Population Genetic Studies on Sodium and Potassium in Sugar Beets (Beta Vulgaris L.)[1]

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Introduction

With the recent increase in the use of nitrogen fertilizer in sugar beet production and the resultant decrease in processing quality, interest has been aroused in the possibility of altering the chemical composition of the sugar beet root by breeding methods. To obtain information on this problem population genetic studies at different levels of soil fertility were conducted. The results of studies carried out in 1956 for percentage sucrose, weight of root, and NO_3-N in the petioles were reported by Powers, Robertson, Whitney, and Schmehl (13)[4]. The results of the study of total nitrogen in the roots from this same experiment were reported by Payne, Powers, and Maag (4). The purpose of this paper is to report the results of the analysis of data obtained for the sodium and potassium contents of these same roots. The objective of the study was to obtain information on the genetic and breeding behavior of sodium and potassium in sugar beet roots grown at different soil-fertility levels.

Materials and Methods

The experimental design used in this study is a split-split plot with 40 replications. Fertilizer treatments are the main plots, populations the sub plots, and locations within the single row of each population the sub-sub plots. The fertilizer treatments, populations, and locations are described in detail by Powers, et al. (13).

The fertilizer treatments are fertilization and non-fertilization. The fertilized plots received 100 pounds of N and 250 pounds of P_2O_5 per acre on April 4, 1956, and an additional 100 pounds of N per acre on June 26.

The experimental plant material consists of six populations: A54-1; A54-1, BB; 50-406, BB; 50-406; F_1 hybrid; and 52-307. A54-1 is a commercial variety. A54-1, BB is a broad-base derivative of A54-1 produced by exposing 25 mother beets of

A54-1 to pollen from 22 other populations. Population 50-406, BB is a broad-base derivative of 50-406 produced in a similar manner. Populations 50-406 and 52-307 are inbred lines, while the F_1 hybrid is the cross 50-406 x 52-307. Populations A54-1, BB; A54-1; and 50-406, BB are heterogeneous and heterozygous and will be referred to as the heterogeneous populations. Populations 50-406, F_1 hybrid, and 52-307 will be referred to as the homogeneous populations. Comparisons between the heterogeneous and the homogeneous populations will be called comparisons between geneities.

Each location within a row consisted of a single plant. Since the rows were planted from north to south, the differences between locations represent any north-south gradient in the field.

Each plot was bordered by a row of A54-1. The rows were spaced 22 inches apart and the plants were thinned to a spacing of 20 inches within the row. After thinning there were 12 plants in each plot. Data were taken on eight plants per plot with the end plants being discarded at the time of harvest.

Sodium and potassium concentrations of the beet juices were determined with the Beckman Model DU Spectrophotometer and the flame attachment. Lead acetate filtrate samples were analyzed without dilution or addition of an internal standard. Sodium and potassium concentrations were determined from the transmission at 589 and 768 μ respectively, with the numerical values in ppm being taken from a standard curve. These values were then converted to percent on beets by the appropriate calculations.

The standard curves were prepared by plotting the transmission on varying known amounts of the element in question. In addition to the sodium and potassium, other known impurities were incorporated in the standard solutions as follows: Ca, 50 ppm; Mg, 50 ppm; sucrose, 2%; lead acetate solution, 6.25 ml/100 ml; K, 200 ppm (in Na standard); and Na, 50 ppm (in K standard). Periodically throughout the runs the operation of the spectrophotometer was checked by running a reference standard of this composition (including 200 ppm K and 50 ppm Na).

The data were recorded as percent on beets of sodium and potassium. For ease of handling, the data were changed to parts per 100,000. Three observations are missing for each character. The plot mean was used to replace each missing observation and the appropriate degrees of freedom were reduced to compensate for the missing observations. Since the frequency distributions

are not following the normal curve on an arithmetic scale, the data were transformed to logarithms of parts per 100,000. The transformed data were used in the statistical analyses.

Questions which are of interest in this study are whether differences between main effects exist, whether there are interactions between main effects, whether there are differences between mean variances, whether the residual variances are different from zero, and if so, which are greater. If the residual variances are different from zero the frequency distributions are of interest.

The analysis of variance is used to test the differences between main effects and interactions and to test differences between mean variances. Chi-square is used to test differences between frequency distributions. Regression of variances on means is used to estimate the environmental variances for the sodium data. For details of the statistical methods used see Powers (6, 9); Powers, Locke and Garrett (10); Powers, et al. (13); Powers, Robertson, and Clark (11); and Powers, Robertson, and Remmenga (12). Where a difference is said to be significant, the odds are at least 19:1 against the difference being due to chance unless otherwise stated.

Results

The results will be discussed under three main headings; means, variances, and frequency distributions.

Means

Analyses of variance

The mean squares and F values from the analyses of variance are shown in Table 1. Because differences between geneities exist for some of the interactions involving populations, the sum of squares for populations is broken down into geneities, heterogeneous populations, and homogeneous populations. Similarly the interactions involving populations except R x P x T and the remainder are broken down into their component parts. In Table 1, G represents geneities, He represents heterogeneous populations, and Ho represents homogeneous populations. The error mean squares used in making the F tests are designated by the small letters in columns 2, 6, and 7. The presence of significant differences between main effects or interactions can be determined by comparing the F values in columns 6 and 7 with the appropriate tabular F values in columns 8, 9, 10, and 11.

The F values for all main effects except locations exceed the one percent level for both characters. For sodium the F value for locations exceeds the one percent level, but for potassium no significant differences between locations were found.

Table 1.—Analyses of Variance for Logarithms of Parts per 100,000 of Sodium and Potassium.

Source of Variation	Smaller Mean Square	Mean Square		F Value[3]			Tabular F			
							Sodium		Potassium	
		Sodium	Potassium	D.F.[1]	Sodium	Potassium	5%	1%	5%	1%
Replications		4.5596	0.0891	39	89.05f	6.41f	1.45	1.69	1.45	1.69
Populations		3.9578	1.0777	5	59.43a	77.53f	2.26	3.11	2.26	3.11
Genetics		1.1179	2.1100	1	17.25b	151.80f	4.10	7.35	3.89	6.76
Heterogeneous		5.1561	1.1381	2	59.54c	81.88f	3.11	4.88	3.04	4.71
Homogeneous		4.1794	0.5012	2	87.80d	36.06f	3.11	4.88	3.04	4.71
Treatments		74.4505	1.1254	1	179.53c	53.34e	4.10	7.35	4.10	7.35
Locations		0.0792	0.0073	7	2.82g	1.20g	2.01	2.64	2.01	2.64
R x P	a	0.0666	0.0148	195	1.30f	1.06f	1.26	1.39	1.26	1.39
R x G	b	0.0648	0.0177	39	1.27f	1.27f	1.45	1.69	1.45	1.69
R x He	c	0.0866	0.0158	78	1.69f	1.14f	1.35	1.53	1.35	1.53
R x Ho	d	0.0476	0.0125	78	f	f	1.35	1.53	1.35	1.53
R x T	e	0.4147	0.0211	39	8.10f	1.52f	1.45	1.69	1.45	1.69
P x T		0.2365	0.1978	5	4.62f	14.23f	2.26	3.11	2.26	3.11
G x T		0.0099	0.1170	1	f	8.42f	3.89	6.76	3.89	6.76
He x T		0.4626	0.0141	2	9.04f	1.01f	3.04	4.71	3.04	4.71
Ho x T		0.1237	0.4220	2	2.42f	30.36f	3.04	4.71	3.04	4.71
R x P x T	f	0.0312	0.0139	195	1.82g	2.28g	1.17	1.25	1.17	1.25
Remainder	g	0.0281	0.0061	3350[2]						

1. D.F. designates degree of freedom.
2. Three degrees of freedom are removed from the remainder to account for three missing observations.
3. The small letters after the F values indicate the error mean square used in calculating F.

The R x P interaction in the sodium data is significant at the five percent level. When this interaction is broken down into its component parts, the R x He interaction is significant at the one percent level but neither the R x G nor the R x Ho interaction is significant. None of the components of the R x P interaction in the potassium data is significant.

The R x T interaction exceeds the one percent level for sodium and the five percent level for potassium.

The P x T interaction exceeds the one percent level for both sodium and potassium. When this interaction is broken down for sodium, the He x T component is significant at the one percent level, but neither of the other components is significant. For potassium both the G x T and the Ho x T interactions are significant at the one percent level, but the He x T interaction is not significant.

The R x P x T interaction is significant at the 1 percent level for both characters when tested against the pooled interactions with locations.

Main effects

The means for main effects are presented in Table 2. For ease of presentation and to have a basis for comparison with the NO_3-N petiole analysis reported by Powers, et al. (13), the replications are grouped into five groups and means are reported as group means. From Table 2 it can be seen that the first two replication groups have approximately the same mean sodium

Table 2.—Means of Logarithms of Parts per 100,000 of Sodium and Potassium for Replication Groups, Populations, and Treatments.

Main Effects	Sodium	Potassium
Replication groups		
1-8	1.1721	2.0308
9-16	1.1879	2.0213
17-24	1.2995	2.0088
25-32	1.5206	2.0419
33-40	1.6745	2.0820
Populations		
A51-1	1.4482	2.0940
A54-1, BB	1.4309	2.0741
50-406, BB	1.2848	2.0130
50-406	1.3016	2.0440
F₁ hybrid	1.3130	1.9890
52-307	1.4469	2.0074
Treatments		
Fertilized	1.5102	2.0541
Non-fertilized	1.2317	2.0198

content, the third group is slightly but significantly higher while increases in the last two groups are sharp, indicating a gradient of increasing sodium content from north to south in the field. There is a small, significant decrease in potassium content from replication group 1-8 to group 17-24 and a marked increase in the last two groups.

Examination of the population means reveals dominance for low sodium with 50-406 and the F_1 hybrid both significantly lower than 52-307. Population 50-406, BB is not significantly different from 50-406. The F_1 hybrid has a significantly lower potassium content than either 50-406 or 52-307 indicating heterosis for low potassium. Population 50-406, BB is significantly lower in potassium than 50-406. This is another indication of either dominance or heterosis for low potassium.

The means for the fertilized plots are higher than those for the non-fertilized plots for both sodium and potassium.

First-order interactions

The means for the interaction of replications x treatments are shown in Table 3. The nature of this interaction can be seen for the sodium data by examining the difference between the fertilized and non-fertilized plots for replication groups 1-8 and 33-40. For group 1-8 the difference is 0.3623, while for group 33-40 it is 0.2123. This interaction is of practical significance because it indicates that the magnitude of the response to fertilization, as measured by sodium content, depends on the original fertility level of the soil. That a gradient did exist is shown by Powers, et al. (13).

Table 3.—Means of Logarithms of Parts per 100,000 of Sodium and Potassium for the Interaction of Replication Groups x Treatments.

Character and Treatment	Replication Group				
	1-8	9-16	17-24	25-32	33-40
Sodium					
Non-fertilized	0.9910	1.0328	1.1792	1.3870	1.5683
Fertilized	1.3533	1.3430	1.4198	1.6541	1.7806
Potassium					
Non-fertilized	2.0089	2.0034	1.9926	2.0374	2.0568
Fertilized	2.0527	2.0391	2.0249	2.0464	2.1071

The means for the interaction of replications x populations are shown in Table 4. The interaction of replications with heterogeneous populations is the only significant component of this interaction in the sodium data. This interaction results primarily from the failure of A54-1, BB to increase gradually

Table 4.—Means of Logarithms of Parts per 100,000 of Sodium and Potassium for the Interaction of Replication Groups x Populations.

Character and Replication Group	Population					
	A54-1	A54-1, BB	50-406, BB	50-406	F₁ hybrid	52-307
Sodium						
1-8	1.2692	1.2959	1.0421	1.0823	1.0764	1.2668
9-16	1.2863	1.2108	1.1307	1.1254	1.1037	1.2706
17-24	1.3702	1.3339	1.2090	1.2723	1.2495	1.3622
25-32	1.5607	1.6037	1.4320	1.4549	1.4831	1.5890
33-40	1.7546	1.7104	1.6103	1.5731	1.6525	1.7460
Potassium						
1-8	2.0904	2.0577	1.9923	2.0284	1.9983	2.0177
9-16	2.0517	2.0552	2.0068	2.0324	1.9791	2.0024
17-24	2.0609	2.0367	1.9884	2.0099	1.9653	1.9915
25-32	2.1120	2.0863	1.9967	2.0525	1.9835	2.0204
33-40	2.1548	2.1348	2.0811	2.0969	2.0189	2.0053

in sodium content from the first replication group to the last, whereas the other heterogeneous populations do increase gradually. In the potassium data none of the components of the interaction of replications with populations is significant.

The means for the interaction of populations x treatments are shown in Table 5. The only part of the interaction of populations x treatments that is significant in the sodium data is the interaction of heterogeneous populations with treatments. This interaction is apparently the result of the difference between fertilized and non-fertilized plots being only 0.2257 for 50-406, BB while it is 0.2864 and 0.3329 for A54-1 and A54-1, BB, respectively.

In the potassium data the interaction of geneities x treatments and of homogeneous populations x treatments are both significant at the one percent level. Examination ·of Table 5

Table 5.—Means of Logarithms of Parts per 100,000 of Sodium and Potassium for the Interaction of Populations x Treatments.

Character and Treatment	Population					
	A54-1	A54-1, BB	50-406, BB	50-406	F₁ hybrid	52-307
Sodium						
Non-fertilized	1.3050	1.2645	1.1720	1.1487	1.1788	1.3212
Fertilized	1.5914	1.5974	1.3977	1.4545	1.4472	1.5727
Potassium						
Non-fertilized	2.0767	2.0485	1.9880	2.0070	1.9770	2.0217
Fertilized	2.1112	2.0998	2.0381	2.0811	2.0011	1.9931

reveals that the interaction of homogeneous populations x treatments is caused by a significant increase in potassium from the non-fertilized to the fertilized plots in population 50-406 and a significant decrease from the non-fertilized to the fertilized plots for 52-307. The interaction of geneities with treatments is a result of the interaction of homogeneous populations with treatments since the increase in potassium from the non-fertilized to the fertilized plots for 50-406 and the F_1 hybrid is partly offset by the decrease of 52-307. The net result is a mean difference of 0.0232 between fertility levels for the homogeneous populations as compared with 0.0453 for the heterogeneous populations.

Second-order interaction

The means for the interaction of replication groups x populations x treatments are shown in Table 6. This interaction is of interest in the sodium data because of the effect on dominance relationships in the F_1 hybrid. For the first four replication groups of both the non-fertilized and fertilized plots the means for 50-406 and the F_1 hybrid are not significantly different while in group 33-40 the F_1 mean is intermediate between those for 50-406 and 52-307. Thus depending upon the replication group which is studied, either no dominance or complete dominance for low sodium is indicated.

The F_1 hybrid is significantly lower in potassium than either parent on replication group 25-32 in the non-fertilized plots. In 3 of the other 4 replication groups on the non-fertilized plots the F_1 hybrid was slightly lower than the low parent but none of these differences was statistically significant. The low parent on the non-fertilized plots is 50-406 for all replication groups except 33-40. In replication group 33-40 on the non-fertilized plots and in all replication groups on the fertilized plots, 50-406 is the high parent. On the fertilized plots the F_1 hybrid is not significantly different from the low parent in the first four replication groups but is intermediate in group 33-40. Thus, for potassium, the dominance relationship and the inbred which is the low parent in the cross both vary with the fertilizer treatment and the replication group.

Variances

Analyses of variance of within-plot variances

The mean squares and F values from the analyses of variance of the within-plot variances are shown in Table 7. The sums of squares for populations and the interactions with populations are broken down into their component parts because the differences between geneities are of interest. The F values for popu-

Table 6.—Means of Logarithms of Parts per 100,000 of Sodium and Potassium for the Interaction of Replication Groups x Populations x Treatments.

Character and Population	Treatment and Replication Group									
	Non-fertilized					Fertilized				
	1-8	9-16	17-24	25-32	33-40	1-8	9-16	17-24	25-32	33-40
Sodium										
A54-1	1.0964	1.1126	1.2291	1.4450	1.6417	1.4420	1.4600	1.5112	1.6764	1.8675
A54-1, BB	1.0560	1.0612	1.1944	1.4398	1.5708	1.5357	1.3604	1.4734	1.7675	1.8500
50-406, BB	0.8892	0.9974	1.1246	1.3242	1.5244	1.1950	1.2640	1.2933	1.5399	1.6962
50-406	0.8706	0.9634	1.1286	1.3154	1.4652	1.2940	1.2874	1.4160	1.5944	1.6809
F₁ hybrid	0.9106	0.9413	1.1371	1.3452	1.5600	1.2422	1.2661	1.3618	1.6210	1.7450
52-307	1.1229	1.1210	1.2614	1.4526	1.6478	1.4108	1.4202	1.4630	1.7253	1.8442
Potassium										
A54-1	2.0682	2.0446	2.0473	2.1066	2.1168	2.1126	2.0588	2.0745	2.1173	2.1927
A54-1, BB	2.0235	2.0310	2.0319	2.0626	2.0936	2.0919	2.0794	2.0415	2.1100	2.1760
50-406, BB	1.9647	1.9854	1.9630	1.9813	2.0454	2.0199	2.0282	2.0137	2.0120	2.1167
50-406	1.9759	1.9890	1.9606	2.0291	2.0803	2.0809	2.0758	2.0593	2.0759	2.1134
F₁ hybrid	1.9847	1.9626	1.9472	1.9926	1.9979	2.0120	1.9957	1.9834	1.9745	2.0399
52-307	2.0364	2.0076	2.0057	2.0521	2.0067	1.9989	1.9971	1.9772	1.9886	2.0040

Table 7.—Analyses of Variance of Within-Plot Variances for Logarithms of Parts per 100,000 of Sodium and Potassium.

Source of Variation	Smaller Mean Square	Mean Square		F Value[2]			Tabular F			
		Sodium	Potassium	D.F.[1]	Sodium	Potassium	Sodium 5%	Sodium 1%	Potassium 5%	Potassium 1%
Replications		0.00077611	0.00003382	39	1.65f	2.16f	1.45	1.69	1.45	1.69
Populations		0.01720056	0.00031421	5	36.57f	15.52a	2.26	3.11	2.26	3.11
Genetics		0.06639155	0.00144698	1	173.92g	53.53b	4.10	7.35	4.10	7.35
Heterogeneous		0.00869156	0.00002621	2	10.80h	1.21c	3.11	4.88	3.11	4.88
Homogeneous		0.00111407	0.00003582	2	6.16i	2.31d	3.11	4.88	3.11	4.88
Treatments		0.01489786	0.00000476	1	16.60e	e	4.10	7.35	4.10	7.35
R x P	a	0.00038658	0.00002025	195	f	1.30f	1.26	1.39	1.26	1.39
R x G	b	0.00040364	0.00002703	39	1.06g	1.73f	1.71	2.14	1.45	1.69
R x He	c	0.00059104	0.00002160	78	h	1.38f	1.45	1.70	1.35	1.53
R x Ho	d	0.00017360	0.00001552	78	i	f	1.45	1.70	1.35	1.53
R x T	e	0.00089727	0.00002201	39	1.91f	1.41f	1.45	1.69	1.45	1.69
P x T		0.00079545	0.00003225	5	1.69f	2.06f	2.26	3.11	2.26	3.11
G x T		0.00085478	0.00001413	1	2.24g	f	4.10	7.35	3.89	6.76
He x T		0.00065358	0.00001830	2	h	1.17f	3.11	4.88	3.04	4.71
Ho x T		0.00090766	0.00005527	2	5.02i	3.54f	3.11	4.88	3.04	4.71
R x P x T	f	0.00047040	0.00001563	195						
R x G x T	g	0.00038174	0.00001609	39						
R x He x T	h	0.00080442	0.00001568	78						
R x Ho x T	i	0.00018071	0.00001535	78						

1. D.F. designates degree of freedom.
2. The letter after the F value indicates the error mean square used in calculating F.

lations are significant at the one percent level for both sodium and potassium. F values for all three components of the population sum of squares for sodium are significant at the one percent level. The only significant component of the population sum of squares for potassium is that for geneities. This indicates that for potassium the only differences between population variances are due to the residual variance present in the heterogeneous populations.

Significant differences between treatments are found for sodium but not for potassium. For replications the F value for sodium exceeds the five percent level while that for potassium exceeds the one percent level.

The R x P interaction for sodium is not significant. The R x P interaction for potassium is significant at the five percent level. A breakdown of this interaction reveals that the R x G interaction is significant at the one percent level, the R x He interaction is significant at the five percent level, while the R x Ho interaction is not significant. The R x T interaction for sodium is significant at the one percent level while that for potassium is not significant.

While the P x T interaction is not significant for either sodium or potassium, a breakdown of this sum of squares for sodium reveals that the Ho x T interaction is significant at the one percent level. In the potassium data the Ho x T interaction is significant at five percent level. Neither of the other components of the P x T interaction is significant for either character.

The R x P x T interaction is broken down into its components because the R x He x T interaction in the sodium data is significantly larger than either of the other components. There is no significant difference between the components of the R x P x T interaction in the potassium data.

Main effects

The mean within-plot obtained and residual variances for populations are shown in Table 8. The F_1 hybrid variance was subtracted from each of the other variances to obtain the residual variances. The significance of the residual variances is tested by using the F_1 hybrid variance as the lesser mean square and each of the obtained variances as the dividend in the F test. All the residual variances from the sodium data are significant at the one percent level. This result might seem to indicate genetic segregation within the inbred lines. If the inbred lines are segregating the variance of the F_1 should also be increased. Furthermore, no evidence of genetic segregation within the inbred lines is found in the analysis of the frequency distributions.

Table 8.—Mean Within-Plot Obtained and Residual Variances of Logarithms of Parts per 100,000 of Sodium and Potassium for Populations.

Population	Sodium		Potassium	
	Obtained	Residual	Obtained	Residual
A54-1	0.043171	0.030259	0.008309	0.001220
A54-1, BB	0.048346	0.035434	0.008079	0.003990
50-406, BB	0.028270*	0.015358	0.007223*	0.003134
50-406	0.020338*	0.007426	0.005165	0.001076
F₁ hybrid	0.012912		0.004089	
52-307	0.015972	0.003060	0.003938*	-0.000151

Starred (*) obtained variances have 559 degrees of freedom; all others have 560. Tabular F for comparison between variances is 1.16 at the five percent level and 1.24 at the one percent level.

Of the residual variances obtained from the potassium data, those from the heterogeneous populations are all significant at the one percent level, that from 50-406 barely exceeds the one percent level, while that from 52-307 is not significantly different from zero.

First-order interactions

The mean within-plot obtained and residual variances for the interaction of populations x treatments are shown in Table 9. The F values for testing the significance of the residual variances are all significant at the one percent level for the heterogeneous populations. For sodium the residual variances for 50-406 are significant at the one percent level, but the residual variance for 52-307 is significant only on the non-fertilized plots. For potassium the residual variances for 50-406 are not different from zero. The obtained variance for 52-307 on the fertilized plots is significantly less than that for the F₁ hybrid. The residual variance for 52-307 on the non-fertilized plots is not considered since it was found that the frequency distribution for this population-treatment combination follows a normal curve on the arithmetic rather than the logarithmic scale.

Other comparisons of interest in Table 9 are A54-1 versus A54-1, BB and 50-406 versus 50-406, BB. On the fertilized plots the mean within-plot variances for A54-1 and A54-1, BB are not significantly different for either character. On the non-fertilized plots the F value for comparing A54-1 and A54-1, BB exceeds the five percent point for sodium while for potassium the variance for A54-1 is slightly higher, although not significantly so, than that for A54-1, BB. The F values for comparison of 50-406,

Table 9—Mean Within-Plot and Residual Variances of Logarithms of Parts per 100,000 of Sodium and Potassium for the Interaction of Populations and Treatments.

Treatment and Population	Sodium		Potassium	
	Obtained	Residual	Obtained	Residual
Fertilization				
A54-1	0.051484	0.033719	0.008035	0.003598
A54-1, BB	0.051962	0.034197	0.008543	0.004106
50-406, BB	0.037057	0.019292	0.007845	0.003408
50-406	0.027592	0.009827	0.005631	0.001194
F₁ Hybrid	0.017765		0.004437	
52-307	0.016575 ˙	-0.001190	0.002909 ˙	-0.001528
No fertilization				
A54-1	0.034858	0.026798	0.008582	0.004841
A54-1, BB	0.044729	0.036669	0.007615	0.003874
50-406, BB	0.019482 ˙	0.011422	0.006600 ˙	0.002859
50-406	0.013083 ˙	0.005023	0.004700 ˙	0.000959
F₁ Hybrid	0.008060		0.003741	
52-307	0.015369	0.007309	0.004968	0.001227

Starred variances have 279 degrees of freedom; all others have 280 degrees of freedom. Tabular F for comparison between variances is 1.26 at the 5% level and 1.39 at the 1% level.

BB with 50-406 on the fertilized plots approach the one percent level for both sodium and potassium, while on the non-fertilized plots the F values for comparisons between these populations are significant at the one percent level.

Since the residual variances for the heterogeneous populations are significantly different from zero, the frequency distributions were studied to determine the relative merits of the various population-treatment combinations as sources for selection of individuals high and low in sodium and/or potassium.

Frequency Distributions

Since the analysis of frequency distributions by the methods outlined by Powers, Robertson, and Clark (11), Powers, Robertson, and Remmenga (12), and Powers, et al., (13) depends upon the environmental variability being normally distributed, chi-square was used to test the fit of the frequency distributions obtained from the homogeneous populations to a normal curve. For sodium none of the homogeneous populations were distributed normally. When the data are transformed to logarithms, both the homogeneous and heterogeneous populations give satisfactory fits to a normal curve. Therefore, the transformed data were used in the statistical analyses.

For the potassium data only population 52-307 fits a normal curve satisfactorily when the original data are tested. When the data are transformed to logarithms, only populations 52-307 and 50-406 on the non-fertilized plots give significant chi-square values. For population 52-307 on the fertilized plots the test of whether the data are following the normal curve on the arithmetic or logarithmic scale is not discriminatory since neither chi-square value is significant. The P value for fit of the transformed data to the normal curve is 0.70-0.50, while that for fit of the untransformed data to the normal curve is 0.20-0.10. Similar results were reported by Powers (8). Statistical analyses of the potassium data were done on the transformed data. In the analysis of the individual frequency distributions, 52-307 on the non-fertilized plots was omitted since the data are following the normal curve on the arithmetic scale rather than on the logarithmic scale.

In order to estimate the environmental frequency distributions for the heterogeneous populations it is necessary to know whether the means and variances of the homogeneous populations are associated. Since there is no significant association between the mean within-plot variances and the means, for either sodium or potassium, the F_1 hybrid variance was used in the preceding section to test for the existence of residual variances. The variances to be used in analysing the frequency distributions are the total within-population and treatment variances. Thus it is necessary to examine the association of these variances with the corresponding means. The means and total within-population and treatment variances for the transformed data from the homogeneous populations are shown in Table 10. Regression of the means on the variances in the sodium data accounts for 85.21 percent of the variation among the variances. The m value of —0.0749 is different from zero with odds greater than 99:1 as measured by the t test. Thus even though there is no significant association between the means and the mean within-plot variances, there is a significant association between the means and the total within-population and treatment variances. Because of this relationship, the regression of the means on the variances is used to predict the environmental variances following the methods outlined by Powers, Robertson, and Remmenga (12). The only difference between the total within-plot variances and the total within-population and treatment variances is the addition of the appropriate among-replications variance to each within-plot variance. Hence, the difference between the regression of the means on the mean within-plot variances and the regression of the means on the total within-population and

Table 10.—Means and Total Within Population and Treatment Variances for Logarithms of Parts per 100,000 of Sodium and Potassium for the Interaction of Homogeneous Populations and Treatments.

Treatment and Population	Sodium		Potassium	
	Mean	Variance	Mean	Variance
Fertilized				
50-406	1.4545	0.060825	2.0811	0.006412
F₁ Hybrid	1.4472	0.065401	2.0011	0.006138
52-307	1.5727	0.055824 *	1.9931	0.003655 *
Non-fertilized				
50-406	1.1487	0.079529 *	2.0070	0.007627
F₁ Hybrid	1.1788	0.092901	1.9770	0.004547
52-307	1.3212	0.073846	2.0217	0.006275

Starred (*) variances have 318 degrees of freedom; all others have 319.

treatment variances must be caused by differences in the among-replications variances for the different population-treatment combinations.

The question arises as to the justification for using this type of association in predicting the environmental variances for the heterogeneous populations, since the occurrence of a negative association between means and variances is seldom reported. The criteria of a high percentage of the variability accounted for by regression and a significant m value already have been shown to hold for the means and variances of the homogeneous populations. Examination of the replication group means and variances in the heterogeneous populations reveals a negative environmental relationship between these means and variances in that part of the distribution in which the mean falls. Thus the use of a negative regression to predict environmental variances is justified.

Examination of the regression of means on total within-population and treatment variances for the potassium data reveals that only 20.06 percent of the variation among the variances is accounted for by regression and that the m value is not significantly different from zero. Therefore the F₁ hybrid variance is used as an estimate for the environmental variance.

The logarithmic means, obtained and calculated frequency distributions, and the numbers and proportions of individuals genetically low and high in sodium and potassium are shown in Tables 11-14. Examination of these tables reveals that the heterogeneous populations each fall into three distinct classes as regards the relationship of the obtained and calculated fre-

Table 11.—Obtained and Calculated Frequency Distributions[1], Means of Data Transformed to Logarithms, and Numbers and Proportions of Individuals Genetically High and Low in Sodium, Fertilized Plots.

Population & Distribution	Mean	Upper Class Limits in Parts per 100,000																				Total Genetically	
		0 to 10	20	30	40	50	60	70	80	90	100	110	120	130	140	150	160	170	180	190	Over 190	Low	High
A54-1	1.5914																						
Obtained		7	48	59	47	34	34	32	17	10	9	8	8	1	3	2					1	55	91
Calculated		2	32	67	66	51	35	23	15	10	6	4	3	2	1	1	1	1				34	67
Difference		5	16					9	2		3	4	5	-1	2	1	-1	-1			1	21	24
Proportion		0.71	0.33					0.28	0.12		0.33	0.50	0.62		0.67	0.50					1.00	0.38	0.26
A54-1, BB	1.5974																						
Obtained		9	55	40	48	45	29	24	20	11	9	10	4	7	5	2					2	64	70
Calculated		2	30	65	66	52	36	25	15	10	6	4	3	2	1	1	1	1				32	44
Difference		7	25						5	1	3	6	1	5	4	1	-1	-1			2	32	26
Proportion		0.78	0.45						0.25	0.09	0.33	0.60	0.25	0.71	0.80	0.50					1.00	0.50	0.37
50-406, BB	1.3977																						
Obtained		33	93	73	44	25	13	11	8	7	7	5	1									33	39
Calculated		21	93	84	53	29	17	10	5	3	2	1	1	1								21	23
Difference		12						1	3	4	5	4		-1								12	16
Proportion		0.36						0.09	0.38	0.57	0.71	0.80										0.36	0.41
50-406	1.4545																						
Obtained		10	79	90	54	29	25	10	13	6	1	1	2										
Calculated		12	76	84	58	36	21	13	7	5	3	2	3										
F₁ Hybrid	1.4472																						
Obtained		11	95	82	40	35	21	19	5	2	4	1	2	2		1							
Calculated		12	78	85	58	36	20	12	7	4	3	2	1	1	1								
52-307	1.5727																						
Obtained		3	38	74	74	45	18	21	9	10	15	7	3	2	1								
Calculated		2	37	70	67	49	34	22	14	9	6	3	2	2	1	2							

[1] The calculated frequency distributions were obtained by using the means of the transformed data, the standard errors of a single determination computed from the variances found in Table 10, and Pearson's (5) tables of the normal probability integral.

Table 12.—Obtained and Calculated Frequency Distributions[1], Means of Data Transformed to Logarithms, and Numbers and Proportions of Individuals Genetically High and Low in Sodium, Non-Fertilized Plots.

Population & Distribution	Mean	Upper Class Limits in Parts per 100,000															Total Genetically	
		0 to 10	20	30	40	50	60	70	80	90	100	110	120	130	140	Over 140	Low	High
A54-1	1.3050																	
Obtained		49	126	70	20	17	10	9	4	5	2	2	1		2	3	175	28
Calculated		43	116	77	40	20	11	6	3	2	1	1					159	13
Difference		6	10					3	1	3	1	1	1		2	3	16	15
Proportion		0.12	0.08					0.33	0.25	0.60	0.50	0.50	1.00		1.00	1.00	0.09	0.54
A54-1, BB	1.2645																	
Obtained		72	116	50	30	14	13	6	6	6		2	1		3	1	72	38
Calculated		55	122	72	35	17	8	5	3	1	1	1					55	19
Difference		17					5	1	3	5	-1	1	1		3	1	17	19
Proportion		0.24					0.38	0.17	0.50	0.83		0.50	1.00		1.00	1.00	0.24	0.50
50-406, BB	1.1720																	
Obtained		101	118	61	13	12	3	2	2		3	4	1				101	27
Calculated		89	126	59	25	11	5	3	1	1							89	21
Difference		12				1	-2	-1	1	-1	3	4	1				12	6
Proportion		0.12				0.08			0.50		1.00	1.00	1.00				0.12	0.22
50-406	1.1487																	
Obtained		99	126	57	19	9	2	3	1	3		1						
Calculated		100	121	54	23	10	5	3	1	1	1		1					
F1 Hybrid	1.1788																	
Obtained		90	131	46	19	14	7	3	2	2	1	5						
Calculated		84	130	60	25	11	5	2	1	1		1						
52-307	1.3212																	
Obtained		44	125	62	34	26	13	7	2	1	2		2	2				
Calculated		38	113	78	42	22	12	6	3	2	1	1	1	1				

[1] The calculated frequency distributions were obtained by using the means of the transformed data, the standard errors of a single determination computed from the variances found in Table 10, and Pearson's (5) tables of the normal probability integral.

Table 13.—Obtained and Calculated Frequency Distributions[1], Means of Data Transformed to Logarithms, and Numbers and Proportions of Individuals Genetically High and Low in Potassium, Fertilized Plots.

Population & Distribution	Mean	0 to 60	70	80	90	100	110	120	130	140	150	160	170	180	190	200	210	220	230	240	Over 240	Total Genetically Low	High
A54-1	2.1112																						
Obtained			2	5	14	27	42	47	31	31	32	22	16	22	10	9	4	2	1	2	1	90	51
Calculated			1	6	18	55		49	55	52	39	28	17	10	5	3	1	1				60	20
Difference			2	4	8	9	7							12	5	6	3	1	1	2	1	30	31
Proportion			1.00	0.80	0.57	0.33	0.17							0.55	0.50	0.67	0.75	0.50	1.00	1.00	1.00	0.33	0.61
A54-1, BB	2.0998																						
Obtained			3	6	20	28	52	40	35	22	26	25	19	19	11	9	1	3		1		109	88
Calculated				2	8	23	40	54	56	48	36	24	14	8	1	2	1					73	53
Difference			3	4	12	5	12					1	5	11	7	7		3		1		36	35
Proportion			1.00	0.67	0.60	0.18	0.23					0.04	0.26	0.58	0.64	0.78		1.00		1.00		0.33	0.40
50-406, BB	2.0381																						
Obtained		3	7	19	37	52	67	34	31	17	17	13	7	8	2	3	2			1		66	53
Calculated			2	12	32	54	65	59	44	26	14	7	3	1	1							46	26
Difference		3	5	7	5						3	6	4	7	1	3	2			1		20	27
Proportion		1.00	0.71	0.37	0.14						0.18	0.46	0.57	0.88	0.50	1.00	1.00			1.00		0.30	0.51
50-406	2.0811																						
Obtained			1	3	11	30	61	69	41	43	24	16	7	7	4	2				1			
Calculated				3	13	31	50	60	55	43	29	18	10	5	2	1							
F. Hybrid	2.0011																						
Obtained		2	6	23	60	66	74	47	17	16	6	2	1										
Calculated			7	26	54	71	64	47	27	14	6	3	1										
52-307	1.9931																						
Obtained			5	15	72	·87	79	42	15	3	2												
Calculated		1	8	31	59	73	63	42	24	11	5	2	1										

[1] The environmental standard error used in obtaining the calculated frequency distributions was 0.0783.

Table 14.—Obtained and Calculated Frequency Distributions[1], Means of Data Transformed to Logarithms, and Numbers and Proportions of Individuals Genetically High and Low in Potassium, Non-Fertilized Plots.

Population & Distribution	Mean	0 to 60	70	80	90	100	110	120	130	140	150	160	170	180	190	200	210	220	230	240	Over 240	Total Genetically Low	High
A54-1	2.0767																						
Obtained			4	13	23	28	53	57	32	25	27	21	17	10	5	2		1		1	1	40	85
Calculated				1	9	30	56	69	62	45	26	13	6	2	1							10	48
Difference			4	12	14						1	8	11	8	4	2		1		1	1	30	37
Proportion			1.00	0.92	0.61						0.04	0.38	0.65	0.80	0.80	1.00		1.00		1.00	1.00	0.75	0.44
A54-1, BB	2.0485																						
Obtained		1	4	12	29	50	71	46	38	25	11	15	7	5	2	2	1		1			46	33
Calculated				4	21	50	71	71	50	30	14	6	2	1								25	9
Difference		1	4	8	8							9	5	4	2	2	1		1			21	24
Proportion		1.00	1.00	0.67	0.28							0.60	0.71	0.80	1.00	1.00	1.00		1.00			0.46	0.73
50-406, BB	1.9880																						
Obtained		3	16	36	58	77	52	34	19	10	5	6	1	2	1							55	25
Calculated			5	28	66	84	68	40	19	7	2	1										33	10
Difference		3	11	8						3	3	5	1	2	1							22	15
Proportion		1.00	0.69	0.22						0.30	0.60	0.83	1.00	1.00	1.00							0.40	0.60
50-406	2.0070																						
Obtained			4	29	61	77	59	35	20	9	11	5	5	2	2			1					
Calculated			3	17	50	78	75	52	28	12	4	1											
F₁ Hybrid	1.9770																						
Obtained		2	4	33	82	93	57	31	6	8	3		1										
Calculated		1	7	35	74	85	64	33	14	5	2												
52-307[2]	2.0217																						
Obtained			5	2	11	34	49	92	64	35	21	6	1										

[1] The environmental standard error used in obtaining the calculated frequency distributions was 0.0674.

[2] No calculated frequency distribution is presented for 52-307 because the transformed data do not follow a normal distribution.

quency distributions. Powers, Robertson, and Clark, (11)
designated as identifiable-genetically superior or inferior those
individuals which fell into the classes of the obtained frequency
for which no individuals were expected. In classes at the ends
of the frequency distributions for which more individuals were
obtained than expected, the number in excess of those expected
was called the number of genetic deviates. A similar terminology
is employed in this paper except that the terms genetically high
and genetically low in sodium or potassium are used instead of
genetically superior and inferior, because there is no unanimity
of opinion among authorities as to the level of sodium or potas-
sium which should be considered superior or inferior.

The significance of differences between the obtained and
calculated condensed frequency distributions was tested by the
methods described by Powers, Robertson, and Clark (11). The
divisions used in condensing the frequency distributions are
indicated by the vertical lines in Tables 11-14. Chi-square
and P values obtained from this test are shown in Table 15. For
sodium, only 52-307, fertilized, of the homogeneous populations
has a chi-square which exceeds the five percent level and this
value lies between the five and two percent points. These
results are further evidence that the significant residual variances
obtained for the inbreds are not caused by genetic segregation.

Table 15.—Chi-Square and P Values for Fit of Obtained Condensed Frequency Distributions
to Expected Environmental Frequency Distributions.

Character and Population	Fertilized		Non-Fertilized	
	Chi-Square	P	Chi-Square	P
Sodium				
A54-1	13.7532	0.01 -0.001	9.8806	0.01 -0.001
A54-1, BB	24.4198	0.001-1-inf.	11.4510	0.01 -0.001
50-406, BB	8.2918	0.02 -0.01	2.3138	0.50 -0.30
50-406	0.2530	0.90 -0.80	0.2082	0.95 -0.90
F hybrid	0.4258	0.90 -0.80	4.1580	0.20 -0.10
52-307	6.3342	0.05 -0.02	1.1024	0.70 -0.50
Potassium				
A54-1	28.4158	0.001-1-inf.	38.1160	0.001-1-inf.
A54-1, BB	31.6066	0.001-1-inf.	23.7680	0.001-1-inf.
50-406, BB	17.7190	0.001-1-inf.	14.5766	0.001-1-inf.
50-406	0.2700	0.90 -0.80	13.9034	0.001-1-inf.
F hybrid	0.1667[1]	0.95 -0.90	0.9921[1]	0.70 -0.50
52-307[2]	18.6398	0.001-1-inf.		

[1] These are goodness-of-fit chi-squares; the rest are homogeneity chi-squares.

[2] 52-307, non-fertilized was not included because the transformed data were not following
a normal curve.

All the heterogeneous populations except 50-406, BB on the non-fertilized plots show significant differences between the obtained and calculated frequency distributions if odds of 49:1 are accepted as significant.

All the chi-square values from the heterogeneous populations for potassium are significant with odds greater than 999:1. Of the homogeneous populations, only 50-406, non-fertilized, and 52-307, fertilized have significant chi-square values. Significant chi-square values would be expected from these population-treatment combinations since the obtained variance for 52-307, fertilized is significantly less than that of the F_1 hybrid, and since 50-406, non-fertilized, while fitting a normal curve better on the logarithmic than on the arithmetic scale, still deviates from expected with odds between 99:1 and 999:1.

Study of Tables 11 and 12 reveals that for sodium there are no identifiable genetically low individuals in any of the heterogeneous populations. On the fertilized plots (Table 11) there is one identifiable genetically high individual in population A54-1, two in A54-1, BB, and none in 50-406, BB. On the non-fertilized plots (Table 12) there are six identifiable genetically high individuals in A54-1, five in A54-1, BB, and eight in 50-406, BB. Thus a significant number of identifiable genetically high individuals was found in 50-406, BB even though the chi-square test of the condensed frequency distributions failed to reveal any difference between the obtained and calculated frequency distributions.

Tests of whether the numbers of genetic deviates are significantly different from zero were made by the method outlined by Powers, Robertson, and Clark (11). On the fertilized plots the number of high and low genetic deviates in populations A54-1 and A54-1, BB are different from zero with odds greater than 99:1. For 50-406, BB, the number of high genetic deviates is significant with odds greater than 99:1, while the number of low genetic deviates is significant with odds of 60:1. On the non-fertilized plots the numbers of high genetic deviates in populations A54-1 and A54-1, BB are different from zero with odds greater than 99:1. Only A54-1, BB has a significant number of low genetic deviates on the non-fertilized plots. Population 50-406, BB has no significant number of genetic deviates in either the high or low class on the non-fertilized plots.

The breeding behavior of the heterogeneous populations for potassium is almost identical on the two fertility levels. On the fertilized plots (Table 13) two identifiable genetically low individuals were found in A54-1; three in A54-1, BB; and three

in 50-406, BB. On the non-fertilized plots (Table 14) four identifiable genetically low individuals were found in A54-1; five in A54-1, BB; and three in 50-406, BB. Five identifiable genetically high individuals were found in A54-1; four in A54-1, BB; and six in 50-406, BB on the fertilized plots, while on the non-fertilized plots five were found in A54-1; six in A54-1, BB; and four in 50-406, BB. The numbers of high and low genetic deviates in each population on both fertility levels are different from zero with odds greater than 99:1.

Joint frequency distributions

The joint frequency distributions for sodium and potassium are of interest in determining the possibility of altering sodium and potassium content simultaneously. The four classes, low sodium-low potassium, low sodium-high potassium, high sodium-low potassium, and high sodium-high potassium, are of interest. The four classes are obtained by using the same breaking points as those used in the individual frequency distributions shown in Tables 11-14. The question being asked is: within the classes in which there are genetic deviates for one character, are there genetic deviates for both characters? To determine this, the obtained joint frequency distributions are compared with the joint environmental frequency distributions expected on the basis of independence. The obtained joint frequency distribution for A54-1 on the fertilized plots is shown in Table 16. Study of Tables 11 and 13 reveals that the breaking points are between 110 and 120 for low potassium and between 170 and 180 for high potassium.

For sodium the breaking points are between 20 and 30 and between 60 and 70. The solid black lines in Table 16 delineate the classes formed by using these breaking points. To obtain the number of individuals expected in each of the four classes, the percentage of the total expected in the low and high classes for sodium, as shown in Table 17, and the number of individuals expected in the low and high classes for potassium are used. The numbers of individuals expected for potassium are listed in Tables 13 and 14 under the columns total genetically low and high opposite the row heading calculated. The product of the number expected for potassium and percentage expected for sodium gives the number of individuals expected in a particular class of the joint frequency distribution.

The obtained and calculated numbers and the number and proportion of joint genetic deviates in each of the four classes of interest are shown in Table 18. The number of individuals obtained in the low sodium-low potassium class for A54-1 on

Table 16.—Joint Frequency Distribution of Sodium and Potassium for A54-1, Fertilized Plots[1].

Potassium upper class limits in parts per 100,000	Sodium upper class limits in parts per 100,000																Total
	10	20	30	40	50	60	70	80	90	100	110	120	130	140	150	150 & over	
Over 220						2					1	1					4
220											1			1			2
210							1	1				1			1		4
200				1	2	1		1	1	1	1				1		9
190			1	3		1	2	1		1			1				10
180			1	1	3	4	2	4	2	1	1	1		1		1	22
170		1	1	1		5	2	2		1	2			1			16
160		1	3	4	5	3	2	2	1			1					22
150		6	5	6	3	2	6	1	1			2					32
140		2	8	4	6	2	3	2	1	3							31
130		6	8	2	5	3	2	2	2		1						31
120	3	11	12	6	4	3	6	2									47
110	3	8	10	7	3	4	3		1	1	1	1					42
100	1	9	5	7	1	1	3										27
90		3	4	4	1	1	1										14
80		1	1		1	1				1							5
70			1			1											2
Total	7	48	59	47	34	34	32	17	10	9	8	8	1	3	2	1	320

[1] Solid lines delineate classes formed by break points used in analysis of individual frequency distributions.

Table 17.—Percent of Individuals Expected in Classes Having Genetic Deviates for Sodium Data.

Treatment and Population	Class	
	Low	High
Fertilized		
A54-1	10.38	20.90
A54-1, BB	9.85	14.01
50-406, BB	6.55	7.49
Non-fertilized		
A54-1	49.60	4.18
A54-1, BB	17.11	5.94
50-406, BB	27.76	6.94

the fertilized plots is 25. This number is obtained by adding the numbers in the lower left hand corner of Table 16. The other obtained numbers for A54-1 are the total of the number of individuals in the appropriate corner of Table 16. The calculated number, six, is computed by multiplying 10.38 (see Table 17), the percent expected on the basis of the environmental frequency distribution for sodium, by 60, the number expected on the basis of the environmental distribution for potassium (see Table 14). The other calculated numbers are obtained in a similar manner. The number of individuals opposite the row heading difference in Table 18 are the number of joint genetic deviates for each class.

Examination of Table 18 reveals that for the high-high class the proportion of joint genetic deviates varies from 0.83 to 0.91. Tests of significance of the number of joint genetic deviates by the method of Powers, Robertson, and Clark (11) show that all the numbers of high-high genetic deviates are different from zero with odds of at least 99:1. Thus the choice of a fertility level and a population in which to select for individuals high in both characters depends on the number of individuals falling in the high-high class. The fertilized plots have from two to four times as many individuals in the high-high class as do the non-fertilized plots. Within the fertilized plots, A54-1, BB has the largest number of individuals in this class. Thus A54-1, BB should be the most fruitful source of individuals high in both sodium and potassium. For the low-low class the numbers of genetic deviates are different from zero with odds of at least 99:1 for all population-treatment combinations except 50-406, BB on the fertilized plots. For 50-406, BB the odds are 35:1 that the number of low-low genetic deviates is different from zero. On the fertilized plots A54-1 and A54-1,

Table 18.—Obtained[1] and Calculated Numbers and Numbers and Proportions of Genetic Deviates for Certain Classes of the Joint Frequency Distributions for Sodium and Potassium.

Treatment, Population, and Distribution	Class			
	Low Na Low K	Low Na High K	High Na Low K	High Na High K
Fertilized				
A54-1				
Obtained	25	0	12	31
Calculated	6	2	13	4
Difference	19			27
Proportion	0.76			0.87
A54-1, BB				
Obtained	28	9	9	47
Calculated	7	5	10	7
Difference	21	4		40
Proportion	0.75	0.44		0.85
50-406, BB				
Obtained	8	2	5	21
Calculated	3	2	3	2
Difference	5		2	19
Proportion	0.62		0.40	0.90
Non-fertilized				
A54-1				
Obtained	26	26	2	12
Calculated	5	24	0	2
Difference	21	2	2	10
Proportion	0.81	0.08	1.00	0.83
A54-1, BB				
Obtained	12	2	2	11
Calculated	4	2	1	1
Difference	8		1	10
Proportion	0.67		0.50	0.91
50-406, BB				
Obtained	20	2	2	10
Calculated	9	3	2	1
Difference	11			9
Proportion	0.55			0.90

[1] The obtained and calculated numbers are those obtained and calculated on the basis of the population of 320 individuals.

BB have the largest numbers and proportions of joint genetic deviates in the low-low class, while on the non-fertilized plots A54-1 has the largest number and proportion of low-low genetic deviates. Examination of Tables 11-14 reveals that the individuals in population 50-406, BB fall into lower classes of the frequency distributions than do those of either A54-1 or A54-1, BB. Thus if the plant breeder wanted extremely low sodium and potassium, he probably would want to work within population 50-406, BB.

In the low sodium-high potassium class only A54-1, BB on the fertilized plots and A54-1 on the non-fertilized plots have joint genetic deviates. In neither case are the numbers of deviates significantly different from zero. For the high sodium-low potassium class, joint genetic deviates are found in 50-406, BB on the fertilized plots and in populations A54-1 and A54-1, BB on the non-fertilized plots. For A54-1 the odds are 21:1 that the number of deviates is different from zero. Only two high sodium-low potassium individuals are found in A54-1 on the non-fertilized plots, but these individuals are identifiable as genetically high in sodium and low in potassium since none were expected. Thus it may be possible to select for high sodium and low potassium simultaneously although it will be more difficult than selecting in either the high-high or the low-low classes.

Information on whether the individuals in the classes studied are there because of an environmental relationship or because of genetic reasons can be obtained by applying the chi-square test described by Powers (7) to the joint frequency distributions of the homogeneous populations. The only difference in the application of this test to the sodium and potassium data and the application made by Powers (7) is that in this case five classes, low sodium-low potassium, low sodium-high potassium, high sodium-low potassium, high sodium-high potassium, and the remainder of the joint frequency distribution are used instead of the two classes described by Powers (7). The classes with few individuals are combined so that at least five individuals are expected in each. The expected values are computed by using the mean and standard error of the transformed data for both sodium and potassium except for 52-307 on the nonfertilized plots. Since the potassium data from this population-treatment combination are following the normal curve on the arithmetic scale rather than on the logarithmic scale, the mean and standard error of the untransformed data are used to obtain the number expected in each class for potassium. The mean and standard error of the transformed data are used to obtain the percent expected for sodium. The chi-square and P values from this test are shown in Table 19. None of the chi-square values for either 52-307 or the F_1 hybrid exceeds the five percent level. For 50-406 the chi-square values are significant at the 0.001 probability level on both fertility levels. Since more individuals are obtained in the low-low and high-high classes than are expected, the relationship indicated by the significant chi-square values is positive. Since no evidence of genetic segregation was found for either character in the analysis of the individual fre-

quency distributions for 50-406, this result in the joint frequency distribution indicates an interaction of genotype and environment such that some genotypes show a positive environmental relationship between the two characters while other genotypes show no such relationship.

Table 19.—Chi-Square and P Values for Fit of Obtained Joint Frequency Distributions to Those Expected on the Basis of Independence of Sodium and Potassium for Five Classes of Interest in Homogenous Populations.

Population	Fertilized		Non-Fertilized	
	Chi-Square[1]	P	Chi-Square[1]	P
50-406	33.7268	0.001-1-inf.	53.0221	0.001-1-inf.
F₁ hybrid	6.3887	0.20 -0.10	9.2634	0.10 -0.05
52-307	4.9464	0.30 -0.20	8.8593	0.10 -0.05

[1] Degrees of freedom for chi-square are 4 in every case.

Discussion

Although Rorabaugh and Norman (14) reported that their tests of solubility of sucrose in salt solutions indicated that sodium, in combination with carbonate, chloride, and sulfate ions, was more harmful than potassium, the effect of the presence of sodium and/or potassium ions on the processing quality of sugar beets has not been determined. Neither has the exact role of sodium and potassium in plant metabolism been determined. Finkner and Bauserman (3), in a study of breeding behavior, concluded that sodium, per se, had little effect on sucrose content and that the negative relationship between sucrose and sodium could be easily broken. They stated that sodium content was of little value in the breeding program unless it is extremely important from the processing standpoint. Wood˙ (15), and Wood, et al., (16) in a review of breeding work which has been done for chemical characters, reported significant decreases in sodium content as a result of selection. He stated that the value of reduction in sodium from the processing standpoint was not known. With respect to potassium he reported that differences between 16 varieties of sugar beets, while they might be statistically significant were too small to be of practical value. Doxtator and Calton (2), studying sodium and potassium contents of three varieties in two areas, found significant differences between varieties and areas but no significant interaction of varieties and areas. They reported differences between beets within varieties for both sodium and potassium. Doxtator and Bauserman (1) in limited breeding trials concluded that changing sodium content was

possible by simple breeding methods but that changing potassium content would be more difficult.

Study of the homogeneous populations indicates that low sodium content is dominant. This is true on both the fertilized and the non-fertilized plots. This result indicates that by using inbred lines in a breeding program it should be relatively easy to obtain a low-sodium hybrid. The potassium picture is more complicated since the cross studied shows dominance for low potassium on the high fertility level and heterosis for low potassium on the low fertility level. Furthermore the low parent on the high fertility level is the high parent on the low fertility level. The behavior of the F_1 hybrid might be explained by assuming that the ability to produce low potassium on the fertilized plots, found in 52-307, is dominant, while the ability to store less potassium on the non-fertilized plots than on the fertilized plots, found in 50-406, is also dominant. If such is the case, the F_1 hybrid should show heterosis for low potassium on the non-fertilized plots and it does.

The next aspect of breeding behavior to be examined is that of the variability in populations A54-1 and 50-406 after exposure to pollen from 22 other sources to form broad-base populations. Exposure of A54-1 to 22 other kinds of pollen had little effect on its variability in sodium and potassium contents, while exposure of 50-406 to 22 other kinds of pollen significantly increased its variability. This can be explained by assuming that A54-1 is heterozygous and heterogeneous enough to encompass the range of sodium and potassium contents found in the 22 other populations while assuming that the variability in 50-406, an inbred line, is limited to that due to environmental causes and that the increased variability of 50-406, BB is caused by increased genetic variability.

The analysis of frequency distributions provides most of the information concerning the potential breeding value of the heterogeneous populations. Study of the within plot variances shows that there is residual variance in the heterogeneous populations. The analysis of the frequency distributions reveals that selection for low sodium content can be more readily accomplished on the fertilized plots while selection for high sodium can be more readily accomplished on the non-fertilized plots. Comparisons of populations within treatments reveals that selection for low sodium should be more successful in population A54-1 since this population contains both a larger number and a larger proportion of genetic deviates than either of the other populations. Populations A54-1 and A54-1, BB are superior to

50-406, BB for selection of genetically high-sodium individuals since the genetic deviates fall into higher classes of the frequency distributions and since the numbers and proportions of genetic deviates are higher than in 50-406, BB.

Analysis of the frequency distributions for the potassium data reveals that the breeding behavior of the heterogeneous populations is essentially the same on both soil-fertility levels. Selection for low potassium should be most effective in population 50-406, BB while selection for high potassium should be most effective in A54-1.

Study of the joint frequency distributions for sodium and potassium indicates that it should be relatively easy to select individuals genetically high in both sodium and potassium or genetically low in both sodium and potassium. Selection of individuals genetically high in sodium and low in potassium or low in sodium and high in potassium would be more difficult. Thus a positive relation between sodium and potassium is indicated. A positive correlation between sodium and potassium was reported by Doxtator and Calton (2). It should be remembered in interpreting the results of the analysis of the joint frequency distributions that the joint environmental frequency distributions were calculated on the basis of independence of environmental effects for sodium and potassium. It was found for 52-307 and the F_1 hybrid that this assumption is correct, but that there is a positive environmental relationship between sodium and potassium in population 50-406. Thus the joint genetic deviates may be in the class in which they fall because of linkage, pleiotropy, or an interaction of genotype and environment.

From a practical sugar beet-breeding standpoint, the relation between sodium and potassium in the beet may not be as important as the relation between these characters and sucrose content, weight of root, and nitrogen content of the root. These characters have been studied and reported on (4, 13), but their interrelation with sodium and potassium have not yet been fully evaluated.

Summary

1. Studies of the variability and breeding behavior of sodium and potassium contents in the sugar beet root were made for six populations at two different levels of soil fertility.

2. It was found that low sodium was dominant for both fertility levels, but that low potassium was dominant on the fertilized plots while heterosis for low potassium was exhibited on the non-fertilized plots.

3. An interaction of populations and treatments such that the high-potassium parent on the fertilized plots was the low parent on the non-fertilized plots was found.

4. Analysis of the within-plot variances showed that all the heterogeneous populations contained significant residual variances and that it should be possible to alter their sodium and/or potassium content.

5. A significant negative relation between the means and the total within-population and treatment variances was found in the sodium data.

6. Analysis of the frequency distributions revealed that the sodium data were following a logarithmic rather than an arithmetic scale. The potassium data except for 52-307 on the non-fertilized plots were also following a logarithmic scale. The data from 52-307, non-fertilized, were following an arithmetic scale more closely than a logarithmic. Both the sodium and the potassium data were transformed to logarithms for statistical analyses.

7. Analysis of the individual frequency distributions revealed that it should be possible to select individuals genetically high or low in sodium content. Selection for low sodium could be done more easily on the fertilized plots, while selection for high sodium could be more readily accomplished on the non-fertilized plots.

8. Selection for high or low potassium could be accomplished with equal facility at either soil fertility level. Study of the differences between populations revealed that 50-406, BB would be the most desirable population from which to select for low potassium and that A54-1 would be the most desirable for selection for high potassium.

9. Analysis of the joint frequency distributions revealed that it would be possible to select readily for individuals high or low in both sodium and potassium but that it would be much more difficult to select for individuals high in sodium and low in potassium or high in potassium and low in sodium.

10. Analysis of the joint frequency distributions of the homogeneous populations revealed no environmental relation between sodium and potassium for 52-307 and the F₁ hybrid but a significant environmental relation between sodium and potassium was found for 50-406.

Literature Cited

(1) DOXTATOR, C. W. and BAUSERMAN, H. M. 1950. Parent-progeny tests for sodium and potassium content. Proc. Amer. Soc. Sugar Beet Tech. 319-321.

(2) DOXTATOR, C. W. and CALTON, F. R. 1952. Sodium and potassium content of sugar beet varieties in some western beet growing areas. Proc. Amer. Soc. Sugar Beet Tech. 144-151.

(3) FINKNER, R. E. and BAUSERMAN, H. M. 1957. Breeding of sugar beets with reference to sodium, sucrose, and raffinose content. Jour. Amer. Soc. Sugar Beet Tech. IX (2) : 170-177.

(4) PAYNE, MERLE G., POWERS, LEROY, and MAAG, GRACE W. Population genetic studies on the total nitrogen in sugar beets (Beta vulgaris L.) . X (7) : 631-646.

(5) PEARSON, K. 1930. Tables for statisticians and biometricians. Part I, Ed. 3, 143 pp., illus. Cambridge.

(6) POWERS, LEROY. 1934. The nature and interaction of genes differentiating habit of growth in a cross between varieties of Triticum vulgare. Jour. Agr. Res. 49: 573-605.

(7) POWERS, LEROY. 1945. Strawberry breeding studies involving crosses between the cultivated varieties (X Fragaria ananassa) and the native rocky mountain strawberry (F. ovalis). Jour. Agr. Res. 70: 95-122.

(8) POWERS, LEROY. 1950. Determining scales and the use of transformations in studies on weight per locule of tomato fruit. Biometrics 6: 145-163.

(9) POWERS, LEROY. 1957. Identification of genetically-superior individuals and the prediction of genetic gains in sugar beet breeding programs. Jour. Amer. Soc. Sugar Beet Tech. IX (5) : 408-432.

(10) POWERS, LEROY, LOCKE, L. F., and GARRETT, J. C. 1950. Partitioning method of genetic analysis applied to quantitative characters of tomato crosses. U. S. Dept. Agr. Tech. Bul. 998, 56 pp.

(11) POWERS, LEROY, ROBERTSON, D. W., and CLARK, A. G. 1958. Estimation by the partitioning method of the numbers and proportions of genetic deviates in certain classes of frequency distributions. Jour. Amer. Soc. Sugar Beet Tech. IX (8) : 677-696.

(12) POWERS, LEROY, ROBERTSON, D. W., and REMMENGA, E. E. 1958. Estimation of the environmental variances and testing reliability of residual variances for weight per root in sugar beets. Jour. Amer. Soc. Sugar Beet Tech. IX (8) : 697-708.   .

(13) POWERS, LEROY, ROBERTSON, D. W., WHITNEY, R. S. and SCHMEHL, W. R. 1958. Population genetic studies with sugar beets (Beta vulgaris L.) at different levels of soil fertility. Jour. Amer. Soc. Sugar Beet Tech. IX (8) : 637-676.

(14) RORABAUGH, GUY, and NORMAN, LLOYD W. 1957. The effects of various impurities on the crystallization of sucrose. Jour. Amer. Soc. Sugar Beet Tech. IX (3) : 238-252.

(15) WOOD, R. R. 1954. Breeding for improvement of processing characteristics of sugar beet varieties. Proc. Amer. Soc. Sugar Beet Tech. VIII (2) : 125-133.

(16) WOOD, R. R., BUSH, H. L., and OLDEMEYER, R. K. 1958. The sucrose-sodium relationship in selecting sugar beets. Jour. Amer. Soc. Sugar Beet Tech. X (2) : 133-137.