Evaluation of Three Sugar Beet Breeding Methods[1]

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In spite of its brief history as a cultivated crop (2)[3] the sugar beet (*Beta vulgaris* L.), primarily a cross-fertilized species, is known to be amenable to gross and adaptive change by mass selection. About the beginning of the nineteenth century, it was selected from a near relative of the mangel-wurzel (5). This early selection resulted in the White Silesian beet which was designated by Lippmann (6) as being the mother stock of all sugar beets in the world. Intrapopulation mass selection advanced root yield and percentage sucrose, as well as adaptive traits, until close selection for particular types apparently placed a limitation on the genetic diversity of the progeny. If primarily non-additive genetic variance remained in adapted sugar beet varieties, selection dependent upon additive genetic effects probably would be ineffective. However, Deming (3) has reported considerable difference in general combining ability of inbred lines for root yield and percentage sucrose. Since differences in general combining ability are related primarily to differences in additive genetic effects, it would appear that considerable additive genetic variation remains in the population. Improvement of sugar beet varieties through simple recurrent selection where selection procedures are based on progeny performance (1) is also evidence for the presence of additive genetic variability in these varieties.

The purposes of this research were to partition the frequency distributions and variances in an attempt to determine the type of gene action affecting root weight and sucrose content and, to measure changes in root yield and percentage sucrose effected by breeding methods designed to take advantage of additive genetic variance.

Materials and Methods

Three breeding methods were used: modified mass selection, the polycross method, and recurrent selection for general combining ability. Mean comparisons are accompanied by partitioned frequency distributions and estimates of variance components.

The parental material from which the initial selections were made was a genetically broad-based monogerm population. It was synthesized by pollinating a self-sterile monogerm line with seven genetically diverse multigerm sugar beet varieties and breeding lines. About 750 monogerm segregates were then allowed to interpollinate; the resulting seed was designated as SLC 15 BB$_2$.

Using the Powers (7) method of selection from small units, 47 individuals superior for both root yield and percentage sucrose were selected from about 9,600 plants of SLC 15 BB$_2$. These selections were interpollinated in a modified polycross plot and also propagated asexually. Since the modification involved undivided roots, each selection appeared only once in the polycross plot. Thirty-three selections produced sufficient seed to be included in the polycross test together with the parental population, SLC 15 BB$_2$. Parent-progeny regressions and maternal half-sib correlations in the polycross test were used to estimate additive genetic variance. Forty-two phenotypically superior selections were made within those seven progeny lines with the highest combining ability for both root weight and sucrose percentage. This was a modified recurrent selection for general combining ability.

The five populations as follows were synthesized from the asexual propagations, polycrossed seed, and recurrent selections:

1. The mass-selected population, a composite of seed from all 47 plants in the polycross plot, represents a single cycle of mass selection with an equal genetic contribution from each maternal parent.
2. Polycross A was a composite of polycrossed seed from five of the 47 plants in population 1. These five had the most superior progeny performance for both root yield and percentage sucrose.
3. Polycross B resulted from interpollinating the asexual propagations of the five original selections with the most superior polycross performance for both root weight and percentage sucrose. Hence it represents a recombination of only those five genotypes with the highest general combining ability.

4. Synthetic A resulted from interpollinating the 42 recurrent selections made from within the seven polycross test entries with the highest general combining ability for root weight and sucrose.

5. Synthetic B resulted from interpollinating the five recurrent selections most superior for root weight and sucrose. These five recurrent selections were made from four of the seven high combining polycross test entries. The five roots were divided and were also included in Synthetic A.

These five population designations are not entirely appropriate but are used here in a somewhat general sense. The polycross populations arose from interpollinating individuals with superior progeny performance while the synthetic populations were derived by mating selected progeny from individual plants in the polycross populations. These five populations were included in a population genetic study together with SLC 15 BB$_2$, two inbreds, and two F$_1$ hybrids. The four nonsegregating populations were included for the purpose of estimating environmental variance. The 10 populations were planted in 40 replications of single-row plots, each bordered by a common competitor. The rows were 22 inches apart; plants within rows were 10 inches apart. Ten competitive roots were harvested from each plot, giving a total of 400 individuals in each population. Each root was analyzed individually for weight and percentage sucrose.

Results

Means, total within-plot variances, genetic variances, and broad-sense heritability ratios for root weight and percentage sucrose in the population genetic study are summarized in Table 1. The variances for root weight are calculated from common logarithm transformations in order to eliminate a mean-variance relation. The use of total within-plot variances eliminated variation attributable to replications and replication by population interaction. The genetic variances are total genetic variances which include both additive and nonadditive sources of genetic variability. The heritabilities (h^2) are ratios of total genetic variance to total within-plot variance. The variance of the four nonsegregating populations was used to estimate environmental variance.

In relation to SLC 15 BB$_2$ the sucrose percentage of Synthetic A and B was increased. Mass selection and Polycross A were not different than SLC 15 BB$_2$ while Polycross B showed a decrease. The total within-plot variances can be compared directly using the F test. A total of 360 degrees of freedom are associated with

Table 1.—Means, total within-plot variances, genetic variances, and heritability ratios for percentage sucrose and root weight in kilograms.

| Population | Percentage sucrose | | | | Root weight | | | |
| | Mean | Variance | | | Mean | Variance* | | |
		Total within plot	Genetic	h²		Total within plot	Genetic	h²
	(%)				(kgs.)			
Mass selection	16.83	1.03882	0.25450	0.245	1.076	0.052106	0.024269	0.466
Polycross A	16.80	1.02205	0.23773	0.233	1.111	0.053468	0.025634	0.479
Polycross B	16.52	1.14456	0.36024	0.315	1.206	0.049649	0.021812	0.439
Synthetic A	17.14	1.00740	0.22308	0.221	1.046	0.050259	0.022422	0.446
Synthetic B	17.14	0.86093	0.07661	0.089	1.005	0.063070 ·	0.035233	0.559
SLC 15 BB₂	16.78	1.13314	0.34882	0.308	1.045	0.045139	0.017302	0.383
Homozygous populations	16.39	0.78432			0.863	0.027837		
LSD 0.05	0.14				0.063			

*Variance caluculated from log root weight.

each variance, except those of the homozygous populations which have 1440. Any within-plot variance significantly larger than the estimated environmental variance must also have a genetic variance significantly greater than zero, hence, a significant broad-sense heritability ratio. Synthetic B was the only population without a significant heritability ratio for percentage sucrose, yet the mean was high. The mean of Polycross B was significantly lower than SLC 15 BB₂, yet its genetic variance remained high. For sucrose then, the five individuals with the highest general combining ability apparently have low specific combining ability with each other.

In an examination of root weight means, Table 1 shows that Polycrosses A and B were significant improvements over SLC 15 BB₂. Synthetic B had a significantly larger total within-plot variance than SLC 15 BB₂. The broad-sense heritability ratios were all different than zero. As in the case of percentage sucrose the highest variance for root weight was associated with the lowest mean, and *vice versa*.

The frequency distributions for both percentage sucrose and root weight were partitioned by the methods of Powers, et al. (8). This method adjusts the distributions to eliminate differences between replications within populations and differences between populations. This results in a common mean for all populations. The mean distribution of the four nonsegregating populations was used as the estimated environmental distribution. The distributions of the segregating populations were partitioned at approximate points of intersection of the obtained

and estimated environmental curves. The identifiable numbers of superior and inferior genetic deviates are differences between obtained and estimated environmental distributions to the right and left, respectively, of the distribution partition points (9). Hence all genetic deviates are not included, only those falling in the extreme classes where they are estimable or identifiable. The method used is nonparametric or distribution free, eliminating the necessity of making assumptions about the distributions. However, it remains necessary to assume that the genotype environment interaction is negligible. The identifiable numbers of genetic deviates, from a total of 400 in each population, are listed in Table 2.

Table 2.—Identifiable numbers of genetic deviates for percentage sucrose and log root weight.

Population	Percentage sucrose Identifiable number of genetic deviates			Log root weight Identifiable number of genetic deviates		
	Superior	Inferior	Total	Superior	Inferior	Total
Mass selection	15 ± 4	16 ± 4	31 ± 5	41 ± 6	32 ± 5	73 ± 8
Polycross A	18 ± 4	15 ± 4	33 ± 6	37 ± 6	26 ± 5	63 ± 7
Polycross B	14 ± 4	24 ± 5	38 ± 6	36 ± 6	24 ± 5	60 ± 7
Synthetic A	21 ± 4	14 ± 4	35 ± 6	37 ± 6	30 ± 5	67 ± 7
Synthetic B	8 ± 3	4 ± 2	12 ± 3	65 ± 7	48 ± 6	113 ± 9
SLC 15 BB₂	13 ± 4	24 ± 5	37 ± 6	33 ± 6	20 ± 4	53 ± 7

The correlations between numbers of genetic deviates and heritability ratios as determined by Powers, et al. (8) are shown in Table 3. The only partitioned group that was not significantly correlated with h^2 was the identifiable numbers of superior genetic deviates for percentage sucrose. For a normal distribution the proportion of genetic deviates should be a monotonic (increasing) function of heritability (h^2) and, hence, an equivalent index. For the non-normal case the two indices are no longer equivalent. In the case of percentage sucrose the estimated environmental distribution and that of mass selection deviated significantly from normal. A normality for root weight was the case for mass selection, Polycross B, Synthetic B, and the estimated environmental distribution. In spite of this anormality the correlations with root weight were quite high.

Table 3.—Simple correlation coefficients between heritability ratios and identifiable numbers of genetic deviates for percentage sucrose and log root weight.

Percentage sucrose			Log root weight		
Superior	Inferior	Total	Superior	Inferior	Total
0.39	0.99**	0.94**	0.92**	0.95**	0.94**

The bivariate frequency distribution of each population was partitioned at the same points as the component univariate distributions, resulting in nine sections (8). To avoid the problems introduced by small numbers in certain sections, the sections of interest were grouped. The group designated as superior consisted of the sections with superior sucrose and average weight, superior sucrose and superior weight, and average sucrose and superior weight. The group designated as inferior consisted of the sections with inferior sucrose and average weight, inferior sucrose and inferior weight, and average sucrose and inferior weight. The numbers of genetic deviates within these groups are listed in Table 4. The mean bivariate distribution of the nonsegregating populations was used as an estimate of the environmental distribution. The multiple correlations of superior, inferior, and total numbers of genetic deviates on heritability ratios, [Powers et al. (8)], are 0.27, 0.18, and 0.14, respectively, none of which even approach significance.

Table 4.—Number of genetic deviates in the superior and inferior groups and their total from the partitioned bivariate frequency distributions.

Population	Numbers of genetic deviates		
	Superior	Inferior	Total
Mass selection	33 ± 6	28 ± 5	61 ± 7
Polycross A	22 ± 5	17 ± 4	39 ± 6
Polycross B	36 ± 6	34 ± 6	70 ± 8
Synthetic A	30 ± 5	16 ± 4	46 ± 7
Synthetic B	40 ± 6	33 ± 6	73 ± 8
SLC 15 BB$_2$	40 ± 6	38 ± 6	78 ± 8

Two estimates of the additive genetic variance were obtained from the polycross progeny test. These were from maternal half-sib phenotypic covariance and parent-progeny regression. The component of variance for half-sib families estimates the phenotypic covariance of half sibs which, according to Falconer (4), is 25% of the additive variance, plus 6.25% of the additive by additive component. The latter is a small proportion of the total epistatic variance which can probably be ignored without serious consequence. No deviations due to dominance enter into this covariance between half sibs. The parent progeny regression is derived from the relation between the 33 polycross parents and the means of their respective progeny. Hence, it is the regression of progeny on one parent, and, as such, is an estimate of one-half the heritability. The resulting narrow sense heritability ratios for percentage sucrose are, respectively, 0.26 and 0.32, while the broad sense heritability estimate (ratio of total genetic variance to total within-plot variance) is 0.52. For

root weight these heritability ratios are, respectively, 0.02, 0.16, and 0.36. The covariance of half sibs is likely to provide the most accurate estimate of the additive variance. The likelihood of full sibs and progeny from self pollination being among these half sibs is very low; hence, any slight increase in the heritability estimate caused by the deviation from a strict half-sib relation can be ignored without serious consequence.

Using the covariance between half sibs to estimate the additive genetic variance, the total within-plot variance of pooled polycross progeny lines is partitioned in Table 5 into additive genetic, nonadditive genetic, and environmental variance components. The nonadditive genetic component is the sum of the dominance and interaction components. The total within-plot variance of an F_1 hybrid was used to estimate the environmental variance. The data for root weight were transformed to common logarithms to remove a mean-variance relation. For percentage sucrose the total genetic variance amounts to 52% of the total variance. Slightly more than half of this total genetic variance may be attributed to additive effects of the genes involved.

Table 5.—Partitioning of the variance of pooled polycross progeny lines.

Component of variation	Variance	
	Percentage sucrose	Root weight
Additive genetic	0.616520	0.000976
Nonadditive genetic	0.597333	0.017037
Environmental	1.116493	0.032205
Total within-plot	2.330346	0.050218

For root weight the components of variance in Table 5 indicate that the nonadditive genetic variance is of primary importance. Thirty-six percent of the total variance is genetic with only 2% estimated as additive genetic variance.

When using partitioned frequency distributions of SLC 15 BB_2 and assuming all genetic variance to be additive the predicted advance was 5.4% for percentage sucrose and 14.0% for root weight. The obtained advance of pooled progeny lines was 3.8 and 6.0%, respectively.

Discussion

The individuals selected as parents contributed significantly to the genetic variance of their parent population by virtue of their being genetic deviates from the population mean. The degree to which this superiority was transmitted to their progeny should serve as a check on the expected result. Additive, dominance, and epistatic gene action and environmental effect could account for parental superiority. With the breeding methods

used, all the additive gene effects and one-fourth the additive-by-additive epistatic effects should have been reflected directly in the progeny. There is some indication that the year by population interaction may be of importance. This could affect expected results.

For percentage sucrose the results of the partitioned frequency distributions and genetic variance (assuming that there was no genotype-environment interaction) indicate that some advance should have been expected in all five synthesized populations. The greatest advance should have occurred in Synthetic A and B. The obtained advance of Synthetic A and B indicates that additive gene effects contribute significantly to improvement and that sucrose content can continue to be improved through advanced cycles of selection utilizing superior general combining ability. The significant decrease of Polycross B is not readily explained. The prediction of a 5.4% gain in percentage sucrose based on the partitioned frequency distribution of SLC 15 BB_2 assumes all genetic variance to be additive. The obtained gain of 3.8% from pooled progeny lines indicates that something less than 70% of the total genetic variance should be due to additive gene effects.

Genetic variance component estimates and partitioned frequency distributions indicate that little improvement should be expected in root weight with any of the breeding methods used. However, the obtained advance of Polycross A and B indicates that additive gene effects may be of greater importance than the variance component estimates have indicated. These two populations are related as half sibs and, theoretically, have a genetic correlation of 0.25. This could partially account for their parallel improvement.

When compared with the obtained advance of 6% for pooled progeny lines, the predicted root weight advance of 14% for SLC 15 BB_2 (which assumes that all genetic variance is additive), indicates that the additive genetic variance is about 43% of the total genetic component. The proportion of additive genetic variance estimated from the half-sib covariance is 0.02, but from the parent progeny regression it is 0.16. This indicates that the half-sib covariance may be an underestimate of the actual additive genetic variance component.

Considering root weight and percentage sucrose simultaneously as components of sugar yield, the three breeding methods do not differ significantly. Synthetic B has a lower gross sugar yield than SLC 15 BB_2, but this could be partly attributable to the fact that only five recurrent selections were used in its synthesis.

The inverse relationship of means and genetic variances for both sucrose percentage and root weight can not be readily explained. One's first impression is that superiority for these characters must be rather simply inherited. This is not borne out, however, by variance component estimates and obtained advances in performance. Another factor which could be related is the apparent inverse relation of heritabilities for sucrose and root weight. Among these populations, the ones with the greatest genetic variance for one character have the least genetic variance for the other character. Such an inverse relationship is also common among their means. These relationships seem to indicate that the control of sucrose and yield is not necessarily physiological, but could result from facultative pleiotropy or genetic linkage.

With respect to the analytic methods, the partitioned frequency distributions and estimation of identifiable numbers of genetic deviates provide an evaluation of the genetic potential of a population and provide information not readily apparent from two or more heritability ratios jointly considered. Accompanied by estimates of the genetic variance components the two methods are quite complementary.

It becomes evident that breeding methods designed to capitalize on additive gene effects would not, by themselves, lead to a rapid advance in sugar yield. But these methods should remain valuable as the first stage of a breeding program designed to take advantage of both additive and nonadditive gene effects. When both additive and nonadditive gene effects are present in a population, maximum ultimate yields should be attainable by full utilization of the additive genetic variability prior to extraction of genotypes with high specific combining ability. Another alternative is the use of a breeding system such as reciprocal recurrent selection which utilizes additive and nonadditive genetic variability simultaneously.

Summary

These breeding methods capitalizing principally on additive genetic variance were studied for their effect on root weight and percentage sucrose in sugar beets. Forty-seven superior plants were selected among 9,600 individuals of a genetically broad-based monogerm population. They were polycrossed and asexually propagated. Recurrent selections for high general combining ability of root weight and percentage sucrose were made within the seven most superior polycrossed progeny lines. From asexual propagations, polycrossed seed, and recurrent selections, five populations were synthesized. One population was developed

by mass selection, two by the polycross breeding method, and two by recurrent selection for general combining ability. A sucrose advance was demonstrated in the two populations from recurrent selections. A root weight advance was indicated in the two populations produced by polycross methods. Joint consideration of both characters revealed little difference between breeding methods in relation to gross sugar yield. The estimated additive genetic variance component for sucrose percentage accounted for more than half of the total genetic variance. Additive genetic variance for root weight was negligible relative to the nonadditive component. The breeding methods relying on additive gene effects should be valuable as the first stage of a breeding program capitalizing on additive and nonadditive gene action for sucrose percentage and root weight.

Literature Cited

(1) BREWBAKER, H. E., H. L. BUSH and R. R. WOOD. 1950. A quarter century of progress in sugar beet improvement by the Great Western Sugar Company. Am. Soc. Sugar Beet Technol. Proc. p. 202-207.

(2) COONS, G. H. 1936. Improvement of the sugar beet. Yearbook of Agriculture, U. S. Dept. of Agr. p. 625-656.

(3) DEMING, G. W. 1942. Use of red garden beet in sugar-beet top crosses. Am. Soc. Sugar Beet Technol. Proc. p. 336-341.

(4) FALCONER, D. S. 1960. Introduction to Quantitative Genetics. Ronald Press Company, New York. 365 p.

(5) JOHNSON, R. T. 1952. A comparison between corn and sugar beet breeding methods. Am. Soc. Sugar Beet Technol. Proc. p. 296-306.

(6) LIPPMANN, E. O. VON. 1925. Geschichte der Rübe (Beta) als Kulturpflanze. J. Springer, Berlin. 184 p.

(7) POWERS, L. 1957. Identification of genetically-superior individuals and the prediction of genetic gains in sugar beet breeding programs. J. Am. Soc. Sugar Beet Technol. 9: 408-432.

(8) POWERS, L., E. E. REMMENGA and N. S. URQUHART. 1964. The partitioning method of genetic analysis applied to a study of weight per root and percentage sucrose in sugarbeets (Beta vulgaris L.). Colo. Agr. Exp. Sta. Tech. Bul. 84. 23 p.

(9) POWERS, L., D. W. ROBERTSON and A. G. CLARK. 1958. Estimation by the partitioning method of the numbers and proportions of genetic deviates in certain classes of frequency distributions. J. Am. Soc. Sugar Beet Technol. 9: 677-695.