SOME ILLUSTRATIONS OF METHODS IN PLANT BREEDING[1]

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While most important food plants had already been brought under cultivation before "the dawn of recorded history," as emphasized by several writers, there is, at present, almost an unlimited opportunity to improve the varieties of plants available for various agricultural uses and in some cases to greatly modify their characters. The primary purpose in plant breeding is to obtain or produce varieties or hybrids that are efficient in their use of plant nutrients, that give the greatest return of high quality products per acre or unit area in relation to cost and ease of production and that are adapted to the needs of the grower and consumer. It is also of extreme importance to obtain varieties that are able to withstand extreme conditions because of resistance to pathogenic diseases or insect pests, or that excel in drought or cold resistance. Such qualities help materially to stabilize yields by a partial control of seasonal variations in yield.

Muller (14)[2], early leader in studies of induced mutation, discussed the importance of gene knowledge and control with respect to plant improvement, making the following statement which I quote:

> "Organisms are found to be far more plastic in their hereditary basis than has been believed, and we may confidently look forward to a future in which - if synthetic chemistry shall not have displaced agriculture - the surface of the earth will be overlaid with luxuriant crops, at once easy to raise and to gather, resistant to natural enemies and climate, and readily useful in all their parts."

An appreciation is now available to the public, of the many problems involved in breeding improved varieties of economic plants in United States and some of the accomplishments, from summaries in the Yearbooks (17) of the U. S. Department of Agriculture for 1936 and 1937. A brief statement by Henry A. Wallace, Secretary of Agriculture, who is well known for his own studies of breeding with corn and swine, seems of particular interest. This is quoted as follows:

> "The science of the quality of life as it passes from generation to generation is in many respects the greatest and youngest of all the sciences. While the art of plant and animal breeding is an old one, the science of plant and animal genetics dates only to 1900. So far as known, this Yearbook is the first comprehensive effort to survey superior germ-plasm in the leading plants and animals. The Yearbook shows how much we know and how much more we should know but do not as

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[2]Numbers in parenthesis refer to "Literature Cited," p. 16-17.

yet. True, the science of genetics is still young and growing. I trust that the day will come when humanity will take as great an interest in the creation of superior forms of life as it has taken in past years in the perfection of superior forms of machinery. In the long run superior life forms may prove to have a greater profit for mankind than machinery."

Standardization of Breeding Methods

While new technics in plant breeding are being developed from year to year, certain standardized methods have been developed for particular categories of crop plants and for specialized problems. These can be illustrated best, I think, in relation to their application.

There is a close relation between methods of breeding and normal mode of pollination. Four subdivisions are of major importance altho there is no sharp division between classes.

1. Naturally self pollinated (4% or less of cross pollination). Barley, wheat, oats, tobacco, potatoes, flax, rice, peas, beans, soybeans, cowpeas.

2. Often cross pollinated (self pollination $>$ cross poll.) Cotton, sorghums, some strains of sweet clover.

3. Naturally cross pollinated.
   Maize, rye, clovers, sugar beets, cucurbits, most perennial grasses.
   Self sterile plants.

4. Dioecious. Hops, hemp, spinach, asparagus.

With this classification as a background it seems logical to outline some standardized methods of breeding for particular problems in relation to the biology of the plant and the type of improvement sought. Many changes of viewpoint have taken place during the 30 years that I have been actively engaged in studies of genetics and plant breeding. Early in this period it was often stated that plant breeding was largely an art. While recognizing the importance of the art I shall try to emphasize the value of a knowledge of genetics in its application to problems of crop improvement. About 1915, Dr. Raymond Pearl stated that the breeder of the self-pollinated group of plants used Mendel's Laws as a direct and working guide. In so doing the first standardized breeding program came to be designated as "the pedigree method." It consists of making a cross between parent lines that differ in several important characters followed by selection, during the segregating generations, for the combination of characters desired. Many of the characters of selection value will be related to yielding ability. There will be other genetic factors for yielding ability that can be selected by the breeder only through field trials of sufficient numbers, under proper methods of experimental design, so that the higher yielding strains can be selected on the basis of their performance.

Crossing Followed by Selection During Segregating Generations

The breeding program can be summarized as follows:

The pedigree method

1. Selecting the parents with the view of combining their desirable characters

in a single variety.

2. Making the cross.

3. Growing the F_2 to F_5 generation plants individually spaced so that selection is possible.

4. Studying the progeny by growing seed of individual plants in progeny rows.

5. Placing homozygous types in yield trials, replicated.

6. Increasing and distributing new varieties of promise.

The method may be illustrated by some work now under way in the breeding of improved varieties of oats and wheat as carried out in Minnesota. At present, we are trying to combine resistance to three major diseases and desirable agronomic characters in a single variety of oats. As crossing is difficult in oats the method of making a few crosses followed by selection during the segregating generations seems a desirable plan. The first important step is the selection of the parents.

Parents in oat crosses

Anthony or Iogold	Bond
*Good yield	Fair yield
*Resistance to stem rust	Susceptibility to stem rust
Susceptibility to smuts	*Resistance to smuts
" " crown rust	*Resistance to crown rust
" " drought	* " " drought
Fair straw	*Strong straw

*Characters desired

The crosses from F_2 to F_5 were grown under conditions of disease epidemic for crown rust, stem rust and smuts. Approximately 1000 lines, with a total of 50,000 plants individually spaced, were grown and examined each year. A knowledge of the mode of inheritance has aided in obtaining the combination of characters desired. A condensed summary of the mode of inheritance of important characters, taken from the studies of Hayes, Moore and Stakman (9), is given here.

Inheritance in oat crosses

1. Crown rust, F_1 resistant, F_2, 9 resistant:7 susceptible
2. Stem rust, F_1 " , F_2, 3 resistant:1 susceptible
3. Smuts. Resistance dominant in F_1, 3 major genes.
4. Spikelet disarticulation. F_1 sativa base, F_2 3 sativa base:1 byzantina base.
5. Floret disjunction. 2 major genes. Byzantina type dominant.
6. Basal hairs. Sativa type dominant, F_2, 3 sativa type:1 byzantina type. Close genetic linkage between genes for 4, 5 and 6.
7. Yield is dependent upon multiple factors. Selection for seed plumpness, stooling, and vigor of plant aids in selecting high yielding genotypes.

It seems unnecessary to emphasize the value of a knowledge of the mode of inheritance of these characters as an aid in breeding. Such information aids the breeder in a selection of homozygous strains with the combination of characters desired. Cultivated oats, like wheat, are hexaploids and have 3 sets of 7 pairs of chromosomes or 21 haploid chromosomes in all. The inheritance of spikelet disarticulation, while approaching a 3:1 ratio in F_2, gave some F_3 segregating lines with wide deviations from this ratio. Similar deviations from expectation have been obtained in wheat. It is important for the breeder to know that meiotic instability is more frequent in some strains and hybrids of wheat and oats than in others as emphasized by Powers (15) and Myers and Powers (13) and that selection for regularity of behavior leads in some cases at least to greater genetic stability. Changes in pairing behavior, whereby a chromosome of one set of 7 chromosomes may pair in crosses with those of another set, explain one of the causes at least of meiotic instability.

One of the important contributions of cereal breeders and pathologists has been the development of stem rust resistant varieties of wheat. The isolation of physiologic races of disease organisms is a genetic application. Over 150 such specialized races of stem rust are now known. The breeding of rust resistant wheat has been greatly simplified by the discovery of a type of "mature-plant resistance" that in the Northwest, under field conditions from heading to maturity, causes certain varieties to be resistant to all physiologic races of black stem rust, even tho they may be susceptible to certain prevalent races in the seedling stages.

A brief history of the development of Thatcher wheat, introduced in 1934 by the Minnesota Agricultural Experiment Station, may be of interest (Hayes and others) (9). It resulted from combined studies of plant breeders, plant pathologists and cereal chemists. During the breeding program many varieties and hybrids of wheat were grown under rust epidemic conditions in a rust nursery using prevalent races of the rust organism. Marquis was crossed with a stem rust resistant durum wheat in 1915. From this cross three selections were obtained that resembled common wheat and that were resistant to stem rust under field conditions. In 1918, Kanred winter wheat, a variety immune to many races of stem rust but susceptible to others, was crossed with Marquis and from this cross strains were selected that combined the immunity of Kanred to certain races of stem rust with the spring wheat habit of Marquis. A cross between selections from these two crosses was made in 1921, i.e. a selection of Marquis x Iumillo was crossed with a selection from Marquis x Kanred. Thatcher, selected from this double cross, combines the desirable milling and baking qualities of Marquis, with the immunity of Kanred to certain stem rust races and with resistance to many races in the mature plant stage from heading to maturity obtained from the Iumillo durum parent.

Before introducing Thatcher it was tested extensively under stem rust epidemic conditions and equally careful studies were made of yielding ability and milling and baking quality. Yields in bushels per acre at the Crookston and Morris branch experiment stations from 1929 to 1938, inclusive, and in the years of severe stem rust epidemics in 1935, 1937 and 1938 show clearly the value of stem rust resistance.

The yield of Thatcher and of other varieties given in table 1 shows clearly the value of stem rust resistance in 1935, 1937 and 1938 when there were severe epidemics.

Table 1. Yields in bushels per acre of Thatcher and of other standard varieties.

	1929-38			1935, 1937, 1938[d]		
	Crookston	Morris[a]	Average	Crookston	Morris	Average
Marquis	18	15	17	8	8	8
Thatcher	26	24	25	25	32	29
Ceres	22	18	20	14	14	14
Hope[c]	21	20	21	17	23	20
Reward	21	18[b]	20	18	20[b]	19

a - no data in 1933.
b - comparable average, Reward not grown in 1934.
c - comparable average, Hope not grown in 1938.
d - severe rust epidemics occurred these three years.

The Backcross Method for Self-pollinated Crop Plants

The backcrossing method is now being used widely by breeders because, through its use, one can retain the many desirable characters of one variety and add the characters that it lacks by crossing and selection. Backcrossing has been used extensively by animal breeders. It was suggested by Harlan and Pope (6) in 1922 for use with self-pollinated crop plants. An appreciation of its value is general among corn breeders who are familiar with convergent improvement, which is equivalent to double backcrossing. Its genetic value is dependent upon the obtaining of the genetic complement of the recurrent parent in the 1st, 2nd, 3rd, etc., generations of backcrossing according to the progression 1/2, 3/4, 7/8, etc. The backcross method will be illustrated in relation to wheat breeding. Its applicability is illustrated as follows:

Backcrossing as a method of breeding

1. Selection of parents.

   A. A variety with desirable characters but lacking one or two characters that are dependent upon only a few genetic factors.
   B. A variety containing one or two of the desirable characters that are lacking in (A).

2. Backcross the F_1 and succeeding generations to (A) selecting for the one or two desirable characters of B.

3. Select in self progeny until desirable homozygous strains are obtained.

Its use may be illustrated by the improvement of Thatcher through crossing with Hope, primarily to add leaf rust resistance and retain stem rust resistance. Thatcher is the standard for yielding ability, desirable agronomic characters and milling and baking value. It is not as stem rust resistant as Hope and Thatcher is very susceptible to leaf rust. The following information was furnished by Dr. E. R. Ausemus of the Division of Cereal Crops and Diseases, U. S. Department of Agriculture, who is stationed at University Farm, St. Paul, and who has charge of the wheat breeding program.

History of backcross (Thatcher x Hope) x Thatcher

Year	Place	Plan
1930	Field	Original Cross
1930-31	Greenhouse	1st backcross
1931	Field	2nd "
1932-37	Field	Pedigree selection

Leaf rust epidemics only in 1932, '35
Stem " " each year.

Yield in bushels per acre, test weight, and leaf rust reaction are given in table 2 from trials made in 1938 when there was a severe rust epidemic in the Northwest spring wheat area.

Table 2. Yield in bushels per acre and test weight, rod-row replicated trials University Farm, 1938. Leaf rust reaction in rod rows (Agron.) and in the rust Nursery (R.N.).

Variety	Yield bu.	Test wt.	Rust Percent			
			Leaf		Stem	
			Agron.	R.N.	Agron.	R.N.
Thatcher	18	47	70	80	T	3
B.C., II-31-2	31	55	2	T	T	T
" -6	30	54	T	5	T	T
" -14	32	54	3	T	T	T

Briggs (2,3) in California, has used the backcross method extensively in breeding improved varieties of wheat. He uses desirable adapted varieties of wheat as one parent and has added bunt resistance by backcrossing and selection.

The few illustrations that I have given show how genetic principles have been adapted rather generally by the plant breeder interested in small grains. Similar illustrations could be given by the score for other self-pollinated crop plants.

Development of Standardized Breeding Methods with Corn

With corn, the most important farm crop grown in United States, the breeding of improved hybrid varieties has had the most far-reaching effect of any work in crop improvement in the present century. Standardization of breeding methods, based on genetic principles, has played a large part in the success that has been attained. The studies of East, at the Connecticut Experiment Station, and of Shull at Cold Spring Harbor, were started in 1905. Shull in 1909 suggested a method of using crosses between inbred lines. It was my good fortune to work under East's direction at the Connecticut Agricultural Experiment Station starting in 1909. A statement of his that seemed to me to be very significant is quoted as I remember it. He said, "I started a study of the physiology of inheritance in maize, believing that a knowledge of principles was necessary in the formulation of a logical method of breeding." A bulletin published in 1912 summarized the effects of self fertilization in corn. Hybrid vigor was discussed in relation to evolution and plant breeding. The following statements were taken from this bulletin.

Effects of self fertilization in corn
(After East & Hayes)(5)

1. Loss of vegetative vigor has followed continued self pollination in all inbred lines.
2. Inbred lines exhibit differences in many normal characters. Example: long vs. short ears.
3. Some pure strains are so lacking in vegetative vigor that they can not be propagated.
4. Continued inbreeding leads to purity of type.

All inbreds so far obtained in field corn are less vigorous than open-pollinated corn or a vigorous hybrid.

It will be noticed that the ears of the inbreds are smaller in all cases than the ear of the F_1 cross. In fact inbreds now available do not yield sufficiently well to make the use of a single cross feasible as a commercial method of seed production. Before illustrating methods of breeding, the mendelian explanation of heterosis, or hybrid vigor, will be outlined.

The Mendelian Explanation of Hybrid Vigor

Keeble and Pellew (12) in 1910 gave the first mendelian explanation of heterosis in a cross in peas. The two parents were medium in height; the one had thick stems and short internodes, the other had thin stems and long internodes. The F_1 showed complementary action of the two genes and was taller than either parent. At this time the large number of genetic factors involved in the inheritance of some characters was unappreciated, and for this reason Keeble and Pellew's explanation of hybrid vigor was not widely accepted. It was not easy to see why it was so difficult to obtain new forms breeding true for the extreme vigor of F_1. In 1917 Jones advanced a theory of heterosis based on the dominance of linked growth factors. The more important feature of this extension seems to me to be the large number of factors responsible for many normal characters. Numbers alone make it difficult to obtain all necessary factors in a single homozygous variety. Linkage adds to this difficulty. The dominant linked growth factor hypothesis appears to accord with the available evidence.

Heterosis, or hybrid vigor, is common throughout the entire plant kingdom. As a rule, heterosis is not so common or striking in crosses between varieties or species of self-pollinated plants as in crosses between inbred lines of the cross-pollinated group. This is to be expected on the basis of the mendelian explanation of hybrid vigor, for varieties of self-pollinated plants, on the average, are relatively more vigorous than inbred lines of cross-pollinated plants. Nature and man have been selecting desirable varieties of self-pollinated plants throughout the ages. If the mendelian hypothesis of hybrid vigor is the correct one, it should be possible, as I have outlined, to breed better inbred lines of cross-pollinated plants than are now available and with corn considerable progress has been obtained in this direction.

According to the present viewpoint, many economic characters are the result of the interaction of multiple factors under particular conditions of environment and in crosses between two inbred lines of corn it seems probable that a considerable number of factors in a heterozygous condition are responsible for the hybrid vigor of the F_1 generation. Certain inbred lines of corn when crossed with other inbred lines or with a commercial variety seem to have better combining ability, that is, give greater hybrid vigor, than other inbred lines which in themselves seem equally desirable, and there seems to be a growing body of evidence that combining ability is an inherited character. In one experiment with 110 inbred lines of corn, careful studies were made of 14 characters of the inbreds in relation to the combining ability in inbred-variety crosses using the open-pollinated variety, Minn. 13, as one parent in each cross. Twelve of the 14 characters of the inbred lines were positively and significantly correlated with yielding ability in the inbred-variety crosses. Table 3 lists the characters of the inbred lines used in the study and presents correlation coefficients for all possible relationships including correlations between 14 characters of the inbreds with the yield of inbred-variety crosses designated as 15 in the table.

Table 3. Total correlations between 12 characters of the 110 inbreds and yielding ability of inbred variety crosses (Hayes and Johnson)(8)

Characters correlated*	2	3	4	5	6	7	8	9	10	13	14	15
1	0.5118	0.6081	0.4819	0.6465	0.6193	0.5469	0.3831	0.3741	0.2230	0.0731	-0.0591	0.4742
2	---	0.7560	0.4419	0.4817	0.4294	0.3959	0.2588	0.1855	0.3568	0.2549	0.0812	0.2717
3	---	---	0.4324	0.5388	0.5025	0.4133	0.3522	0.3317	0.2201	0.1512	-0.0074	0.4110
4	---	---	---	0.4954	0.4417	0.4797	0.3959	0.2893	0.1847	0.2040	0.0815	0.2889
5	---	---	---	---	0.7623	0.5095	0.6013	0.4052	0.2085	0.1484	0.0352	0.4486
6	---	---	---	---	---	0.5545	0.7424	0.3896	0.2894	0.1947	0.0320	0.5430
7	---	---	---	---	---	---	0.5355	0.2384	0.2674	0.2065	0.1549	0.4069
8	---	---	---	---	---	---	---	0.2559	0.2245	0.2025	0.0683	0.4463
9	---	---	---	---	---	---	---	---	0.1990	-0.0029	-0.0342	0.1902
10	---	---	---	---	---	---	---	---	---	0.3451	0.3202	0.2566
13	---	---	---	---	---	---	---	---	---	---	0.6403	0.2474
14	----	---	---	---	---	---	---	---	---	---	---	0.2768
15	---	---	---	---	---	---	---	---	---	---	---	---

Significant value of r for P of .05 = 0.188
Significant value of r for P of .01 = 0.246

*Key to characters:

1 Inbred date silked
2 Inbred plant height
3 Inbred ear height
4 Inbred leaf area
5 Inbred pulling resistance
6 Inbred root volume
7 Inbred stalk diameter
8 Inbred total brace roots
9 Inbred tassel index
10 Inbred pollen yield
13 Inbred yield index
14 Inbred ear length
15 Inbred-variety cross yield

From this study it was found that the multiple correlation between 12 of these characters in the inbreds and yield in the inbred-variety crosses was .67. Date of silking was held constant and a partial multiple correlation coefficient was found where the multiple correlation R, holding constant date of silking, is obtained from the following formulae:

$$1 - R^2_{15.2,3,4,5,6,7,8,9,10,11,12|1|} = \frac{1-R^2_{15.1------12}}{1-R^2_{15.1}}$$

The computed value of R in this case was 0.5310.

These results show that the characters of inbred lines which are responsible for their relative vigor of growth are also to a considerable extent responsible for the combining ability of the inbreds themselves, as measured by yield in inbred-variety crosses.

The mendelian explanation of hybrid vigor is essential in an understanding of breeding methods with cross-pollinated crop plants. If the explanation is a correct one it would seem possible to breed improved inbred lines that approach homozygosity and that approach the F_1 in vigor of growth. With different cross-pollinated plants the difficulties would seem to be in direct relation to the number of growth factors involved, i.e., the extent of heterozygosity. Throughout the corn belt most and perhaps all corn breeders are endeavoring to obtain more vigorous inbred lines. The breeding methods available are not greatly different than those that have been illustrated with small grains but may be repeated here for corn. Before discussing the breeding of improved inbreds, the commercial value of three-way and double crosses will be illustrated.

Commercial Value of Three-way and Double Crosses

Two types of crosses are being utilized by the commercial grower, the three-way and double cross. A three-way cross utilizes three inbred lines and a double cross is made using four inbreds. Minhybrid 301 illustrates a three-way cross that has been grown extensively in southern Minnesota. Minhybrid 403, a double cross, also has been grown extensively.

The double cross plan is illustrated for Minhybrid 403.

Inbred lines	11 14	374 375
Single crosses	(11x14)	(374x375)
Double cross	(11x14) (374x375)	

Comparative yields of Minhybrids 301 and 403 and commercial varieties illustrate the value of the method. Ability to withstand lodging and resistance to diseases such as smut and ear and stalk rots are some of the reasons why hybrids are more desirable than commercial varieties. The comparative yields given in tables 4 and 5 indicate rather clearly the value of hybrids to the commercial grower. The yields in table 4 represent results from demonstration trials where the hybrids were planted in strip plots in commercial fields. The results in table 5 are from randomized block trials, replicated five times at each location. Murdock was used as a standard open-pollinated variety. All tests are on the basis of bushels per acre, 14 percent moisture basis.

Table 4. Yield in bushels per acre of Minhybrids 301 and 403 compared with farm varieties.

	Minhybrid 403	Minhybrid 301
No. of trials	85	454
Yield of hybrid	58.3	54.6
Yield of farm variety	49.7	46.6
Increase - bushels	8.6	8.0

Table 5. Yield in bushels per acre of Minhybrids 301, 403 and Murdock, 1937-38.

Location (county)	Minhybrid 301	Minhybrid 403	Murdock
Brown-Cottonwood	60.1	62.5	50.2
Rock	66.2	70.6	54.1
Waseca-Faribault	63.0	66.2	53.1
Fillmore-Houston	68.8	72.4	57.3
Average	64.5	67.9	53.7
Bu. increase over Murdock	10.7	14.2	

The data given in tables 4 and 5 show clearly the value of these two hybrids in comparison with open-pollinated varieties that are similar to these hybrids in date of maturity.

Breeding Improved Inbred Lines of Corn

Two methods of breeding improved inbred lines of corn are being used rather extensively in the Corn Belt. These are backcrossing and convergent improvement.

An undesirable character of the three-way cross, Minhybrid 301, is the susceptibility to smut of the inbred B164. This inbred has been changed by backcrossing. The method may be illustrated as follows:

Improvement of B164 by backcrossing with particular reference to smut resistance

B 164	Early inbred, C37
Smut susceptible	Smut resistance

Method

1. (B164 x 37) x B164
2. [(B164 x 37) x B164] x B164

   Selection in 1 and 2 for smut resistance.
3. Self pollination and selection (2 years).
4. Select a desirable smut resistant line resembling B164.

In a field trial in 1938 and 1939 several such lines were obtained that were highly smut resistant in comparison with B164.

Convergent improvement, first suggested by Richey (16) in 1927 (equivalent to double backcrossing), is a method of improving each of two inbreds without modifying their combining ability when crossed together. It may be illustrated with two of the inbred lines used in Minhybrid 403. Some of the differential characters of the inbred lines 11 and 375 are given here.

Characters of the parental inbreds

11	375
Smut susceptible	Smut resistant*
Large seed*	Small seed
Premature germination	Good quality seed*
Fair root system	Excellent root system*

*Characters desired

The methods followed are given in outline form.

Convergent improvement

1.	1st backcross	(11x375) 375	(11x375) 11
2.	2nd "	$(11x375)\ 375_2$	$(11x375)\ 11_2$
3.	3rd "	$(11x375)\ 375_3$	$(11x375)\ 11_3$
		Select for seed size.	Select for smut resistance. " " good seed quality. " " strong root system.

4. Self pollination and selection for characters desired (2 years).

The inbred parents 11 and 14 were improved in standing ability and in smut resistance. Inbred line 11 was improved in quality of seed while inbred 14 was improved in seed size and in ear length. Inbreds 374 and 375 were improved in ear type.

Another method used extensively in Minnesota to breed improved inbreds is the so-called pedigree method illustrated as follows, which has been described by Hayes and Johnson (8).

Breeding improved inbreds by the pedigree method

1. Select inbreds that excel in the characters desired.
   ex., one parent resistant to smut, the other to lodging.

2. Make several crosses of unrelated inbreds.

3. Continue selection in self-pollinated lines for smut resistance, strength of stalk and other desirable characters for 5 or 6 years.

4. Combine the better lines using crosses between lines of different genetic origin.

Introduced inbreds that excelled in strength of stalk were used as one parent of several of the original crosses. As standing ability was difficult to select in commercial varieties, later maturing inbreds with good standing ability were introduced from other breeders.

These introduced inbreds were crossed with early maturing inbreds selected in Minnesota, and selection was practiced during the segregating generations. Some characters of selection value that have been used in making selections from F_3 to F_6 are of interest.

Some characters of selection value

1. Length of ear and ear production.
2. Period of maturity.
3. Vigor of plant.
4. Well developed root system.
5. Smut resistance.

After obtaining the best possible inbreds (110 were selected at University Farm and about the same number were available from the Waseca studies) the following methods have been used in further work.

Selecting crosses from inbred lines available

1. Determine best combiners in inbred-variety crosses.
2. Make all possible single crosses between unrelated lines.
3. Predict yield of double crosses.
4. Make yield trials of actual double crosses.

Jenkins (10) compared various methods of testing the combining ability of inbred lines in double crosses using single crosses as one method of predicting the yielding ability of double crosses. Doxtator and Johnson (4) made a further study of single crosses as a means of predicting the yield of a particular double cross. The following data is taken from the work of Anderson (1) and shows how single crosses are used to make such a prediction. The yield of a particular double cross may be determined with accuracy from the average yield of the four single crosses not used as parents in the double cross. From any four inbred lines six single crosses can be made and three different double crosses. One of these three double crosses frequently yields more than the other two.

The inbreds that yield well in inbred-variety crosses may be tested in single crosses and their yielding ability in double crosses predicted, as illustrated from data presented by Anderson.

Method of predicting double cross yields from single cross data

(23x24) x (26x27)

(23x26)	62.6
(23x27)	70.8
(24x26)	65.6
(24x27)	72.1
Av.	67.8

(23x26) x (24x27)

(23x24)	41.7
(23x27)	70.8
(26x24)	65.6
(26x27)	64.2
Av.	60.6

(23x27) x (24x26)

(23x24)	41.7
(23x26)	62.6
(24x27)	72.1
(26x27)	64.2
Av.	60.2

A comparison of actual and predicted yields of double crosses by Anderson is given to show the value of the method.

A comparison of actual and predicted yields (after Anderson)

Lines combined	Bu. per A. Actual	Bu. per A. Predicted
23,24,26,27		
(23x24) x (26x27)	68.8	67.8
(23x26) x (24x27)	62.4	60.6
(23x27) x (24x26)	62.0	60.2
23,24,26,28		
(23x24) x (26x28)	65.0	65.5
(23x26) x (24x28)	59.8	58.0
(23x28) x (24x26)	56.0	58.5

(continued)

23,24,27,28		
(23x24) x (27x28)	71.1	69.2
(23x27) x (24x28)	58.1	59.4
(23x28) x (24x27)	58.0	60.4
Diff. for signif.	5.26	3.41

Inbred lines selected at Waseca and University Farm were combined in single crosses using unrelated lines. The inbreds used in one cross illustrate the method without the necessity of detailed description. It will be noted that inbreds A96, A163, A116 and A131 were selected from crosses between inbreds (64xH), (43x47), (49x9) and (11-28 x 15-28), respectively. After crossing, self pollination and selection was practiced six years before inbreds were selected for use in crosses. A96, A163, A116, A131 and other inbreds used as parents of double crosses were first tested for combining ability and only good combiners were selected.

Genetic diversity of inbreds

Original parent inbreds	Source
64	N.W. Dent
H (Reid's)	From Holbert, Ill.
43, 47, 49, 11-28	Four Minn. #13 inbreds
9	Wis. Golden Glow
15-28	Rustler

Inbreds selected	Origin
A 96	64 x H
A163	43 x 47
A116	49 x 9
A131	11-28 x 15-28

The yielding ability in a double cross in bushels per acre on a 14 percent moisture basis and the moisture percentage (% M) at harvest, used to show relative time of maturity, is illustrated in the following summary for the double cross (A96 x A163) x (A116 x A131).

Method of predicting yield and actual results

Av. yields 4 stations, 3 replications per station, 1938

59.1 bu. (A96xA163)	47.0 bu. (A116xA131)	
Cross	Bu.	% M.
A96 x A116	57.6	20.5
" x A131	58.7	22.0
A163 x A116	65.3	20.4
" x A131	68.2	22.5
Av.	62.5	21.4
Minhybrid 401	60.0	24.2
" 402	54.3	21.3

From this summary we conclude that the double cross (A96 x A163) x (A116 x A131) may be expected to yield as much or more than the later maturing hybrid, Minhybrid 401, and mature as early as Minhybrid 402.

Four double crosses that were tested in southern Minnesota in 1938 and 1939 illustrate many other comparisons that have been made in recent years. Yield in bushels per acre, 14% moisture basis, for predicted doubles grown in 1938, yield in bushels per acre from actual doubles grown in 1939, and moisture percentage at harvest is given in table 6. The results given are an average of trials in three or four locations in randomized blocks with three replications per location.

Table 6. Predicted yield of double crosses in 1938 and actual yield 1939, compared with standards, Minhybrids 401 and 403.

	Yield bu.*			Moisture %*		
Double Cross	1938	1939	Av.	1938	1939	Av.
(42x144) x (57x92)	72.6	77.3	75.0	28.6	29.4	29.0
(134x144) x (57x92)	80.7	82.9	81.8	29.6	28.4	29.0
(122x134) x (57x144)	80.2	83.0	81.6	30.8	27.0	28.9
(134x375) x (122x30)	83.1	86.4	84.8	35.8	33.2	34.5
Minhybrid 401	62.5	59.7	61.1	28.8	27.3	28.1
" 403	79.4	71.8	75.6	31.6	32.3	32.0

*1938 yield and moisture predicted from results from F_1 crosses.
1938 yields and moisture obtained in regular tests of these double crosses.

These results illustrate the many cases where prediction of the yielding ability of double crosses from yields of singles may be used. This greatly simplifies the testing of many double cross combinations for the predicted yields of over one million double crosses can be obtained from testing 1770 single crosses, that in turn can be obtained from all possible combinations between only 60 inbred lines.

A study of F_1 crosses between the inbreds available has shown the importance of genetic diversity of inbred lines used in double crosses. Three groups of lines based on relationship were used and the yields of single crosses were compared on the basis of origin. The three groups on the basis of origin are illustrated as follows.

Original Cross	Inbred cultures selected
A48 x H	A94, A96
A9 x A26	A102, A111, A116, A122, A124
A9 x A39	A99
A39 x A26	A136, A143, A145

Group I, no parents in common, i.e., A94 x A102, etc.
" II, one parent in common, i.e., A102 x A99, etc.
" III, both parents in common, i.e., A 102 x A111, etc.

Results of yield trials from an average of three localities are given in table 7.

Table 7. Yield of single crosses in comparison with standards, Minhybrids 401 and 402, in relation to the origin of the inbred lines. Randomized block trials average of three locations, 3 replications per location.

Group origin of inbreds	Single crosses as desirable as Minhybrids 401 or 402a	Less desirable
	No. of single crosses	
1. Unrelated	28	15
2. One parent in common	6	9
3. Two parents in common	1	14

[a]Minhybrids 401 and 402 have proven desirable double crosses in North Central Minnesota from extensive yield trials.

These results show that single crosses between unrelated inbreds yield better, on the average than either group 2 or 3. When both inbreds were selected from an inbred cross with two parents in common, most of the single crosses were low in yielding ability. Genetic diversity of inbreds used in making single crosses seems essential in relation to obtaining high yielding single crosses.

Single crosses from combinations of unrelated inbreds were tested in yield trials and the yields of predicted double crosses were determined. From each 4 inbred lines 3 predicted double crosses can be made and as a rule one of these appears somewhat superior to the other two as has been emphasized. In the summary in table 8 only the best double cross from each 4 inbred lines was used.

Table 8. Yields of predicted double crosses using unrelated inbreds compared with standard double crosses. Predicted double crosses of comparable maturity to Minhybrids 401, 301, or 403. Those yielding as well or better than standard double crosses are summarized as E, early, M, medium maturity, etc. Those classified as undesirable were lower in yielding ability than standard Minhybrids 401, 301 and 403.

Cross	E	M	L	V.L.	Undesirable
Group		No. of lines in each group			
Early	10	7			
Medium	2			2	
Late	2	7	10	4	5
E x M	11	10	7		12
M x L		3	21	12	4
Total	23	29	38	18	21

Out of a total of 129 such double crosses 108 were equal or superior to the standard recommended hybrids. The breeding methods used, therefore, show what can be accomplished by the use of genetic methods in planning a definite breeding program.

Some Concluding Remarks

Continued intensive studies of genetics and other plant sciences and their aplication to breeding problems may be expected to yield handsome dividends in the development of more efficient crop plants and more efficient breeding methods than are now available. While much has been accomplished already, the possibilities of further improvement seem almost unlimited.

I have discussed the breeding of self-pollinated crop plants and of corn because breeding methods, with these crops, have become standardized to such an extent that it is possible in many cases to plan the breeding program with the definite expectation of obtaining certain desired results. I have spent considerable time in presenting methods of breeding with corn because some of the principles learned seemed to have a direct bearing on the program for improvement of other cross-pollinated plants such as sugar beets.

The breeder of grasses has accepted, for the time being at any rate, the English plan of strain building. Instead of breeding many varieties this plan consists of isolating favorable germ plasm and the recombining in a single variety of the best germ plasm available. When self pollination is possible inbred lines may be isolated. This makes possible the isolation of relatively pure breeding types. The combining ability of such inbreds can be determined by methods similar to those used with corn. Synthetic varieties can be developed from the use of inbreds when such methods prove feasible. It would seem desirable to test combining ability of the inbreds and use in the synthetic variety only those that show the greatest hybrid vigor. It is possible that methods may be developed with some crop plants, such as sugar beets, for the more direct utilization of hybrid vigor by using first crosses between inbred lines for the commercial crop. Several members of your association have emphasized the desirability of this plan.

In our studies with corn at Minnesota, we have learned the importance of selecting inbreds for use in a particular double cross that are as genetically diverse as possible. In presenting the history of sugar beet improvement, Dr. Coons has pointed out that sugar beet varieties are rather closely related from the standpoint of their origin. Some method of adding greater diversity of genetic origin may be important in sugar beets in relation to the utilization of hybrid vigor in the breeding of improved varieties.

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