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Ray Tissues as an Indirect Measure of Relative Sap-Sugar Concentration in Sugar Maple

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Abstract

Attempts to correlate ray tissue as a percentage of total wood volume with sap-sugar concentrations of sugar maple progenies were unsuccessful. These results raise doubts about our ability to use a relatively constant value such as ray-tissue volume in a selection program designed to increase the sap-sugar concentration of sugar maple seedlings.

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Introduction

For hundreds of years in the United States and Canada, sugar maple, red maple, and several birch species have been wounded to provide sweet sap. Because sugar maple produces the largest quantities and the sweetest sap, investigators have been studying this species in some detail for more than a century. Yet, there remain important questions that need to be answered. Gabriel and Seegrist (1977) studied 21,000 trees in several states and found a considerable amount of variation in sap-sugar content within and between stands. The average reading of all trees was 2.5 percent. Stressed trees in pastures and along roads had slightly higher readings. There are reports in the literature stating that trees producing sap with a high sugar content also produce large volumes of sap (Marvin et al. 1967). Other researchers have maintained that such a correlation does not exist (Tressler and Zimmerman 1942). Some reports suggest that trees with one or both of these traits tend to maintain their relative ranking year after year despite fluctuations in absolute values due to environmental factors (McIntyre 1932; Tressler and Zimmerman 1942; Taylor 1956).

If it is true that individual trees are always sweeter, or always produce larger volumes of sap than other trees, there is little research to suggest why this might be so, and even less evidence that these are heritable traits that will be expressed in progeny of "select" trees (Wilkinson 1985). Nor have we produced data to show that vegetatively propagated material is similar to the ortet from which it was derived, or that it is more uniform than nonrelated ramets. In fact, the only data we have suggest that this probably is not true. Santamour and Cunningham (1964) looked at variation in sugar content on budded sugar maple of a single clone and compared that with sugar content of seedlings of unselected parents. Their data showed that the variation among ramets of this clone was as great as the variation among seedlings. Demeritt (1985) obtained similar results with grafted trees in the clone bank at Grand Isle, Vermont. The variation among clonal ramets was as great as that among clones.

Recent analysis of long-term data from progeny trials of "sweet" trees has raised questions about the original selection methods. Sap-sugar concentrations in sugar maple vary from season to season, day to day, and even hour to hour, making it difficult to assign a "sweetness" value to individual trees. Finding a trait that is correlated with sweetness, and one that remains relatively constant over time, might be a better method of predicting the potential of a tree to produce sap of a given sugar content. Ray parenchyma cells are known to be the primary storage sites for the sugars in trees (Gregory 1977, 1978; Gregory and Hawley 1983). If the quantity of this tissue as a proportion of total tissue in the stem is correlated with sap-sugar concentration, one could select on the basis of the more constant tissue rather than fluctuating sugar concentration. Selection has been restricted to several weeks in the spring when sap is flowing, but the use of ray tissue would allow that activity to take place at any time.

Gregory (1981) worked out simple techniques for estimating ray volume based on maximum ray width, maximum ray height, and number of multiseriate rays/mm^2 of tangential area. Gregory (1982) then suggested that individual trees may inherently produce more ray tissue, and that if this is so, the volume of ray tissue could be manipulated genetically. Morselli et al. (1978) and Gregory reported that ray area is strongly correlated with sap sugar. Wallner and Gregory (1980) reported that this positive relationship between sap-sugar concentration and the amount of ray tissue per unit of xylem does exist, but they also found considerable overlap in the amount of ray tissue between individuals in the high and low sap-sugar groups of trees. They concluded that factors other than storage space are involved in regulating (increasing) sap-sugar concentrations. Fast-growing trees would use more reserve and currently produced carbohydrates, which would mean that less starch is available for overwinter storage despite greater storage space. Also, the secretion of sucrose into vessel sap is controlled by enzymes (Jones 1932; Jones and Bradley 1933; Sauter et al. 1973) rather than passive flow as suggested by Munch (1930). And enzymatic activity may vary from tree to tree because of genetic control of those activities.

The possibility of regulating sap-sugar concentration has long been a goal of researchers working with sugar maple. Earlier work had been based largely on stand manipulation. The work of Gregory, Morselli, and others with ray tissue, and their suggestions that real differences in sap sugar may be associated with volume of ray parenchyma tissue, prompted our study. If regulation of sap—sugar concentration is possible, it is essential that this be a heriteble trait that can be passed from a select tree to its progeny. In the 1960's, the USDA Forest Service established a series of sugar maple progeny trials in several states. These plantings contained material that could be used to study inheritance patterns useful in tree improvement programs to increase the quantity and/or quality of sap.

Methods and Results

In the spring of 1968, the Sugar Maple Project of the Northeastern Forest Experiment Station, then located at Burlington, Vermont, established rangewide provenance/progeny trials in several states. In 1982 that program was terminated and all of the tree improvement activities were transferred to the Genetics Project at the Northeastern Forest Experiment Station's laboratory at Durham, New Hampshire. When the trees in these progeny trials were 17 years old, the planting on the Fernow Experimental Forest near Parsons, West Virginia, was selected for additional studies on inheritance of response to wounding. One tree in each two-tree plot was wounded and 7 months later the wounded trees were cut. Portions of the main stem were brought to the Durham Laboratory for additional sectioning and analysis. The trees averaged 3.16 inches in diameter at 4.5 feet above ground. Stem sections from each cut tree were stored under refrigeration (34°F) until used in the current study.

Because this was an exploratory study, it was decided to limit our initial investigations to a few progenies and individuals that our records indicated had diverse sugar readings over the previous 6- to 10-year period, and later expand it to other progenies if the data warranted it. For this study we chose two seed sources with relatively high sap sugar (31-Cass County, MN; 34-Mille Lacs County, MN) and five seed sources with lower readings (17-Berkshire County, MA; 23-Franklin County, ME; 28-Iron County, MI; 29-Quebec, Canada; and 36-Chittenden County, VT).

Thin sections of the last growth ring (tangential surface) were made of each stem section. Two sections were made from each block and microphotographs were made of three random fields on each of the two sections (Fig. 1). Using the same magnification for each photograph provided a uniform field size for further analysis. Tracings were then made of each photograph filling in every uniseriate and multiseriate ray (Fig. 2). The tracings were sent to Decagon Devices Inc., Pullman, WA, which used its Delta-T Area Meter to provide ray tissue as a percentage of total field. Each tracing passed through the meter 3 times with an accuracy of slightly better than 98 percent.

In addition to the sections from the West Virginia planting that were taken from a position approximately 4.5 feet above ground, we looked at other portions of the stem of a sugar maple to see if there might be variation related to stem position. A single tree in southern Maine was felled

Figure 1.—Microphotograph shows multi- and uniseriate rays on tangential surface of sugar maple (field of view 1.05 x 0.79 mm).

Figure 2.—Tracing of Figure 1 showing only ray tissue.

Table 1.—Percentage of ray tissue in sample sugar maple tree

Height (feet)	North	East	South	West	Average
Stump	12.70	11.97	13.77	14.20	13.16
3.5	14.37	14.43	14.60	14.30	14.43
4.5	13.17	13.97	12.67	11.83	12.91
5.5	10.50	11.13	11.47	12.57	11.42
14.0	11.57	12.00	10.87	10.57	11.25
23.0	10.37	11.63	11.03	11.70	11.18
Average	12.11	12.52	12.40	12.52	12.39

and sections taken from the stump area and 3.5, 4.5, 5.5, 14.0, and 23.0 feet above ground. At each of these points sections were made at each of the four cardinal directions for a total of 24 sampling points (6 heights x 4 directions). Again, two sections and three fields of each sections were photographed for a total of 144 measurements from this tree. There were no differences in amount of ray tissue due to direction (Table 1), nor were there differences in ray tissue as a percentage of total wood tissue due to height except for a slight increase just above the stump. The amount of ray tissue in this sugar maple tree was essentially the same at all points in the main stem, which suggests that the sampling point in our main study should provide a valid measure of ray-tissue volume.

Using one-way analysis of variance, we then looked at variation in percentage of ray tissue between sources and found highly significant differences (Table 2). Next, we used the same test to determine variation between families within sources, but we found little variation (Table 3).

We then plotted ray tissue (percent) over sap-sugar concentration (percent) for every tree in the study regardless of source or family. We found no apparent correlation (Fig. 3), which suggests that trees with more ray tissue can have either high or low sugar concentrations, and that the same can be true of trees with small amounts of ray tissue.

We also looked at possible correlations between ray tissue and sap sugar for individual trees within sources. Some were slightly positive while others were slightly negative, but all were weak (Fig. 4).

Table 2.—Comparison among sources using Approximate Student Newman-Keuls test; one-way analysis of variance

Source No.	Number of samples	Percent ray tissue			
34	8	15.81	A		
28	19	15.63	A		
23	14	15.11	A	B	
17	21	15.07	A	B	
31	8	14.56	A	B	C
29	15	13.95		B	C
36	26	13.43			C

Variation	df	SS	MS	F
Total	110	367.03	3.34	
Source	6	81.35	13.56	4.94**
Error	104	285.68	2.75	

Note: Ray tissue of sources sharing a common letter are not significantly different ($P \leq 0.05$).

** = < 0.01 level of significance.

Table 3.—Comparison of variation between families within sources

Variation	df	SS	MS	F
Source 17 (Berkshire County, MA)				
Total	20	36.32	1.87	
Family	7	7.93	1.13	.50 ns
Error	13	29.39	2.26	
Source 23 (Franklin County, ME)				
Total	13	22.11	1.70	
Family	6	17.92	2.99	4.98
Error	7	4.20	.60	
Source 28 (Iron County, MI)				
Total	18	54.55	3.03	
Family	6	28.48	4.75	2.18 ns
Error	12	26.07	2.17	
Source 29 (Quebec, Canada)				
Total	14	56.71	4.05	
Family	6	41.17	6.86	3.53 ns
Error	8	15.54	1.94	
Source 31 (Cass County, MN)				
Total	7	11.30	1.61	
Family	4	7.95	1.99	1.78 ns
Error	3	3.35	1.12	
Source 34 (Mille Lacs County, MN)				
Total	7	39.05	5.58	
Family	6	37.25	6.21	3.44 ns
Error	1	1.80	1.80	
Source 36 (Chittenden County, VT)				
Total	25	64.64	2.59	
Family	7	11.55	1.65	.56 ns
Error	18	53.09	2.95	

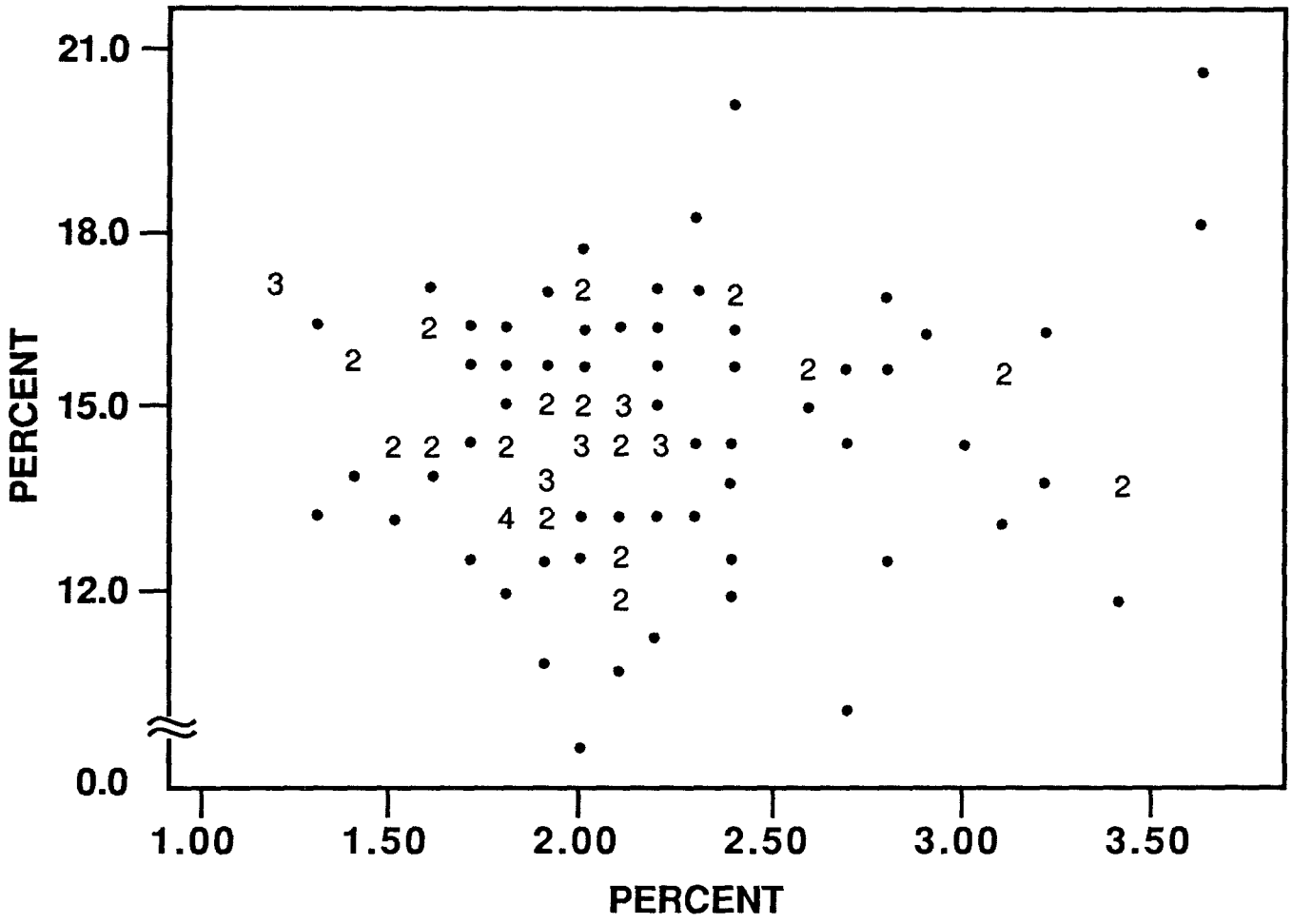

Figure 3.—Percentage of ray tissue over sap-sugar concentration for all trees.

Conclusions

The easiest conclusion to draw from these results is that there is no apparent correlation between the amount of sugar storage tissue (ray cells) and sap-sugar concentration (sweetness) in sugar maple trees. If this is true, then it would not be possible to use core samples of trees to predict and select "sweet trees." If our ray-tissue measurements reflect conditions across the growth rings and if this is constant with size of the tree, 17.9-percent ray cells (Meyer 1922) may be high. Our data indicate that this figure may be more on the order of 14.5 percent.

Our failure to find correlations between sap-sugar readings for the parent trees and progeny from the parent tree in the bush or in the seed orchard, or to find any patterns between ray tissue and sap sugar, might mean there is no correlation. Or these negative results might be due to our inability to obtain reliable readings of sap sugar. If the standard method of taking one or several readings over several years produces inaccurate values, then anything correlated with the true values would appear to be uncorrelated.

While our data failed to establish a connection between ray

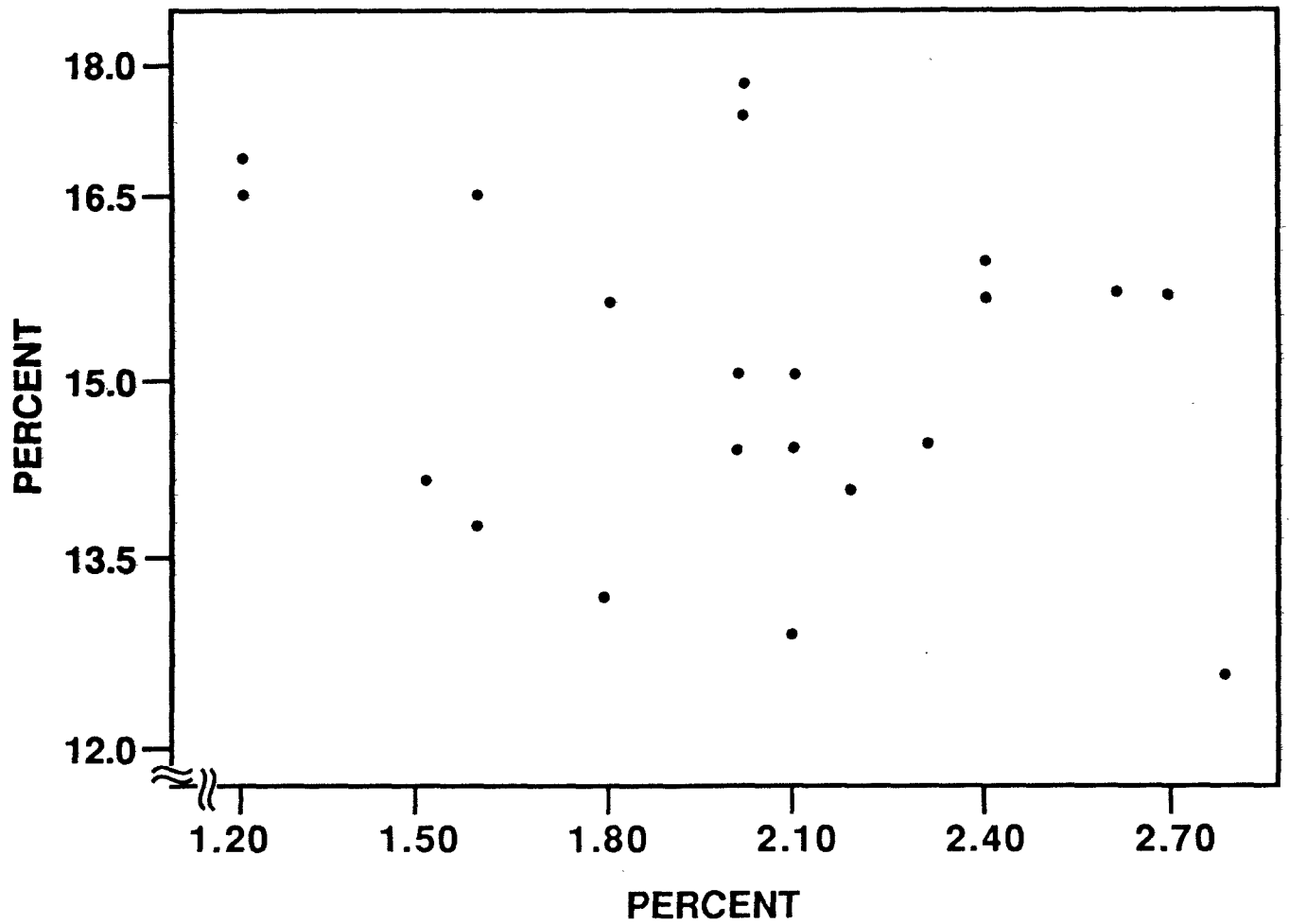

Figure 4.—Source 17 (Berkshire County, MA)—correlation of –0.282 for ray tissue and sap sugar for all trees from this source.

tissue and sap-sugar readings in sugar maple, we do know more about ray tissue in this species. We now know that the amount of ray tissue is similar on all sides of a tree and does not vary by distance along the main stem except for a small but nonsignificant increase just above ground level. We also know that there is significant variation between sources or populations of sugar maple, though we did not include enough sources in this study to determine if there are geographic patterns to this variation. Finally, our data indicate that there is little or no variation between families within any particular source.

That ray cells are the primary storage sites for sugars in maple and other species is well documented. How the abundance of such tissue might influence the concentration of xylem sugar during the spring sap-flow period could not be answered by this study. Additional work is needed on the problem of evaluating relative sap-sugar concentration among trees.

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