes as F_1 plants, provided there is no selective elimination. Kiesselbach (1930) reported the results of advanced generation crosses to be approximately the same as crosses of first generation hybrids. The Burr-Leaming hybrid, described in the Storrs Connecticut Station Extension Bulletin 108, has been produced as a double cross of first and second generation hybrids. The yields for two years compare as follows:

	1923	1924	Average
$(21 \times 20)F_1 \times (243 \times 237)F_1$	49	49	49
$(21 \times 20)F_2 \times (243 \times 237)F_2$	40	55	48

The difference in average yield is not significant. In appearance, time of maturity and quality of grain, the two lots appeared to be the same. The seed produced on F_2 plants was more variable and less attractive in appearance.

Multiple Crosses

Instead of using first or later generation crosses for the production of hybrid seed, it is possible to combine a number of inbreds to form a new synthetic variety, and to cross two of these. This has been done in the case of the Burr Leaming hybrid. Eight inbreds out of Burr White were combined in pairs by hand pollination. The F_1 seed was mixed and planted in an isolated field and allowed to interpollinate. The same thing was done with eight Leaming inbreds. Both lots have been continued by natural pollination in isolated fields for several years with selection for certain ear characters in each lot.

FIGURE 110. Increase field of Whipple inbred C2.

In 1933 the Multiple Burr Leaming, produced by crossing these two composites, was compared with the original double cross made both ways. The results in bushels of grain per acre were as follows:

Multiple Burr Leaming	61 ± 1.5
Double Crossed Burr Leaming	64 ± 1.9
Reciprocal Double Cross	67 ± 1.2

Although the original double cross made both ways yielded more than the cross of the composite, the differences are not significant.

It might be expected that in later generations reduction in yield would be less for multiple than for double crosses. There is always a tendency for the corn grower to save his own seed from high yielding hybrids. In many cases this would be desirable provided the sacrifice in yield were not too great.

A comparison was made between the first and second generations of the Canada Leaming hybrid. This is a first generation cross of two composites similar to Burr Leaming. One is a Canada Flint type, the other the same Leaming as used in Burr Leaming. The first generation yielded 59.5 ± .05, and the second 46.0 ± .92, a decrease of 22 per cent.

Richey (1934) compared the yields of 10 first and second generation double crosses. The reductions ranged from 5 to 24 per cent. In single crosses this percentage is usually higher. The senior writer (1924) found a reduction of 32 per cent between the first and the second generations of two long-inbred Leaming strains. The crosses were grown over a period of six years. With every type of cross using inbred strains in both parents, either singly or in combination with others, there is an appreciable loss of yielding power after the first generation. This makes it advisable to use only freshly crossed seed each year.

Variety-inbred Crosses

Lindstrom (1931) called attention to the practical value of variety by inbred crosses which he calls top crosses, a term borrowed from animal breeding. In 1917 a number of crosses of local Connecticut varieties of flint and dent corn were made with an inbred Leaming strain No. 243. These were grown with a number of single crosses, about 60 in all. Ten of them yielded more than 100 bushels per acre. Eight of the ten were variety-inbred crosses. The combination of Canada Yellow Flint variety by Leaming inbred 243 gave the highest yield. The grain was well matured and uniform in its intermediate flint-dent type. Twenty-two variety-inbred crosses averaged 95 ± 1.4. Under the same conditions 49 single crosses yielded 91 ± 1.3 (Jones 1922). This method of producing seed is now widely used with both field and sweet corn and gives excellent results, especially when distinctly different types of maize are brought together.

The Crosby variety of sweet corn crossed by an Evergreen inbred, Connecticut 77, gives a productive and fast growing corn of good canning quality. Spancross C2*, Marcross C6, Whipcross P39 and Bancross P39, are other variety-inbred crosses using Spanish Gold, Golden Early Market, Whipple Yellow, and Golden Bantam, that have outstanding value either in early maturing, large size of ears, productiveness or quality. From the standpoint of ease of producing seed and the adaptability of this seed as compared to that of single crosses, there is much to be said in favor of variety-inbred crosses.

Single Plant Crosses

In sweet corn for canning, single plant lines have been used for field production where the uniformity of kernel type is more important than gross yield. These single plant lines are the descendants by natural pollination of an individual plant, selected on the basis of the progeny per-

*According to this system of naming hybrids, a syllable of the varietal name is combined with the word "cross". The letters and figures following indicate the source of the inbred (C=Connecticut, P=Purdue) and its pedigree number. One figure shows that it is a variety-inbred cross, two figures a single cross, etc.

formance test. Davis (1934) has shown that two generation selfed lines, crossed with open-pollinated varieties, yield as well as those crossed with lines that are inbred longer, although they are undoubtedly more variable and more subject to change. This suggests that single plant lines can be used for crossing with homozygous inbreds to give high yielding hybrids with more uniformity and fixity of type than a variety by inbred combination. These single plant lines may be open-pollinated, selfed, or offed for one or two generations, depending upon the vigor and yielding ability required in the seed parent, and the uniformity and constancy desired in

FIGURE 111. Uniformity in plant and ear characters and in time of maturity is characteristic of single crosses.

the hybrid. A simple way to find a good combination of this kind is to self individual plants, save part of the pollen and apply this to an inbred selected as a tentative pollen parent. A series of such crosses would indicate the most desirable combinations and these could be tested more thoroughly by using the mixed progeny of the once inbred line as the seed parent. This method is now being tried with sweet corn.

Crosses of two, open-pollinated, single plant lines may have value and should be tried. The earlier work with ear-row selections, in which part of the rows were detasseled and crossed with the other lines, indicated

that individual plants had outstanding productiveness. If there were any way of maintaining this yielding ability from year to year without the expense and delay of fixing it by inbreeding, it would be a real saving.

METHOD OF PRODUCING INBRED STRAINS

Up to the present time inbred strains have been produced chiefly by self-fertilization. It is theoretically possible (Haldane, 1931) to obtain a more thorough recombination of desirable genetic factors by other forms of inbreeding where homozygosity is more slowly approached. Brother and sister mating, or sib-crossing as applied to plants, offers a more convenient method of inbreeding than self-fertilization, from the hand-pollination standpoint. It may also have a distinct advantage in permitting freer recombination of genetic factors.

This method is being applied to early sweet corn as described in Bulletin 361. Individual plants were self-fertilized the first year and from each of the ears harvested six seeds were taken and wrapped in tissue paper. Each lot was planted singly in hills, and thinned to three stalks in each. Two plants in each hill were sib-pollinated, using pollen from each other or from the third plant, whichever tasseled at the right time. At harvest the two hand-pollinated ears were examined and one was discarded in the field. In this way each ear represented an inbred line. No labeling and staking were needed at any time. This method has produced some early maturing inbred lines of sweet corn with remarkable yielding ability when crossed.

If bulk seed is used, the first generation plants should be selfed, since sib-mating the first time would be about the same as natural intercrossing. If individual open-pollinated ears are used at the start, they may be sib-pollinated from the beginning. After three or more generations of such off-pollination, the surviving lines may be grown in rows having a sufficient number of plants to give an estimate of their uniformity and type, and provide ample plants for crossing.

Previous studies emphasize the importance of having the largest possible number of lines to select from, after some degree of uniformity and constancy has been obtained. Also there is little value in selecting during the inbreeding process unless for particular characters which have major importance. Taking the most vigorous and productive plants for progenitors in each generation usually delays the reduction to uniformity and constancy. By growing only a few plants each year, little selection is possible. Therefore the resulting inbred strains represent more nearly a random sample of the genetic recombinations possible and this is desired. The importance of selection comes after some degree of uniformity and fixity of type has been obtained from among the available inbred lines. If the desired qualities are not all recombined, then the method of convergent improvement can be used to good advantage.

THE EFFECT OF A DELETERIOUS FACTOR ON YIELD

The following experiment was devised to determine the effect of a noticeably harmful recessive gene, when used in crosses. A Leaming line in the second generation was noted as segregating for golden plants. Several of these were self-fertilized and the progeny grown the following year. In each generation a progeny segregating for golden plants was selected for continuing the line, always through one normal green plant carrying the recessive golden gene. In the seventh generation, both green and golden plants were self-fertilized, and the following year, homozygous golden and green progenies were crossed with a third uniform inbred strain of the same variety.

Having been self-pollinated for seven generations, it was assumed that the green and golden plants would have practically the same composition except for this one chlorophyll determiner. In appearance the two types were closely alike except that the golden plants were smaller and less vigorous due to poor nutrition.

The two crosses were compared in yield by growing nine alternating plots, five with seed from the cross of golden × green, and four with seed from the cross of homozygous green × green. Both lots of crossed plants were green, one Gg in composition, the other GG. They were identical in appearance. The average yields of grain were 56 ± 1.2 bushels from the cross with the golden parent and 59 ± 1.2 from the cross with the green parent. The difference in yield of 3 ± 1.7 in favor of the homozygous green plants is not significant.

Mangelsdorf found homozygous dominant plants slightly taller than heterozygous plants in a progeny segregating for a lethal defective seed character. In this case no fair comparison in yield of grain could be made on account of the lethal factor reducing the number of normal seeds on the heterozygous plants.

Even if a significant increase in yield were obtained, one could not be sure that the difference was due to the specific gene being studied. Adjacent loci could also be in the heterozygous condition. From these results it may be concluded that some deleterious recessive genes may be present in a heterozygous condition without any serious effect upon the ability of the hybrid to grow and to produce. Furthermore, it indicates that the removal of abnormal genes of this type is not the most important function of inbreeding.

SEED PRODUCTION

Various details essential to the production of crossed corn seed were discussed in Bulletin 361 and need not be reviewed here. The statement often made, that seed corn should not be planted more than 100 miles from its place of production, has been shown to be a too sweeping generalization and not in line with the facts (Jones and Huntington, 1935). There seems to be a distinct advantage in producing varietal seed in a climatic region less favorable to growth than that in which the crop is to be planted. However this may be, it should be realized that the production of naturally pollinated varietal seed is distinctly different from

the production of crossed corn seed from the standpoint of adaptation and dispersal.

Seed of double crossed Burr-Leaming has been produced in Virginia, Maryland, Ohio and Spain and grown in Connecticut in comparison with local seed. The single crosses used in producing this combination were all raised in Connecticut; the seed of each parental single cross was mixed in one lot and some was sent to each of the above mentioned places. The yields of grain are given in Table 10. In most cases the yields for each year represent the average of five plots. The five-year average (1925 to 1930) gives 61 ± 2.0 bushels per acre for Connecticut-, and 67 ± 2.8 for Virginia-grown seed. The difference of 6 ± 3.4 bushels indicates that there is no distinction in results wherever seed is produced for use in Connecticut. The time of maturity and quality of grain are apparently similar.

TABLE 10. THE YIELD OF DOUBLE CROSSED BURR-LEAMING IN BUSHELS PER ACRE, WHEN GROWN IN CONNECTICUT FROM SEED PRODUCED IN VARIOUS PLACES.

Year grown	Place where seed was produced				
	Connecticut	Virginia	Maryland	Ohio	Spain
1924	54*				56
1925	63	81		85	
1926	64	70	67	70	
1927	59	57			
1928	68	68			
1930	51	59			
Average	61	67			

*Not included in average.

Likewise, seed of Redgreen sweet corn, a single cross, has been produced in Indiana and Connecticut and the first generation crossed plants grown in both places. The average yield in pounds per plot for the two lots of seed grown in Connecticut three years was 9.4 ± .01 for native, and 10.3 ± .07 for Indiana seed, a significant difference of .9 ± .07 in favor of the Indiana-grown seed. The results are given in Table 11. In all years and in both places the Indiana-grown seed yielded more and the plants grew taller than those from Connecticut-grown seed, although this hybrid originated in Connecticut from types that had long been grown there. It is a type that suffers severely from low humidity and high temperatures and is usually unproductive in the Central States.

TABLE 11. THE PERFORMANCE OF REDGREEN SWEET CORN WHEN GROWN IN CONNECTICUT AND IN INDIANA FROM SEED PRODUCED IN BOTH REGIONS.

Place where seed was produced	Yield in pounds of dry ears per plot and height of plant in inches					
	1925 Yield	1926 Yield	1927 Yield		1927 Height	
	Conn.	Conn.	Conn.	Ind.	Conn.	Ind.
Connecticut	9.9	9.0	9.3	8.3	88	75
Indiana	10.4	9.7	10.8	10.7	89	83

The change from Connecticut to Indiana is not extreme, although Indiana produces 10 bushels less grain corn per acre according to the 20-year average. To have the seed produced under as widely different climatic conditions as possible, inbred seed from the same self-pollinated ears was planted in Texas and in Connecticut and the cross-pollination made by hand. In Texas the two inbreds grew less than two feet high and produced only a few seeds. This was largely the result of moving corn to a shorter growing day. In Connecticut both inbreds normally grow from five to six feet or more in height and produce well filled ears. The crossed seed from both places was grown in adjacent rows in Connecticut the following year. There was only enough seed of the Texas crop to plant one row. The weight of dry ears from the two plots was 4.8 pounds from the Texas-grown seed, and 3.7 pounds from the Connecticut-grown seed. The plants tasseled and silked on the same days and were identical in appearance. The average height of plants from Texas seed was $77 \pm .6$ and for the Connecticut seed, $77 \pm .9$ inches.

Another cross of two long inbred dent strains, 14–4 and 112–1, was also produced in Texas and in this State and both lots were grown here. There was only enough seed from Texas to grow one row in Connecticut. The ears were so badly eaten by birds that no yields could be taken. In height of plant, the averages were 80 ± 1.7 for Texas- and $84 \pm .7$ for Connecticut-grown seed. Here the difference of 4 ± 1.8 is not significant.

All of these results indicate clearly that either there is no difference in the seed of hybrids grown away from the place of origin or, if there is any significant difference, it is in favor of seed grown in the new locality. In all of these cases the new region is less favorable for the production of corn, as shown by the 20-year average production of grain corn per acre. Tests should be made to see whether hybrids originating in other districts yield less in their native home when seed is produced in Connecticut or other favorable corn growing regions.

There are many economic reasons for producing seed in those regions where a good crop can be obtained every year. High yields reduce the cost of production. Well developed and matured seeds insure strong germination. When seeds of naturally pollinated varieties are raised in such regions, they are likely to lose productive capacity when planted under less favorable conditions. If this is also true, even in a less degree, for crossed corn, it should be known and given careful consideration. Crosses of inbred strains are uniform and fixed in their type and do not become adapted to the region in which the seed is grown as quickly as do open-pollinated varieties. The reasons for this are obvious.

The evidence at hand indicates that it is possible to produce crossed seed wherever it can be grown to the best advantage, taking into consideration cost and quality of the matured seed. This is especially true of single crosses and probably also of other types of crosses. To insure proper maturity, quality, and other essential details, the foundation inbred stock seed should be grown where it is originally produced. When this is increased, the crosses may be made in a region most favorable to seed production. Seed that is one or a few generations removed from this foundation seed will probably be all right in most cases. Continued production in a different region however, will in time tend to change the genetic constitution of the inbred stock by natural selection, and the rapidity of this change will depend upon the amount of germinal variation within it.

SUMMARY

Briefly stated, the results of Part I of this series of experiments, as summarized in Station Bulletin 266, were as follows: Selection during the inbreeding process of such specific characters as plant height, height of the ear from the ground, number of tillers, and resistance to disease, produced inbred strains that transmitted these characters to the first generation hybrid. However, it was impossible to foretell before crossing, with any high degree of certainty, which inbred strain would give the largest grain yield when crossed. In other words, selection for the dominant growth genes responsible for heterosis was of little or no value. Selection must be based upon the progeny of the inbreds when crossed.

The findings of Part II (this bulletin) corroborate in general the previous conclusions. Several types of corn were used in the demonstration with the following results:

1. In two sets of experiments with both Burwell's Yellow Flint and Leaming Dent, the inbreds were classified, before crossing, as good or poor in one case, and as productive, intermediate and unproductive in another case. In no case were the highest average yields obtained from strains that had been classified as unproductive. The opposite also held true, although once in the dent and twice in the flint, the highest or lowest average yield was obtained from a strain in the intermediate class. In different matings of good and poor inbreds, the good × good produced the largest yield; the good × poor, intermediate; and the poor × poor, the lowest. The differences, however, were not significant.

2. In double crosses combining from none to three good strains, there was a barely significant increase in the crosses having three good strains over those having none. The double cross combining four good strains was not tested.

3. Specific characters in the inbred parents that appeared in the F_1 hybrid were: Short ear, long slender ear, cylindrical ear and tapering ear.

4. In a series of white flint corn inbreds, all crossed by a multiple Leaming variety, selection of the best inbreds was of little avail. By choosing one-third of the best inbreds before crossing, we were able to obtain one-half of the most productive crosses. It is doubtful if any normal lines should be eliminated before crossing.

5. In Evergreen sweet corn the most productive F_1 hybrid had a serious root weakness, contributed largely by the C–63 parent. In an effort to correct this, remnant seed from three progenies in the second generation of lines 50 and 63 were grown, and 61 new lines were started. These were selfed for three generations, always using erect plants. The new 50 lines were then crossed with the new 63 lines and the F_1 hybrids tested. No hybrids were found that were materially better than the original cross. This emphasizes the futility of carrying on many lines after the plants have been selfed for two generations. It probably would have been better to start a great many lines and to carry on only one progeny from each originally selfed plant.

6. In a series of Whipple sweet corn inbreds, 106 lines were started and 74 remained after three generations of self pollination. Of these, 23

were noted as promising on the basis either of stalk growth or of ear characters. With one exception, all of the best F_1 hybrids resulted from crossing these 23 inbreds in various combinations. As the experiment turned out in this one case, the rest of the inbreds could have been profitably discarded. However, these results held for this lot only and cannot be relied upon as an effective method of procedure.

7. In the Whipple series, positive correlations of the inbreds and the F_1 hybrids were found between number and weight of ears, and number of tillers per plant. There was also a positive correlation between number of tillers and yield of marketable ears. Selection of inbreds with many tillers is advisable provided the tillers do not produce ears.

8. Inbreds can be tested by crossing them by other inbreds (single cross), by crossing an F_1 hybrid × an inbred (three way cross), by crossing two F_1 hybrids together (double cross), by crossing later generation hybrids together (advanced generation cross), by crossing an inbred by a variety (top-cross), or by crossing two synthetic varieties together (multiple cross). Doubtless other combinations could be devised. One of the greatest problems confronting the maize breeders today is how to test inbreds most advantageously after good inbreds have been secured. Each of the testing methods is discussed in this bulletin.

9. A larger number of inbred lines can be produced with minimum effort by growing only one hill of each line. This method is described in the bulletin. It has proved advantageous in isolating good inbred lines of Spanish Gold, an extra early sweet corn.

10. First generation hybrids heterozygous for Gg (the golden plant character) were grown in comparison with similar hybrids of GG composition. There was no difference in yield.

11. Crossed seed of the same inbred parents was produced under widely different conditions of latitude and climate. No differences in yield of the F_1 hybrids were obtained when all lots were grown in Connecticut.

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