

PHENOTYPIC VARIATION IN SAP SUGAR AMONG SUGAR MAPLE
STANDS IN NORTHEASTERN UNITED STATES

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INTRODUCTION

Sugar maple is a species that is unique among forest trees. Not only is it a source of valuable timber, but it also provides the raw material for a food product other than a nut or a fruit. Because of its attractive flavor, maple syrup promises to become an increasingly popular food, if supplies can be made more plentiful.

The quantity of maple syrup produced is directly related to the sugar content of the sap. Thus, one of the means of increasing the supply of syrup is through the genetic improvement of sap sugar.

The first step in the improvement program was to study the variation in sap sugar by sampling a large number of sugarbushes throughout the important maple-producing states in Northeastern United States. The data from this study were used in setting up guidelines and criteria for making phenotypic selections (Gabriel 1972). The sampling data have been used to estimate components of variation for factors that may affect sugar content in sap. This paper summarizes this information according to state.

BACKGROUND

The significance of variation in sap-sugar content in the manufacture of maple syrup was recognized by a number of earlier researchers (Stevenson and Bartoo 1940; Anderson et al 1949; Moore et al 1951; and others). Probably the most intensive of the earlier studies of variation was carried out by Taylor (1956) at the Vermont Agricultural Experiment Station. Tests made on 4,500 trees over a period of 12 years in one county in Northern Vermont showed that individual trees had a consistent pattern of performance within and between seasons. Trees that were ranked high in sap sweetness tended to maintain this superiority during and between sugaring seasons in relation to other trees. This information was most encouraging to one who was about to embark on a program for the genetic improvement of sugar content in sap.

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It is common knowledge that there is a trend toward lower sap-sugar content as the syrup season progresses and that these values may vary from year to year for trees and stands.

The literature has proven to be inadequate in explaining environmental effects on sap-sugar production. Production has been found to be related with certain characters of the tree itself, such as crown size and shape, and tree diameter (Morrow 1955; Toma 1961; and Blum 1971). As far as edaphic effects are concerned, with the exception of one study on the effect of fertilization (Watterston et al 1963), very little has been published in this respect.

Finally, there is an indication that stress may be an important factor in determining sap-sugar content. It is well known that old, decadent trees are consistently higher in sugar content than healthy ones. A part of this paper will deal with the effects of other sources of stress originating through roadside effects and livestock grazing in sugarbushes.

METHODS AND MATERIALS

Sugar maple is widely distributed throughout Northeastern United States and it is in this area that the bulk of the maple syrup is produced in this country. Consequently, our survey was conducted here, since we were dependent on trees that were tapped to get our sap samples for testing.

Sugar readings were made with a hand-held refractometer on 21,080 sugar maple trees from 279 sugarbushes, distributed over the 6-State area of Maine, New Hampshire, Vermont, Massachusetts, New York, and Pennsylvania. Readings were taken along a randomly selected transect through each sugarbush. Exception to this are roadside trees where generally all trees on both sides of the road were tested. Although a sample size of 100 trees was sought from each bush, sometimes fewer trees were tested and we ended up with an average sample size of 74.9 trees per bush.

To improve the sensitivity of the survey, fieldmen were asked to classify the sugarbushes, or groups of tapped trees, as (1) ungrazed, (2) grazed, and (3) roadside. We were guided in making these divisions by the broad differences in environment and by exploratory sampling data that indicated variations in sap-sugar content.

We calculated a sample mean and standard deviation for each sugarbush and summarized these by state and bush class. Analyses of variance and Scheffe's method were used to test for significance of difference associated with the source of variation. Selection differentials were calculated for each plus-tree that was found. Table 1

RESULTS AND DISCUSSION

A summary of the variation in sap sugar, according to our sampling in the 6-State area, is found in Table 1, values are consistently lower in the ungrazed sugarbushes that are relatively undisturbed. Apparently, the presence of livestock and the proximity to roads causes an increase in sap sweetness. We believe that soil compaction and root damage from grazing creates a stress that is reflected in higher sugar content. In the case of roadside trees, these stress factors might be road salt and gas emissions, among others.

From Table 1, we can see that most of the sugaring operations in Northern New England take place in ungrazed stands. However, going towards the south there is a trend toward more grazing of stands and the increased use of roadside trees.

The original data suggested that there was a relationship between sugarbush sugar-content averages and variation. When bush means were plotted against their respective standard deviations, we found them to be linearly and positively related. Thus, the larger the mean, the larger will be its corresponding standard deviation. We attribute this to a number of low-sugar-producing trees that are consistently present within bushes. As the number of high-producing trees increased in a stand, both the mean and the variance increased. Correlations coefficients that were calculated between the mean and standard deviation ranged from a high of .74 for Maine to .22 for Pennsylvania.

The bulk of our attention was directed toward the data collected from ungrazed sugarbushes because most of the bushes in the survey were in this class, providing the largest source from which selections were made. Sap-sugar averages in this class ranged from a low of 2.29% for Massachusetts and Pennsylvania, to a high of 2.64% for New York. The overall average was 2.50%. An analysis of variance of these data shows significant differences between bushes within states. Table 2. Between states differences were also found to be highly significant (Table 2). But none of the paired differences between states was significant when tested by Scheffe's method. The significant analysis of variance implies that there is at least one significant contrast among state means, but the significant contrast is not a paired difference. Figure 1.

The sap-sugar means (Table 1) suggests geographical differences in sap-sugar content. The more southern states of Massachusetts and Pennsylvania have the same low averages of 2.29%, with standard deviations among these bushes of 0.39 and 0.35% respectively, indicating that variation, as well as the level of sap sugar, is very similar. We decided to look more closely at the data from interconnecting sugar-bushes in southeastern New York. The bush average in this area was found to be 2.41% (Figure 1). From this we infer that with respect to sap-sugar content, there may be two populations of sugar maples. One population is made up of the northern tier of New England States and most of New York State, and a second consists of the more southern syrup-producing states and the southeastern corner of New York. There is no indication from the original data that the variation is continuous or clinal in nature as we can see from the data in south central New York. Table 3.

The analysis of differences between sugarbush classes was inconclusive because of the small number of grazed and roadside sugarbushes sampled (Table 3). Eight out of 12 comparisons were not significant. However, when the data are averaged over all states, the differences between (1) ungrazed and grazed stands, and (2) ungrazed and roadside stands are significant. Differences between grazed and roadside classes are not significant. Thus, the data suggest that ungrazed stands of sugar maple that are relatively undisturbed are not as sweet as grazed and roadside stands which have similar sap-sugar contents.

Between-sugarbush variances (Table 1) are highly significant for all three classes. For ungrazed bushes it is 67% of the within-bush variance. For grazed and roadside classes it is 48% and 33%, respectively. Thus, the data suggest that the variability within sugarbushes, for all classes, is greater than between bushes.

The early results of the sap-sugar survey played an important role in setting up guidelines and criteria for making phenotypic selections. However, we departed from the classical baseline approach to making selections where a stand mean is estimated and best tree in that stand is selected. In our method we used adjacent comparison trees in order to minimize environmental effects when selecting plus-trees. This decision was based on the fact that we could not satisfactorily assess changes in environment in terms of sugar content in sap.

In the course of sampling sugarbushes, a number of field selections were made that met our criteria of having a sugar content that was 30% or higher than the average of neighboring standard trees and exceeding the sweetest standard by at least 0.5%. After a rigorous screening, 43 of these were chosen as plus-trees. Table 4. We have compared these trees, selected by the comparison-tree method, with the estimated means of their respective stands, and calculated the selection differential for each one (Table 4). Differentials, in terms of within-bush standard deviation from the mean, averaged 2.54 and ranged in value' from 0.83 to 5.36.

We found a positive linear relation when the means of standard tree units were plotted against the means of respective sugarbushes. Correlation analysis also indicated a high degree of association between these statistics ($r=.843$). The differences between 43 pairs of bush and standard means were not significant when subjected to Student's t test. With respect to ranking, in 16 pairs, the bush averages were higher than standard, and in 24 they were lower. We concluded from the analysis of this data that there is no evidence that the standard trees used for comparison in making sap-sugar selections are any more closely related to themselves than they are to the rest of the trees in the stand.

SUMMARY

In a study of the nature and extent of phenotypic variation in the sugar content in sap, a survey was conducted in 6 of the important maple syrup-producing states in the Northeast, where 279 sugarbushes were sampled, and 21,080 trees were tested.

Sugar maple stands showed a high degree of heterogeneity in sap-sugar content. There is significant variation within and between stands and between states.

The species appears to be divided into 2 broad populations on the basis of sugar production: One extends across the Northern tier of New England states and most of New York State; the second is located in the more southern of the syrup-producing states.

The significantly higher sap-sugar values found in grazed and roadside stands compared to relatively undisturbed, ungrazed stands are attributed to stress factors associated with the environment.

Sugarbush means and standard deviations are highly correlated: the larger the mean, the larger is the variation.

Selection differentials averaged 2.54 for 43 trees selected for superior sugar content in sap. The plus-trees were selected using the comparison-tree method.

The average sugar content of ungrazed sugarbushes in Northeastern United States is 2.5%.

Figure 1 Average sap-sugar values In percent according to states and specific regions within New York state.

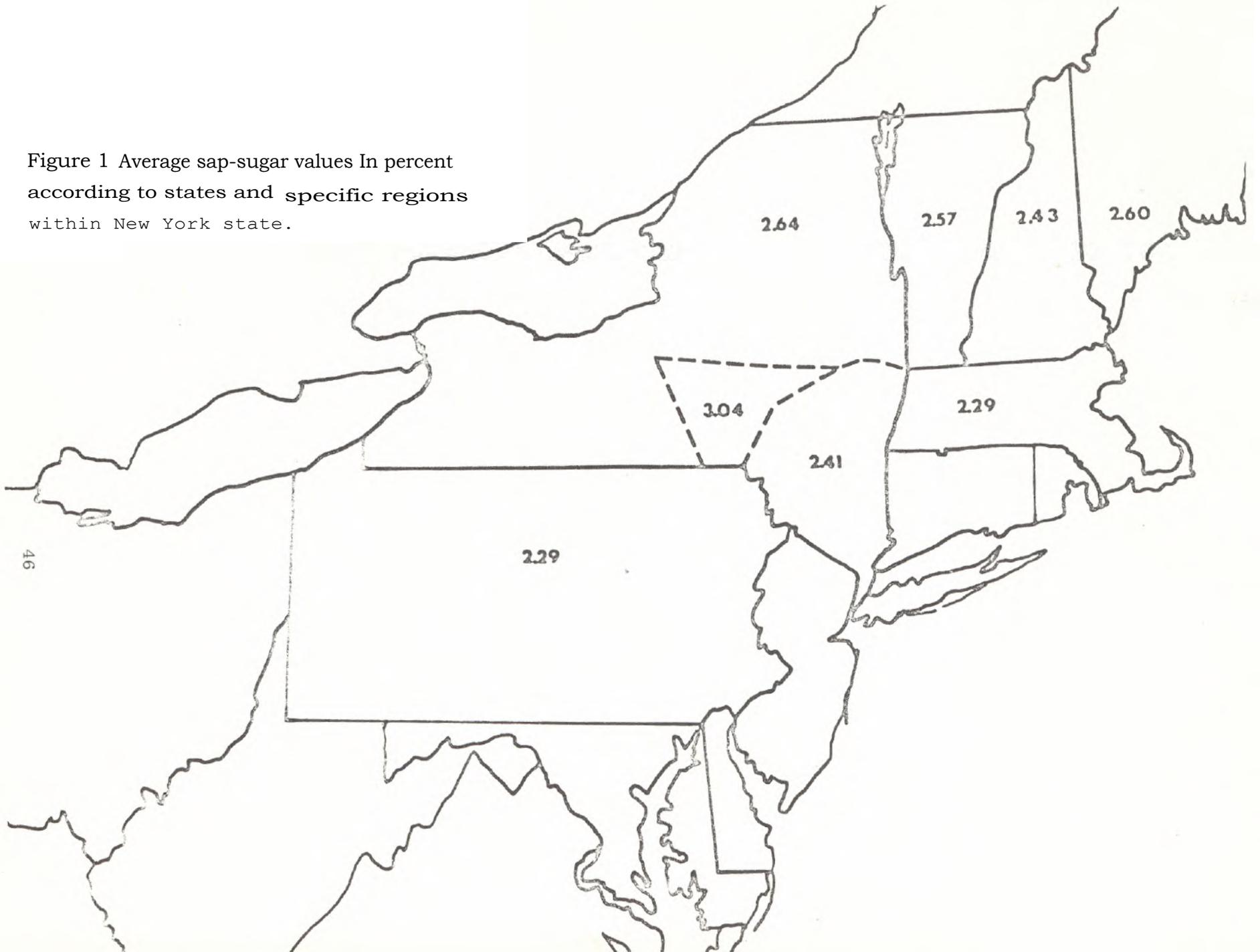


Table 1. Sap-sugar means, standard deviations and average deviations calculated for three sugarbush classes in six states.

State	Sugarbush Class	Number	Trees-per-bush Mean	Sap-sugar Mean	Standard Deviation	
					Among-bush Means	Within-bush Means
Vermont	Ungrazed	81	86.5	2.57	0.44	0.52
	Roadside	6	55.8	2.82	0.28	0.62
	Grazed	3	47.7	3.07	0.69	0.73
		90	83.2	2.60	0.44	0.54
Maine	Ungrazed	8	69.1	2.60	0.47	0.64
	Roadside	1	41.8	3.89	-	0.66
	Grazed	-	-	-	-	-
		9	66.0	2.74	0.47	0.64
New Hampshire	Ungrazed	21	79.4	2.43	0.58	0.52
	Roadside	3	82.3	2.93	0.45	0.71
	Grazed	-	-	-	-	-
		24	78.0	2.49	0.56	0.54
Massachusetts	Ungrazed	24	55.5	2.29	0.39	0.58
	Roadside	12	75.7	2.65	0.52	0.71
	Grazed	-	-	-	-	-
		36	62.2	2.41	0.43	0.63
Pennsylvania	Ungrazed	31	81.0	2.29	0.35	0.66
	Roadside	6	51.0	2.68	0.41	0.88
	Grazed	12	83.2	2.90	0.27	0.74
		49	77.9	2.49	0.34	0.71
New York	Ungrazed	51	76.8	2.64	0.53	0.55
	Roadside	19	48.6	3.02	0.50	0.62
	Grazed	2	62.0	3.40	0.54	0.51
		72	68.9	2.76	0.52	0.57
All States	Ungrazed	216	78.4	2.50	0.46	0.56
	Roadside	47	58.7	2.87	0.48	0.69
	Grazed	17	74.3	2.99	0.41	0.71
		280	74.9	2.59	0.46	0.60

Table 2. Analysis of between-states variation for three sugarbush classes.

Source	df	MS	F
Between States			
Ungrazed bushes	5	0.8010	3.58** ^{1/}
Roadside bushes	5	0.4582	2.04ns ^{2/}
Grazed bushes	2	0.2231	0.99ns
Among Sugarbush Means			
All States and stands	265	0.2236	

^{1/} = Highly significant

^{2/} = Not significant

Table 3. Variance ratio (F values) for comparison among sugarbush class means.

Source	Comparison		
	Ungrazed versus roadside	Ungrazed versus grazed	Roadside versus grazed
Vermont	1.64ns	3.41ns	1.01ns
Maine	6.99**	-	-
New Hampshire	3.10ns	-	-
Massachusetts	4.89* ^{1/}	=====	
Pennsylvania	3.61ns	3.30ns	0.91ns
New York	9.44**	5.41*	1.23 ns
Average all states	22.29**	17.88**	0.84ns

^{1/} = Significant

Table 4. Range and average selection intensity for selected sap-sugar phenotypes in six states.

State	Selected Phenotypes	Range Intensity <u>1/</u>	
	Number	Range	Average
Vermont	11	1.02 - 4.92 <u>2/</u>	2.54 *
Maine	2	2.28 - 2.47	2.38
New Hampshire	5	1.62 - 3.09	2.27
Massachusetts	5	2.44 - 4.38	3.28
Pennsylvania	7	0.95 - 4.28	2.26
New York	13	0.83 - 5.36	2.53
All States	43	0.83 - 5.36	2.54

$$1/ \text{ Selection Intensity (I) } = (X_i - \bar{X}_i) / S_i$$

X_i = value of selected tree in Ith sugarbush

\bar{X}_i = sample mean of Ith sugarbush

S_i = sample standard deviation of Ith sugarbush