SITE AND AGE DIFFERENCES IN FAMILY HERITABILITY ESTIMATES FOR BOLE DIAMETER AND SUGAR CONCENTRATION OF SAP FROM OPEN-POLLINATED PROGENY TESTS OF SUGAR MAPLE

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Abstract.--Sugar concentration of sap from sugar maples (*Acer saccharum* Marsh.) growing in open-pollinated progeny tests planted at Underhill, VT (Proctor) and Williamstown, MA (Hopkins) in 1960 was measured in each of either 8 or 9 years between 1973 and 1983, and diameters were measured in either 1969-77, and 1983 or 1970-78, 1981, and 1984 in the two plantations; respectively. Family heritability estimates for both sap-sugar concentration and diameter generally were higher at Proctor, a poor site with shallow soils, than they were at Hopkins, a good site where the trees are more vigorous and taller. At Proctor, heritability estimates were consistently high for all measurement years. At Hopkins, heritability estimates were lowest in the last few years that sap-sugar concentration and diameter were measured. Phenotypic correlations between sap-sugar concentration and diameter were positive and fairly high in most years in both plantations. Genetic correlations were high and positive at Proctor, but after the first few years they were low or negative at Hopkins. These patterns may reflect the onset of competition for growing space among trees in plots as crown closure occurred at Hopkins before 1978, whereas crown closure has not yet occurred at Proctor.

Sugar content of sap is a characteristic of sugar maples (Acer *saccharum* Marsh.) that is of special economic importance to the maple syrup industry. The amount of sap required to produce a given volume of syrup varies inversely with the sugar content of the sap as it comes from the trees. Sap collection from only high sugar-yielding trees would result in significant cost reductions. For that reason, there has been a steady but unfulfilled demand for genetically "sweet" seedlings ever since the Northeastern Forest Experiment Station's program for progeny testing sugar maples selected for superior sap-sugar content started in 1956.

Individual sugar maples vary in sugar concentration (Taylor 1956; Gabriel and Seegrist 1977), and some trees are found with more than double the average of 2.5 percent sap sugar characteristic of maples in sugarbushes in the Northeast. There is also evidence that this individual-tree variation in sugar concentration is inherited. A preliminary estimate of narrow-sense heritability from a controlled breeding experiment was 0.60 (Kriebel and Gabriel 1969). Nevertheless, progress has been slowed by the time required to make reliable genetic evaluations of selected material. In the oldest progeny test experiments that were planted in 1960, sap-sugar concentration of half-sib

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offspring--measured in almost every year between 1973 and 1983-- from selected parents is no higher than that of average parents; and parent-progeny correlations for sap sugar in each year are close to zero (Wilkinson and Hawley 1986). In a younger progeny test that is based on a more recent, extensive and stringent selection of parents (Gabriel 1982a), the parent-progeny correlation following a single year measurement of sap sugar in 1983 was $r = -.33$. In that test, a maple that averaged 8.6 percent sap sugar over several years produced half-sib progeny that averaged 2.7 percent. Another maple that averaged 2.4 percent produced progeny with an average sugar concentration of 3.9 percent.

The absence of a positive parent-progeny correlation, coupled with relatively high heritability estimates for sap-sugar concentration based on variance component analyses in the progeny tests, suggests that early selection in the progeny tests themselves may be more effective than phenotypic superior tree selection in sugar bushes. Making selections for the genetic improvement of sap-sugar concentration in these tests is complicated by fluctuations in sugar concentration that can occur in an individual tree from year to year, from day to day, and even from hour to hour (Gregory and Hawley 1983; Kriebel 1960; Wilkinson 1985). Wilkinson (1985) has suggested potential improvements in methods for evaluating sap-sugar concentration of families and individual trees in sugar maple progeny tests that may reduce the impact of these problems.

However, I have found that sap-sugar concentration and bole diameter are closely interrelated in young sugar maples, though they are only weakly associated in older trees (Blum 1973; Leaf and Watterston 1964). Conditions in progeny test plantations, such as spacing, stocking, and competition, that affect growth rates also may affect sap-sugar concentration. In this paper I present heritability estimates for sap-sugar concentration and bole diameter measured each year for several, years along with phenotypic and genetic correlations between these two characteristics in two open-pollinated progeny tests. Differences in proportions of genetic and environmental variances encountered at the two sites and at different ages may affect selection procedures.

METHODS

Measurements of sap-sugar concentration and bole diameter were made in two open-pollinated progeny test plantations, one on *the Hopkins* Memorial Forest, Williamstown, MA; and the other at the University of Vermont Proctor Maple Research Farm, Underhill, VT. The Hopkins plantation is on a good site with normally abundant soil moisture. By contrast, the Proctor plantation is on a poor site with shallow soils and numerous rock outcrops. Mean height of maples in the Hopkins plantation was 12.8 meters 23 years after planting, but mean height was only 9.7 meters in the Proctor plantation 25 years after planting.

Both plantations were established in 1960 and each has the same 20 open-pollinated families from parent trees selected for sap with a high sugar content (mean = 4.3 percent; range 3.4 to 5.6 percent) and 5 families from parent trees that were near average (mean = 2.8 percent; range 2.3 to 3.2 percent). The Proctor test has seven additional families that were not planted at Hopkins and were not examined in this study. Each family in each plantation is represented by four-tree plots randomly located in four blocks (Hopkins) or six blocks (Proctor) with a spacing of 10 feet between trees. Maples in two blocks in the Proctor plantation were not tested for sugar content of sap as frequently as the others, and incomplete data sets from those trees were excluded from the analyses.

Sugar concentration of sap collected from mini-taps of the type described by Gabriel (1982b) and Wilkinson (1985) was measured with a temperature calibrated refractometer once during the sap-flow season in 8 (Proctor) or 9 (Hopkins) years from 1973-83. Diameters (at 30.5 cm above the ground from 1969–75, at 45.7 cm from 1976-81, and at breast height in 1983 and 1984) were measured in 1969-77 and in 1983 at Proctor, and in 1970-78 and in 1981 and 1984 at Hopkins. All analyses were made using complete data sets from those trees still living in 1984. In 1984, when the trees were 27 years old, survival was 92 percent (367 trees) in the Hopkins plantation and 95 percent (379 trees) in four blocks at the Proctor Farm.

Data sets for each year were analyzed separately by analysis of variance. Degrees of freedom were 3, 24, and 72 for block, family, and family x block; respectively, and 279 for tree-within-plot at Proctor and 267 for tree-within-plot at Hopkins. Family and error variance components were estimated from the mean square for all variables. Family heritabilities were estimated by a standard equation for one-parent progeny tests:

$$\text{Family heritability} = \frac{Vf}{Ve/NB + Vfb/B + Vf}$$

where: Ve, Vfb, and Vf are variances due to tree-within-plot, family x block, and family; and B and N are number of blocks and the harmonic mean of the number of trees per plot, respectively. Genetic and phenotypic correlations between diameters and sap-sugar concentrations were obtained from cross-product analyses using diameters that were measured at the time of tapping in early spring or in the previous fall.

Family heritability estimates also were calculated for sap-sugar concentration over all measurement years at each progeny test location by plot mean analysis of variance and the following equation:

$$\text{Family heritability} = \frac{Vf}{Ve/BY + Vfb/B + Vfy/Y + Vf}$$

where: Ve, Vfb, Vfy, and Vf are variances due to error, family x block within location, family x year, and family; and B and Y are the number of blocks within location and number of years, respectively.

RESULTS AND DISCUSSION

Family heritability estimates for sap-sugar concentration over all measurement years were .376 for the Hopkins progeny test and .620 for the Proctor progeny test. Family variances for sap-sugar concentration in the two plantations were equal, but family x block variance was 2.8 times greater and family x year variance was 2.4 times greater at Hopkins than at Proctor. Heritability estimates for sap-sugar concentration in individual years were similar in the two plantations, but there was a decline in values after a peak in 1976 in the Hopkins plantation, with no corresponding change at Proctor (Table 1).

Table 1.--Family heritability estimates for sap-sugar concentrations and bole diameters measured between 1969 and 1984 in two open-pollinated progeny tests of sugar maple.

	Hopkins Memorial Forest Williamstown, MA		Proctor Maple Research Farm Underhill, VT	
Year	Diameter[a]	Sap-sugar	Diameter[a]	Sap-sugar
1969	--	--	.621	--
1970	.267	--	.634	--
1971	.187	--	.657	--
1972	.254	--	.663	--
1973	.255	.584	.640	.498
1974	.274	.464	.668	.628
1975	.253	.615	.682	.566
1976	.236	.693	.641	.500
1977	.220	.410	.629	.478
1978	.099	.355	--	.470
1979	--	.457	--	.503
1981	.082	.367	--	--
1983	--	.224	.731	.550
1984	.049	--	--	--

[a] Diameters were measured at 12 inches above the ground from 1969-75 at 18 inches from 1976-81, and at breast height in 1983 and 1984.

Heritability estimates for diameter were much higher for progenies growing on the poor site at Proctor than they were at Hopkins. At Proctor, four families were clearly better adapted to the site conditions and grew more rapidly than the other families; their average diameters in 1983 were an inch or more greater than the plantation mean of 4.8 inches. Four other families grew poorly. Their average diameters were an inch or more less than the plantation mean. All of the families grew well on the good site at Hopkins. The average diameters of 18 families in 1984 were no more than 0.3 inch above or below the plantation mean of 5.8 inches. The coefficient of variability for family mean diameters was 15.7 at Proctor and 7.2 at Hopkins.

Heritability estimates for bole diameter at Hopkins, like those for sap-sugar concentration, were lowest in the last few years. This trend may be analagous to the large changes in the relative magnitude of genetic and environmental effects on height growth during stand development that have been reported for several coniferous species (Namkoong et al. 1972; Namkoong and Conkle 1976; Franklin 1979). The changes are thought to be caused by the onset of cohort competition in stands and their timing is thus related to factors of environment such as site quality and stocking.

The Hopkins plantation was thinned after the 1984 growing season. At that time, I removed a segment of the bole near breast height from each of 116 trees that were at least 10 cm in diameter, and measured increment along the shortest and longest radii for each year from 1967 through 1984. I also calculated the basal-area increment for each year using the average of the two radial measurements. The low heritability estimates for diameter at Hopkins in the last several years followed the peak diameter growth years for most trees--1974-76 for radial increment and 1975-77 for basal-area increment--and coincided with a period of rapidly declining growth rates that may have been caused by intensification of competition for crown and/or root space (Table 2).

Table 2.--Average annual radial and basal area increment of 116 sugar maples from 1967-84 in Hopkins progeny test, and percentage of trees reaching their peak growth rate in each year.

Year	Radial increment (cm)	Percent of trees at peak growth	Basal-area increment (cm)	Percent of trees at peak growth
1984	.20	0.0	9.7	4.6
1983	.15	0.0	7.1	0.0
1982	.23	0.0	9.7	0.0
1981	.25	0.0	10.3	2.3
1980	.28	0.0	11.0	6.0
1979	.30	0.0	11.6	3.0
1978	.41	2.5	13.5	11.5
1977	.48	8.7	14.8	27.7
1976	.53	23.6	14.2	22.3
1975	.56	26.7	13.5	17.7
1974	.53	16.8	11.0	3.0
1973	.46	6.2	8.4	1.5
1972	.48	6.2	7.1	0.0
1971	.43	3.7	5.2	0.0
1970	.38	4.3	3.9	0.0
1969	.33	1.2	2.6	0.0
1968	.23	0.0	1.3	0.0
1967	.15	0.0	0.6	0.0

Sap-sugar concentration and bole diameter are closely interrelated in young sugar maples, most likely through their mutual correlation with crown area in closed stands and live crown ratio in more open stands. This relationship for sap-sugar concentration measured in 1983 and diameters measured in 1983 at Proctor and 1981 at Hopkins is summarized in Table 3. In each year a similar relationship was observed to a varying degree; sap-sugar concentration in both plantations generally was highest in large-diameter trees. Changing environmental conditions during stand development that affect genetic variances for diameter might, therefore, be expected to affect covariances between diameter and sugar concentration of sap.

Table 3.--Sap sugar concentration of sugar maples in two one-parent progeny tests in 1983, by diameter class.

Diameter class[a] (cm)	Hopkins Memorial Forest Williamstown, MA No. trees	Percent sap sugar	Percent above mean[b]	Proctor Maple Research Farm Underhill, VT No. trees	Percent sap sugar	Percent above mean[b]
<5.1	6	1.6	0.0	8	2.4	12.5
5.1-7.4	7	1.7	0.0	37	2.4	13.5
7.6-9.9	32	2.1	15.6	57	2.6	31.6
10.2-12.9	70	2.3	31.4	92	2.9	51.1
12.7-15.0	103	2.5	38.8	108	3.0	58.3
15.2-17.5	74	2.8	71.6	50	3.2	62.0
17.8-20.1	60	2.9	75.0	21	3.1	61.9
20.3>	14	2.9	71.4	6	3.5	83.3

[a] Diameter at Hopkins measured in 1981 at 45.7 cm; diameter at Proctor measured in 1983 at breast height.

[b] Percent of trees in diameter class above plantation mean of 2.54 percent sap sugar at Hopkins and 2.87 at Proctor.

Phenotypic correlations between sap-sugar concentration and diameter varied from year to year, but they were always positive in both plantations (Table 4). Genetic correlations, on the other hand, were fairly high and positive at Proctor; but after 1975 they were low or negative at Hopkins. In the first few years that sap-sugar measurements were made at Hopkins, families with the largest diameter trees generally had the highest concentration of sugar in sap. By 1983, after size differences among families had diminished, the trees with the highest concentrations of sugar generally were the largest trees within the families with the overall smallest diameters. Changes in family and within family rank in diameter may partially account for large year-to-year changes in family rank for sap-sugar concentration reported by Wilkinson (1985).

Maples need maximum crown development for expression of their full sugar-making potential. Selection for high sap-sugar concentration in progeny tests is complicated by changing genetic and environmental variances and covariances with diameter, especially on good sites at relatively close spacing where the period of free growth in the establishment phase is short and competition between trees starts early. This problem has not been encountered in tests at the Ohio Agricultural Research Center, Wooster, Ohio, where spacing between trees is up to 30 feet and heritabilities for sugar concentration have been consistently high (Howard B. Kriebel, pers. comm. 1983).

Table 4.--Phenotypic and genetic correlations between sap-sugar concentrations and bole diameters at the time of tapping in two open-pollinated progeny tests of sugar maple.

	Hopkins Memorial Forest Williamstown, MA		Proctor Maple Research Farm Underhill, VT	
Year	Phenotypic	Genetic	Phenotypic	Genetic
	Correlation coefficent r			
1973	.38	.57	.57	.77
1974	.55	.77	.42	.83
1975	.35	.58	.30	.53
1976	.31	.15	.32	.63
1977	.22	-.18	.27	.58
1978	.40	.22	.50	.72
1979	.51	-.32	--	--
1981	.51	-1.00	--	--
1983[a/]	.53	-1.00	.42	.68

[a/] Correlations with diameter in 1981.

Kriebel (1960) has claimed that there is no relationship between age and sugar content of maple sap and that accurate progeny appraisals can be made by the time that the trees are 10 year old. Selection at age 13, following an evaluation period of 3 years, offers several advantages. During the evaluation period, sap-sugar concentration should be measured as many as 10 times in each sap-flow season in early spring (Wilkinson 1985) with possible supplemental measurements in the fall (Gibbs 1969). Progeny tests can be designed with a large number of replications at a fairly narrow spacing, possibly with single-tree plots to avoid competition for growing space among members of fast-growing families. The only thinning required would be for conversion to a seedling seed orchard. Selection would coincide with a period of high heritability for sap-sugar, diameter, and genetic covariances between the two. Using a method described by Wood and Hanover (1981) for accelerating growth of sugar maple seedlings for early plantation establishment may further reduce the time required for genotypic progeny evaluations.

So long as young maples have ample growing space, there appears to be a positive genetic correlation between bole diameter and sap-sugar concentration so selection for high sugar concentration could be restricted to only the fastest growing trees with the greatest degree of crown development. Trees too small to provide sufficient sap for sugar measurement by age 10 could be ignored. Simultaneous selection for early fast growth, adaptability, and sugar concentration might shorten the time between selection and orchard seed production and the time from planting until the progeny reach productive size in sugarbushes.

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