Measurement of the Difference Between "Sugar Type" and "Yield Type" Sugar Beets

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One of the best opportunities for further improvement in the sugar beet crop lies in a better understanding and utilization of the large correlations existing between physiological characteristics of the beet. The general conditions producing correlations between the characteristics of sucrose, glutamic acid and root weight may be formulated as follows: Solar energy absorbed by the beet plant is either utilized in the growth processes or is stored—chiefly in the form of sucrose. Soil nitrogen is likewise absorbed, and either utilized for growth or stored—chiefly in the form of glutamine (which is measured as glutamic acid in the laboratory).

, In such a situation, genetic and environmental factors of three general types can be postulated to explain the wide variability observed in these characteristics, namely:

1. Factors altering the balance between growth and storage in the direction of less growth should favor a higher content of both sucrose and glutamic acid.
2. Factors increasing the total amount of energy absorbed should favor both greater size of beet and higher sucrose and glutamic acid content if adequate soil nitrogen is available. If soil nitrogen is inadequate, additional energy would cause glutamic acid to decrease.
3. Factors increasing the amount of nitrogen available to the plant tend to raise glutamic acid and decrease sucrose (1, 2)[3] while increasing growth to a maximum; in the presence of excessive nitrogen, root weight decreases.

The problem here is to evaluate both the size and direction of these factors. Two single factors, e. g., a single gene change and a constant difference in temperature actually might be very different, but would still give results indistinguishable in measurements on sucrose, glutamic acid and weight if they belonged to the same type. Any single factor might give a change intermediate to the three general types but classifiable as effecting a certain amount of change in each type.

One possible approach to a solution of this complicated situation is offered by the use of the discriminant function suggested by R. A. Fisher (3). When a number of concomitant measurements on the same experimental material are available, the discriminant function shows the linear combination of the measurements giving the greatest significance for comparisons among experimental groups. In variety trials on sugar beets, where considerable correlation between the measured quantities is usual, the most significant difference is not obtained in the direction of any one measurement but is in a direction intermediate to the various measurements.

As an example of the use of discriminant functions, a variety trial at Salinas, California, in 1946, was selected. This experiment[4] on 12 varieties of sugar beets originally contained 12 replications, but two of these were

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deleted for the present calculation because of their unfortunate arrangement in the field. Ten beet samples were taken from each plot for analysis, and portions of the pulp were frozen and analyzed for glutamic acid (2) and sucrose (4) the following spring. Results are shown in columns 1, 2, and 3 of Table 1. Errors in the experiment, as shown by the size of the least difference required for significance, were relatively large due to large variations in fertility, and to inadequate sample size for accurate glutamic

Table 1.—A Comp; of 12 Varieties Tested at Salinas in 1946.

Variety	Sucrose	**Glutamic Acid %**	**Yield Tons/Acre**	**Storage Potential (X)**	**Growth Potential <z>**
SL 222 (US22/2)	ITo	Ti	29Tl	*To7i*	23
SL 922 (US22)	13.8	.15	28.2	10.9	25
SL 315 (US15)	14.1	.17	28.3	11.3	27
SL 36 (US22/2 Select.)	14.4	.13	28.1	11.5	25
SL 333 (US33)	14.8	.14	28.0	12.0	27
SL 456 (US56)	15.0	.12	27.4	12.6	25
SL 411 (US22/2 Select.)	14.5	.10	26.7	12.7	20
SL 53 (US22/3 Select.)	14.4	.08	25.4	13.6	**16**
SL 4108 (US22 MS X CT_8)	15.0	.06	25.0	14.4	15
SL 52 (US22/3 Select.)	15.4	.09	25.5	14.7	**21**
SL 1-300 (Old Type)	15.5	.08	24.0	16.0	19
SL 54 (US35)	15.5	.10	22-6	17.4	20
LSD (5%)	1.2	69%	2-6	2.7	**6**

Arrangement: Randomized complete blocks with 10 replications
Plots: 4 rows 65 feet long
Samples: 10 beets per plot
Planted April 4, 1946. Harvested October 21-25, 1946.

acid and sucrose determinations. Differences among variety averages barely reached significance (Table 2) for sucrose and glutamic acid but were highly significant for yield. Average stands at harvest were fairly uniform, ranging from 101 (SL 4108) to 121 (SL 52) beets per 100 row feet.

Primary Varietal Difference

Calculation of the major varietal difference present follows the calculation given by Mather (3) . A table of mean squares and mean cross products (Table 3) is set up in the usual way. It is then possible to write an equation in the parameter 0 as follows, the constants of which may be identified in Table 3:

$$\begin{vmatrix} 1.9274(110)-3.5559(11)\phi & -.24408(110)+.40575(11)\phi & -1.9216(110)+9.6587(11)\phi \\ -.24408(110)+.40575(11)\phi & .074801(110)-.15751(11)\phi & .40045(110)-1.7324(11)\phi \\ -1.9216(110)+9.6587(11)\phi & .40045(110)-1.7324(11)\phi & 12.062(110)-40.712(11)\phi \end{vmatrix}$$

This equation is solved for the smallest real root of ϕ by trial and error, yielding the determinant:

$$\begin{vmatrix} 103.36 & -14.381 & 85.409 \\ -14.381 & 3.3944 & -9.1824 \\ 85.409 & -9.1824 & 75.812 \end{vmatrix} = 0; \text{ at } \phi = 2.7934$$

If this determinant has been verified by expanding down the first column the three minors $M_{11} = 173.02$, $M_{12} = -306.01$, and $M_{13} = -157.85$ will be available. The discriminant function maximizing varietal differences is of the form: $X = AS + BG + CW$ where S = % sucrose, $G = 1 + \log$ % glutamic acid, and W = tons beets per acre. If A, the coefficient of S, is arbitrarily taken as 1, $B = -M_{12}/M_{11} = 1.8$ and $C = M_{13}/M_{11} = -0.9$. In order to eliminate negative values and give results more comparable between experiments, the discriminant function is expressed in terms formally equivalent to % sucrose at 0.15% glutamic acid and 25 tons per acre yield by adding the constant —1.8 (1 + log. 0.15) + .9 (25) = 22.2. This gives:

$$X = S + 1.8G - 0.9W + 22.2 \qquad \text{Eq. 1}$$

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We have called this quantity an estimate of the storage potential of the variety. It gives differences more highly significant than the original measurements (sucrose, GA and weight) or any other linear combination of them (Tables 1, 2 and 3) . There is a nine percent increase in the F value (Table 2) over the largest individual difference, that of weight. In other experiments carried out at Woodland the advantage of the discriminant function has been usually much greater. Similar equations were obtained maximizing varietal differences in five experiments, in which values of B ranging from 1 to 10 and C ranging from —0.1 to —2.0 were found. Evidently the values of both B and C vary with both the set of varieties chosen and the environmental conditions.

Table 2.—Variance Ratios and Correlation Coefficients.

F Values

	Varieties	Blocks
D.F.	11/99	9/99
% Sucrose (S)	2.02[1]	10.42[3]
1 + Log % Glutamic Acid (G)	2.40[2]	4.27[3]
Tons per Acre (W)	4.59[3]	5.91[3]
Storage Potential (X)	5.02[3]	6.06[3]
Growth Potential (Z)	3.66[3]	2.56[1]
Nitrogen Status (Y)	1.42	8.09[3]

Correlation Coefficients

	Varieties	Blocks	Error
D.F.	10	8	90
SG	—.50	—.92[3]	—.67[3]
SW	—.89[3]	—.55	—.27[3]
GW	.68[1]	.73[1]	.33[3]

[1] Exceeds the 5% point of significance.
[2] Exceeds the 1% point of significance.
[3] Exceeds the 0.1% point of significance.

Since small beets with high sugar give large values of storage potential, while large beets with low sugar give low storage potentials, it is evident that this quantity gives a numerical measure of the difference between the "sugar type" and the "yield" or "tonnage type" of sugar beet. The inclusion of a third component, glutamic acid, in this numerical measure has definite advantages because it eliminates confusion of other genetic and environmental effects. On the basis of sucrose and weight, a sugar-type beet grown in high nitrogen soil could not be differentiated easily from a yield-type beet grown in soil of average nitrogen, but its higher glutamic acid and storage potential would distinguish it as a sugar type.

One would predict from equation 1 that high storage potential beets would tend to have high glutamic acid and we have generally found this to be the case. The opposite results shown by the variety averages in the present case appear to have a quite different cause and will be discussed later.

From the initial discussion it appears that an increase in the storage potential, tending to raise sucrose and glutamic acid as weight decreases, is governed by a group of factors tending to divert energy from growth to storage. Since significant effects were observed in both variety and block comparisons, both genetic and environmental factors are operating. It seems quite possible that further measurements, especially one of top weight, might give additional information on the nature of the genetic changes involved.

Table 3.—Mean Squares and Mean Cross Products.

D.F.	Varieties 11	Blocks 9	Error 99	Varieties + Error 110
S^2	3.5359	18.171	1.7486	1.9274
G^2	.15731	.28008	.065633	.074801
W^2	40.712	34.695	8.8783	12.062
SG	—.40575	—2.0634	—.22612	—.21108
SW	—9.6587	—13.767	—1.0620	—1.9216
GW	1.7324	2.2744	.25246	.40045

Secondary Varietal Difference

When more than two measurements are made on a set of data it is clearly possible that secondary maxima in the various possible F values, resulting from different directions of measurement, be present. If it is assumed that the standard deviation constitutes a rational unit of measure for each measurement, it is possible to calculate a second discriminant giving the greatest significance in directions perpendicular to the first discriminant:

Thus if the three variables S, G, and W are each measured from their general mean and a set of discriminant planes

$$X = AS + BG + CW \qquad \text{Eq. 2}$$

has been calculated as above, it can be shown that the line which passes through the origin and which would be perpendicular to X if S, G and W were measured in units of their standard deviations is

$$\frac{S}{AV_S} = \frac{G}{BV_G} = \frac{W}{CV_W} \qquad \text{Eq. 3}$$

where V_S = variance of S, etc. The point of intersection of 2 and 3 gives the expected value of $S\,(=S_E)$ and $G\,(=G_E)$ for given X:

$$S_E = AV_S\,X/K \text{ and } G_E = BV_G\,X/K \qquad \text{Eq. 4}$$

where $K = A^2V_S + B^2V_G + C^2V_W$. The deviations of each measurement of S and G from its expectancy are given by Eq. 5

$$\Delta S = S - S_E = S - AV_S\,X/K \text{ and}$$

$$\Delta G = G - G_E = G - BV_G\,X/K$$

Thus the quantities

$$K\Delta S = (B^2V_G + C^2V_W)S - ABV_S G - ACV_S W \text{ and} \qquad \text{Eq. 6}$$

$$K\Delta G = -ABV_G S + (A^2V_S + C^2V_W)G - BSV_G W$$

are proportional to that part of the variation which cannot be attributed to variations in X. A discriminant function can then be calculated which maximizes differences in ΔS and ΔG

$$Z' = K\Delta S + D(K\Delta G) \qquad \text{Eq. 7}$$

Z' may then be expressed in terms of S, G and W by use of equation 6 and any one of the coefficients of S, G or W given an arbitrary value. This might give, for example,

$$Z = ES + FG + W \qquad \text{Eq. 8}$$

as the "secondary discriminant" giving the most significant differences perpendicular to the ordinary discriminant function, $X = AS + BG + W$, if S, G and W are measured in units of the standard deviation.

In the present experiment

$$K\Delta S = 7.5957S - 3.0930G + 1.5954W$$
$$K\Delta G = -.11609S + 9.1390G + .10592W$$

Analysis of variance and calculation of a discriminant maximizing differences in ΔS and ΔG gives

$$Z' = K\Delta S + 7.1682\ K\Delta G$$
$$= 6.7635S + 62.417G + 2.3546W$$

It is convenient to divide by 2.3546, giving

$$Z = 2.9S + 27G + W$$

This equation is made formally equivalent to the weight in tons per acre at 15 percent sucrose and 0.15 percent glutamic acid by adding the constant $-2.9\,(15) - 27\,(1 + \log.\ 0.15) = -48$. Therefore

$$Z = 2.9S + 27G + W - 48 \qquad \text{Eq. 9}$$

This secondary discriminant, perpendicular to the storage potential, is designated **growth potential.** Being characterized by positive coefficients for S, G and W it appears to be a measure of the total "vigor" or energy absorption of the plant. Very significant differences are present among the varieties tested. Strains which have proved to be commercially useful, such as SL 922, 333, 315 and 456, have uniformly a high growth potential. Strains with significantly lower growth potential, especially SL 53 and 4108, would be expected to have no direct commercial value. Low growth potential might be caused by either low innate vigor or low resistance to adverse environmental conditions perhaps peculiar to this experiment.

In this experiment the large coefficient of glutamic acid in the growth potential equation 9 explains why the tonnage-type beets (those with low storage potential) unexpectedly had relatively high glutamic acid. The greater growth potential, tending to increase glutamic acid at adequate nitrogen levels, more than compensated for the low storage potential which tends to divert nitrogen from storage.

In other experiments, the growth potential has been found to be a major component of the environmental variation, so that varietal differences in this direction are not easily measurable. The coefficient of S has been found to vary from 2 to 15, while the coefficient of G has varied from —22 (at very low N) to the present +27.

Residual Independent Variation

If the measured variables in the storage potential and growth potential equations are expressed in terms of their standard deviations ($S' = S/\sigma S$, etc.) the following equations are obtained:

$$X = 1.32S' + 0.45G' - 2.72W' + 22.2 \qquad \text{Eq. 10}$$
$$Z = 3.80S' + 6.79G' + 2.98W' - 48 \qquad \text{Eq. 11}$$

The set of planes perpendicular to these two is

$$Y = -3.56S' + 2.56G' - 1.30W' \qquad \text{Eq. 12}$$

Expressed in ordinary units, this is equal to

$$Y = -2.7S + 10G - .44W \qquad \text{Eq. 13}$$

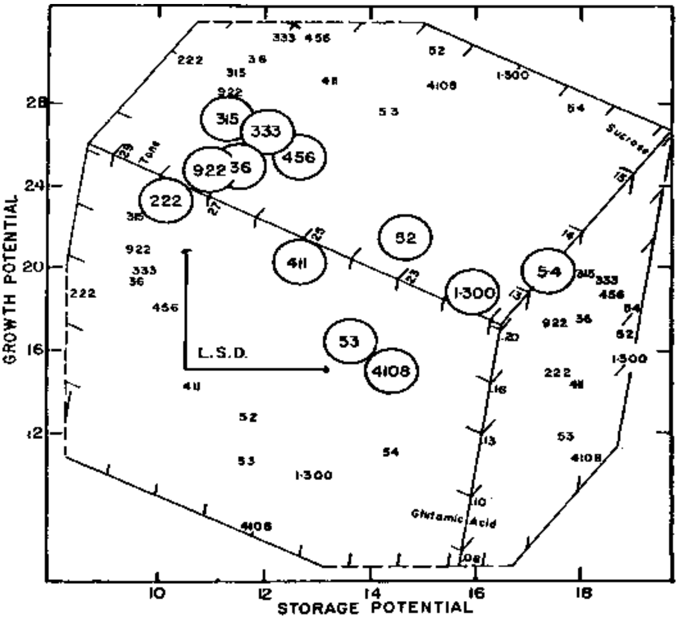

Figure 1.—An orthogonal projection of a three-dimensional graph of varietal averages of sucrose, weight and glutamic acid, viewed from the particular direction showing storage potential and growth potential as perpendicular measurements. Storage potential gives the greatest significance among varietal comparisons, and growth potential gives the greatest significance in the residual variation perpendicular to changes in storage potential. Projections of the varietal averages on the boundary planes are shown as uncircled numbers.

This function is nearly identical with that one found (5) to give the most highly significant difference between levels of applied nitrogen fertilizer and is designated nitrogen status. No significant difference in nitrogen status was detectable in the varieties in this experiment. Nitrogen status accounts for a major part of the block variation and presumably of the error variation. Calculation of secondary discriminants and residual independent variation are artifices to be used when the experiment has not incorporated other classifications, the maximization of which can indicate the proper directions of measurement. Thus testing of varieties at two levels of nitrogen, not too widely separated, would permit the direct calculation of nitrogen status. Treatments producing pure changes in storage potential and growth potential have not yet been identified.

Discussion

The transformation of axes from sugar, weight and GA to storage potential, growth potential and nitrogen status which has been carried out by the above calculations is depicted graphically in Figure 1. It is a representation of a three-dimensional graph of the varietal averages viewed in the direction of changing nitrogen status. Such transformation is useful in many ways. It explains why the difference between sugar-type and tonnage-type beets is sometimes manifested chiefly in differences in sugar, and other times, as in this case, in differences in weight. Storage potential, the difference between these different types, is measured with optimum accuracy. The nature of the change in storage potential is shown by solution of the three discriminant functions (equations 1, 9, 13) obtained for weight and glutamic acid at constant growth potential and nitrogen status. This shows that weight increases 4.7 tons for each percent sucrose lost as the beets approach more of a tonnage type. This implies that gross sugar per acre improves as lower storage potential beets are obtained. Similarly, glutamic acid increases 16 percent for each percent sucrose gained as beets approach more in the direction of the true sugar type or high storage potential beets. This relationship may be compared to that found by Skuderna et. al. (6) in a comparison of two European yield-type strains to two European sugar-type strains. The general weighted average showed a gain of 2.59 tons for each percent sucrose lost, while tests in California averaged 4.8 tons for each percent sucrose lost.

Difficulties in the method lie in the absence of a procedure for determining the error of the discriminant function coefficients when differences among more than two varieties are maximized. Results could be unduly affected by choice of varieties studied or the nature of the error encountered. Finally, sampling errors of the standard deviation can affect the direction of any secondary discriminants calculated.

Summary

Methods have been described for calculating the direction of the most significant difference between varieties when measurements on sucrose, weight and glutamic acid are available. Storage potential, the primary discriminant function thus obtained, differentiates between varieties even under conditions of widely varying fertility. Beets of high storage potential are

true "sugar type" with high sucrose, low weight and **high** glutamic acid; those of low storage potential are true "yield type" having low sucrose, high weight and **low** glutamic acid.

High vigor, measured by a secondary discriminant, tends to increase the glutamic acid content of the beet. Varieties with low nitrogen foraging ability are distinguished by high sucrose, low yield and low glutamic acid. A method for calculating a secondary discriminant function perpendicular to the primary one has been developed.

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