A Comparison Between Corn and Sugar Beet Breeding Methods

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The exact origin of corn is lost in antiquity but its value as a food was recognized and exploited by many of the primitive people of South and Central America. The sculptures depicting corn plants found in the remains of Mayan, Inca and Aztec villages are evidence of the dominant part corn played in those ancient civilizations.

It is probable that those people exercised some selection with corn because by the time Columbus discovered the New World the natives were cultivating five distinct types. These types were dent, flint, flour, sweet and pop corn; not greatly different from those same types we grow today. Their method of propagation was, in all probability, the saving of good ears each year as a seed supply for the following year. Some of these peoples made a practice of planting seeds of different colors in each hill. Their purpose of doing so is not known, but in effect it may have helped maintain heterozygosity and prevent reduction in vigor through inbreeding.

The variability in corn made it readily adaptable to a wide variety of climatic conditions so that its culture spread from the tropics of Central and South America to the temperate regions of North America. The Pilgrims, upon landing in Massachussetts in 1620 found the Indians there cultivating corn. As settlement moved westward in this country corn was, from the beginning, one of the major agricultural crops. Until the early part of the present century the predominant breeding methods used with corn consisted of selecting ears of a desired type from healthy plants in the field at harvest time and using these as seed for the subsequent crop. This method is called mass selection and is essentially the same as had been used by the Indians for centuries. It is doubtful if it resulted in any particular genetic improvement of the crop beyond adaptation to particular environments and possibly some disease resistance.

In contrast to corn, the origin of the sugar beet, as it exists at present, is known and the steps in its development are quite accurately recorded as reviewed by Coons (4)[2]. Marggraf first produced crystal sugar from *Beta rubra* and *Beta alba* in 1747, but it was his pupil, Achard, who developed the agricultural and processing methods to initiate the beet sugar industry. Achard began his experiments with beets as a source of sugar in 1784 and from the "Runkelruben," a near relative of the mangel-wurtzel, he carried on a selection program which produced the White Silesian beet. His selection methods included the evaluation of purity and sucrose content of the roots in addition to visible characteristics of the beet plants.

In 1856, Vilmorin, of the French seed firm of the same name, while working with sugar beets developed a breeding principle which stands as one of the earliest and still most fundamental principles of the science of plant breeding. He found that the breeding value of an individual was not dependent upon the excellence of that particular individual but upon its

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2 Numbers in parentheses refer to literature cited.

ability to transmit desirable characteristics to its offspring. The demonstration of this principle is commonly called the progeny test and is the basis for all breeding programs on crops which are propagated through seed. By use of this principle together with newer and more rapid methods of selection for sucrose content of the root, Vilmorin developed strains which, in yield and sucrose content, were probably similar to the varieties which are grown at present.

As pointed out before, mass selection had little effect in the genetic improvement of the corn crop. In fact, when selection is very rigid for a particular character, there is often a reduction in the yield of the crop. This is apparently due to the limitation placed on the genetic diversity of the progeny by a close selection for a particular type. Hayes and Alexander (8) showed this in selecting for certain ear types in corn. Winter (28) reported the results of twenty-eight years of selection for oil and protein content of corn. Although no yield data are given, it seems reasonable to assume that a reduction in vigor accompanied the rigid selections for oil and protein because the experiment was modified twice to prevent too close inbreeding. This same situation is found in sugar beets. In selecting for high sucrose content of the beets a reduction in root weight of the progeny is often observed.

In 1899, Hopkins, at Illinois, initiated in his corn breeding program a type of progency test which was called *ear-to-row* selection. This consisted of planting a row of corn from each ear selected the previous year, and continued selection within the better yielding rows. Modifications of this method included detasseling part of the rows to prevent too close inbreeding, and saving remnants from each ear so composites could be made of the higher yielding selections. Some early reports indicated that some progress was made by using this method, but later reports (24) demonstrated that it had been of little value in increasing yields.

This method had two basic weaknesses. The field plot techniques used were not precise enough to correctly evaluate the material and those lines which were inherently high-yielding were a mixture of complex hybrids which could not be duplicated. A method very similar to this and commonly called "family breeding" has been used in sugar beet breeding also, and some results are discussed by Brewbaker and McGreevy (2). Although sound field plot techniques were apparently used, only slight, if any, improvement other than adaptation could be attributed to this method when lines were maintained without controlled pollination.

About 1905 East, at the Connecticut station, and Shull, at Cold Spring Harbor, began studying the effects of inbreeding and cross breeding corn. In 1908 Shull suggested the use of F_1 crosses between inbreds, but this method was never used much because of the high cost of seed due to the low seed yields produced on weak inbreds. In 1909 East suggested the more practical method of hybridization in corn, making crosses between varieties without inbreeding. This method had been suggested earlier by Beal at Michigan in 1880, but had apparently not been used. Varietal hybridization was carried on to a very limited extent from 1909 to about 1920.

Jones (16) in 1918 suggested the possibility of the use of double cross seed for the commercial crop. This eliminated seed cost as a prohibitive element because seed for the commercial crop would be produced on vigorous single cross plants and per acre seed yields would be high. Interest was renewed in inbreeding and subsequent crossing of lines. With an economically sound method of utilizing hybrid vigor available, two problems faced the corn breeder: 1. the production of desirable inbred lines, and 2. the most advantageous use of these lines in hybrid combinations.

As a result of the increased interest and research conducted with corn, an ever increasing fund of information has been contributing to a better understanding of the principles and methods involved in developing better corn hybrids.

Richey and Mayer (22) in 1925 found no difference in yield of single crosses between inbred lines selfed three and five generations. Davis (6) in 1927 first used the inbred-variety or top-cross as a method of determining combining ability. Jenkins and Brunson (14) in 1932 showed a comparison of the top-cross performance with the average performance of the single crosses involving a particular inbred as a method of evaluating combining ability of inbred lines. They showed relatively high correlation between yields of inbred-variety crosses and the average performance of a line in single crosses.

The importance of producing hybrids from unrelated inbreds (genetic diversity) has been pointed out by several (5) (9) (15). In general these experiments have shown that hybrids produced from unrelated inbreds have consistently yielded more than hybrids whose parental inbreds were related. The importance of genetic diversity in sugar beet breeding has been pointed out by Brewbaker, et al (1).

That combining ability is a heritable character in corn has been demonstrated by Johnson and Hayes (15) and Cowan (5). Lines selected from the progenies of single crosses whose component inbred parents were low combiners produced significantly lower yielding single crosses than lines derived from single crosses made from two high combining lines or one high and one low combining line.

Jenkins (12) has developed a method by which the yield of double crosses can be predicted from the performance of single crosses. From four inbred lines, six different single crosses can be made and three different double crosses utilizing all four inbreds. Of four methods tested, Jenkins found the correlation between predicted and actual yields of double cross hybrids to be highest when using the average yield of the four non-parental single crosses as the predicted value.

Based on this increasing supply of information, a more or less generally accepted method of producing corn hybrids evolved. It consisted of selecting and self-pollinating outstanding individuals from an open-pollinated variety. Progeny rows were grown from this selfed seed the following year and the best plants from the more promising rows were selected for further self pollination. This process continued for three to five generations at which time the remaining selected lines were crossed to a tester variety to determine the average or general combining ability of each line. Based on the performance of this top cross seed, the best lines were tested in specific single cross combinations. From the results of the single cross trials, double cross yields were predicted and the most promising combinations were made. These double cross hybrids were then grown in comparison with standard varieties to determine what progress had been made.

As desirable inbred lines became available, planned crosses between two such inbreds became a valuable source for isolating new inbreds. This method of obtaining inbreds from planned crosses is probably the greatest source of inbred lines of corn at the present time.

During the time the corn breeders were making such rapid strides in the development of corn hybrids, sugar beet breeders were faced with the problem of developing a sugar beet variety which would withstand the ravages of certain disease conditions. In most of the sugar-beet-growing areas west of the Rocky Mountains, an insect-borne virus which caused a disease known as beet blight or curlytop threatened the survival of the entire sugar beet industry. Many beet sugar factories were abandoned because of successive crop failures due to this single disease.

In 1934 the first so-called curly-top-resistant variety, U. S. I, developed by the U. S. Department of Agriculture, was made commercially available. By present-day standards, the resistance possessed by this variety was only slight, but it represented the first of a series of improvements which have led to the highly resistant variety, U. S. 22, and its derivatives.

These varieties have made possible the growing of a successful crop of sugar beets in areas which had previouly been abandoned for sugar beet culture, and stand as a tribute to those individuals who took part in their development. These varieties have been produced largely by mass selection and although they will produce a satisfactory crop under severe disease conditions, numerous tests have shown that in the absence of disease their performance is about equal to the European varieties from which they were derived. This is additional evidence that mass selection is of little value in increasing the inherent yielding ability in an adapted variety.

In many areas east of the Rocky Mountains a leaf spot disease caused by the fungus, *Cercospora beticola,* caused considerable damage, particularly in reducing the sucrose content of the beets in certain years. Mass selection had not been effective in developing any resistance to this organism. The first source of resistent material appeared in fourteen of some two hundred strains of beets which had been selected on the basis of certain morphological characteristics. Those strains showing some resistance were inbred in an attempt to obtain some lines homozygous for resistance. Later, five of the best lines were combined to form the synthetic variety, U. S. 17, which was introduced in 1937. Continued improvement has led to the variety U. S. 215 x 216 which is presently grown on considerable acreage in areas subject to leaf spot epidemics. This variety, however, in a year without serious leaf spot conditions, performed no better, if as well, than a composite of European varieties. This is not surprising even in view of the fact that this variety was produced from somewhat inbred lines. The lines were selected on the basis of disease resistance and probably represented random lines with regard to combining ability. Another reason may be that, if the lines were self-fertile enough to be maintained as inbreds by self pollination, considerable self-pollination in the seed fields may account for some reduction in vigor.

With the major disease problems in sugar beets somewhat alleviated, the attention of plant breeders was turned more to the commercial utilization of hybrid vigor. Some investigators demonstrated experimentally that hybrid vigor was apparent in some crosses between varieties and between inbreds of sugar beets (7) (27). In general, the hybrid vigor expressed has been in the form of increased root weight rather than increased sucrose percentage. The commercial exploitation of this phenomenon, however, encountered difficulty from the start. Most selected individual beets could not produce self-pollinated seed due to an inherent condition of self sterility (17). This precluded the possibility of developing inbred lines from all selected individuals. Some individuals, however, would produce some self-pollinated seed. A few individuals were found to be rather highly self fertile. From these self-fertile beets, inbred lines could be produced but the utilization of the inbreds was difficult.

Unlike the monoecious corn flower in which the male and female portions of the flowers are widely separated and easily emasculated, the sugar beet has a perfect flower in which the male and female portions are adjacent to each other. To insure cross fertilization in self fertile strains of hermaphoditic beets each flower on the plant or branch to be used as the seed parent of the cross must be hand emasculated. While this practice is satisfactory to produce small experimental lots of seed, it is obviously not practical on a commercial scale.

Recently, Owen (18) reported the finding of a type of male sterility in sugar beets which was dependent for its expression upon both cytoplasmic and genetic factors. A male sterile plant produces no viable pollen and, therefore, can function only as a female or seed parent. This discovery has opened a way by which it now seems possible that inbred lines of sugar beets may be developed and utilized to produce superior hybrid varieties. To main completely male sterile lines, however, pollen must be supplied to them from an hermaphroditic line so genetically constituted that, when crossed to a male sterile, all offspring are also male sterile. Such hermaphroditic lines have been called "O" types and the genotypes of these lines are described by Owen. They apparently occur with varying frequency in most open-pollinated populations. Therefore, for each male sterile line maintained, a specific pollen-producing line must be also maintained in order to insure a continued supply of completely male sterile plants each generation. At the present time there is a considerable effort being put forth by sugar beet breeders in the search for genotypes of "O" type beets.

In self fertile material, by self-pollinating the "O" types and at the same time backcrossing them to male sterile strains in each of several generations, two inbreds are developed which approach being genetic equivalents except that one is an hermaphrodite, and, due to the cytoplasm of the other, it is male sterile. In self sterile material, the "O" types and their developed male sterile equivalents will represent a much more heterogeneous population than in the case o£ the self fertile material. Self-sterile type "O" plants will be isolated from paired crosses or clones because they cannot be self pollinated. It seems possible that such male steriles may be of value as a tester for combining ability of inbred lines because of the broader genetic base they would possess, but their value seems doubtful in a long range program for use in commercial hybrids.

Some male-sterile hybrid varieties of sugar beets are now being produced on a limited scale. These hybrids fall into two types: those which are made using male-sterile equivalents of self fertile inbred lines, and those using male-sterile strains of relatively self-sterile material. Hybrids made from self-fertile material utilize complete male sterility or are rogued very carefully in the seed field to prevent pollen shedding from any plants of the seed parent. This procedure is necessary because a small amount of self-pollinated seed could easily nullify the desirability of the seed which was true hybrid. In those hybrids using relatively self sterile material, while complete male sterility would be highly desirable, partially or "semi" male sterile plants which shed some pollen would not be as deleterious as with self fertile inbreds because the resultant seed would be a mixture of hybrid and the female parent. Very little actual self pollination would occur under such circumstances. Such a hybrid would represent the average combining ability of each population in combination with the other. While such hybrid may be an improvement over present open-pollinated varieties, it seems possible that lines of higher than average combining ability could be isolated from each population. It would seem that, in the long range program, hybrids from inbreds offers more promise than hybrids between the more heterogeneous populations of relatively self-sterile material.

Some of the main points in the commercial production of hybrid sugar beets are still to be worked out. It is quite possible that the production of single cross hybrids, as was found with corn, may not be economically feasible. The commercial seed crop would have to be produced on inbreds and the seed yield may be so low that the cost would be too high to be practical. Owen (19) has suggested the use of three-way crosses which might be represented as (A x B) x C. In this case, inbred "A" would have to be a male sterile line. Inbred "B" would have to be of type "O" so the single cross on which the commercial seed crop was to be harvested would be male sterile. Inbred "C" could be any high combining line. Its genotype regarding male sterility would be immaterial because the commercial portion of the sugar beets is the vegetative part of the plant. This appears to be a satisfactory type of cross if the pollen inbred used in the final cross will produce sufficient pollen to provide adequate seed setting. Such a cross would require the maintenance of a minimum of four inbred lines; B, C and both the male sterile and hermaphroditic phases of line "A." In actual practice the two phases of an inbred line will be maintained in the same isolation whether it be by space or bagging. Separation will be maintained in the planting and harvesting of them. A minimum of six lines would be required to produce a double cross hybrid comparable to the corn hybrids used.

The problem of preliminary testing for combining ability is also not completely solved. For those inbred lines on which both the male sterile and male fertile equivalents are being produced, the testing can probably closely parallel the testing of corn. An adapted variety of beets with a broad genetic base to be used as the tester parent can be interplanted between the rows of male sterile lines. All pollen in the field then should come from the tester parent and seed harvested from the various lines in such a plot would be top-crossed seed.

Performance trials conducted with seed harvested from each line should give an adequate test of general combining ability. Although such a test would be made only on the male sterile equivalent phase of each line, the results should be indicative of the combining ability of the male fertile phase also, provided such test was not made in the early back-cross generations. It is obvious that tests made on the male sterile phases early in the back-crossing program would not reflect the combining ability of the hermaphroditic phase which would be the recurrent parent of the backcross. The only exception to this would be the case in which the same male sterile inbred was used to initiate the development of the male sterile equivalents for all hermaphroditic lines to be tested in any given test. In this event, such a test would be similar to a breeding method called "gamete selection" in corn (26) , which is discussed later in this paper.

In the process of developing inbreds, many of the strains will be found to neither be nor segregate for the type "O" genotype and, consequently, their male sterile equivalents cannot be readily developed. Bcause a considerable portion of the genotype of each hybrid will be contributed from inbreds which need not necessarily be type "O," it does not seem to be a sound practice to discard these if they are highly desirable otherwise. The evaluation of general combining ability of these lines will probably present a problem. Top-cross tests as described above would be unsatisfactory because each of these lines would produce pollen and, being self fertile, probably ten percent or less of the seed produced would be crossed seed. Hand emasculation to insure crossing would be so time-consuming as to make it impractical. A male-sterile strain, preferably not an inbred, might be used as a tester, but this method would require bagging or a separate space isolation for each line to be tested. As the number of lines to be tested increased, the problem of providing satisfactory space isolations would become progressively more difficult. Another possibility for evaluating a group of such lines would be to conduct comparative tests on the inbreds themselves, after careful selection for disease resistance and other observable characteristics.

Disease resistance, because of its extreme importance in sugar beet breeding, may make possible a much more rigid selection of lines in sugar beets than is possible with many other crops.

In the continuing attempt to find more efficient methods of developing new corn inbreds, several breeding methods have been suggested. Some of these have been accepted as sound breeding practices and others have been the subject of much controversy. A few of them are mentioned very briefly here because they may have some possibility of use in a sugar beet breeding program with some modifications.

Jenkins (13) presented some data from top-crosses made after successive generations of inbreeding from which he concluded that the combining ability of a line becomes fixed relatively early in the inbreeding program and it maintains that level quite constant through the succeeding generations. This principle has become known as early testing and has received considerable support from Sprague (25) .

As practiced at Iowa, early testing involves the outcrossing to a tester at the same time as the first selfing, selecting only 10-15 percent of the selfs on the basis of the top-cross yield trial, for carrying on in the inbreeding program, and top-crossing again in S_4 for the final evaluation of general combining ability. Early testing has met considerable criticism from several corn breeders. Richey (20) , in a reanalysis of Jenkin's data, points out that the families did change relative positions with regard to combining ability prior to S_4, but that Jenkin's conclusions were based on successful selections in S_4 and the fact that the combining ability of the families remained constant after that. From Sprague's data Richey maintains that only fifteen percent of the material could be discarded on the basis of early testing without discarding desirable parental material. Singleton and Nelson (23) presented data from early testing of sweet corn and concluded that the method is not genetically sound before S_3, and, even if sound, would be of doubtful value on the basis of expense involved. Both early and late testing are still being practiced.

Stadler (26) has suggested a method called gamete selection. It consists of crossing gametes from a selected source with an inbred of known performance, selfing as many of the resulting plants as there are gametes to be tested, and at the same time outcrossing to a suitable tester. For comparison the inbred is also crossed onto the tester. Any increase of (gamete x inbred) x tester over inbred x tester is assumed to be due to the gamete. Therefore, the selfed seed from the high yielding gamete x inbred top crosses should be a good source of further inbreeding and selection. This method assumes early testing to be a valid corn breeding principle. Stadler states the advantages of this method are: 1. increased frequency of exceptional zygotes, 2. gamete x inbred crosses will be at least heterozygous for all desirable agronomic characters possessed by the inbred, and 3. further possibilities of improvement by selection in superior gamete x inbred crosses. Hayes, Rinke and Tsiang (10) have questioned the necessity for the gamete x inbred top crosses to outyield inbred top crosses in order to be desirable parental material, pointing out that recombinations during the segregating generations of selfing from some of the lines giving lower yielding crosses may lead to desirable inbreds. Brewbaker and Wood (3) have reported a modification of this breeding method as adapted to sugar beets.

In 1945, Hull (11) outlined his method of recurrent selection for specific combining ability. This consists of going into an open-pollinated field and selfing 100 plants and at the same time outcrossing each of them onto a suitable inbred as a tester. A yield trial is conducted with the outcrossed seed and, from the results of this, the selfed seed representing the highest ten outcrosses is planted in rows and intercrosses made between rows. Seed from these intercrosses is bulked for the start of the next cycle. Hull maintains that continuing through three such cycles is equivalent to testing twelve thousand plants in the original population. The commercial seed would be obtained by crossing plants from the intercrossed seed of the last cycle with the inbred used as a tester throughout the program. The criticism of this method is that if, during the process or after completion, the inbred tester was found to be susceptible to some new destructive disease, the whole process may have been wasted effort since the whole project is dependent upon the specific combining ability of the intercrossed progeny with a particular inbred tester.

Richey (21) has suggested a method which he calls multiple convergence, which is supposed to combine several small streams of germ plasm into one superior hybrid. This method is accomplished by improving two inbreds by using different non-recurrent parents in a backcross plan, and later crossing the recovered lines. The final cross could be represented as follows: $(A_b \times A_c) \times (X_y \times X_z)$ where A_b represents a recovered line of A using b as the non-recurrent parent and A_c a recovered line of A using c as the non-recurrent parent and so on. Mechanically this will be a double cross, but genetically it will be a single cross except for the characters retained from the non-recurrent parents. Data were presented on only one-half of this cross. The average yield of the recovered lines was greater than the original parent. The average of crosses between recovered lines using different non-recurrent parents was higher, but not significantly so, than the average of crosses between recovered lines using the same non-recurrent parent. This method will depend upon further results before becoming widely used, but it does appear to have possibilities of approaching the value of a single cross and still make seed production economically feasible.

Good sources of inherently self-fertile sugar beets are now available. A working understanding of the development and maintenance of male sterile strains is known. The dangers of crop failures due to diseases are somewhat alleviated by resistant varieties. It would seem that the problems of the sugar beet breeder today, as recognized by the corn breeders of some twenty-five years ago are: 1. the isolation of desirable inbreds, and 2. the utilization of these inbreds to produce superior hybrids.

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