The Interrelation of 3-Hydroxytyramine and Polyphenoloxidase with Weight Per Root and Percent Sucrose in Sugar Beets[1]

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Introduction

In recent years several studies have been made on the possible role of phenolic compounds in leaf spot resistance in sugar beets. One of the most important of these compounds in sugar beet leaves is 3-hydroxytyramine. The activity of the oxidizing enzyme, polyphenoloxidase, and the subsequent oxidation products from phenolic compounds, also function in the expression of leaf spot resistance. This paper discusses experiments conducted in 1963, 1964 and 1965 on the interrelation of 3-hydroxytyramine content and polyphenoloxidase of sugar beet leaves to weight per root and percentage sucrose. The purpose was to obtain information about the distribution and variability of 3-hydroxytyramine and polyphenoloxidase between and within sugar beet genotypes and varieties. Such information is needed if 3-hydroxytyramine relations are found to be of direct value in breeding, pathologic and physiologic studies, to increase leaf spot resistance in sugar beets. Equally important is the relation of 3-hydroxytyramine to yield and quality characters. This is necessary for the simultaneous improvement of all the economic characters.

Literature Review

Interest was generated for further research on the phenolic compounds in sugar beets (*Beta vulgaris* L.) when Harrison et al (3)[3] discovered that one of these phenolic compounds is positively associated with Cercospora leaf spot resistance. When this

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[3] Numbers in parentheses refer to literature cited.

compound is oxidized in beet leaf extract it becomes highly toxic to *Cercospora beticola* Sacc. grown in pure culture. This phenolic compound was later identified as 3-hydroxytyramine by Gardner (1). The methods for chemical determination of 3-hydroxytyramine and its oxidizing enzyme, polyphenoloxidase, are described by Harrison et al. (2). The results of a study of the distribution of these two compounds in one population (A56-3) of sugar beets, as well as other chemical characters, and the mathematical transformations required to obtain normality, are described by Maag et al. (5). The distribution and variability of 3-hydroxytyramine in this one sugar beet population for one year was such that the possibility of genetic change by selection appears very likely. Differences between populations also indicate excellent potential for genetic change [Harrison et al. (2)]. However, the relation to sucrose and yield are not well defined. It is known that 3-hydroxytyramine content is highly variable and that extreme differences occur between and within leaves from the same plant, and from different plants of the same variety. These differences are apparently affected by local environmental conditions. A study of this variability, and of the development of a sampling procedure to obtain consistent estimates of 3-hydroxytyramine content, is also reported by Harrison et al. (2).

The distributions of weight per root and sucrose and their interrelations have been reported by Powers et al. (9), Payne et al. (6) and Powers and Payne (7). These relations, where they are informative, will be presented here, but major emphasis will be placed on 3-hydroxytyramine content and its relation to root yield and sucrose content. The analysis will follow the general pattern described by Powers et al. (8).

Materials and Methods

We used the following populations of sugar beets in the three experiments. The leaf spot resistance is given at the right of each population; mr, moderately resistant; r, resistant; unk, unknown resistance.

A56-3, a multigerm open-pollinated commercial variety, was used all three years. The hybrid (52-305CMS $\times$ 52-408, F_1) was used in both 1964 and 1965. Hence eight different populations were used over the three years. SP 5481-0 (2n) and (4n) are diploid and tetraploid equivalents of a multigerm open-pollinated variety. US 401 (4n) is the tetraploid equivalent of US 401, a multigerm open-pollinated diploid variety. Among the four inbred parents involved in the three hybrid populations, 52-305CMS is moderately high in leaf spot resistance while the other three are quite susceptible.

Variety	Leaf spot resistance
1963	
A56-3	mr
US 401 (4n)	mr
(52-305CMS × 52-407, F_1)	mr
1964	
A56-3	mr
SP 5481-0 (2n)	r
SP 5481-0 (4n)	r
(52-305CMS × 52-408, F_1)	unk
1965	
A56-3	mr
FC 901	mr
[52-305CMS × (52-430 × 52-407, F_1)] OP	unk
(52-305CMS × 52-408, F_1)	unk

The experimental materials were grown under irrigation at the Colorado State University Agronomy Research Center, Fort Collins, Colorado, and were planted on April 8, April 23, and April 8 in 1963, 1964, 1965, respectively. The average growing season in Fort Collins is about 145 days. The field design was a randomized block with 40 replicates. In 1963, ten plants were harvested per plot for a total of 400 plants per population. Twelve plants were harvested for each plot in 1964 and 1965, for a total of 480 observations for each character in each population. The same design was used in all years. However, in 1965, two replicates were deleted from the analysis because of missing plots for two characters.

Individual plant data were obtained on all populations in all years for weight per root, percentage sucrose and 3-hydroxytyramine content. Leaf samples for 3-hydroxytyramine were taken in mid-July in 1963 and 1964 and the first week of August in 1965. In 1963 and 1964, the same leaves were used for polyphenoloxidase determinations. Complete analysis for polyphenoloxidase was made in 1964 only and sufficient material was available in only 26 replicates for this determination. Incomplete polyphenoloxidase data were available in 1963. The chemical methods used for determination of 3-hydroxytyramine and polyphenoloxidase are the same as described by Harrison et al. (2).

The data were transformed to scales indicated by Maag et al. (5) and the transformed data were checked for normality and independence of means and variance. Population means and

variances were obtained for each year and analyses of variance were computed within and between years for each character. Genetic variances and heritabilities were computed for each character each year by using the F_1 variance as an estimate of environmental variance. Correlations within populations were computed by using individual plant data for each pair of characters within years, and estimates obtained of genetic correlation. Univariate and bivariate frequency distributions were made and studied for identifiable numbers of genetic deviates.

The univariate frequency distributions were partitioned for all populations for all years by methods of Powers et al. (8). This method adjusts the distributions to eliminate differences between replications within populations and differences between populations, resulting in a common mean for all populations. Using the nonsegregating population as an estimate of the environmental distribution, the distributions of the segregating populations each year were partitioned at approximate points of intersection of the obtained and the estimated environmental curves. The identifiable numbers of genetic deviates were differences between obtained and estimated environmental distributions. The same partition points were used in the bivariate distributions for estimation of the identifiable numbers of genetic deviates for combination of two characters.

Results

The population means and their standard errors for the 3 years are reported in Table 1. The mean weight per root in kilograms and percentage sucrose show year and population differences as expected.

The means for 3-hydroxytyramine show extreme differences between years and between populations. Some of the year effects between 1963 and 1964 are probably due to changes in analytic methods since the determination method was modified in 1964. However, there is undoubtedly a true year effect as there is with weight per root and percentage sucrose, although year effect cannot be isolated from chemical technique for this variable in 1963 and 1964. In the standard error for 3-hydroxytyramine from year to year, there is a corresponding change which may be partly due to changes in chemical procedure. But a positive relation between the means and variances appears to be partly responsible for these year-to-year differences. However, the correlations between 3-hydroxytyramine and weight and sucrose should not be affected by this change in chemical procedure.

The highest levels of 3-hydroxytyramine each year occur in the F_1 hybrids. All of these hybrids in this particular study

Table 1.—Population means and their standard errors within years.

Population and year	Leaf spot[1] classification	Root weight	Percentage sucrose	3-hydroxy-tyramine	Polyphenol-oxidase
		kg	%	mg/100ml	optical density
1963					
A56-3	mr	1.174±0.032	15.38±0.069	6.64±0.242	0.797±0.056
US 401 (4n)	mr	1.127±0.034	14.60±0.086	7.96±0.271	1.015±0.038
52-305CMS × 52-407. F_1	mr	0.974±0.017	16.15±0.050	17.76±0.265	0.497
1964					
A56-3	mr	0.551±0.012	19.01±0.046	12.14±0.530	1.005±0.015
SP 5481-0 (2n)	r	0.502±0.011	18.76±0.043	8.67±0.390	1.052±0.014
SP 5481-0 (4n)	r	0.572±0.014	18.50±0.056	12.31±0.393	1.009±0.014
52-305CMS × 52-408. F_1	unk	0.556±0.009	20.03±0.030	23.55±0.550	0.790±0.015
1965					
A56-3	mr	0.689±0.016	15.43±0.060	34.76±1.495	
FC 901	mr	0.516±0.013	14.27±0.069	27.85±1.237	
52-305 CMS × (52-430 × 52-407. F_1)	unk	0.417±0.009	15.37±0.048	103.19±2.338	
52-305CMS × 52-408. F_1	unk	0.566±0.009	15.28±0.033	63.31±1.192	

[1] mr = moderately resistant.
r = resistant.
unk = unknown resistance.

have the same female parent, 52-305CMS. The hybrid (52-305CMS × 52-407, F_1) is rated as moderately resistant to leaf spot; as is A56-3 which in 1963 had less than one-half as much 3-hydroxytyramine. In 1964, SP 5481-0 (2n) had the least amount of 3-hydroxytyramine but is classed as being a resistant variety, superior to A56-3 and the F_1.

The population differences are such that genetic manipulation of the amounts of 3-hydroxytyramine present should be possible. From the population means, it would appear that 3-hydroxytyramine is not closely related either to root weight or percentage sucrose. High levels of all three characters occurred in the hybrid (52-305CMS × 52-408, F_1) in 1964; whereas, in 1963 the highest level of 3-hydroxytyramine occurred with the lowest yielding population and the lowest level of 3-hydroxytyramine occurred with the highest yielding population.

Complete polyphenoloxidase data (on 26 replications) were available only in 1964 with some partial data in 1963. Fairly large population differences exist for quantity of this enzyme. The lower levels of polyphenoloxidase occur in those populations which have high levels of 3-hydroxytyramine and vice versa. It is difficult to infer a relation between polyphenoloxidase and weight per root or percentage sucrose from 1 year with only four populations. but as with 3-hydroxytyramine, a close relation probably does not exist.

For variance and correlation analysis each of the characters in each year were transformed to the scale indicated by Maag et al. (5). That is, the weight per root and 3-hydroxytyramine were transformed to square roots, the sucrose was untransformed and the polyphenoloxidase was transformed to the antilog_{10}. Tests were performed on each set to determine whether or not the transformations were successful in removing any relations between the means and variances which have commonly existed in these types of data, and to determine if the data on the transformed scale are sufficiently normal for valid tests following the analyses of variance.

Tests using the third and fourth moments about the mean were run on each variable, transformed to the scale recommended by Maag et al. (5), for each population in each year to determine whether or not the data were normally distributed. The tests were sensitive with the sample sizes used here. Many variables were significantly non-normal, considering variable within years within populations. For example, square root of weight per root was negatively skewed in three cases, positively skewed in one case and acceptably normal in seven cases. Sucrose, which was handled on the arithmetic scale (the usual practice) was

found to be negatively skewed in eight cases, positively skewed in two cases and acceptably normal only once. Obviously, no transformation can possibly produce overall normality when one population is negatively skewed and another positively skewed in the same year. The chosen transformations are superior to no transformations and possibly allow an acceptable analysis.

The relation between the means and variances for each variable for each population in each year was also studied. The same lack of pattern was found with some significant positive relations, some significant negative relations and some non-significant relations. It is impossible to remove the relation between means and variances in all cases with a uniform transformation. The mean-variance relation for the F_1's used as a measure of environmental variability has been removed or decreased in most cases, however.

Analyses of variance were performed on the transformed data for each character for each year and reported in Table 2. The population and replication effects were significant for nearly all characters in all years; however, the magnitude of these differences is such that the population effect is of greatest concern. The population by replication interaction was significant for all characters except root weight. Environmental differences,

Table 2.—Analyses of variance for weight per root (kg), percentage sucrose, 3-hydroxytyramine (mg/100ml), and polyphenoloxidase (optical density), for three years.

Year and source of variation	Degrees of freedom	Mean square			
		$\sqrt{\text{Root Weight}}$	Sucrose	$\sqrt{\text{3-hydroxytyramine}}$	Antilog[1] polyphenol-oxidase
1963					
Populations	2	0.5817**	240.1743**	360.2464**	
Replications	39	0.0732	24.5461**	9.0966**	
P × R	78	0.0633	6.0961**	2.0861**	
Residual	1080	0.0780	1.8333	0.6972	
1964					
Populations	3	0.2161**	213.7442**	317.4579**	1686.3915**
Replications	39	0.0400**	12.6754**	32.8003**	679.2404**
P × R	117	0.0194	3.8082**	4.0648**	86.0740**
Residual	1760	0.0310	0.9648	1.5617	38.9127
1965					
Populations	3	2.5526**	136.8993**	2384.8758**	
Replications	37	0.0503*	33.7621**	37.0614**	
P × R	111	0.0288	4.5814**	12.2164**	
Residual	1672	0.0299	1.3317	4.9647	

[1] Degrees of freedom are 3, 25, 75, and 1112, respectively, for each source of variation for polyphenoloxidase.

as indicated by the replication effects and the replication × population interactions, are minor as compared to the population effects.

Combined analyses of variance were computed to evaluate the year effects and the population × year interactions (Table 3). A56-3 was used in all years and A56-3 and the F_1 (52-305CMS × 52-408) were common to 1964 and 1965. The anticipated year-effect is significant for all characters (when considering A56-3 only). For A56-3 and (52-305CMS × 52-408) F_1 which were common to 1964 and 1965, the year effect, the population effect and the year-by-population interaction were all highly significant statistically. But, because these tests involve only two populations in two years, the results should be interpreted cautiously. A study of the means (Table 1) indicates that the yearly population interaction (Table 3) exists but also indicates that if a population has a high yield, sucrose content or 3-hydroxytyramine content in any year, that population will probably be relatively high in all years. The interaction stems from the fact that the population differences vary within years even though the general ranking is the same.

Table 3.—Analyses of variance for weight per root (kgs), percentage sucrose, and 3-hydroxytyramine (transformations as noted), three years (1963, 1964, 1965) combined.

Source of variation	Degrees of freedom	Mean square		
		√ Root weight	Sucrose	√ 3-hydroxytyramine
Years	2	38.3445**	8843.1000**	7690.8741**
Populations within years	8	1.1712**	191.5349**	1103.4368**
Replications within years	115	0.0546	23.4855**	26.1326**
P × R within years	306	0.0340	4.6719**	6.5173**
Residual	4512	0.0418	1.3086	2.6158
A-56-3 only				
Between years	2	11.8058**	2002.4538**	1064.4171**
A56-3 and (52-305CMS × 52-408) F_1				
Years	1	0.9493**	8104.2380**	3443.7843**
Populations	1	0.2953**	93.3355**	1641.6128**
Y × P	1	0.6564**	158.2373**	98.0632**

The correlations within populations and within years for each pair of characters are shown in Table 4. These correlations were calculated from individual plant determinations and include both the genetic and environmental correlation. None of the correlations are large but many are significant. The correlation between sucrose and weight is negative in most cases as is generally expected.

Table 4.—Simple correlation coefficients (r) within populations and years.

Year and character combination	Population			
1963	A56-3	US 401 (4n)	52-305CMS × 52-407, F_1	
$\sqrt{\text{Root weight}}$ vs. sucrose	—0.131**	0.093	—0.391**	
$\sqrt{\text{Root weight}}$ vs. $\sqrt{\text{3-hydroxytyramine}}$	0.147**	0.156**	0.280**	
Sucrose vs. $\sqrt{\text{3-hydroxytyramine}}$	0.197**	0.204**	0.100*	
3-hydroxytyramine vs. polyphenoloxidase	—0.537**			
1964	A56-3	SP 5481-0(2n)	SP 5481-0(4n)	52-305CMS × 52-408, F_1
$\sqrt{\text{Root weight}}$ vs. sucrose	—0.175**	—0.053	—0.007	—0.412**
$\sqrt{\text{Root weight}}$ vs. $\sqrt{\text{3-hydroxytyramine}}$	0.059	0.180**	0.117**	0.239**
$\sqrt{\text{Root weight}}$ vs. antilog polyphenoloxidase	—0.037	—0.046	—0.100	—0.030
Sucrose vs. $\sqrt{\text{3-hydroxytyramine}}$	0.047	0.030	0.076	—0.130**
Sucrose vs. antilog polyphenoloxidase	0.037	0.196**	0.048	0.154**
$\sqrt{\text{3-hydroxytyramine}}$ vs. antilog polyphenoloxidase	—0.406**	—0.283**	—0.209**	—0.330**
1965	A56-3	FC 901	52-305CMS × (52-430 × 52-407, F_1)	52-305CMS × 52-408. F_1
$\sqrt{\text{Root weight}}$ vs. sucrose	—0.115*	0.116*	—0.056	0.008
$\sqrt{\text{Root weight}}$ vs. $\sqrt{\text{3-hydroxytyramine}}$	0.163**	0.070	0.063	0.044
Sucrose vs. $\sqrt{\text{3-hydroxytyramine}}$	—0.012	0.139**	—0.119**	—0.080

Weight and 3-hydroxytyramine are positively related in all populations and years in this study. This relation is not large but is significantly greater than zero in most cases, indicating genetic linkage, epistasis or interallelic interaction.

The relation between sucrose and 3-hydroxytyramine is somewhat erratic. Significant correlations exist in all years, and both significant positive and negative relations exist in 1965. These correlations are neither as high nor consistent as those between weight and 3-hydroxytyramine. Simultaneous selection for high sucrose and high 3-hydroxytyramine will probably present the same problems as selection for high sucrose and high root yield.

A significant negative relation exists between 3-hydroxytyramine and polyphenoloxidase. The correlations of polyphenoloxidase with weight per root are negative but not significant; whereas the correlations with sucrose are positive, with two significant. This pattern is consistent with the preceding discussion as well as the patterns previously reported by Maag et al. (5).

The genetic correlations are presented in Table 5. These correlation coefficients were calculated from estimates of the genetic variances and covariances which, in turn, were estimated as differences between the respective variances and covariances of the segregating and nonsegregating populations. These genetic correlations should represent the genotypic relationship of the various characters. In testing these genetic correlations for significance, the degrees of freedom for the genetic variances and covariances, and thus the genetic correlations were obtained from the theoretical form of the variance of the estimates of genetic variances and covariances. The number of degrees of freedom is generally considered to be the divisor in the equation for a variance. In this case if σ_g^2 (or cov_g) = 0, the number of degrees of freedom is one-half that of the total within plot correlation. Even a sizeable value for σ_g^2 will change this value only slightly; hence the degrees of freedom used for testing the genetic correlations were considered as a good approximation of the true number of degrees of freedom. It is apparent from the correlations of root weight with 3-hydroxytyramine for A56-3 over the three years that a year by genotype interaction is present and has considerable effect. The difference between populations is marked, indicating that the genes conditioning each character must be different in the different populations. In other words, each of these characters seems to be conditioned by several genes.

The total genetic variance was computed for each population for each year based on the total within-plot variance of each population and using the total within-plot variance of the

Table 5.—Genetic correlations within populations and years.

Year and character combination	Degree of freedom (for testing r)	Population		
1963		A56-3	US 401 (4n)	
$\sqrt{\text{Root weight}}$ vs. sucrose	178	0.122	0.419**	
$\sqrt{\text{Root weight}}$ vs. $\sqrt{\text{3-hydroxytyramine}}$	178	0.038	0.011	
Sucrose vs. $\sqrt{\text{3-hydroxytyramine}}$	178	0.420**	0.336**	
1964		A56-3	SP 5481-0 (2n)	SP 5481-0 (4n)
$\sqrt{\text{Root weight}}$ vs. sucrose	218	—0.059	0.363**	0.279**
$\sqrt{\text{Root weight}}$ vs. $\sqrt{\text{3-hydroxytyramine}}$	218	—0.902**		
$\sqrt{\text{Root weight}}$ vs. antilog polyphenoloxidase	143	—0.008	—0.074	—0.203*
Sucrose vs. $\sqrt{\text{3-hydroxytyramine}}$	218	0.100		
Sucrose vs. antilog polyphenoloxidase	143	—0.031	0.156	—0.204*
1965		A56-3	FC 901	52-305CMS × (52-430 × 52-407, F_1)
$\sqrt{\text{Root weight}}$ vs. sucrose	226	—0.140*	0.198**	—0.022
$\sqrt{\text{Root weight}}$ vs. $\sqrt{\text{3-hydroxytyramine}}$	226	0.210**	—0.047	—0.065
Sucrose vs. $\sqrt{\text{3-hydroxytyramine}}$	226	0.093	0.216**	—0.129

nonsegregating F_1 as an estimate of the environmental variance. Broad sense heritability ratio estimates were computed for each population for which an estimate of genetic variance could be obtained and are presented in Table 6.

The heritability ratios for root weight and sucrose are quite consistent and little affected by years. However, the heritability ratios for 3-hydroxytyramine are affected by years. Therefore, the variability in quantity of 3-hydroxytyramine is affected both by the environment and by genotype and tends to detract from the value of the heritability ratios. It appears that little can be accomplished by a comprehensive study of the variability of 3-hydroxytyramine until its environmental influences are more clearly defined.

The estimates of identifiable numbers of superior and inferior genetic deviates are also included in Table 6. These estimates are expected numbers of genetically inferior and superior individuals in each population for each character and, as such, provide an empirical comparison of the relative breeding value of each segregating population. These expected numbers of genetic deviates in the case of 3-hydroxytyramine are of dubious value since the population variance can be greatly influenced by unknown environmental factors. One thing worthy of note and further study is that the estimate of superior genetic deviates is usually less than the estimate of inferior ones (classing high 3-hydroxytyramine as superior). Identifiable numbers of genetic deviates should serve as comparative breeding values in the case of root weight and sucrose percentage.

The association between the expected number of genetic deviates (in percent of the total) and heritability can be determined according to Powers et al. (8), by their correlation. This correlation, if high, would indicate that the populations were normally distributed, since Hecker (4) states that under conditions of normality the proportion of genetic deviates should be a monotonic (increasing) function of heritability and, hence, an equivalent index. These correlations were calculated. For 3-hydroxytyramine the coefficients were 0.88 and 0.85, respectively, for heritability with the identifiable numbers of superior and inferior genetic deviates. These same correlations are also relatively high for root weight and percentage sucrose: 0.92, 0.97 and 0.90, 0.86. In this experiment the heritability ratios and identifiable numbers of genetic deviates provide equivalent information, except that the identifiable numbers of genetic deviates allow one to see whether or not high and low deviates contribute equally to the genetic variability of the population.

Table 6.—Heritability ratios (h^2) and identifiable numbers of superior and inferior genetic deviates, expressed as percent of the total population.

Year and population	√ Weight per root			Percentage sucrose			√ 3-hydroxytyramine			Antilog$_{10}$ polyphenoloxidase		
	h^2	Number of deviates		h^2	Number of deviates		h^2	Number of deviates		h^2	Number of deviates	
		Sup.	Inf.		Sup.	Inf.		Sup.	Inf.		Sup.	Inf.
		%	%		%	%		%	%		%	%
1963												
A56-3	0.623	13.2	14.5	0.484	7.5	8.5	0.342	8.2	13.0			
US 401 (4n)	0.689	14.5	16.8	0.615	11.2	8.0	0.355	6.5	10.2			
1964												
A56-3	0.403	5.8	7.3	0.582	9.2	8.5	0.048	1.5	6.9	0.421	7.0	9.3
SP 5481-0 (2n)	0.418	8.1	7.5	0.530	9.6	8.1	0.000	2.1	7.7	0.452	9.3	11.9
SP 5481-0 (4n)	0.579	9.6	11.7	0.725	12.7	11.5	0.000	1.2	3.8	0.374	7.7	11.9
1965												
A56-3	0.643	13.4	13.2	0.689	16.2	11.0	0.483	7.9	11.2			
FC 901	0.595	9.9	11.2	0.767	18.6	13.4	0.479	8.1	11.8			
52-305CMS × (52-430 × 52-407, F_1)	0.343	6.8	5.7	0.508	9.6	9.2	0.650	19.7	13.2			

The partitioned bivariate distributions provide the identifiable numbers of genetic deviates for combinations of two characters (Table 7). These are average numbers of individuals superior or inferior for two characters simultaneously. These values are a function of the correlation of two characters and their heritabilities, but they provide information not readily observable by studying the correlations and heritability ratios. For instance, it is apparent from Table 7 that there are no individuals superior for both 3-hydroxytyramine and polyphenoloxidase. This was not readily observable by studying the correlation coefficients and the heritability ratios. It would apparently be futile to select for high 3-hydroxytyramine and high polyphenoloxidase in the three populations studied in 1964. Genetic deviates superior for 3-hydroxytyramine and weight or sucrose occur with about equal frequency in all populations. However, the frequency is not very high indicating some difficulty in selecting for these combinations. Genetic deviates superior for both weight and sucrose occur more frequently than any other combination of characters but there is a considerable difference between populations and possibly some difference between years.

Discussion

It is apparent from the means and partitioned univariate frequency distributions that there is considerable variability in quantity of 3-hydroxytyramine due to genotype. According to Maag et al. (5), a larger proportion of this variability may be due to additive gene effects than in the case of root weight and sucrose percentage. So it should be possible to shift the quantity of 3-hydroxytyramine by selection or choice of parents in a hybrid combination, provided the considerable environmental effect on 3-hydroxytyramine can be separated from the genetic effect. Further studies are currently under way in an attempt to determine the environmental factors influencing 3-hydroxytyramine. Some difficulty might be experienced in advancing both root yield and quantity of 3-hydroxytyramine, as well as sucrose content and 3-hydroxytyramine. From those populations grown in 1964 it appears impossible to increase quantities of 3-hydroxytyramine and polyphenoloxidase simultaneously. Since certain of these 1964 populations were quite heterogenous this relationship might be expected to extend extensively through the species.

Even though positive associations between quantity of 3-hydroxytyramine and leaf spot resistance have been established by Harrison et al. (3) and Maag et al. (5), these data and those of Harrison et al. (2) show that there are exceptions to this

Table 7.—Heritability ratios (h^2) for the respective characters in order and identifiable number of genetic deviates, expressed as percent of the total population, in sections 4, 5, and 6 (superior) and in sections 1, 2, and 8 (inferior) for the bivariate frequency distributions.

Year, character, and population	Heritability ratio 1st Var. h^2	Heritability ratio 2nd Var. h^2	Identifiable numbers of genetic deviates Sup. %	Identifiable numbers of genetic deviates Inf. %
1963				
√ Weight vs. sucrose (n=400)				
A56-3	0.623	0.484	9.0	11.0
US 401 (4n)	0.689	0.615	8.5	8.5
√ Weight vs. √ 3-hydroxytyramine (n=400)				
A56-3	0.623	0.342	10.0	9.5
US 401 (4n)	0.689	0.355	8.8	8.8
√ 3-hydroxytyramine vs. sucrose (n=400)				
A56-3	0.342	0.484	8.0	9.0
US 401 (4n)	0.355	0.615	9.8	2.5
1964				
√ Weight vs. sucrose (n=480)				
A56-3	0.403	0.582	10.6	8.3
SP 5481-0 (2n)	0.418	0.530	13.5	9.4
SP 5481-0 (4n)	0.579	0.725	8.8	10.8
√ Weight vs. √ 3-hydroxytyramine (n=480)				
A56-3	0.403	0.048	3.3	9.6
SP 5481-0 (2n)	0.418		1.6	9.8
SP 5481-0 (4n)	0.579		5.4	7.7
√ 3-hydroxytyramine vs. sucrose (n=480)				
A56-3	0.048	0.582	7.9	9.4
SP 5481-0 (2n)		0.530	7.5	6.0
SP 5481-0 (4n)		0.725	6.2	4.0
√ Weight vs. antilog$_{10}$ polyphenoloxidase (n=312)				
A56-3	0.403	0.421	—1.3	5.8
SP 5481-0 (2n)	0.418	0.452	5.4	7.4
SP 5481-0 (4n)	0.579	0.374	4.5	9.3
Sucrose vs. antilog$_{10}$ polyphenoloxidase (n=312)				
A56-3	0.582	0.421	5.1	5.8
SP 5481-0 (2n)	0.530	0.452	11.2	10.6
SP 5481-0 (4n)	0.725	0.374	10.3	11.5
√ 3-hydroxytyramine vs. antilog$_{10}$ polyphenoloxidase (n=312)				
A56-3	0.048	0.421	—3.5	—1.0
SP 5481-0 (2n)		0.452	—4.8	2.6
SP 5481-0 (4n)		0.374	—5.1	4.5
1965				
√ Weight vs. sucrose (n=456)				
A56-3	0.643	0.689	17.1	9.6
FC 901	0.595	0.767	21.3	16.9
52-305CMS × (52-430 × 52-407, F$_3$)	0.343	0.508	11.0	7.9
√ Weight vs. √ 3-hydroxytyramine (n=456)				
A56-3	0.643	0.483	12.3	11.6
FC 901	0.595	0.479	6.1	11.4
52-305CMS × (52-430 × 52-407, F$_3$)	0.343	0.650	15.1	11.2
√ 3-hydroxytyramine vs. sucrose (n=456)				
A56-3	0.483	0.689	12.1	7.2
FC 901	0.479	0.767	11.4	4.2
52-305CMS × (52-430 × 52-407, F$_3$)	0.650	0.508	13.2	6.6

relationship. It is not a one-to-one association. It would appear that quantity of 3-hydroxytyramine cannot be used directly as a measure of leaf spot resistance. Further studies are being conducted to determine the exact relationship of these two characters and the relationship of leaf spot resistance with related phenolic compounds and their oxidizing enzymes. A direct quantitative determination of some compound as a precise measure of leaf spot resistance would be extremely valuable; but considering the number of alternative pathways that exist for most metabolic processes it would appear unlikely that any single chemical determination could serve as a direct and precise measure of leaf spot resistance. However, a combination of two or more determinations might be a more precise and economic measure of leaf spot resistance than actual plant observations under leaf spot conditions.

Summary

Studies were made of the distribution and variability of 3-hydroxytyramine and its oxidizing enzyme in sugar beet leaves between and within varieties to determine the quantity and relationships of this phenolic compound with root yield and sucrose content.

The study was conducted over 3 years and included eight different varieties and hybrids. Population differences in quantity of 3-hydroxytyramine and polyphenoloxidase were of sufficient magnitude to indicate that genetic manipulation of each should be possible. Differences due to environment, years and replications, were also significant. Even though the variety by year interaction was significant, the general ranking of their means was the same over years.

Total correlations between 3-hydroxytyramine and weight per root were small but positive and generally significant. Correlations of 3-hydroxytyramine and sucrose percentage were positive and negative but low. Polyphenoloxidase and 3-hydroxytyramine were consistently negatively correlated and relatively high. The polyphenoloxidase correlations with weight and sucrose were small and generally not significant.

Genetic correlations indicate an effect of environment on genetic expression and that different genes are active in all populations for all characters.

Broad sense heritability ratios were quite consistent for weight per root and sucrose content over years and populations, ranging from 0.403 to 0.689 and 0.484 to 0.767, respectively. Heritability of 3-hydroxytyramine was affected considerably by unaccountable environmental variability and ranged from 0 to 0.650.

Identifiable numbers of genetic deviates for both univariate and bivariate frequency distributions were estimated. Using identifiable numbers of genetic deviates as expected breeding values, they correspond very closely to the heritability estimates. They have the advantage of showing whether or not high and low deviates contribute equally to the genetic variability of the population. They also indicate the potential for simultaneous increase of any two characters. There were superior and inferior genetic deviates for all combinations of characters except 3-hydroxytyramine and polyphenoloxidase.

It appears that quantity of 3-hydroxytyramine cannot be used as a direct measure of leaf spot resistance even though there is a general relationship between them.

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