being a convenient place in which to store small lots of roots of breeding strains, provided conditions which were equal to those in the silo, insofar as loss in sucrose was concerned. In other words, the cellar was fully as good as the silo in holding the metabolic rate at a low figure.

A CRITICAL STUDY OF FAMILY AND GROUP BREEDING METHODS FOR SUGAR BEETS

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Introductory

The Vilmorin principle of selection which was developed by Louis Leveque de Vilmorin and his father Louis de Vilmorin in connection with their studies of vegetables and sugar beets was published in a monograph in 1856. It became known as the progeny test principle since it provided for the growing and examination of the progeny of an individual as the only method for determining its value.

This principle quickly became an essential feature of the breeding methods for many crops including sugar beets. In sugar beets it is still the essential feature of much of the breeding work, particularly in Europe, as was graphically presented by Dr. G. H. Coons in the U. S. Dept. of Agriculture Yearbook of Agriculture (1).

Since it is the intention of this paper to refer frequently to various phases of the breeding work with corn, inasmuch as the two crops are similar with respect to the fact of being largely cross-pollinated, it is well to observe that the ear-to-row methods for corn are essentially similar to the family and group methods for sugar beets.

While the pure line methods of breeding were adopted for small grains at Svalof, Sweden, in 1891, it was not until after Johannsen in 1903 and 1906 conducted his famous selection experiments with beans and barley that the pure-line theory was developed. These being naturally self-pollinated crops, he showed that variation within the progeny of a single individual could not be retained, in other words, there was a complete regression back to the average in the progeny of both the plus and minus variations. It is the pure line concept which underlies the important recent advances in breeding work with many naturally cross-pollinated crops. The ear-to-row methods which were adopted for corn by early breeders have given way almost completely to pure-line methods. It is the intention in this analysis to study statistically, so far as possible, the results obtained from an extensive application of the progeny test or family and group breeding methods employed over a period of years by the research department of The Great Western Sugar Co. Without attempting to claim any undue credit or responsibility, the experiments from which these studies were made probably constitute the most extensive application of this breeding method to the sugar beet crop in America.

The statement was made by one of the foremost European beet breeders a few years ago that "a sugar beet breeder could well consider his life a success if he was able to increase sucrose by 1 percent and at the same time maintain yielding ability." Certain it is that such would be a real accomplishment, but in this country we have seen increased yield to the extent of saving an industry in several western states through resistance to the curly top disease alone. And we are probably soon to witness, perhaps less actual contribution in the form of increased production, but no less striking similar accomplishments from varieties nearly immune to the Cercospora leaf spot. In no other important crop have the plant breeders contributed a more brilliant page to the history of improved varieties than for sugar beets in the curly top area, and for breeding strains of sugar beets resistant to leaf spot in the areas subject to this disease.

Historical Sketch of Great Western Breeding

The breeding work of The Great Western Sugar Company was started by Hans Mendelson at Edgar, Montana, in 1910.

The greater part of the breeding was carried on at Edgar, supplemented by work at Longmont under the direction of A. C. Maxson, who started the Experiment Station at that place in 1910, until 1915 when Longmont became the seat of all Great Western breeding operations, the work being under the direction of Mr. Mendelson until 1925 at which time H. W. Dahlberg, Research Manager, took over the work of Mr. Mendelson.

During this early period the source of the material used consisted of selections from commercial yield, normal and sugar types of leading European producers; strains developed at Brookings, S.D., Experiment Station; and an Elite mother stock secured from a European producer.

In the early work progeny tests based on siloed roots analyzed in the spring formed the basis for family selection. Individuals were selected from the best families on the basis of individual weight and polarization.

Groups of from a few to a hundred or more selected roots were set out for increase. These groups were based on family performance and not on the type of stock out of which the original selection was made.

The breeding work was reorganized in 1925. Since that time family performance has been determined by a fall test of an unselected population. Only desirable families have been siloed.

In the final judgment of families the performance of preceding generations is given consideration. Only lines having a consistently good performance for several generations are finally alloted a place in the breeding program.

Selection of individuals is based on the weight and sucrose % of the individual and the physical characters of the root. Selected individuals must exceed the family means for weight and % sucrose, the emphasis being placed on each depending upon the family tendencies.

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Heritable differences of selection value exist between individuals and families within a group. It may seem trite and unnecessary to prove such is the case before a group of geneticists and plant breeders. But upon this fact hinges the possibility for improvement, and we shall present some pertinent data. The correlation of weight and % sucrose was determined for 1028 individual roots taken at random from Old Type in 1915. The stand in the field from which these beets were taken was spotted, with considerable variability in competition between individuals. An r value of -.6310 was obtained, which is somewhat larger than commonly reported for this relationship. From this population 15 individuals from the high weight, high sucrose corner were taken for a group increase and 15 others from the low weight, low sucrose corner for a similar group, both of which were grown for seed in 1916 and a mass increase from each tested in 1917. The yields obtained from the two lots were about the same but the sucrose was 1.35% higher in the progeny of the high sucrose selections. In any case the regression from the extremes, back toward the average, was rather significant.

Schneider (8) conducted a progeny test in which the descendants of a group of large and another group of small beets from the same original mother were tested for yield and sucrose. Two such comparisons were made with results as follows:

Family	Size of previous generation	Yield of Progeny in Kg per hectare	% Sucrose
171	large	40500 ± 507	20.18 ± .06
"	small	39900 ± 543	20.34 ± .06
224	large	38200 ± 634	20.19 ± .09
"	small	38800 ± 416	20.25 ± .09

The conclusion was reached that selection resulted in no change, and that it is not a question of fixed hereditary differences, but of modification resulting from the place where the beets were cultivated. The results obtained confirm Schneider's conclusions but it is doubtful if many of us would agree to this as a general conclusion based on one generation of selection, realizing, as we do, that the character of yield must be a very complex one, and that several generations of selection would be necessary to establish the value or ineffectiveness of such selection.

In 1934 two Great Western groups were made up from beets of the same family. In one case the beets were of medium weight and % sucrose while in the other they were of medium weight and relatively high % sucrose. Following are the results of performance of progeny families:

Group	No. of Families	Selected beets Wt. (g)	Selected beets % Suc.	Performance of Progeny % of Check Yield	Performance of Progeny % of Check % Sucrose	Performance of Progeny % of Check Sucrose Yield
344	28	727	17.16	85.84	106.97	91.85
348	6	816	18.80	78.72	110.25	86.87
Difference			+ 1.64	- 7.12**	+ 3.28**	- 4.98**
			"t"	- 4.39	+ 3.50	- 2.95

**Sig. to P = .01 level

The differences between the progeny of the two groups are highly significant for yield, % sucrose and sucrose yield per acre. It is very important to note that the % sucrose in the progeny followed the mother selections but that the yield of roots was negatively correlated with % sucrose in the progeny in spite of the fact that the selected mothers used for Group 348 were high in both weight and % sucrose.

In a study of variation in yield within groups very significant differences between strains were indicated, the strain variance greatly exceeding the error variance. There are commonly represented in a group several families from each of one or more mothers. We may call the several families descending from a single mother a "class." Differences between classes was found to be significant in one out of 4 groups tested, while in the other 3 significance was approached. Differences within classes were found to be very significant. Such differences would be expected to be largely conditioned by heredity, and would be expected, on the basis of their face value, to be of measurable plant breeding interest.

In this connection the correlation of various genetic and economic characters is of interest:

	r	t	Regression
Wt. and % sucrose of selected beets	- .1839**	4.20	
Wt. mother and Wt. progeny	+ .0669	1.51	
" " " % sucrose of progeny	- .0626	1.41	
% sucrese mother and Wt. of progeny	- .1565**	3.65	- .227 (% Std. for 1% Std. in % sucrose) W on S
" " " " % sucrose progeny	+ .0781	1.76	
(581 observation, 77 classes, 503 DF for r			
Yield family and yield of progeny	+ .089	0.72	
% sucrose " " suc. of progeny	.121	0.99	
(66 DF for r within groups)			
Wt. seed per plant and yield progeny	+ .1065	2.0	0.23% per ounce
" ". " " " % suc. "	+ .1482	2.5	-0.12% of Std.per ounce
(261 DF for r)			
Leafspot (a and yield, Brush (1936)	- .1904**	2.7	
" " % sucrose " "	- .2666**	3.5	
(154 DF for r within groups)			
Leafspot and yield, Longmont (1937)	- .3545**	3.3	- 3.62% Std.(Y on LS)
" " % sucrose " "	- .1954**	3.1	- 0.80% " (%S on LS)
(239 DF for r within groups)			
Vigor (b (June 6) and yield,Longmont 1937	-.2099**	3.3	- 2.53 % Std. (Y on V)
" (Oct. 1) " " "	-.0960	1.5	
" " " leafspot " "	+.1762**	2.7	

**Significant to P = .05 level

a) Leaf spot scale 1 to 10. 1 = trace, 10 = completely burned down.

b) Vigor scale 1 to 10. 1 = very vigorous, 10 = very weak

Immer (4) has shown a correlation between % sucrose and apparent purity of .7096.

The r values for weight and % sucrose of selected beets is - .1839, which is highly significant but much less than noted previously for an unselected population (- .6310). The weight of the mother was not shown to be significantly correlated with either the weight or % sucrose of the progeny. The correlation of % sucrose of mother with weight of progeny was shown to be significant but low in value (r = - .1565). This is in line with a considerable mass of evidence indicating a danger in loss of yielding ability by selecting beets of unusually high sugar content (refer to groups 344 and 348 cited previously). From this it would seem that % sucrose should be correlated in the progeny test but while the correlation between % sucrose in the mother and family with the progeny is positive it is not significant in either case cited.

Yield in the family was not significantly correlated with yield of the progeny, however, the number of observations is small.

The weight of seed is positively correlated with yield and negatively with % sucrose in the progeny, *r* being barely significant for the first case and quite significant for the latter. It must be remembered in this case as well as the others cited that the mothers used were selected usually above the average in both weight and % sucrose.

As would be expected leaf spot was significantly correlated with both yield and percent sucrose, both at Brush in 1936 and Longmont in 1937. In the latter for each unit of 1 on the scale of 1 to 10 for resistance vs. susceptibility there was an increase of 3.62% yield and .80% sucrose, the percentages being of the Standard used. The most resistant strains rated as low as 1 while the susceptible Standard rated up to 8 in some plots. This extreme difference could account for 25.34% (7 x 3.62) loss in yield and 5.6% (7 x .80) loss in % sucrose.

A vigor estimate (Scale 1 = vigorous to 10 = weak) on June 6, when the plants were about to cover the row, was correlated with final yielding ability with *r* = - .2099, indicating a definite, although small, positive relationship between vigor at that time and yield. A later observation on Oct. 1 was undoubtedly influenced materially by leaf spot burning, the *r* value of - .0960 having no statistical significance. The correlation between leaf spot and vigor was + .1732 which indicates a positive lowering of the vigor rating with heavier leaf spot incidence.

Trends in Great Western Commercial 1922 to 1936

From the historical sketch given previously it was shown that before 1926 the selection was based on a test of individuals taken from a selected population. There was no progeny test estimation of the random population from each mother; only a selected lot of roots were used for this purpose. Furthermore, the selection of mothers was based on an evaluation scale which placed the major emphasis on percent sucrose.

We have charted (Fig. 1) in % of Great Western Standard a 3-year moving average the course of the performance of Great Western commercial and one of the leading normal type European commercials. Each point on the graph represents a 3 year mean including the two years previous to the year for which the point on the graph occurs. A material drop in yield, and somewhat compensatory increase in % sucrose appeared in both the Great Western and European for the 1924 and 1925 points. Following this period a material rise in yield and to some extent a consistent drop in sucrose % occurred in both varieties, the high being reached by the European variety in 1929, and by the Great Western in 1931. A rapid drop back in yield was thereafter noted for the European while the Great Western remained more or less otherwise constant. There appears to be some correlation between the performance of the two varieties for the period from 1922 to 1931 and it may be assumed that to

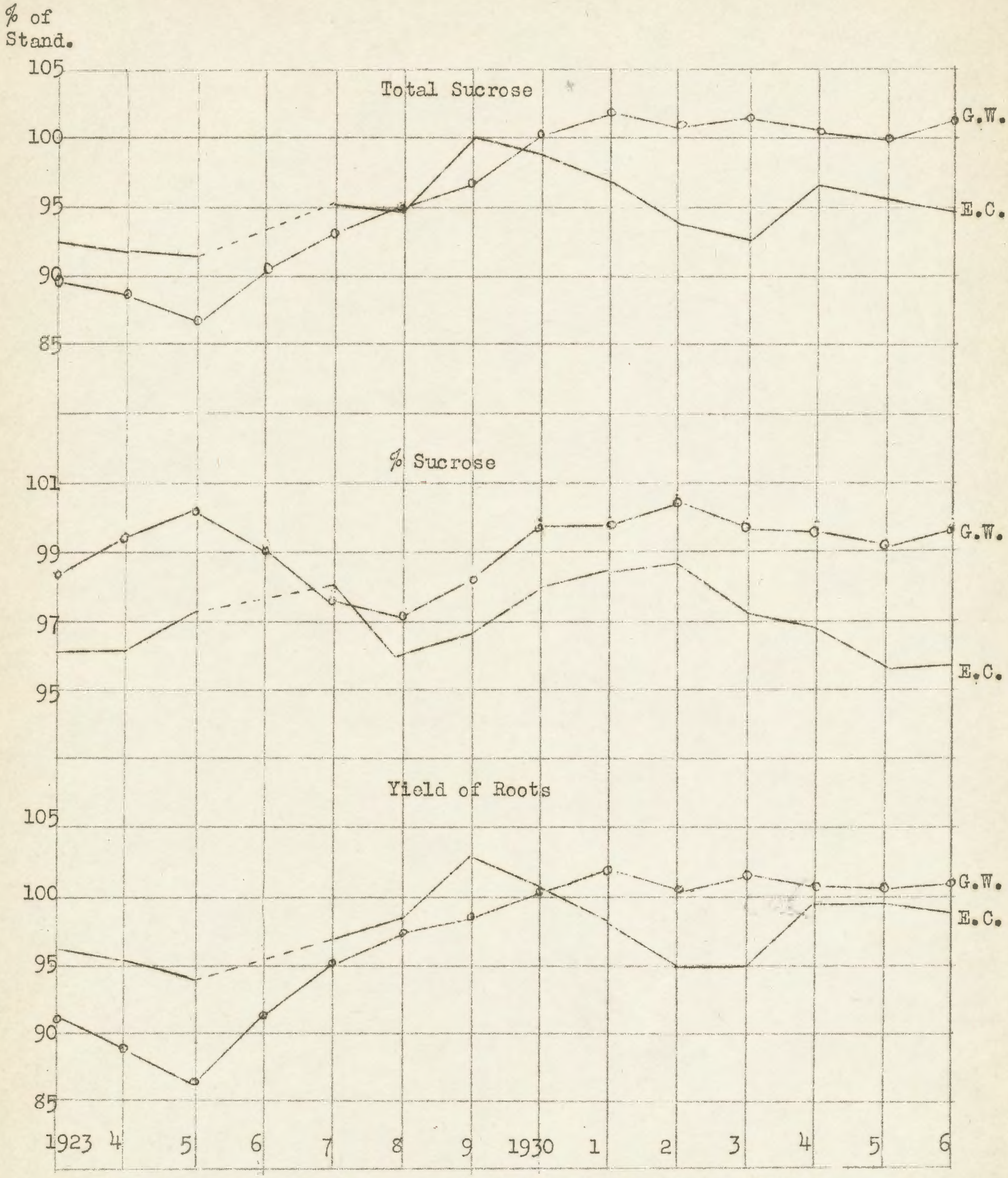

Fig. 1. Three year moving average Great Western Commercial (G.W.) and a leading European Commercial (E.C.) in % of Standard

some extent, at least the conditions under which these tests were conducted were responsible for the relative performance.

It is chiefly our concern to offer some explanation for the Great Western curve. In the first place, the drop in yield for the years 1922 to 1925 may be due in part to the unbalanced selection at that time, giving greater emphasis to sucrose percentage. Following 1925 emphasis was placed on the progeny test, which has continued to the present. The yield increase for the period 1925 - 1931 was very significant.

Following 1930-31 in spite of refinement in testing and continuous extensive selection, there has been no material change in the performance of the commercial.

It is, perhaps, worthwhile noting the apparent drop in % sucrose for 3 or 4 generations following 1925, with recovery following this depression to about the previous level from which there was little change from year to year, the average being well above the European commercial, the latter having exhibited a material and consistent regression downward in recent years in relation to the Standard.

In total sugar the curve follows the "yield" curve rather consistently, the spread between the two varieties being greater in later years, however, due to the additive effect of yield plus % sucrose.

The Great Western commercial is both a high yield and high sucrose variety. In a test in 1937 at four locations in Northern Colorado and Western Nebraska, Great Western was found to be higher in purity than all other varieties at each location, the average being 1.7 points above the average for the other varieties. In this test Great Western showed 14.0% greater sucrose yield per acre than the average of the four varieties. In addition, it possesses some degree of leaf spot resistance, or perhaps better called tolerance, since it may appear only slightly less heavily affected than the European commercials but still yields definitely higher.

The tests shown in the graph were conducted at Longmont where leaf-spot is not serious except in occasional years. If they had been conducted in Eastern Colorado where leaf spot is much more of a determining factor in yield the spread between Great Western and the European commercial would, no doubt, have been greater in recent years.

Great Western is also characterized by long smooth roots.

Discussion

The results of the progeny test or family and group methods for sugar beets, as we have attempted to analyze them, are the source of considerable satisfaction and, at the same time much concern. For it appears from the information presented, and from wide commercial tests, that the Great Western variety as now grown extensively is a real improvement over the European varieties available.

At the same time it is somewhat disconcerting to note that the curve of improvement in yield for Great Western commercial seems to have flattened out in spite of improved methods of field plot testing to isolate the more desirable lines more efficiently. It may well be that there is still sufficient improvement, slow though it may be, taking place to justify the method. Recent groupings for leaf spot resistance indicate that a high degree of resistance may be obtained, and from the regression of yield on leaf spot presented we may confidently expect a real increase in yield resulting from increased leaf spot resistance. After this point is attained further improvement by this method appears doubtful, or at least, very slow and inefficient to an American plant breeder.

An analogy with the results obtained by the corn breeders would seem pertinent in this case. The two crops are similar in being naturally cross pollinated. The ear-to-row test used by the early corn breeders is similar to the methods as outlined here for sugar beets. We cannot go into the results obtained for corn (See Richey, 7) more than to record that it is the concensus of opinion of the corn breeders that ear-to-row methods are most effective in adapting a variety to new climatic conditions, but that the effect is not cumulative from the yield standpoint.

Perhaps the most outstanding example of progeny test selection available was conducted with corn at the Illinois Experiment Station (5). Continuous selection has been made for high and low protein and high and low oil for 38 generations. The results in 1934 after 38 generations of selection are as follows:

Strain	Analysis
High protein	23.79 % protein
Low "	10.73 " "
High oil	11.36 % oil
Low "	1.04 % oil

The efficacy of selection for the characters in question cannot be doubted. Even the more recent results show continued cumulative and positive effects of the selection. It is of vital interest from the breeding standpoint, however, that in spite of efforts used to counteract the tendency to decreased yields the yielding ability has been reduced at least 30 percent (3) in each of these selected lines. Experience with sugar beets indicate that a similar result could easily be obtained by placing first emphasis on sucrose percentage, with a corresponding probable loss in yield of roots.

It appears to be relatively simple to show improvement for one character by selection methods with group pollination, but that it becomes exceedingly more difficult, if not impossible, to show continuous improvement for a complexity of characters such as are required for corn where yield is of major importance or for sugar beets where both quality and quantity are of equal importance and where other characters such as shape of root and crown and resistance to disease are of great importance.

Pursuing the analogy with corn still further, it is sufficient to observe that ear-to-row methods were discarded several years ago and pure line methods substituted in their place. By the pure line method Hayes (2) was able to show as much increase in protein content in 4 generations without loss in yield, using the pure line method, as was obtained in the Illinois selection experiment in 15 generations. In an extensive corn yield contest in Iowa the latest published results in 1936 (6) show the average yield of hybrids, employing inbred lines, to exceed the open-pollinated entries by 30.8 percent. Farmers are not quick to purchase seed when it is so easy to pick their own, as in corn, but at least 50 percent of all commercial cornfields in the corn belt will be planted to crossed corn in 1938 - this fact alone constituting an impressive testimony to the superiority of the varieties produced by pure line methods.

The pure line method is genetically sound. While it has been used for sugar beets for several years by the U. S. Department of Agriculture the extent of the work was necessarily very limited as compared with the accumulated experience with corn. Moreover, most of the selfing was by space isolation which is not absolute in prevention of crossing as are bagging or caging methods. The inbreeding method seems to hold much possibility for the future of improvement for the sugar beet crop.

In the popular search for new genes the wild relatives of the commercial sugar beet, as well as, the garden beet and stock beet types are not being overlooked. In the final analysis the plant breeder's task is to locate and synthesize the valuable genes into a commercial product. This task, at least, is a romantic one.

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