Identification of Genetically-Superior Individuals and the Prediction of Genetic Gains in Sugar Beet Breeding Programs[1]

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The identification of genetically- superior individuals and the prediction of genetic gains should add materially to the effectiveness of the breeding programs with sugar beets and other crops. The purposes of this article are to present methods and formulas used to identify genetically-superior individuals and to predict genetic gains in segregating and heterogeneous populations. Applications of these methods and formulas are illustrated.

Literature Review

Wright (28)[3] discusses the genetic principles governing the rate of progress of livestock breeding. These principles are equally basic to plant breeding.

Dickerson and Hazel (3) and Lush (11) have developed methods and formulas for predicting genetic gains applicable to animal breeding. Robinson, Comstock, and Harvey (21) and Robinson, Mann, and Comstock (22) developed somewhat similar methods and formulas for predicting genetic gains in plant breeding.

The immediate genetic theory basic to the development of the methods of identifying genetically-superior individuals has to do with the partitioning of variance into its components and the partitioning method of genetic analysis. This is also true of the methods used in predicting genetic gains.

Fisher (4) was the first to provide a statistical method of partitioning variance into its environmental and genetic components. Fisher, Immer, and Tedin (6) elaborated on this method and gave several formulas for further partitioning genetic variance, using barley data to illustrate the application of the formulas. Wright (24, 25, 26, and 27) independently developed formulas and methods for studying variance components. These methods have been applied and extended by research workers in the animal and plant fields (see Lush, 11; Comstock and Robinson, 1; Robinson, Comstock, and Harvey, 19 and 20; Mather, 12; Lerner, 9; and Powers, 17).

Powers (14, 16, and 17) and Powers, Locke, and Garrett (18) have presented methods and formulas in addition to the above that are basic to the methods presented in this article for identifying genetically-superior individuals and predicting genetic gains in segregating and heterogeneous populations.

Lerner and Hazel (10) applied the method developed by Dickerson and Hazel (3) to egg production in poultry. The predicted gain per bird

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[3] Numbers in parentheses refer to literature cited.

per year was 5.28 eggs and the actual gain was 5.6 eggs per bird per year. It is obvious that the agreement between the rate of improvement expected from selection and that obtained is remarkably close.

Materials and Experimental Design

The characters studied were percentage sucrose and weight per root in sugar beets (*Beta vulgaris* L.). The experiment was conducted during the growing period of 1955.

Six populations were included in the study. The F_1 hybrid resulted from crossing two inbred lines, 50-406 with 52-307. GW359-52R is the variety being grown by farmers producing beets for the Great Western Sugar Company in the Rocky Mountain Region. SP 53104-0 is a United States Department of Agriculture production under development as a variety carrying resistance to curly top and leaf spot. US 201 is not a commercial variety but a closebred strain extremely high in leaf-spot resistance and is very valuable as a parent to furnish genes conditioning resistance to the organism causing this disease. The inbred lines 50-449 and 52-305 were produced by the late G. W. Deming. The exact number of generations of inbreeding is not known. However, Mr. Deming stated that 52-305 had resulted from many generations of inbreeding and was included in the studies because he believed it to be relatively homozygous.

Inbred line 52-305 and the F_1 hybrid were included in the experiment to obtain a measure of environmental variability and to furnish some measure of the reliability of the methods used. The inbred line 50-406 has recessive-green hypocotyls and 52-307 has dominant-red hypocotyls. Hence, the F_1 plants produced by seed harvested from 50-406 could be identified by hypocotyl color. During thinning, the green hypocotyl plants were eliminated, thus insuring that only F_1 hybrid plants were left. At the time of harvest, all roots were found to have pink buds, and in this manner the F_1 cultures were checked for possible self- or intra-fertilized plants.

In planting the different cultures of the experiment, the rows were spaced 40 inches apart and subsequently the beets were thinned to a spacing of 20 inches between beets within the row. The wide spacing between and within rows was used to minimize competition between beets. At time of thinning each culture was reduced to 12 plants and only 8 plants were harvested per culture. Any beets showing visual evidence of disease, either before or after being pulled, were discarded.

The field design of the experiment was a randomized complete block composed of two parts. The first part included the six populations listed in Table 1, and the second part included 52-307 in place of the F_1 hybrid. The first part was composed of 20 blocks and the second part of 60 blocks. Since, for the second part of the experiment, eight roots were not available for all plots the number was reduced, by random elimination, to six before analysing the data. Hence, there was a total of 160 plants per population available for statistical analysis in the first part of the experiment and 360 available for analysis in the second part of the experiment. Five of the populations occur in both parts, making a total of 520 plants for these populations. The present article reports on the analysis of the populations involving 160 individuals and those involving 520 individuals.

Table 1.—Population Frequency Distributions Expressed in Percentages for Percentage Sucrose[1 2]

Population	Upper limit of Class in Percent														
	0 to 6.75	7.50	8.25	9.00	9.75	10.50	11.25	12.00	12.75	13.50	14.25	15.00	15.75	16.50	17.25 & >
	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%
F_1 hybrid						1.9	7.5	21.9	14.4	28.8	15.6	8.7	1.2		
GW359-52R		0.6	0.6	1.9	0.6	8.8	10.0	15.6	21.9	14.4	13.1	5.0	3.8	2.5	1.2
SP 53104-0	1.2	2.5	5.0	1.9	8.7	8.1	14.4	21.9	11.2	14.4	6.9	3.8			
US 201	1.9	2.5	6.2	5.6	8.8	15.6	20.6	19.4	5.0	8.1	3.8	0.6	1.9		
50-449	0.6	2.5	5.0	7.5	8.1	21.3	20.6	18.1	7.5	5.6	1.3	1.9			
52-305					0.6	6.9	12.5	18.8	25.6	23.1	11.9		0.6		

[1] Number of plants per population = 160.

[2] The percentage of any given frequency distribution enclosed in brakets is the proportion identified as genetically superior.

Identification of Genetically-Superior Individuals for Percentage Sucrose

The frequency distributions of the populations for percentage sucrose having N values of 160 are listed in Table 1. In reality identification of genetically-superior individuals and the prediction of genetic gains involve analyses of these frequency distributions. The frequency distributions are expressed in percent rather than number of plants, and the upper limits of the classes are given. By so doing the analyses of the data are facilitated.

One of the first steps in analysing the frequency distributions is to partition the variances into their components. To do this it is necessary to have a measure of the environmental variability. Inbred line 52-305 and the F_1 hybrid 50-406 x 52-307 were included in the experiment to measure the environmental variability. An examination of Table 1 reveals that the ranges (number and values of classes in which individuals occur) are not greatly different for the frequency distributions of 52-305 and the F_1 hybrid and are considerably less than those for the other populations. It appears that either, or both, of these populations furnish a satisfactory estimate of the environmental variability. Whether this assumption is correct will be determined as the analyses of the data proceed. For percentage surcrose, data from inbred 52-305 are used to estimate the environmental variance and those from the F_1 hybrid to give a practical check on the methods and formulas employed.

It is important to determine which populations have genetic variances. Those not showing any genetic variability would not be expected to possess any genetically-superior individuals nor would genetic gains be possible by breeding within them. Hence, the data from 52-305 and the F_1 hybrid compared with the data from the segregating populations serve somewhat as a practical check on the reliability of the methods employed to identify genetically-superior individuals and to predict genetic gains.

The means, total variances, and genetic variances of populations for percentage sucrose are listed in Table 2. The information in this table indicates whether there are differences between means of populations, in which populations genetically-superior individuals occur, and finally in which populations it is possible to make genetic gains by application of suitable breeding methods.

As given by footnote 2 of Table 2 the F value obtained by analysis of variance is 21.13 for differences between means of populations. That required for significance at the one percent level is 4.40. There are differences between means of populations as regards percentage sucrose. At least, the means fall into two classes; the F_1 hybrid, GW359-52R, and 52-305 comprising one class, and SP 53104-0, US 201, and 50-449 comprising the other class.

The total variance of 52-305 listed in Table 2 is used as an estimate of the environmental variance. The genetic variances listed in the fourth column of this table are obtained by subtracting this estimate (1.1533) from the total variances of column 3.

A comparison of the genetic variances with their standard errors reveals that all except the variance of the F_1 hybrid are significantly different from zero. The estimated genetic variance of the F_1 hybrid should not be significantly different from zero if both parents are relatively homozygous. This confirms that either 52-305 data or the data of the F_1 hybrid, or both, are suitable for estimating the environmental variability of percentage sucrose.

Table 2.—Means, Total Variances, and Genetic Variances for Percentage Sucrose and Populations[1].

Population	Mean[2] Sucrose	Variance[3] Total	Genetic
	Percent		
F_1 hybrid	12.8	1.2578±0.1411	0.1045±0.1914
GW359-52R	12.5	2.9929±0.3357	1.8396±0.3597
SP 53104-0	11.3	3.7125±0.4164	2.5592±0.4360
US 201	10.7	3.7695±0.4228	2.6162±0.4421
50-449	10.7	2.6376±0.2958	1.4843±0.3229
52-305	12.3	1.1533±0.1293	——— ———

[1] The number of plants per population 160.

[2] The F value for populations is 21.13, the degrees of freedom are 5, and for populations times replications, which variance was used as an estimate of error, the degrees of freedom are 95. The mean square used in calculation of the F value for populations is derived from culture totals (total of 8 plants).

[3] These are the within population variances calculated from individual plant data. The standard errors of the total variances are calculated from a formula given by Fisher (5, page 78). The standard errors for the genetic variances are calculated from the well known formula for the standard error of a difference.

In identifying genetically-superior individuals it is assumed that the proportion of individuals in each class of Table 1 can be estimated and the deviations of the estimates from the obtained frequency distributions will not be greater than expected by chance. This assumption can be tested for the F_1 hybrid and 52-305 populations by testing for agreement using the chi square frequency distribution. The means of the population under consideration, the standard error calculated from the environmental variance (variance of 52-305, see Table 2), and Pearson's (13) normal probability tables are employed. For details of the method see Powers (15) and Leonard, Mann, and Powers (8). For both of these populations the deviations from the calculated and obtained frequency distributions are no greater than expected due to chance. All of the data necessary to carry out the calculations are given in Tables 1 and 2.

The finding that the frequency distributions based on environmental variation can be predicted within the limits of random sampling, justifies proceeding with the analysis pertaining to the identification of individuals genetically superior and to prediction of genetic gains. To do this it is necessary to determine an upper class beyond which the odds are great that individuals will not occur due solely to environmental variability. That is, the odds are great that the individuals occurring beyond the upper limit of this class are genetically superior to the average of the population. Stated in still another way these individuals have values greater than those delimited by chance fluctuations due to the environmental variability. The methods and formulas used in determining the upper limit of the class beyond which only individuals genetically superior to the average of the population would be expected to occur are given in a previous publication (Powers, 16). Certain minor modifications and extensions of the use of these methods and formulas are necessary in identifying genetically-superior individuals and in predicting genetic gains. Therefore their application to percentage sucrose will be given in some detail.

The formula for predicting the mean of sub-group frequency distributions is $y = z - s_d x'$ (Powers, 16). In identifying genetically-superior individuals the z values given in Table 3 are obtained by application of the formula $z = \bar{x} + s_d x'$. This formula is easily derived from the formula $y = z - s_d x'$, in which $\bar{x}$ is substituted for y. In the application of these formulas the symbols used and those given in Table 3 have the following connotations.

y = predicted mean
$\bar{x}$ = obtained mean
z = upper limit of class
s_d = estimated standard error calculated from the environment variance of 52-305 (total variance of Table 2).
$p = 1 - q$
$q = \frac{1}{2}(1 + a)$ Pearson's (13) tables
x' = x of Pearson's (13) tables

Table 3.—Percentage of Identified-Genetically-Superior Individuals and Estimated Means of Sub-Group Frequency Distributions in Which These Individuals Occur For Percentage Sucrose and Populations[1], [2].

Populations	Value of z for p = 0.003	Value z Used	Superior Individuals[3]	Value of x'	Mean: Obtained $\bar{x}$	Mean: Predicted, y: Superior Individuals[3]	Predicted, y: 12.5%	Predicted, y: 37.5%
	Percent	Percent	Percent		Percent	Percent	Percent	Percent
F_1 hybrid	15.70	15.75	0.0	——	12.8	——	——	——
GW359-52R	15.40	15.75	3.7	1.79	12.5	13.8	14.5	15.4
SP 53104-0	14.20	14.25	3.8	1.78	11.3	12.3	13.0	13.9
US 201	13.60	14.25	2.5	1.96	10.7	12.1	13.0	13.9
50-449	13.60	14.25	1.9	2.07	10.7	12.0	13.0	13.9
52-305	15.20	15.75	0.0	——	12.3	——	——	——

[1] The number of plants per population = 160.

[2] The variance of 52-305 is 1.1533 (see Table 2) and the standard error (s_d) is 1.0739. This variance and this standard error were used as estimates of the environmental variance and environmental standard error, respectively.

[3] These means are estimated from the percents listed under the column heading "Superior individuals" and the superior individuals are the percentages of individuals in classes of Table 1 falling beyond the values of z used (3rd column of Table 3).

In identifying genetically-superior individuals it is necessary to determine the value of p to be employed. The value of p that should be used is dependent upon the number of individuals in the population and the intensity of the selection to be practiced. Another way of stating the problem that may help to clarify this point is as follows: The decision as to what value of p to use is based on the number of individuals the investigator wishes to select for further study and breeding, and the number of genetically-superior individuals it is possible to identify in the population under consideration.

For example, if a p value of 0.003 is employed, as shown previously the value of z may be calculated from the formula $z = \bar{x} + s_d x'$. The calculations for GW359-52R are as follows:

$\bar{x} = 12.5$ (see Table 3)

$s_d = 1.0739$ (see footnote of Table 2)

$p = 0.003$ (chosen value)

$q = 0.997$ (l-p)

$x' = 2.70$ (value of x in Pearson's (13) tables for $\frac{1 + a}{2}$ equals 0.997)

$z = 12.5 + (1.0739 \times 2.70) = 15.40$ as given in the second column of Table 3

The values of z for the other population given in the second column of Table 3 are calculated in a similar manner.

Since, in this example, p was chosen as 0.003 only one individual in a population of 333 would be expected to equal or exceed the value of 15.40 percent sucrose. Hence, the probability of two individuals in a population of 160 exceeding 15.40 percent sucrose is very small. Consequently the p value of 0.003 should be satisfactory for studying the frequency distributions of Table 1 providing, due to genetic superiority, there are a sufficient number of individuals exceeding the value of z used.

The value of z as calculated above seldom corresponds to an upper class limit, as is necessary to identify the genetically-superior individuals in frequency distributions such as those listed in Table 1. From an examination of the frequency distribution of GW359-52R given in Table 1 it can be seen that the calculated z value (15.40) falls into the class having an upper limit of 15.75 percent sucrose. Hence, the value of z selected is 15.75 as shown in the third column of Table 3. The other values of z listed in this column were determined in a similar manner. It should be pointed out that if the investigator desires to work with calculated values of z, such as 15.40, he can do so by referring to the data from which the frequency distributions were compiled.

The value of 3.7 listed in the fourth column of Table 3 is the percentage of individuals in the frequency distribution of GW359-52R that exceeded 15.75 percent sucrose. As the fourth column heading indicates, the percentages listed under it are those cumulated for all the classes whose upper limits exceed the value of z used.

For GW359-52R, the number of individuals having an upper class limit greater than 15.75 is 6 (3.7 percent of 160). The chances are very good that all six of these individuals are genetically superior as regards percentage sucrose, and it is reasonably certain that at least five of them fall into this category. By labeling all beets at time of harvest with culture and plant number these individuals can be selected for further use in the breeding program and for further studies.

It is apparent that the percentages listed in column 4 of Table 3 are the proportions of identifiable-genetically-superior individuals in the respective populations. As stated previously, if the beets are labeled at time of harvest the procedures and calculations outlined provide a means of identifying some of the genetically-superior individuals. It is equally apparent that these are not all the genetically-superior individuals in the population. In all probability they are not even a preponderant proportion of such individuals.

Predicting Genetic Gains in Percentage Sucrose

The percentages of identifiable-genetically-superior individuals listed in the fourth column of Table 3 provide a basis of predicting genetic gains in percentage sucrose. It is clear that these individuals are members of a sub-group frequency distribution having a mean larger than that of the population in which they occur. Environmental variability and probably to some extent genetic variability are causing them to fluctuate and hence form a sub-group within the population frequency distribution. The problem has resolved into one of estimating the means of these sub-group frequency distributions of which these genetically-superior individuals are members.

The formula employed to predict the means of these sub-group frequency distributions is $y = z - s_d x'$ (see Powers, 16) and the connotations of the symbols are as given previously in this article. The number of individuals in this sub-group frequency distribution is not known, and therefore the proportion that the genetically-superior individuals are of this sub-group is not known. However, what proportion they are of the respective populations in which they occur is known. For GW 359-52R the identifiable-genetically-superior individuals constitute 3.7 percent of the population.

Using the percentage for GW359-52R a conservative estimate (underestimate) of the sub-group mean can be calculated. As stated above, the formula employed is $y = z - s_d x'$. The calculations are as follows: Converted to decimal fractions the proportion of genetically-superior individuals is 0.037. This is the value of p. The value of q is l-p, or 0.963, and it is designated as ½ (1 + a) in Pearson's (13) tables. As taken from Pearson's tables the corresponding value of x′ is 1.79. The x′ values for all populations are listed in the fifth column of Table 3. The value of z used for GW359-52R is 15.75 (see Table 3). This is a conservative estimate of z, because, as can be determined from Table 1, 1.2 percent of the population exceeded 16.50 percent sucrose. By substituting the proper values in the formula given at the beginning of this paragraph, $y = 15.75 - (1.79 \times 1.0739)$. By completing the calculations a value of 13.8 percent sucrose is obtained, as listed in the seventh column of Table 3. The predicted genetic gain in percentage sucrose for GW359-52R is 13.8 minus 12.5 (column 7 minus column 6), or 1.3 percent. The values for the other populations are calculated similarly.

The values listed under columns 8 and 9 of Table 3 (heading 12.5% and 37.5%, respectively) were obtained by substituting 12.5% and 37.5% for the values of column 4 of Table 3 and carrying out the calculations as given in the immediately preceding paragraph. The values listed in column 9 compared with the obtained means (column 6) represent maximum genetic gains that may be possible by breeding within the populations listed in Table 3. The genetic levels that can be reached for these populations, by appropriate methods of breeding, probably lie somewhere between the values listed in column 7 and those listed in column 9.

The values for percentage sucrose listed in column 7 of Table 3 compared with those given in column 6 show the expected genetic gains based on a conservative estimate of the means of the sub-group frequency distributions. These gains for the populations starting with GW359-52R and going down the table in order are 1.3, 1.0, 1.4, and 1.3 percents, respectively. The increases expressed as percentages of the obtained means are 10.4, 8.8, 13.1, and 12.1 percents, respectively.

Identification of Genetically-Superior Individuals and Prediction of Genetic Gains for Weight per Root

The methods and formulas used in the identification of genetically-superior individuals and to predict genetic gains for weight per root are essentially the same as those for percentage sucrose. The differences that do exist are attributable to the positive relation between the means and environmental variances for weight per root. Hence the variances of the non-segregating populations cannot be used directly as an estimate of the environmental variance for the segregating populations. For such characters as weight per root, regression may be used to estimate the environmental variances of the segregating populations (see Powers, 14). This method of estimation assumes a straight line relation between the means and environmental variances. Consequently, to employ this method two points on the line are essential. In the present study these are furnished by the means and variances of the F_1 hybrid and inbred line 52-305. When studying characters that exhibit heterosis, such as weight per root, it is desirable to include at least one F_1 hybrid and at least one inbred line. This usually assures that two rather widely separated points on the regression line will be available for estimating the environmental variances of the segregating populations.

The population frequency distributions for weight per root are given in Table 4. The smallest range is for 52-305 and the greatest range is for GW359-52R. The range for the F_1 hybrid is considerably greater than that for 52-305 and the frequency distribution lies in classes having a greater weight per root. This is to be expected if both the mean weight per root and the environmental variance are greater for the F_1 hybrid. As was the case for percentage sucrose, the identification of genetically-superior individuals and prediction of genetic gains for weight per root involve analyses of the frequency distributions which are listed in Table 4.

Table 4.—Population Frequency Distributions Expressed in Percentages for Weight Per Root[1], [2].

Population	Upper Limit of Class in Pounds																
	0 to 0.75	1.50	2.25	3.00	3.75	4.50	5.25	6.00	6.75	7.50	8.25	9.00	9.75	10.50	11.25	12.00	12.75 & >
	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%
F_1 hybrid				7.5	13.1	25.0	21.9	16.3	10.0	4.4	1.2	0.6					
GW359-52R		1.9	0.6	1.9	3.7	11.9	12.5	13.1	12.5	10.0	10.6	8.8	4.4	5.0	0.6	[0.6	1.9]
SP 53104-0			4.4	10.6	13.1	24.4	16.9	16.3	6.9	6.2		[1.2]					
US 201	3.1	11.3	15.0	26.9	18.8	14.4	8.1	[0.6	1.2	0.6]							
50-449		5.6	11.9	33.8	23.8	16.2	6.2	1.9			[0.6]						
52-305		3.1	45.7	45.0	5.6	0.6											

[1] Number of plants per population = 160.

[2] The percentage of any given frequency distribution enclosed in brackets is the proportion identified as genetically superior.

Again, as for percentage sucrose, the analyses of these frequency distributions for weight per root assume that the proportion of individuals in the different classes of the frequency distribution can be estimated by employing Pearson's (13) normal probability tables and formulas given by Powers (16). These formulas for calculating the theoretical frequency distributions make use of the obtained means and environmental standard errors. Whether the calculated theoretical proportion of individuals in the different classes agrees with those obtained can be determined for the F_1 hybrid and 52-305 populations. For both populations applications of chi square for agreement revealed that the deviations between the obtained and calculated proportions in the different classes of the frequency distributions are no greater than expected by chance. All the data necessary for making the test are given in Tables 4 and 5. This finding justifies proceeding with the analyses of the data.

The means, total variances, within-culture variances, within-culture environmental variances, and within-culture genetic variances for weight per root are listed in Table 5.

Table 5.—Means, Total Variances, Within-Culture Total Variances, Within-Culture Environmental Variances, and Within-Culture Genetic Variances for Weight Per Root and Populations[1].

Population	Mean	Variance			
		Total[2]	Within Cultures[3]		
			Total	Environmental	Genetic
	Lbs.				
F_1 hybrid	4.74	1.4194±0.1592	1.0145±0.1327	1.0145±0.1327	——— ———
GW359-52R	6.44	5.1248±0.5748	5.0596±0.6429	1.5729±0.2182	3.4867±0.6723
SP 53104-0	4.56	1.9520±0.2189	1.7879±0.1871	0.9469±0.1296	0.8410±0.1634
US 201	2.94	1.6270±0.1825	1.4861±0.1992	0.4196±0.0819	1.0665±0.1841
50-449	3.09	1.1246±0.1261	1.0139±0.1789	0.4417±0.0700	0.5721±0.1688
52-305	2.29	0.2349±0.0263	0.1825±0.0374	0.1825±0.0374	——— ———

[1] The number of plants per population = 160.

[2] The standard errors of these variances are calculated from a formula given by Fisher (5, page 78).

[3] The standard errors of these variances are calculated from the data, variances for cultures within populations. For the details of calculating the variances of these variances see Powers (17, pages 9 and 10).

The t test in which standard errors were calculated for each population from the data within each population shows that there are significant differences between means of populations. However, since there is a positive relation between the means and variances, the results from the analysis of variance must be interpreted with this in mind. The analysis of variance together with the results from the t test seem to justify the following conclusions. The F values obtained from an analysis of variance led to the same conclusions. The means compose four levels of weight per root; GW359-52R composes one level, the F_1 hybrid and SP 53104-0 another, US 201 and 50-449 another, and 52-305 the fourth level.

There are four different columns of variances listed in Table 5. These are given to illustrate the difference in estimating the genetic variances for percentage sucrose in which there is no relation between the means and environmental variances and weight per root in which there is a positive relation between the means and variances.

It will be remembered that in Table 2 the genetic variances were calculated by subtracting the total variance of 52-305 from the total variances of the other populations. The variances given in the 3rd column of Table 5 correspond to the variances given in the third column of Table 2. The within-culture total variances given in the fourth column of Table 5 were calculated from the eight plants of each culture of a given population. The errors were calculated by standard methods using the 20 estimated variances for a given population. It is interesting to note the rather close agreement between the errors for the total variances (column 3) calculated by use of Fisher's formula (5) and those (column 4) obtained from the data for the within-culture total variances.

Likewise the within-culture environmental variances (column 5) were calculated on the basis of cultures, and the standard errors were obtained by use of standard methods applied to the 20 variances of a given population. Finally, on the basis of cultures, the within-culture genetic variances were calculated by subtracting the corresponding within-culture environmental variance from the within-culture total variance. Again the standard error for any given population was calculated from the 20 genetic variances so estimated.

Table 6.—Percentage of Identified-Genetically-Superior Individuals and Estimated Means of Sub-Group Frequency Distributions in Which These Individuals Occur for Weight Per Root and Population[1].

Population	Value of z Used[2]	Environmental Standard Error[3]	Superior Individuals	Value x'	Mean: Obtained X	Mean: Predicted, y: Superior Individuals	Mean: Predicted, y: 12.5%	Mean: Predicted, y: 37.5%
	Lbs.		%		Lbs.	Lbs.	Lbs.	Lbs.
F1 hybrid	9.00	1.1914	0.0	—	4.74	—	—	—
GW359-52R	11.25	1.4971	2.5	1.96	6.44	8.32	9.53	10.77
SP 53104-0	8.25	1.1543	1.2	2.25	4.56	5.65	6.92	7.88
US 201	5.25	0.7410	2.4	1.97	2.94	3.79	4.40	5.01
50-449	6.00	0.7884	0.6	2.49	3.09	4.04	5.09	5.75
52-305	4.50	0.4847	0.0	—	2.29	—	—	—

[1] The number of plants per population = 160.

[2] The value of p for the values of z used are equal to or less than 0.001.

[3] The variances giving rise to these standard errors for the heterogeneous populations are calculated from the mean of the respective population and the means and total variances (column 3 of Table 5) of the F1 hybrid and 52-305 (for method see Powers, 14).

By comparing the genetic variances with their standard errors it is clear that they are significantly different from zero for GW359-52R, SP 53104-0, US 201, and 50-449. In these populations it should be possible to identify genetically-superior individuals and to predict genetic gains.

The percentage of identified-genetically-superior individuals and estimated means of the sub-group frequency distributions in which these individuals occur are given in Table 6. The variances giving rise to the standard errors listed in the third column of Table 6 are calculated by regression involving the mean of the respective population and the m and b constants in the formula $y' = mx + b$. The symbols in the formula have the following connotations:

y' = environmental variance

m = the slope of the regression line

b = the point of intercept of the regression line and the ordinate

x = the mean of the population whose variance is being estimated

In application of the above formula m and b are calculated from the means and variances of the F_1 hybrid and 52-305. For details of the method for estimating the environmental variances of the heterogeneous populations see Powers (14).

The genetically-superior individuals identified are those composing the percentage values listed in the fourth column of Table 6. The number of identified-genetically-superior individuals for GW359-52R and US 201 populations is four (0.025 X 160), for SP 53104-0 is two, and for 50-449 is one. Since the value of p used in calculating the percentage of identifiable-genetically-superior individuals was 0.001 the chances are good that most, if not all, of the 11 individuals representing the percentages listed in column 4 of Table 6 are genetically superior. The chances are very small that two of them would occur in these classes due to environmental variability.

A conservative estimate of the genetic gains possible by application of the proper breeding methods is obtained by comparing the values listed under mean and obtained, with those listed under mean and superior individuals. The increases expected for the heterogeneous populations starting with GW359-52R and proceeding down Table 6 are 29.2, 23.9, 28.9, and 30.7 percent, respectively. Hence, according to the conservative estimates, decided advances can be made in weight per root. The increased levels of yield are even higher for the columns listed under 12.5 percent and 37.5 percent. However, these latter levels of yield would be much more difficult to attain.

Percentage Sucrose and Weight per Root Considered Simultaneously

So far the analysis of the data has considered the identification of genetically-superior individuals for either percentage sucrose or weight per root, but not both simultaneously. In any breeding program both characters must be taken into consideration. At least, the breeder attempts to maintain the level of one of these characters while improving the other.

Table 7.—Frequency Distributions of GW359-52R Expressed in Percentages for Percentage Sucrose and Weight per root[1, 2, 3].

Weight Per Root Upper Limit of Class in Pounds	Percentage Sucrose Upper Limit of Class in Percent														
	0 to 7.50	8.25	9.00	9.75	10.50	11.25	12.00	12.75	13.50	14.25	15.00	15.75	16.50	17.25 & >	Total
	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%
0 to 1.50								0.2	0.2	0.2	0.2			0.2	1.0
2.25								0.2	0.6	0.2		0.4			1.4
3.00						0.2		0.4	0.7	0.4	0.2		0.2	0.2	2.3
3.75					0.2	0.2	0.4	0.8	1.1	1.5	1.3	1.2	0.2		6.9
4.50				0.2	0.4	0.6	1.0	1.7	2.3	1.5	2.1	1.3		0.2	11.3
5.25	0.2	0.4	0.4		0.4	0.8	1.2	2.3	3.3	1.9	1.3	0.8	0.5		13.5
6.00					0.6	0.8	1.9	2.5	2.5	3.1	1.1	1.1	0.4		14.0
6.75			0.2	0.2	0.4	0.2	2.7	2.5	2.7	1.9	1.1	0.8	0.2		12.9
7.50			0.2	0.2	0.6	1.3	2.1	1.9	1.2	2.3	1.0				10.8
8.25			0.2	0.3	0.7	0.6	1.3	2.9	1.2	1.2			0.2		8.6
9.00				0.2	0.8	1.7	1.1	1.2	1.1	0.6					6.7
9.75		0.2		0.2		1.1	0.8	0.9	0.8	0.4					4.4
10.50					0.6	0.6	0.7	0.6	0.2	0.2					2.9
11.25		0.2			0.4		0.2	0.2							1.0
12.00					0.3	0.2	0.2	0.4			0.2				1.3
12.75 & >	0.2				0.2	0.4			0.2						1.0
Total	0.4	0.8	1.0	1.3	5.6	8.7	13.6	18.7	18.1	15.4	8.5	5.6	1.7	0.6	100.0

[1] The number of plants = 520.

[2] The mean percent sucrose = 12.7.

[3] The mean weight per root = 6.19 lbs.

The study of percentage sucrose and weight per root simultaneously involves the analysis of the frequency distribution for both characters. The frequency distribution for percentage sucrose and weight per root is given in Table 7. From Table 3 it can be determined that for GW359-52R the identified-genetically-superior individuals exceeded 15.75 percent sucrose and from Table 6 that the identified-genetically-superior individuals exceeded 11.25 pounds per root. The percent of this population meeting this requirement for percentage sucrose is 3.7, and for weight per root is 2.5. The expected proportion of the population exceeding the upper class limits for both characters would be the product of their separate probabilities on the basis that they are independent. In this case it is 0.037 times 0.025 or 0.000925. If these two characters are independent, approximately one individual in a thousand would be expected to fall into categories that would identify them as genetically superior for both characters. Hence, in a population of 520 individuals, none would be expected and none were obtained, as can be seen from Table 7.

An examination of the frequency distribution for GW359-52R given in Table 7 shows that there is a negative relation between percentage sucrose and weight per root. How this negative relation affects the probability of obtaining some genetic gain in both characters can be determined to some extent by studying that portion of the frequency distribution delimited by a solid black line. The solid black line delimits those individuals that exceed the limits of the class in which the averages of the characters fall. The percent of the individuals for percentage sucrose falling in this area of the frequency distribution is 36.7 and for weight per root is 49.9. The expected percent for both characters on the basis of independence is 18.3. The percent obtained is 10.8. Among 520 individuals and on the basis of independence, 95 would be expected to fall within the area of Table 7 delimited by the solid line. The number obtained is 56. The chi square value for testing agreement between the two ratios (425:95 and 464:56) has a p value less than 0.01. The entire frequency distribution confirms that the two characters are not independent. The relation is negative.

It has been shown that on the basis of independence, only one beet in a thousand could be identified as genetically-superior for both percentage sucrose and weight per root. This means that on the basis of independence, to obtain 10 such beets would require a population of 10,000. Since the relation is negative between percentage sucrose and weight per root more individuals would be required. An examination of the data of Table 7 indicates that the negative relation between percentage sucrose and weight per root in this population is reasonably linear. It is apparent that very large populations would be required to identify fifty or more individuals in GW359-52R genetically superior for both characters.

Whether this same negative relation between percentage sucrose and weight per root exists for other populations and, if so, whether the regression is linear within and between populations should be determined. To obtain some information the total covariances and genetic covariances were calculated for all the segregating populations. They are listed in Table 8.

Table 8.—Within Cultures Total Covariances and Genetic Covariances for Percentage Sucrose and Weight Per Root[1].

Population	Covariance within cultures	
	Total	Genetic
F_1 hybrid	-0.2133 ± 0.0555	—— ——
GW359-52R	-1.8109 ± 0.3615	-1.6520 ± 0.3657
SP 53104-0	-0.3787 ± 0.1883	-0.2197 ± 0.1908
US 201	-0.2059 ± 0.1299	-0.0470 ± 0.1393
50-449	-0.3626 ± 0.1356	-0.2036 ± 0.1473
52-305	-0.1046 ± 0.0235	—— ——

[1] The number of plants per population = 160.

The covariances, both total and genetic, were calculated from individual plant data within cultures and populations. Their standard errors were calculated from the covariances within a population (for details of the method see Powers 17, pages 9 and 10). The total covariances for the F_1 hybrid and 52-305 populations are environmental covariances. They are significantly different from zero, as the covariance for the F_1 hybrid is 3.84 times its standard error and that for 52-305 is 4.45 times its standard error. In fact, with the possible exception of US 201, all of the total covariances are significantly different from zero.

From the data given in Table 8 and as determined by a comparison with their standard errors the only genetic covariance significantly different from zero is the one for GW359-52R. However, the genetic covariances for the other three populations are negative and hence furnish some evidence that even in these populations a slight negative relation may exist between percentage sucrose and weight per root. It is clear that the degree of the relation is similar for SP 53104-0, US 201, and 50-449; but of very little importance as compared with the extent to which this relation exists in the GW359-52R population. An understanding of the biological phenomena responsible for this difference between GW359-52R and the other segregating populations may be of fundamental importance to the sugar beet breeding program.

The frequency distributions for other populations involving percentage sucrose and weight per root may furnish some information pertaining to this problem. Such a frequency distribution for US 201 is given in Table 9. Again the solid line delimits individuals falling into classes beyond those in which the means occur. The second solid black line within this larger group delimits the classes in which it would be possible to identify the individuals genetically-superior for both characters, if any occur. As was also true for GW359-52R, it was not possible in the US 201 population to identify any individuals genetically superior for both characters. On the basis of independence of the two characters, only six such individuals would be expected in a population of 10,000. Hence, none would be expected in a population of 520 individuals and as can be seen none occurred.

Table 9.—Frequency Distributions of US 201 Expressed in Percentages for Percentage Sucrose and Weight Per Root[1, 2, 3].

Weight Per Root Upper Limit of Class in Pounds	Percentage Sucrose Upper Limit of Class in Percent														
	0 to 6.75	7.50	8.25	9.00	9.75	10.50	11.25	12.00	12.75	13.50	14.25	15.00	15.75	16.50 & >	Total
	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%
0 to 0.75						0.2	0.3	0.2		0.2	0.2			0.2	1.3
1.50	0.2			1.0	0.8	1.1	1.0	1.7	0.4	0.9	0.6	0.4	0.7		8.8
2.25	1.0	0.6	1.0	1.0	1.3	1.7	2.1	3.8	1.5	1.0	1.2				16.2
3.00	0.6	0.6	1.2	1.5	1.9	3.7	4.8	6.5	2.7	1.7	1.5	0.4	0.4		27.5
3.75		0.2	0.4	1.5	2.3	2.3	3.3	4.2	2.1	2.5	1.4	0.6			20.8
4.50			0.4	0.6	1.5	2.9	2.5	2.5	1.3	1.1	0.4	0.6			13.8
5.25				0.4	0.4	1.0	1.1	1.5	0.6	1.7		0.2			6.9
6.00					0.2	0.2	0.8	0.8	0.4		0.7				3.1
6.75						0.2	0.2	0.4				0.2			1.0
7.50						0.4									0.4
8.25 & >										0.2					0.2
Total	1.8	1.4	3.0	6.0	8.4	13.7	16.1	21.6	9.0	9.3	6.0	2.4	1.1	0.2	100.0

[1] The number of plants = 520.
[2] The mean percent sucrose = 11.1.
[3] The mean weight per root = 3.02 lbs.

Another interesting fact concerning the frequency distribution given in Table 9 is that for weight per root 2.7 percent of the population fall into those classes identifying them as genetically superior as regards weight per root and superior to the mean as regards percentage sucrose. For percentage sucrose the situation is quite different as all seven (1.3 percent of 520) of the individuals identified as genetically superior for percentage sucrose fall into classes having values lower than the mean for weight per root. This indicates that within that portion of the population having higher percentage sucrose the same negative relation noted between this character and weight of root for GW359-52R might exist for US 201. Since GW359-52R has both higher percentage sucrose and greater weight per root than US 201, this raises the question whether a threshold exists beyond which the negative relation between percentage sucrose and weight per root becomes pronounced.

If such were the case and most of the individuals for the three populations other than GW359-52R were to fall below this threshold, the small negative and statistically non-significant genetic covariances noted might be expected. Likewise, this same tendency of the identifiable-genetically-superior individuals for percentage sucrose to have lower weight per root is evident in the frequency distributions of populations SP 53104-0 and 50-449.

Another biological phenomenon that needs to be considered as a possible factor in bringing about the relation noted between percentage sucrose and weight per root is that the physiology of root growth and formation of sucrose is such that some of the physiological-genetic processes favorable to increased weight per root are not favorable to increased percentage sucrose. The fact that the environmental covariances for the F_1 hybrid and 52-305 populations are significantly different from zero (Table 8) would tend to support this explanation. If thresholds are involved, such a fact would lend further support to the conclusion that the physiology of the plant at certain levels of weight of root or certain levels of percentage sucrose does not favor both increased weight per root and increased percentage sucrose.

The frequency distribution of GW359-52R given in Table 7 does not furnish evidence of a threshold operating within this population, as the regression involving percentage sucrose and weight per root seems to be linear. In other words, the relation noted seems to exist to about the same degree throughout the population. It should be noted that the lower levels of percentage sucrose and weight per root are well within those of the other three segregating populations. This finding does not support the theory of a threshold at which increase in one character is associated with a decrease in the other character.

Discussion

Negative Genetic Covariances

Of interest are the possible explanations for the negative genetic covariance between percentage sucrose and weight of root in GW359-52R. For other segregating populations a tendency for this same relation was noted only among those plants having high percentage sucrose. The data presented in this study do not provide a full, nor perhaps adequate, hypothesis to explain this relation. Even though evidence furnished by the data are not conclusive they should be of value in helping to clarify the problems involved and in designing further experiments.

The possibility of thresholds, at which the negative relation noted for percentage sucrose and weight per root becomes pronounced, has already been mentioned. The fact that percentage sucrose and weight per root are higher for GW359-52R and the negative relation is much more pronounced is evidence that thresholds may be playing some part. The frequency distributions of GW359-52R and other populations show considerable overlapping. Then, that thresholds are not the sole casual phenomenon is indicated by the apparent linearity of regression of these two characters (see Table 7) throughout the frequency distribution of the GW359-52R population. For other segregating populations, the tendency for this same negative relation to exist among the plants having the higher percentages of sucrose is further evidence that thresholds may be playing some part.

Another possible explanation for the negative relation noted in GW359-52R is linkage between a preponderance of the genes conditioning very high percentage sucrose with a preponderance of those conditioning low weight per root. Since the genetic covariances for the other segregating populations are not statistically significant, the data from these populations do not confirm linkage as a causal agency. However, neither do they disprove linkage, as a balanced system may be involved.

A third possible explanation is pleiotropy. Again, if pleiotropy were one of the causal agencies, at least some of the genes conditioning percentage sucrose and some of them conditioning weight per root would be pleiotropic in GW359-52R and those conditioning these two characters in the other segregating populations would exhibit pleiotropy to a very limited extent. Stated another way, at least some of the physiological-genetic processes tending to produce high percentage sucrose tend to produce lower weight per root in GW359-52R; but such a relation exists to a very limited extent (if at all) in the other segregating populations. The physiological-genetic hypothesis is supported by the finding that those varieties possessing only environmental variability have statistically significant negative environmental covariances.

It should be kept in mind that all of these biological phenomena, and others not considered here, may be playing some part in producing the negative relation noted between percentage sucrose and weight per root. They may differ according to the population under consideration.

An understanding of the biological phenomena responsible for the negative relation between percentage sucrose and weight per root would be of value in conducting the breeding programs. Such knowledge should materially facilitate recombining the desirable genes for percentage sucrose with the desirable genes for weight per root. Also, an understanding of these biological phenomena should provide information as to what extent these two characters can be increased simultaneously and provide other information of value to the planning and promulgation of the breeding programs.

Evaluation of Breeding Stocks

In starting breeding programs and throughout their duration it is desirable to evaluate the different material available as breeding stocks. The methods and formulas presented in this article provide one means of so doing. Their application should provide the following information: The extent of genetic variability, the proportion in the population of the identifiable-genetically-superior individuals, genetic gains possible, and the relation between the characters the breeder is striving to recombine or increase. Such information would make possible the selection of superior stocks with which to start the breeding program, and also the production of superior breeding stocks. These superior breeding stocks can be produced in the following ways: Hybridization between identified-genetically-superior individuals selected from a given population, hybridization between genetically-superior populations, and, finally, hybridization between identifiable-genetically-superior individuals of superior populations. Also, the relative merits of these different breeding stocks so selected and produced can be evaluated by application of the methods and formulas outlined in this article.

Value to the Breeding Program

The methods and formulas are equally valuable throughout the pursuance of the breeding programs.

In asexually propagated material in which mutations may have given rise to heterogeneity, they can be used to select the individual identifiable as genetically superior. The same applies to self-fertilized crops. Also, where different methods of producing mutations are being tested the methods and formulas may be used to determine the most effective mutagenic agencies, and to determine just how effective they are in producing variability.

The application of the methods and formulas to the breeding of cross-fertilized crops will be considered in more detail. Heterosis may be of decided importance in breeding some cross-fertilized crops, and some characters may exhibit heterosis and others may not do so. In the present study, heterosis plays very little part in conditioning percentage sucrose, whereas in conditioning weight per root it plays a very decided part. This is brought out very clearly by comparing the frequency distributions within Table 1 (percentage sucrose) and those within Table 4 (weight per root). In Table 1 there is no tendency for the frequency distributions of the inbred populations to occur in the lower classes, whereas there is a decided tendency for such to be the case in Table 4 (weight per root). The selection of breeding methods in cross-fertilized crops is influenced materially by whether or not heterosis plays a decided part in conditioning the character being studied.

For those characters not exhibiting heterosis, mass selection within the cross-fertilized crops would be expected to bring about an increase in the desirable trait. In the mass selection program genetically-superior individuals can be identified by applying the methods and formulas presented in this article. The objective is to obtain as high a concentration as possible of those genes tending to increase the expression of the desirable character and those having favorable interallelic interactions.

For those characters exhibiting heterosis, the methods of breeding most generally employed are designed to utilize general combining ability, specific combining ability, or both. The polycross (Tysdal, Kiesselbach, and Westover, 23) is most commonly used to take advantage of general combining ability and the recurrent selection (Hull, 7) and reciprocal recurrent selection methods (Comstock, Robinson, and Harvey, 2) are designed to take advantage of both general and specific combining ability. The inbred line method of breeding followed by hybridization is designed to take advantage of specific combining ability. For the polycross and recurrent selection methods the different cycles of selection should be tested for proportion of identifiable-genetically-superior individuals and for genetic gains possible. The original breeding stocks and those varieties and strains that the breeding program is designed to replace should be included in these tests for purposes of comparison. Such a test should furnish information as to the progress being made and the advisability of continuing cycles of crossing followed by progeny testing and selection.

For the reciprocal recurrent selection method, the testing of the two sources of the different cycles for proportion of genetically-superior individuals and for genetic gains possible in comparison with the original material provides some information as to the desirability of continuing selection in further cycles. The inclusion of strains and varieties that the breeding program is designed to replace would serve to evaluate the two sources as possible synthetic varieties. The analysis of the frequency distribution of the hybrid between the two sources by methods and formulas given in this article would evaluate the progress being made (if any) as well as provide information concerning the desirability of continuing the hybridization, progeny testing, and selection cycles. If the proportion of individuals identifiable as genetically superior is low or if the genetically-superior individuals are inferior to those of other populations, further cycles of breeding would be of questionable value.

Inbred lines produced from one source of the reciprocal recurrent selection program should combine well with those produced from the other source. The possibility of getting inbreds whose hybrids would excel the hybrid between the two sources would be shown by testing the two sources and their hybrid for proportion of genetically-superior individuals and genetic gains possible. These tests are those discussed in the immediately preceding paragraph. The number of inbred lines that it would be necessary to produce and maintain should be comparatively few, if the reciprocal recurrent selection program is successful.

Probably one of the most important functions of the methods and formulas presented in this article is to provide a means of evaluating the breeding program as it proceeds. Likewise, whether the methods and formulas accomplish the purposes for which they were designed is subject to test as the breeding programs progress. The reliability of the methods and formulas will be indicated early in the breeding programs. However, if so desired, progeny performance tests can be made to ascertain the reliability of the methods and formulas for identifying genetically-superior individuals and predicting genetic gains possible.

Experimental Design for Selecting Individuals Genetically-Superior for Both Percentage Sucrose and Weight per Root in GW359-52R

A randomized complete block experimental design for selecting individuals genetically-superior for both percentage sucrose and weight per root in sugar beets is given in Table 10. The number of plants per culture is 24 and as can be seen from Table 10 the number of entries is 12 and the number of replications is 100. This makes a total of 28,800 plants in the experiment.

Table 10.—Randomized Complete Block Design for Selecting Individuals in GW359-52R Genetically Superior as Regards Percentage Sucrose and Weight Per Root.

Population	Entry Number	Replication and Culture Number						
		1	2	3	.	.	.	100
F_1 hybrid	1	6	17	28	.	.	.	1200
Inbred	2	7	13	26	.	.	.	1192
GW359-52R	3	2	21	34	.	.	.	1199
GW359-52R	4	1	18	31	.	.	.	1194
GW359-52R	5	11	24	33	.	.	.	1189
GW359-52R	6	9	19	35	.	.	.	1198
GW359-52R	7	4	16	25	.	.	.	1191
GW359-52R	8	8	15	32	.	.	.	1195
GW359-52R	9	12	14	27	.	.	.	1196
GW359-52R	10	3	20	29	.	.	.	1190
GW359-52R	11	10	22	30	.	.	.	1193
GW359-52R	12	5	23	36	.	.	.	1197

From Table 7 it can be seen that 2.3 percent of the GW359-52R population was identified as genetically superior for weight per root. The number of GW359-52R plants in the experiment outlined in table 10 is 24,000. Of this number 552 plants (2.3 percent of 24,000) would be expected to be genetically superior for weight per root. On the basis of independence also 2.3 percent of these plants should be identifiable as genetically superior for percentage sucrose. Hence, probably approximately 12 plants should be identifiable as genetically superior for both characters. The data show that the two characters are not independent and that the relation between them is negative. Hence, considerably less than 12 plants can be identified as genetically superior for both characters. An examination of Table 7 shows that only 0.2 percent of the individuals identifiable as genetically superior for percentage sucrose fell beyond the average for weight per root. Then, it is doubtful if even one of these 552 individuals, identifiable as genetically superior for weight per root, could be identified as genetically superior for percentage sucrose. It seems that individuals identifiable as genetically superior for both characters cannot be selected in one growing season from a population of 24,000 plants.

Another approach is to save ten percent of the roots having the greatest weight, analyze these for percentage sucrose, and save those individuals that can be identified as genetically superior for this latter character. Then, again select from this 10 percent another group which can be identified as genetically superior for weight per root and which have the highest percentages of sucrose. If among these 2,400 heavier beets any do occur which are identifiable as genetically superior for both characters, they should be saved as such and grown in a crossing plot by themselves. The other two groups should be grown in another crossing plot. In both crossing plots the seed should be saved on an individual plant basis. Asexual propagations should be made from all of the beets selected for parents and grown in the crossing plots mentioned in this paragraph. The progeny from both crossing plots should be tested in an experiment with GW359-52R to determine if any improvement has occurred in weight per root and percentage sucrose. If so, the asexually propagated roots of these progenies should be used for further breeding purposes.

When crossing the above roots selected from the experiment outlined in Table 10, provisions should be made to test for both general and specific combining ability. This can be done by cutting each root into four parts and planting two cuttings from each selection in a polycross breeding plot. In the second crossing plot composed of the other two quarters of each beet the reciprocal recurrent selection method of breeding should be employed. Those roots in which identifiable-genetically-superior individuals for percentage sucrose had been selected would be used as one source and those roots in which identifiable-genetically-superior individuals for weight of root had been selected would be used as the other source. The mechanics of the procedure outlined above have been solved and the pertinent information is being prepared for publication by Powers, Finkner, and Doxtator.

Summary

The principles and formulas developed in connection with the partitioning of variance into its components and in connection with the partitioning method of genetic analysis are applied to the identification of genetically-superior individuals of populations and to the predicting of genetic gains possible by application of suitable breeding methods within these populations.

The identification of genetically-superior individuals and prediction of the genetic gains involve analyses of the population frequency distributions.

The method of identifying genetically-superior individuals by use of the formula $z = \bar{X} + s_a x'$ is given in some detail and is illustrated. The methods of determining the values of p and z are given and are illustrated.

The methods employed identify only a portion of the genetically-superior individuals in any given population, probably a minor portion.

The percentage of identified-genetically-superior individuals listed in the fourth column of Table 3 provide a basis of predicting genetic gains.

The identified-genetically-superior individuals for any given population are members of a sub-group frequency distribution having a mean larger than that of the population in which they occur.

Predicting genetic gains involves estimating the means of these subgroup frequency distributions of which the genetically-superior individuals are members. The formula employed is $y = z - s_a x'$. Its application is illustrated.

The identification of genetically-superior individuals for percentage sucrose and weight per root simultaneously is considered.

The study of percentage sucrose and weight per root simultaneously involves the analysis of the frequency distribution for both characters.

The genetic covariance for percentage sucrose and weight per root was found to be highly statistically significant and negative for GW359-52R. For the other segregating populations the genetic covariances are negative but taken individually none are statistically significant. The biological phenomena that might be responsible for this genetic relation between the two characters are discussed.

The application of the identification of genetically-superior individuals and prediction of genetic gains to the evaluation of breeding stocks, and to the promulgation and evaluation of the breeding program, is given. In the discussion, application to the following breeding methods is stressed: Mass selection, polycross, recurrent selection, reciprocal recurrent selection, and production and hybridization of inbred lines.

An experimental design for selecting individuals genetically-superior for both percentage sucrose and weight per root in GW359-52R and its use on the basis of the findings reported herein are discussed.

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