YEAR-TO-YEAR VARIATION IN SAP-SUGAR CONCENTRATION OF SUGAR MAPLE PROGENIES AND ITS POTENTIAL EFFECTS ON GENETIC SELECTION FOR HIGH SAP SUGAR

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ABSTRACT.--Sugar concentration of sap from almost 400 sugar maples (Acer saccharum Marsh.) in each of two one-parent progeny test plantations was measured once in each of either 8 or 9 years between 1973 and 1983. Differences in sugar concentration among years were highly significant and accounted for the highest proportion of total variation in both plantations. Highly significant family x year interactions were also found. Only 1 family of 25 in each plantation was ranked among the 5 families highest in sap sugar in every year. The maximum change in yearly rank of several families occurred between consecutive years. Only one tree in each plantation was among the highest 10 percent of all trees in sap sugar in every year, and less than 10 percent of all trees were consistently above the plantation mean. A large proportion of the families or trees with the highest sap-sugar concentrations in 1983 would not be included among selections that would have been made if trees had been selected for high sugar content in any of the previous years. Measuring sap-sugar concentration several times within the sap-flow season may be a better method for characterizing progenies than single-day measurements made over a period of several years.

CONCENTRATION OF SUGAR in sap from sugar maples (Acer saccharum Marsh.) varies from year to year. The average sugar yield from sugar bushes in the Northeast is 2.5 percent (Gabriel and Seegrist 1977), but producers of maple syrup are well acquainted with low-yield years. In those years, more sap is required to produce a gallon of syrup, which raises production costs and reduces profits.

Year-to-year fluctuations in sap-sugar concentration can also be important to breeding programs for improvement

of sap-sugar yield. Ranking among mature maples in natural stands and sugar bushes for sap-sugar content tends to be consistent over a period of years (Marvin et al. 1967; Taylor 1956). However, young individual trees and families in progeny test plantations, which must be evaluated for their sugar-producing potential at an early age, do not respond synchronously to varying environmental conditions responsible for annual differences in sap-sugar production in maples, at least not when their sap-sugar content is based on an annual single-day measurement.

In this study I have compared annual sap-sugar measurements made between 1973 and 1983 in two one-parent progeny test plantations of sugar maple. My objectives were: (1) to evaluate how well combining ability of parents selected for high sap sugar can be judged on the basis of annual single-day measurements of sap sugar of progenies, (2) to examine the effects that year-to-year variation in sugar content of progenies would have on selections that must be made prior to thinning and conversion of the plantations to seedling seed orchards, and (3) to suggest potential improvements in methods for evaluating sap-sugar concentration of families and individual trees in sugar maple progeny tests.

METHODS

Measurements of sap-sugar concentration were made in two one-parent progeny test plantations, one on the Hopkins Memorial Forest, Williamstown, Massachusetts, and the other at the University of Vermont Proctor Maple Research Farm, Underhill, Vermont. Both plantations were established in 1960 and each contains the same 25 open-pollinated families from selected parents that have been previously described by Gabriel (1972). The Proctor test has seven additional families that were not examined in this study. Each family in each plantation is represented by four-tree plots in four randomized blocks. In 1983, when the trees were 26 years old, survival was 92 percent (367 trees) in the Hopkins test and 95 percent (379 trees) at the Proctor Farm.

Sap-sugar concentration of all trees from the 25 families common to both plantations was measured once during the sap-flow season in each year from 1973 through 1979, in 1983, and in 1981 in the Hopkins test only. The trees were tapped by drilling a 7/64-inch hole into the south side of the stem at 18 inches from the ground and inserting a sterilized piece of 13-gauge hypodermic needle tubing about 3 inches long. In most years, the 15th to 20th

drop of sap flowing from the end of the tubing in each tree was collected on the plate of a temperature calibrated refractometer, and the percentage of solids in the sap was read. In 1976 and 1978, sap was collected in containers for several hours before refractometer readings were made. From midfall until midspring, refractometer measurements of the total amount of solids dissolved in the sap give a highly accurate estimate of sap-sucrose concentration (Gregory and Hawley 1983). Similar methods for mini-tapping young sugar maples for sap-sugar testing have been described by Gabriel (1969; 1982).

Differences in sap-sugar concentration among families, years, and their interaction in each plantation were tested for significance by analyses of variance. Changes in family rank for sap-sugar concentration from year to year over the entire 11-year period were examined. Consistency of individual tree sugar content from year to year was evaluated by a series of correlation analyses between all measurement years. The number of years that each tree was among the approximately upper 10 percent of all trees in sap-sugar concentration and the number of years that each tree exceeded the plantation mean were used as additional measures of consistency. The potential effects of year-to-year variation in sap-sugar content and genotype x year interactions on selection within the progeny test plantations were tested by examining the 1983 sap-sugar concentration of families and individual trees with the highest levels of sap sugar in each of the previous years and over all years prior to 1983. The 1983 sap sugar of these selected families and trees was then compared with selections that would be made exclusively on the basis of 1983 sap sugar in terms of selection differential and numbers of families or trees in common. All comparisons and analyses were made using measurements of sap sugar from only those trees living in 1983.

RESULTS

Differences in average sap-sugar concentration between years reached a high of 1.37 percent sap sugar at Hopkins (Table 1) and 1.22 percent at Proctor (Table 2). These percentages are about half of the average values for the plantations over all years. In both plantations, differences in sap sugar among years were highly significant and accounted for the largest proportion of total variation (Table 3). Family x year interactions in both plantations were also highly significant.

Substantial changes in family rank occurred. These changes in each plantation are summarized in Table 4. Only one family in each plantation was ranked among the five families highest in sap-sugar concentration in every year --family 640 at Hopkins and 227 at Proctor. In each plantation, 14 different families were ranked among the top 5 families in at least one year, and in both plantations combined, all 25 families were included in this category. Conversely, only three families were never ranked among the five families lowest in sap-sugar concentration in at least one of the two plantations in at least one year. For some families change in rank from the highest to the lowest recorded, or the opposite, was not a gradual change over the 11-year measurement period. In the Hopkins and Proctor plantations, respectively, the highest and lowest ranks of 8 and 10 families occurred in consecutive years.

One reason for the extreme changes in family rank from year to year is that within any one year the numerical differences in sap-sugar concentrations of the highest and lowest ranked families are quite small (Tables 1 and 2). However, variation in sap-sugar rank from year to year was prevalent among individual trees as well as among families. Overall, correlations between yearly sap-sugar concentrations for individual trees were fairly low (Table 5). Sap-sugar content of individual maples in any year tended to be most highly correlated with concentration of sugar in the previous or following year. There were some exceptions, however. Sap-sugar concentration of maples at the Proctor Farm in 1973, 1976, and 1977 was most highly correlated with sap sugar in 1975, 1979, and 1974, respectively.

As was true for families, trees with high sap-sugar levels in any one year rarely retained their superiority over other trees in subsequent years. Only one tree in each plantation maintained a ranking among the approximately upper 10 percent of all trees in sap-sugar concentration over the entire measurement period (Table 6). Moreover, less than 10 percent of the trees in each plantation were consistently above the yearly plantation mean in sap-sugar content.

The potential effects of year-to-year variation in sap-sugar rank among families and individual maples on selection within the progeny tests are presented in Table 7. Individual tree selections, if they had been made in almost any single year prior to 1983, would have included less than 50 percent of the trees with the highest levels of sap sugar in 1983. In this example, selection differ-

erentials, and therefore gains from selection, would only be a fraction of what they would have been if selection was delayed until 1983. Similar results would have been obtained following early family selection. But, selection of the highest ranking families alone may not be desirable in these two plantations because family differences in sap sugar were small in most years, while differences between individual trees were much greater. Selection based on average sap-sugar concentration of individual trees over all years prior to 1983 would have produced only slightly more favorable results than selection based on most single-year measurements. Selections based on 7- or 8-year average sap-sugar concentrations would have had to include 72 percent of the trees at Hopkins or 79 percent at Proctor to include the 20 percent of the trees with the highest concentrations of sugar in 1983.

DISCUSSION AND CONCLUSIONS

Examining selections that might actually have been made in the progeny tests is useful for pointing out potential problems caused by genotype x year interactions in sap-sugar concentration. It must be remembered, however, that unlike early selection for mature height, 1983 sap sugar in these two plantations is no more reliable for characterizing progenies than sap sugar in any other year. If the same pattern holds true, then a new set of families or trees will have the highest sap-sugar concentration in 1984.

One would think that average sap sugar from several years of measurements would be a useful selection criterion, but 1983 sap-sugar content of the trees with the highest 7- or 8-year averages was not as high as it was in many other trees. One problem in using average sap-sugar concentration over years is that the average is weighted heavily in favor of those trees that had high sap-sugar levels in high sap-sugar years.

However, it is clear that single-day measurements of sap-sugar content of progenies, even if they are made and averaged over a period of several years, are not adequate for identifying the trees or families that will be the sweetest at maturity. Judging the effectiveness of plus-tree selection for high sap-sugar yield and the combining ability of parental selections will have to be delayed until sap-sugar concentration in the progenies stabilizes, or until methods that are better than annual single-day measurements of sap sugar for evaluating sugar maple progeny tests are found.

There is another related problem of more immediate concern that is caused by genotype x year interactions in sap-sugar concentration. Sap-sugar concentration of maples in these two progeny tests has now been measured in 8 or 9 different years, but we still cannot identify all of the poorest families or trees that should be removed in thinnings, or those that should be retained as a seed orchard breeding population. This is a serious problem because the trees were planted on a 10- x 10-foot spacing and at least half of the trees should have been removed in 1978, or even earlier, to allow the crown development necessary for the trees to realize full sugar-making potential. This same problem will, undoubtedly, recur in several other progeny tests planted since 1978.

Kriebel (1960) has claimed that there is no relationship between age and sugar content of maples and that accurate progeny appraisals can be made by the time that the trees are 10 years old. It is possible, therefore, that the instability in sap-sugar content of the progenies that I have reported on here is not an age related or developmental phenomenon. Kriebel (1963) has also pointed out, however, that hourly and daily variation in sugar concentration of maples is great enough to require several measurements of sap sugar within a year, as well as measurements over a period of at least 2 or 3 years, for an accurate assessment of a tree's relative sweetness.

Variation in sap-sugar concentration among years may have been less, and perhaps the genotype x year interaction of less significance, in the two progeny tests that I examined if the average of several sugar measurements made within the sap-flow season of each year had been available. Taylor (1956) found that year-to-year differences in average sugar content of sugar bushes based on single-day measurements could be as high as 2.5 percent sap sugar over a 12-year period. But, the maximum difference in the bush with the greatest variation was only 1.4 percent when the averages of several measurements made within each year were compared.

What I have called genotype x year interactions may, in reality, be reflections of nonsynchronous changes in sap sugar of progenies within a single season because there is no way that single-day measurements of sap sugar could be made under the same climatic conditions from one year to the next. If within-season variation in sugar content of the progenies that I examined had been accounted for, then maybe Taylor's 1956 assertion that a sweet tree is a sweet tree relative to it's neighbors year after year

would have held true. Repeated measurements of sap-sugar concentration made within each of several years should be tested as a potentially better way to evaluate sugar maple progeny tests in the future. On the other hand, sap-sugar concentration of maples may vary in response to and interact with climatic and other environmental changes to such an extent that it may be impossible to predict future sugar content of progenies with a high degree of certainty.

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Table 1.--Average sap-sugar concentration of sugar maple families in the Hopkins Memorial Forest 1-parent progeny test plantation by year.

F number	1973	1974	1975	1976	1977	1978	1979	1981	1983	9-year average
226	2.82	2.22	2.73	3.15	3.66	2.62	3.48	3.08	2.34	2.90
227	2.80	2.22	2.77	3.20	3.08	2.52	3.33	2.99	2.48	2.82
232	2.49	2.03	2.47	3.14	3.33	2.59	3.72	3.25	2.57	2.83
234	2.39	1.94	2.45	2.97	2.99	2.50	3.05	2.97	2.33	2.63
263	2.33	1.95	2.44	3.28	3.73	2.77	3.52	3.50	2.68	2.92
269	2.67	2.24	2.87	2.87	3.23	2.35	3.18	3.19	2.29	2.75
303	2.84	2.29	2.63	3.25	3.52	2.63	3.56	3.39	2.51	2.96
397	2.63	2.43	2.93	3.16	3.39	3.07	3.81	3.65	2.83	3.10
457	2.41	2.23	2.66	3.01	3.20	2.39	3.17	3.09	2.43	2.74
463	2.60	2.03	2.44	3.40	3.75	2.82	3.99	3.23	2.58	3.00
491	2.49	2.20	2.71	3.24	3.34	2.48	3.35	3.07	2.50	2.81
545	2.63	2.28	2.70	3.33	3.58	2.82	3.86	3.39	2.84	3.05
572	2.37	2.26	2.65	2.96	3.47	2.78	3.61	3.23	2.33	2.86
573	2.43	2.24	2.71	2.92	3.23	2.81	3.57	3.00	2.66	2.83
574	2.57	2.12	2.55	3.19	3.32	2.27	3.37	2.79	2.35	2.73
575	2.19	1.97	2.51	2.79	3.06	2.57	3.16	2.82	2.34	2.59
576	2.33	2.14	2.45	2.97	3.20	2.54	3.38	2.99	2.43	2.73
577	2.92	2.26	2.76	3.28	3.68	2.86	3.94	3.20	2.51	3.06
583	3.13	2.56	3.05	3.73	4.08	3.23	3.85	3.51	2.92	3.34
585	2.80	2.36	2.89	3.26	3.39	2.91	3.89	3.04	2.66	3.02
624	2.79	2.27	2.79	3.16	3.32	2.73	3.65	3.02	2.43	2.91
632	2.76	2.10	2.44	3.53	3.44	3.05	4.00	2.86	2.61	2.97
640	3.07	2.52	2.95	4.00	4.17	3.11	3.96	3.91	2.69	3.39
645	2.71	2.34	2.60	3.18	3.60	2.61	3.55	3.22	2.53	2.91
664	2.40	2.11	2.56	3.21	3.50	2.84	3.74	2.86	2.79	2.89
Plantation mean	2.62	2.21	2.67	3.20	3.44	2.71	3.58	3.17	2.54	2.91

Table 2.--Average sap-sugar concentration of sugar maple families in the Proctor Maple Research Farm 1-parent progeny test plantation by year.

Family number	1973	1974	1975	1976	1977	1978	1979	1983	8-year average
226	1.88	2.40	1.95	2.98	2.23	2.50	2.46	2.77	2.41
227	2.22	2.89	2.24	3.08	2.99	2.68	2.83	3.11	2.76
232	1.44	2.25	1.79	2.82	2.39	2.59	2.29	2.90	2.32
234	1.52	2.25	1.72	2.62	2.02	2.34	2.21	2.83	2.19
263	1.40	2.20	1.86	2.66	2.26	2.36	2.30	2.84	2.24
269	1.64	2.36	1.92	2.48	2.42	2.23	2.25	2.42	2.22
303	1.65	2.19	1.83	2.60	2.20	2.27	2.29	2.97	2.23
397	1.56	2.39	1.98	2.67	1.94	2.48	2.42	2.98	2.29
457	1.76	2.39	1.75	2.72	2.29	2.45	2.44	2.95	2.36
463	1.68	2.41	1.78	3.05	2.28	2.49	2.50	3.15	2.42
491	1.76	2.50	2.05	2.84	2.22	2.58	2.49	2.80	2.41
545	1.45	2.08	1.68	2.76	1.92	2.28	2.28	2.42	2.10
572	1.71	2.44	1.91	2.76	2.13	2.39	2.19	2.70	2.27
573	1.74	2.55	1.90	3.02	2.26	2.46	2.54	3.35	2.48
574	1.49	2.36	1.84	3.14	2.07	2.39	2.54	3.03	2.36
575	1.27	2.01	1.73	2.46	2.07	1.96	2.10	2.69	2.05
576	1.56	2.24	1.59	2.91	2.11	2.41	2.38	2.83	2.25
577	1.48	2.14	1.71	2.89	2.08	2.14	2.24	2.60	2.17
583	1.69	2.56	1.95	2.98	2.44	2.69	2.75	3.18	2.54
585	1.85	2.44	1.84	2.98	2.22	2.48	2.71	2.73	2.41
624	1.63	2.24	1.79	2.74	2.01	2.30	2.30	2.81	2.23
632	1.66	2.20	1.71	2.90	2.30	2.47	2.31	2.63	2.28
640	1.78	2.51	1.91	3.00	2.54	2.76	2.66	2.96	2.52
645	1.71	2.27	1.71	2.81	2.16	2.41	2.27	2.93	2.29
664	1.62	2.35	1.89	2.86	2.11	2.65	2.46	3.15	2.38
Plantation mean	1.65	2.35	1.84	2.83	2.23	2.43	2.41	2.87	2.33

Table 3.--Mean squares and estimates of variances of each component in analyses of variance for sap-sugar concentration measured from 1973 through 1983 in two 1-parent progeny tests of sugar maple.

Component	Progeny test					
	Hopkins Memorial Forest			Proctor Maple Research Farm		
	D.f.	Mean square	Variance	D.f.	Mean square	Variance
Family	24	1.253 N.S.	.015	24	0.744**	.015
Block	3	2.945**	.013	3	3.395**	.017
Family x block	72	0.715**	.075	72	0.259**	.027
year	8	21.346**	.208	7	18.291**	.177
Family x year	192	0.106**	.017	168	0.071**	.007
Block x year	24	0.514**	.019	21	0.604**	.022
Family x block x year	576	0.038	.038	504	0.045	.045

N.S. Non-significant
** Significant at the 1-percent level of probability

Table 4.--Range of family rank for sap-sugar concentration between 1973 and 1983 in two 1-parent progeny test plantations.

Family Number	Progeny test			
	Hopkins Memorial Forest		Proctor Maple Research Farm	
	Highest rank	Lowest rank	Highest rank	Lowest rank
226	5	22	2	18
227	6	23	1	5
232	7	21	5	23
234	21	25	14	23
263	4	24	9	24
269	5	25	4	25
303	4	15	8	23
397	2	16	3	24
457	13	23	5	19
463	2	24	3	17
491	10	22	2	13
545	2	13	16	25
572	9	24	6	24
573	8	23	1	12
574	13	25	1	20
575	18	25	19	25
576	17	24	9	25
577	3	14	11	24
583	1	7	2	10
585	4	16	3	19
624	6	19	15	23
632	1	25	6	22
640	1	5	1	9
645	5	16	9	22
664	4	23	4	18

Table 5.--Correlations between sap-sugar concentrations measured between 1973 and 1983 for individual trees in two 1-parent progeny tests of sugar maples.

Progeny test and year	Year measured							
	1974	1975	1976	1977	1978	1979	1981	1983
	---- -Correlation coefficient r----------							
Hopkins Memorial Forest								
1973	.68	.59	.61	.46	.50	.53	.42	.45
1974		.68	.62	.45	.54	.67	.57	.56
1975			.53	.42	.51	.50	.49	.46
1976				.69	.64	.66	.53	.60
1977					.60	.54	.50	.47
1978						.73	.59	.60
1979							.66	.65
1981								.63
Proctor Maple Research Farm								
1973	.63	.68	.36	.34	.58	.55		.33
1974		.57	.33	.40	.60	.53		.33
1975			.24	.32	.56	.40		.27
1976				.30	.60	.62		.52
1977					.34	.29		.26
1978						.75		.59
1979								.64

Table 6.--Numbers of trees with high (upper 7 to 13 percent of all trees) and above average sap sugar in one or more ysars in two 1-parent progeny test plantations .

Progeny test	Number of years								
	9	8	7	6	5	4	3	2	1
HIGH SAP SUGAR									
Hopkins Memorial Forest	1	1	3	7	10	18	11	28	48
Proctor Maple Research Farm	--	1	1	3	3	15	9	26	83
ABOVE AVERAGE SAP SUGAR									
Hopkins Memorial Forest	34	34	27	34	33	32	39	34	34
Proctor Maple Research Farm	--	31	37	44	37	32	40	44	61

a Trees above average in sap sugar were 37 to 51 percent of all trees in the plantation depending on year.

Table 7.--Response of 1983 sap-sugar concentration in two 1-parent progeny tests of sugar maple to simulated early selection for high sap sugar.

Selection year	Percentage of 1983 selection differential		Percentage of families or trees with the highest sap sugar in 1983 selected	
	Family selection[a]	Individual tree selection[b]	Family selection[a]	Individual tree selection[b]
	HOPKINS MEMORIAL FOREST			
1973	40	40	40	42
1974	69	44	60	46
1975	51	34	60	37
1976	70	61	60	50
1977	50	45	40	47
1978	88	55	80	57
1979	26	60	20	53
1981	81	64	60	58
8-year average	81	66	80	64
	PROCTOR MAPLE RESEARCH FARM			
1973	0	32	20	35
1974	66	32	60	42
1975	31	19	40	32
1976	78	61	60	54
1977	14	29	40	35
1978	59	66	60	48
1979	51	67	60	49
7-year average	25	68	40	50

[a]Based on selection of the five families with the highest sap sugar concentration in each year.

[b]Based on selection of 68 to 92 trees (approximately 20 percent) with the highest sap sugar concentration in each year.