Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Soil nutrients affect sweetness of sugar maple sap

Adam D. Wild*, Ruth D. Yanai

State University of New York College of Environmental Science and Forestry, United States

ARTICLE INFO

Article history: Received 17 October 2014 Received in revised form 18 December 2014 Accepted 21 December 2014

Keywords: Sugar concentration Nitrogen Calcium Phosphorus Foliage Tree health

1. Introduction

Maple syrup and maple sugar are the most important non-timber forest products in the northeastern United States and southeastern Canada (Whitney and Upmeyer, 2004). The maple sugar industry has been experiencing a renaissance in the last decade after declining through the 1900s (Farrell and Chabot, 2012). Maple sugar products produced in the United States are valued at US\$81 million a year (Farrell and Chabot, 2012) and well over CAN\$300 million in Canada (Statistics Canada, 2013). Maple sugar is produced by boiling off water from sap collected from trees in the *Acer* genus of which sugar maple (*Acer saccharum* Marsh.) has the sweetest sap and is most commonly tapped.

Sap flows in late winter when subfreezing temperatures at night are followed by thawing during the day (Marvin, 1958; Marvin et al., 1971). Pressure in the sapwood is lower than in the atmosphere during the night and greater during the day (Tyree, 1983; Cirelli et al., 2008), which allows sap to flow from tap holes (Gregory, 1982).

Maple sap typically has a sugar concentration of 1-5% (Gregory and Hawley, 1983; Larochelle et al., 1997). Sap sweetness, in addition to the volume of sap collected, determines the amount of maple syrup or maple sugar that can be produced (Taylor, 1956) and the time and energy required to boil the sap into syrup. Thus much attention has been focused on factors controlling sap sweetness. Faster growing trees produce more ray cells, which store

* Corresponding author. E-mail address: adamdwild@gmail.com (A.D. Wild).

ABSTRACT

Understanding how soil nutrients affect sap sweetness of sugar maples (*Acer saccharum* Marsh.) is important for producing maple syrup, an economically important non-timber forest product in the northeastern USA and southeastern Canada. Sugar maples were sampled for sap sweetness in 21 plots distributed across five stands in the White Mountains of New Hampshire. Sugar concentrations in maple sap were higher in plots with greater native soil nitrogen availability, indicated by N mineralization in laboratory incubations (p = 0.01). To test whether nutrient additions can improve sap sweetness, treatment plots were fertilized with N, P, N and P, or Ca. Addition of 30 kg N ha⁻¹ yr⁻¹ increased sap sweetness two years after initial treatment. Foliar P had a negative correlation with sap sweetness (p = 0.02) while trees with higher foliar N:P had sweeter sap (p < 0.001). By selecting sites with higher soil nitrogen or fertilizing N-limited sites with N, maple sugar producers may be able to collect sweeter maple sap.

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starch and release sugar during the tapping season (Gregory, 1977; Morselli et al., 1978). Healthier trees with larger crowns and greater growth rates tend to have sweeter sap (Morrow, 1955; Taylor, 1956; Blum, 1973; Laing and Howard, 1990).

Sugar maple decline has been observed for the past half century in forests of the northeastern United States (Horsley et al., 2002; Bailey et al., 2004) and southeastern Canada (Moore et al., 2012). Deficiencies of soil calcium and magnesium have been associated with sugar maple decline on the Allegheny Plateau of Pennsylvania and New York (Horsley et al., 2000; Bailey et al., 2004), Green Mountains in Vermont (Schaberg et al., 2006) and the Adirondacks of New York (Sullivan et al., 2013). Leaching losses of soil Ca and Mg are attributed to acid rain caused by air pollution (Driscoll et al., 2001). Liming, the addition of Ca carbonate (or Ca and Mg in dolomite) to soils, has reversed the symptoms of maple decline (Long et al., 2011; Moore et al., 2012). It is not clear whether the effect of liming on sugar maple health is due to the direct effect of Ca and Mg additions or the indirect effect of carbonate dissolution in lowering soil acidity, which reduces the toxicity of aluminum and manganese (Schaberg et al., 2006; Long et al., 2009). One study added Ca silicate instead of Ca carbonate, and found improvements to sugar maple health and seedling fitness (Juice et al., 2006; Battles et al., 2013). None of the liming studies of maple decline have investigated the sugar content of sap, although sap sweetness has been linked to maple health in other studies, as described above.

There have been many fertilization trials studying the effects of nutrient additions to soils on sap sweetness in forests used for maple sugar production (Yawney and Walters, 1973), but results







have been mixed. Adding N increased sap sweetness in a study in Ohio (Kriebel, 1961) but had no effect in central New York (Watterston et al., 1963) or New Brunswick (Bary and Roy, 1998). Adding P decreased sap sweetness of trees in central New York (Watterston et al., 1963). Potassium, Ca, and Mg together increased sap sweetness in northern Vermont (Wilmot and Perkins, 2004) but not in northwestern New Brunswick (Bary and Roy, 1998). Often, N, P, and K are added together, with positive effects (LaValley, 1969; Leech and Kim, 1990) or no effect (Watterston et al., 1963; Wilmot et al., 1995) on sap sweetness.

These previous studies of the effects of nutrients on sap sweetness shared certain limitations. Commercial P fertilizers all contain Ca, which means that a response to P fertilization could be a response to Ca addition. Liming studies cannot distinguish the effects of Ca from the effects of elevated pH, which affects P availability, as well as the availability of Al and Mn. The effects of N and P on sap sweetness have never been studied in a full factorial experiment, which would permit the identification of synergy or antagonism. And many fertilization studies have been limited to a single site.

Northern hardwood forests respond variously to N, P, and Ca fertilization, with N fertilization consistently having the greatest response. At some sites (of the 35 fertilization studies surveyed), there was a greater growth response when P or Ca was also added (Vadeboncoeur, 2010). Sugar maple was the only species studied to respond to Ca addition alone. At the Bartlett Experimental Forest, where some of our stands were located, sugar maple increased in diameter growth by 19% over controls after a lime addition and doubled in growth after a lime plus NPK addition (Safford, 1973). Jeffers Brook, our other site, is more nutrient rich (Bae, 2013). We selected these study sites because of their marked differences in native fertility and because they have been further manipulated by N, P, and Ca additions.

The objective of this study was to better define the effects of soil nutrients on the sugar concentration of maple sap, using a unique fertilization experiment in the White Mountains of New Hampshire. The effects of N and P were studied in a full-factorial, randomized complete block design in four stands. The effects of Ca were studied in four stands in which Ca silicate was added. We also measured foliar nutrient concentrations, photosynthesis, growth, canopy health, and pre-treatment soil nutrient availability as potential predictor variables. Identifying which factors control maple sap sweetness could have important economic benefits.

2. Methods

2.1. Site description

This study was conducted in the White Mountains of New Hampshire, USA. Three stands were located in the Bartlett Experimental Forest and two stands were located near Jeffers Brook on the western edge of the White Mountain National Forest (Table 1). Soils were Spodosols developed in glacial drift (Fisk et al., 2014). Temperature in the White Mountain region averages 19 °C in July and -12° C in January with a frost free period of about 120 days (Smith and Martin, 2001). Average annual precipitation in the Bartlett Experimental Forest is 127 cm with snow often accumulating 150–180 cm.

Stands originated by natural regeneration following clearcutting and varied in age from 28 to 130 years in 2013, the time of sampling (Table 1). Average basal area was $34 \text{ m}^2 \text{ ha}^{-1}$ for three mature stands and $31 \text{ m}^2 \text{ ha}^{-1}$ for the younger stands. Overstory vegetation in the mature stands at Bartlett was primarily sugar maple, yellow birch (*Betula alleghaniensis* Britton), and American beech (*Fagus grandifolia* Ehrh.) with occasional white ash (*Fraxinus americana* L.) and red maple (*Acer rubrum* L.) (Fatemi et al., 2011). The younger stand at Bartlett had beech, red maple, white ash, white birch (*Betula papyrifera* Marsh.), yellow birch, pin cherry (*Prunus pennsylvanica* L.f.) and sugar maple. The older stand at Jeffers Brook was dominated by sugar maple and yellow birch with occasional beech. The younger stand at Jeffers Brook had sugar maple, yellow birch, white birch, quaking aspen (*Populus tremuloides* Michx), bigtooth aspen (*Populus grandidentata* Michx) and pin cherry.

These stands are part of a larger study of Multiple Element Limitation in Northern Hardwood Ecosystems (http://www.esf.edu/ melnhe/). Stands contained treatment plots for addition of Ca, N, P, N + P, and a control. Calcium was applied once in the fall of 2011 as CaSiO₃ at the rate of 1150 kg Ca ha⁻¹. Beginning in the spring of 2011, N was applied as NH₄NO₃ at the rate of 30 kg N ha⁻¹ yr⁻¹, and P was applied as NaH₂PO₄ at the rate of 10 kg P ha⁻¹ yr⁻¹ (Fisk et al., 2014). Nitrogen and P were applied twice a year (spring and mid-summer) in 2011, 2012 and 2013.

Treatment plots were 50 m \times 50 m and trees were sampled in a 30 m \times 30 m measurement area, except for the younger stand at Jeffers Brook where the treatment plots were 30 m \times 30 m and the measurement area was 20 m \times 20 m. We sampled from 4 stands with Ca treatments and 4 stands with N and P treatments (Table 1): stand C9 did not have a Ca plot, and C6 had too few sugar

Table 1		
Description of the five stands and 21	treatment plots used in th	is study.

Site	Stand	Treatments	Year of harvest	Coordinates	Elevation (m)	Slope	Slope aspect	Soil pH	Number tapped of trees in C, N, P, NP, Ca	BA (m²/ha ⁻¹)	BA of sugar maple (m ² /ha ⁻¹)	DBH of tapped trees (cm)
Bartlett	C8 Mature	Control, N, P, NP, Ca	1883	44°03′N 71°18′W	330	5-35%	NE	4.26	12, 12, 13, 12, 13	34.7	14.1	13.1-58.0
	C9 Mature	Control, N, P, NP	1890	44°03′N 71°17′W	440	10-45%	NE	4.63	11, 17, 14, 13	32.7	17.1	10.5-82.5
	C6 Mid	Control, Ca	1975	44°02′N 71°16′W	460	13-20%	NNW	4.22	10, 10	34.6	1.2	11.5–29.6
Jeffers Brook	Mature	Control, N, P, NP, Ca	$\sim \! 1900$	44°03′N 71°88′W	730	30-40%	WNW	4.65	24, 25, 25, 25, 24	34.2	27.0	10.3-41.5
	Mid	Control, N, P, NP, Ca	1985	44°03′N 71°88′W	730	25-35%	WNW	4.57	12, 6, 10, 11, 14	27.3	3.5	10.0-22.1

maples to sample, except in the Ca plot, so control trees were selected at least 15 m from the edge of the Ca treatment. All sugar maples with a diameter at breast height (DBH) of 10 cm or greater were sampled (10–18 trees per plot; Table 1), with the exception of the older stand in Jeffers Brook, which was dominated by sugar maple, where 25 trees were randomly selected for sampling in each plot.

2.2. Maple sap sampling

Each site was sampled three or four times in 2013. Sites at Bartlett and Jeffers Brook were sampled on separate back-to-back days and the two sampling days were considered one sampling period. On February 24, only Bartlett C8 mature was sampled. On March 10 and 11, March 24 and 25, and March 30 and 31, all stands were sampled. This time period covered the majority of the sap flow season during 2013. The order of sites and plots within a day was varied to avoid bias due to time of sampling.

Sap was sampled from each tree using a mini-tapping procedure (Gabriel, 1982). A 2-mm diameter hole was drilled approximately 1 cm into the south side of the tree approximately 1.3 m above the ground. A 16-gauge syringe needle was then inserted into the tree as a sap spile. When sampling, a plastic 50 ml test tube was hung on the end of the syringe needle to collect sap. When rain or snow was falling, the top of the test tube was covered to prevent dilution. After 15 min, when at least 1.5 ml of sap was collected in the test tube, sugar concentration of the sap was measured with a MISCO PA201 digital temperature-compensating refractometer (MISCO, Cleveland OH) on a Brix scale (Gregory and Hawley, 1983). The refractometer was calibrated with de-ionized water prior to sampling and after sampling every ten trees. The prism of the refractometer was cleaned after every sample with isopropyl alcohol and dried with a tissue wipe. In total, 298 trees provided sap for analysis.

A composite sap sample from each plot for each sampling date was collected by combining ~2 ml of sap from each tree and freezing immediately upon returning from the field. Sap samples were later filtered through #1 Whatman filter paper and two drops of nitric acid were added for stabilization. The sap samples were then analyzed by inductively coupled plasma-optical emission spectrometry (ICP-OES) using a PerkinElmer Optima 3300 DV (Perkin-Elmer Inc., Waltham MA) for the concentration of P, Ca, Mg, K, and Mn.

2.3. Soil nutrients

Soil nutrients and pH were measured in late June 2009, prior to the onset of fertilization, in the N and P treatment plots and associated controls (Fisk et al., 2014). In each plot, ~30 soil cores 2 cm in diameter and 10 cm deep were collected, separated into Oe, Oa, and mineral soil, and composited by horizon.

Nitrogen mineralization was measured in 21-day laboratory incubations (Fisk et al., 2014). Soil P was analyzed by extracting with pH 8.5 bicarbonate (DeForest and Scott, 2010). Exchangeable soil Ca was determined by extracting with NH_4Cl (Naples and Fisk, 2010). Soil Ca and P concentrations and N mineralization rates were averaged across horizons to characterize nutrient availability for each plot.

Resin-available N was measured using six anion exchange resin strips buried for two weeks in the Oa horizon of each plot in July 2011, after the first year's fertilizer additions (Fisk et al., 2014). Available N was extracted from the strips by shaking rinsed strips in 30 ml of 1 M KCl (Fisk et al., 2014).

2.4. Foliage collection and gas exchange measurements

Foliar nutrients and gas exchange were measured for the two trees with the highest average sugar concentration and the two trees with the lowest average sugar concentration in each plot on July 24 (Bartlett C8), July 25 (Bartlett C6 and C9), or July 27 (Jeffers Brook mid and old), 2013. Trees were chosen randomly if there were more than two trees with the same sap sweetness. At least 15 sun-exposed leaves from the upper canopy were collected from each tree using a shotgun. Only leaves free from shot holes, disease and insect herbivory were used. Foliage was sampled between 10 am and 2 pm on sunny days to ensure the leaves were dry and photosynthesizing. The removed branches were immediately placed in water to sustain transpiration for gas exchange measurements.

A single healthy leaf from each tree was sampled for potential photosynthesis and stomatal conductance within a few minutes of being shot down, while it was still attached to the branch (Schaberg et al., 1997). Leaf gas exchange was measured with a LI 6400 (Licor Inc., Lincoln, NE) using a 6400-02B LED light source cuvette on 6 cm² of leaf area. Environmental conditions in the chamber during measurement were maintained at a temperature of 26 °C, 400 µmol/mol CO₂ concentration, 500 µmol s⁻¹ flow rate, and 1800 µmol m⁻² s⁻¹ photosynthetically active radiation. Ten measurements were taken for each leaf and averaged for potential photosynthesis and stomatal conductance.

2.5. Foliar nutrients

After gas exchange measurements, leaves were dried at 65 °C for 24 h and ground using a Wiley Mill with a 40-mesh screen (Thomas Scientific, Swedesboro, NJ). Foliar P, Ca, Mg, K and Mn concentrations were determined by ashing 0.25 g of sample in a muffle furnace at 470 °C overnight, digesting in 6 N HNO₃ on a hot plate for 20 min, and filtering the digested solution through Whatman #42 filter paper and rinsing with de-ionized water (Wilde et al., 1979). The digested solution was analyzed by ICP-OES for P, Ca, Mg, K, and Mn concentrations; blanks were high for Al and thus foliar Al is not reported here. Nitrogen was analyzed with a C and N elemental analyzer (Flash EA 1112 series, CE Elantech Inc., Lakewood, NJ).

2.6. Tree health and growth

Canopy health of all sampled trees was assessed from July 12 to 19, 2013 using the procedure developed by the North American Maple Project (Miller et al., 1991). Two individuals were trained and certified through the Vermont Department of Forest, Parks and Recreation to perform the assessment by viewing a tree from two different angles. The assessment rated the tree for overall vigor, canopy transparency, percent dieback, live crown ratio, and the overall density of the canopy.

Growth rates were determined from DBH measurements taken in 2008, 2011 and 2013. Trees in the Ca plots were not measured in 2008, before the plots were established. Control trees outside these plots were not measured until 2013 and growth rates could not be estimated for these trees. Some trees were selected in the treatment buffers and others grew in to measureable size between 2008 and 2013. The growth rate per tree was fit by linear regression to the available observations. Diameter growth rates could be estimated for 256 trees of the 298 in the study.

2.7. Data analyses

Correlation was used to test for relationships of sap sweetness to stem diameter, diameter growth, and canopy health measures using the average sap sweetness for all 298 trees. For the 84 trees



Fig. 1. Trees with higher foliar N:P ratio had sweeter sap (p < 0.001).

sampled for foliage, sap sweetness was correlated with foliar nutrient concentrations, photosynthesis, and stomatal conductance. For soil nutrients, which were measured at the plot level, not for each tree, sap sweetness was averaged by plot and correlated with soil extractable Ca, P, and N mineralization. For sap nutrients, which were also measured at the plot level, correlations were also conducted using average sap sweetness by plot.

The effect of nutrient treatments was tested using analyses of variance and covariance with a randomized incomplete block design on plot means of sap sweetness, with stand as the blocking variable. Pretreatment soil measurements were included as covariates to control for differences in nutrient availability not associated with nutrient additions. Soil measurements were not available from the Ca plots or the C6 control trees (selected near the Ca plot), thus these plots were not included in the analysis of covariance. We performed the analysis of variance on the same reduced data set (16 plots instead of 21 plots). The effect of sap nutrients on sap sweetness was tested using repeated measures analysis of variance for sap samples collected March 10 and March 31. Dunnett's test was used to test for differences between treatments, which allows comparison of several treatments against a single control. Residuals of all three models met the assumption of normality. Statistical analyses were conducted in SAS version 8 (SAS Institute Inc., Cary, NC).

3. Results

Sugar concentrations of maple sap ranged from 1.4% to 4.6%, based on the average of 3-4 sampling periods for each of 298 trees. Sap sweetness did not vary significantly across dates (p = 0.42). Foliar N:P was positively correlated with sap sweetness (r = 0.38, p < 0.001, Fig. 1), based on foliage sampled from the four trees with the highest and lowest sap sweetness in each plot (84 trees from 21 plots across 5 stands). Trees with higher N concentrations in leaves had sweeter sap (Fig. 2B), but this correlation was not statistically strong (r = 0.16, p = 0.15); the negative relationship of foliar P to sap sweetness was stronger (r = -0.25, p = 0.02, Fig. 2B). Foliar K was also negatively correlated with sap sweetness (r = -0.22, p = 0.05), probably because foliar K was positively correlated with foliar P (r = 0.31, p = 0.004). There was no relationship of foliar Ca or Mg to sap sweetness (r = -0.03, p = 0.79 for Ca and r = -0.11, p = 0.32 for Mg). All of the trees were below the threshold for Mn toxicity (1.6 mg/g; Kolb and McCormick, 1993; Moore and Ouimet, 2010), and there was no correlation between foliar Mn and sap sweetness (r = -0.17, p = 0.12). Comparison of foliar concentrations with deficiency thresholds showed N to be more commonly near deficiency than P or K (35% compared to 0-8%) in the trees we studied, while 24% were below the deficiency threshold



Fig. 2. (A) Sap sweetness as a function of soil exchangeable Ca, potential N mineralization, and extractable P. Plots with higher potential N mineralization had trees with sweeter sap. (B) Sap sweetness as a function of foliar Ca, N, P, by tree. The vertical dashed lines represent thresholds for nutrient deficiency (Kolb and McCormick, 1993; Moore and Ouimet, 2010).



Fig. 3. Sap sweetness after two years of addition of N (30 kg ha⁻¹ yr⁻¹), P (10 kg ha⁻¹ yr⁻¹), N (30 kg ha⁻¹ yr⁻¹) and P (10 kg ha⁻¹ yr⁻¹), and Ca (1150 kg ha⁻¹). The control is represented by "C." Boxes show the interquartile range, the line shows the median, and outliers are shown with stars. Sample sizes are shown in Table 1.

for Ca (Fig. 2). The only element more often below deficiency than N was Mg (61%; data not shown).

At the plot level, the average sap sweetness of maple trees was positively correlated with soil N mineralization, based on soil measurements made in 2009, before the onset of fertilization treatments. Plots with higher potential soil N mineralization had higher sugar concentration in the sap (r = 0.65, p = 0.007, Fig. 2A), based on data from 16 plots across 4 stands. Resin-strip nitrate measured in 2011, the first year of fertilization, had a similar correlation with sap sweetness (r = 0.60, p = 0.008; data not shown). Neither exchangeable Ca (r = 0.28, p = 0.28, Fig. 2A), bicarbonate-extractable P (r = -0.22, p = 0.42, Fig. 2A), nor soil pH (r = 0.4, p = 0.13) was significantly correlated with sap sweetness (Fig. 2).

At the time of sap collection, plots had been fertilized for two years with N, P, N + P, Ca, or kept untreated as a control. Treatment effects on sap sweetness, including all fertilizer treatments, were not significant in an unbalanced analysis of variance (p = 0.21, Fig. 3 and Table 2) (the analysis of variance was unbalanced because not all treatments were present in all the stands). For the N, P, N + P and control treatments, which were balanced across four stands, we could use pretreatment soil characteristics as covariates. The effect of fertilizer treatment on sap sweetness was more significant if pretreatment soil N mineralization was used as a covariate (p = 0.09, Table 2). Pretreatment exchangeable Ca and bicarbonate-extractable P were not significant covariates in explaining variation in sap sweetness ($p \ge 0.22$). The improvement in the significance of the analysis with N as a covariate was not due to dropping 5 plots from the analysis, as evidenced by an insignificant effect of treatments (p = 0.23) in analysis of variance on the same 16 plots (Model 2, Table 2). The mean sap sweetness in N-fertilized plots was 2.52%, compared to 2.27% in the controls (based on least-squares means) (p = 0.04). The other nutrient additions (P, N + P, and Ca) did not significantly affect sap sweetness (Table 2).

None of the measures of canopy health (vigor, live crown ratio, density, transparency, or dieback of the crown) were significantly correlated with sap sweetness across all 298 trees ($p \ge 0.41$). The variation in canopy health across trees was very low. Vigor was 1.5 ± 0.65 (mean \pm standard deviation), with 1 being a healthy tree and 5 being dead. The live crown ratio was $45\% \pm 10.45$ and the density of the crown was $49\% \pm 10.82$. Mean light transparency in the canopy was $14\% \pm 4.91$ and the average branch dieback was $6.1\% \pm 2.87$. There was a weak positive correlation of sap sweetness and diameter increment (r = 0.12, p = 0.06), with faster-growing trees having higher concentrations of sugar in their sap, as expected.

Photosynthetic capacity of leaves from the 84 trees from which foliage was sampled was weakly positively correlated with sap sweetness (r = 0.23, p = 0.04). There was no relationship of stomatal conductance to sap sweetness (r = -0.06, p = 0.57). Both photosynthetic capacity (r = 0.40, p < 0.001) and stomatal conductance (r = 0.26, p = 0.02) were positively correlated with foliar N concentration, but foliar N had only a weak positive relationship with sap sweetness, as described above.

The chemical composition of sap was measured in samples composited at the plot level. None of the elements measured (Ca, P, Mg, Mn, K, Al) were significantly correlated with sap sweetness ($p \ge 0.14$). Plots treated with P had higher concentrations of P in the sap (p = 0.03) while plots treated with N had higher concentrations of Mn in the sap (p = 0.05). All measured sap nutrient concentrations varied significantly across stands ($p \le 0.04$). Sap nutrients varied across sampling dates for Al, Ca, Mg, K ($p \le 0.04$).

4. Discussion

Results of this study point toward N as the limiting nutrient for sap sweetness. Soil N mineralization was correlated with higher sap sweetness, and N fertilization was also associated with sweeter sap (Fig. 1 and Table 2). In addition, trees with higher foliar N:P had

Table 2

Sources of variability, *p*-values, and least-squares means for the analysis of sap sweetness. Model 1 is a randomized incomplete block design ANOVA with all five treatments: control, N, P, N and P, and Ca. Model 2 is a balanced ANOVA with four treatments: control, N, P, and N and P. Model 3 is a balanced ANOVA using pre-treatment soil N mineralization as a covariate.

Source	Model 1		Model 2		Model 3		
	df	<i>p</i> -value	df	p-value	df	p-value	
Stand	4	<0.001	3	0.005	3	0.12	
Soil N mineralization					1	0.11	
Treatment	4	0.21	3	0.23	3	0.09	
Error	12		12		8		
RMSE	0.15		0.16		0.14		
Sap sweetness (%)							
LS Means & Error	Model 1 LS Means		Model 2 LS Means		Model 3 LS Means**		
Control	2.31 (0.066)		2.24 (0.081)		2.27 (0.075) b		
Ν	2.56 (0.078)		2.47 (0.081)		2.52 (0.077) a		
Р	2.38 (0.078)		2.29 (0.081)		2.26 (0.074) b		
NP	2.35 (0.078)		2.26 (0.081)		2.21 (0.078) b		
Ca	2.34 (0.076)		. ,		. ,		

* Standard error is presented in parentheses.

** Values with the same letter within a column do not differ at α = 0.10.

sweeter sap. Across the northeastern US, sugar maple grows faster on sites with higher soil N (Thomas et al., 2010). In northern Vermont, sugar maple on sites with higher soil N had healthier canopies (Liu et al., 1997) and trees with higher foliar N had higher photosynthetic potential (Ellsworth and Liu, 1994). The importance of N to sweeter sap is likely related to N limitation of photosynthesis. Higher foliar N was associated with higher photosynthesis rates, which would be expected to allow for higher production of sugars. Our study included five stands at two sites, which makes the findings more robust than those conducted in just one or two stands (Kriebel, 1961; Watterston et al., 1963; Bary and Roy, 1998).

The lower sap sweetness we found in trees with higher foliar P was surprising (Figs. 1 and 2). Since foliar N and P were inversely correlated, it would be possible for the apparent negative effect of P to be due to the positive relationship with N. However, the negative correlation with foliar P was stronger than the positive correlation with foliar N (Fig. 2), and combining N and P (N:P) gave the strongest correlation (Fig. 1). The results of fertilizer treatments further supported a negative effect of P on sap sweetness. While N fertilization increased sap sweetness, the addition of P with N did not result in sweeter sap (Table 2). Other studies have found negative relationships with P in sugar maple. Foliar P was higher in declining than healthy sugar maples in Vermont (Liu et al., 1997). An experimental addition of P to sugar maple stands decreased sap sweetness in central New York (Watterston et al., 1963). However, ours is the first study to report a negative relationship of foliar P to sap sweetness. No study has found P to have a positive effect on sap sweetness, but studies in central Ontario (Gradowski and Thomas, 2006) and Quebec (Paré and Bernier, 1989) have found P to be limiting to sugar maple growth.

Calcium influences the health of sugar maples (Sullivan et al., 2013), so it was surprising that we found no relationship of Ca to sap sweetness, either with soil or foliar Ca (Fig. 2) or with Ca addition (Fig. 3 and Table 2). We expected to see an effect because the application rate of Ca silicate was high, and foliage showed elevated silica (data not shown). Although soil Ca is important to the health of sugar maples (Horsley et al., 2002; Schaberg et al., 2006; Sullivan et al., 2013) and healthier trees have higher sap sweetness (Noland et al., 2006) the relationship of Ca to sap sweetness had not previously been tested. It is possible that a wider range of soil conditions would show a relationship between sap sweetness and soil or foliar Ca. Most (76%) of the trees in our study were in the sufficiency range for foliar Ca concentrations (Fig. 2). Measurements of canopy health confirmed that a majority of our trees were healthy.

We did not find a relationship between any of our measures of canopy health and sap sweetness. Previous studies have found sweeter sap in trees with greater crown density (Moore et al., 1951; Taylor, 1956) or crown diameter (Morrow, 1955; Blum, 1973), suggesting that healthier trees would have sweeter sap. However, there was little variation in tree health across our stands. Wilmot et al. (1995) also failed to find a correlation between canopy dieback and sugar production. Live crown ratio was expected to affect sap sweetness because the size of the canopy influences sap sweetness (Morrow, 1955). However, crown diameter is probably more important than the height of the crown because sun does not reach lower parts of the tree in a closed canopy forest (Morrow, 1955).

5. Implications for management

Sap sweetness is economically important because of the cost of removing the water and its effect on the amount of sugar produced per gallon of sap. Large producers now use reverse osmosis in their operations (Boulet et al., 2005), which has reduced the cost of water removal (Perkins and van den Berg, 2009). The magnitude of the effects we saw (11% higher sugar concentrations from N fertilization) would translate directly into increased production, if the volume of sap collected were not affected. Our study did not address sap volume, but positive relationships have been reported between sap sweetness and sap volume (Blum, 1973; LaValley, 1969), presumably because both reflect tree health and C balance. If soil N improves sap volume as well as sap sweetness, the benefits of fertilization would be even greater than those reported here.

Consumption of maple sugar in the United States increased by 155% per capita from 1975 to 2009 (Farrell and Chabot, 2012). Thus the acreage of sugar bushes is expanding and the importance of soil fertility, particularly with regard to N, could be relevant to site selection. The majority of the resource is still untapped, with 9.3 million taps currently in operation of a total possible 2.2 billion, based on the size and number of sugar and red maples in the United States (Farrell and Chabot, 2012). Avoiding high P relative to N could also be a consideration; more study is needed of this relationship. Although Ca additions in our study did not increase sap sweetness, low soil Ca is known to predispose sugar maple to decline (Long et al., 2011; Sullivan et al., 2013).

In sites that are not naturally high in N, fertilization may increase sugar production and has been found to increase profit 25% over five years after fertilization cost (LaValley, 1969). We estimated costs of fertilizing a sugar bush with 60 kg N ha⁻¹ at \$110 per ha⁻¹, including an application cost of \$74 per ha⁻¹ (Fox et al., 2007). For the 11% increase we observed in sugar concentration, the cost of fertilization would be recovered within five years if the profit before fertilization was at least \$200 per ha⁻¹ (Boulet et al., 2005).

Assessing the nutrient status of a stand is important to predicting the benefits of fertilization (Wilmot and Perkins, 2004). We found that P had a negative effect on sap sweetness in our stands, but P additions could be beneficial in P-deficient stands (Gradowski and Thomas, 2006; Casson et al., 2012). We were unable to test this as all of our trees were sufficient in foliar P (Fig. 1). Adding too much N could be detrimental; in a study in Quebec, application of 95 kg N ha⁻¹ yr⁻¹ for 8 years was enough to cause maple decline, while 26 kg N ha⁻¹ yr⁻¹ did not (Moore and Houle, 2013). By selecting sites with adequate soil N or fertilizing N-limited sites with N, maple syrup producers may be able to collect maple sap with higher sugar concentrations.

Acknowledgments

Tim Wilmot, Tim Perkins, and Steve Childs gave advice on sap sampling, and Eric Randall provided spiles and tubes. Mike Wild helped collect sap and took photos. Chris Costello managed the site and the snowmobiles. Heidi Asbjornsen provided a LiCor 6400; Adan Hernández and Katherine Sinacore helped with photosynthetic measurements. Eric MacPherson conducted canopy health assessment and Sandy Wilmot provided training. The MELNHE summer field crew, led by Craig See, helped to collect leaves and measure tree growth. Melany Fisk provided the soils data. Chris Nowak, Colin Beier and Mike Farrell provided reviews of an earlier version of the manuscript. The USDA Forest Service maintains the Bartlett Experimental Forest and the White Mountain National Forest. The MELNHE project is funded by the US National Science Foundation through Ecosystem Science (DEB-0949324) and the Long-Term Ecological Research (LTER) Program (DEB-1114804). Funding for the sap sweetness project was provided by the Northeastern States Research Cooperative in cooperation with the USDA Forest Service.

References

- Bae, K., 2013. Below Ground Carbon Fluxes Respond to Nutrient Availability in a Northern Hardwood Forest, Ph.D. Dissertation. State University of New York College of Environmental Science and Forestry.
- Bailey, S.W., Horsley, S.B., Long, R.P., Hallett, R.A., 2004. Influence of edaphic factors on sugar maple nutrition and health on the allegheny plateau. Soil Sci. Soc. Am. J. 68 (1), 243–252.
- Bary, R., Roy, L., 1998. Effects of Maple Fertilization on Sugar Production (Phase 4). National Research Council of Canada Research Report.
- Battles, J.J., Fahey, T.J., Driscoll, C.T., Blum, J.D., Johnson, C.E., 2013. Restoring soil calcium reverses forest decline. Environ. Sci. Technol. Lett. 1 (1), 15–19.
- Blum, B.M., 1973. Relation of sap and sugar yields to physical characteristics of sugar maple trees. Forest Sci. 19 (3), 175–179.
- Boulet, S., Deschênes, C., Aubin, J., Beaudoin, J., Deschênes, J., Durand, M., Fontaine, D., Gagné, F., Lemieux, N., Deschênes, J., 2005. Study on the Cost of (bulk) Maple Svrup Production in Quebec in 2003 Bibliothéque Nationale du Québec Directorate for Policies on Risk Management. Translated to English.
- Casson, N.J., Eimers, M.C., Watmough, S.A., 2012. An assessment of the nutrient status of sugar maple in Ontario: indications of phosphorus limitation. Environ. Monit. Assess. 184 (10), 5917-5927. http://dx.doi.org/10.1007/s10661-011-2390-2
- Cirelli, D., Jagels, R., Tyree, M.T., 2008. Toward and improved model of maple sap exudation: the location and role of osmotic barriers in sugar maple, butternut and white birch. Tree Phys. 28, 1145-1155.
- DeForest, J.L., Scott, L.G., 2010. Available organic soil phosphorus has an important influence on microbial community composition. Soil Sci. Soc. Am. J. 74 (6), 2059-2066
- Driscoll, C.T., Lawrence, G.B., Bulger, A.J., Butler, T.J., Cronan, C.S., Eagar, C., Lambert, K.F., Likens, G.E., Stoddard, J.L., Weathers, K.C., 2001. Acidic deposition in the northeastern U.S.: sources and inputs, ecosystems effects, and management strategies. Bioscience 51, 180-198.
- Ellsworth, D.S., Liu, X., 1994. Photosynthesis and canopy nutrition of four sugar maple forests on acid soils in northern Vermont, Can. J. For, Res. 24, 2118-2127
- Farrell, M.L., Chabot, B.F., 2012. Assessing the growth potential and economic impact of the U.S. maple syrup industry. J. Agric. Food Syst. Community Dev. 2 $(2)^{-}11-27$
- Fatemi, F.R., Yanai, R.D., Hamburg, S.P., Vadeboncouer, M.A., Arthur, M.A., Briggs, R.D., Levine, C.R., 2011. Allometric equations for young northern hardwoods: the importance of age-specific equations for estimating aboveground biomass. Can. J. For. Res. 41, 881-891.
- Fisk, M.C., Ratliff, T.J., Goswami, S., Yanai, R.D., 2014. Synergistic soil response to nitrogen plus phosphorus fertilization in hardwood forests. Biogeochemistry 118, 195-204.
- Fox, T.R., Allen, H.L., Albaugh, T.J., Rubilar, R., Carlson, C.A., 2007. Tree nutrition and forest fertilization of pine plantations in the southern United States. South. J. Appl. For. 31 (1), 5–11
- Gabriel, W.J., 1982. Mini-Tapping Sugar Maples for Sap-Sugar Testing. USDA Forest Service, Northeastern Forest Experiment Station Research Note NE-305.
- Gradowski, T., Thomas, S.C., 2006. Phosphorus limitation of sugar maple growth in central Ontario. For. Ecol. Manage. 226 (1-3), 104-109.
- Gregory, R.A., Hawley, G.J., 1983. Sap extraction and measurement of soluble sap sugars in sugar maple. Can. J. For. Res. 13, 400-404.
- Gregory, R.A., 1977. Cambial activity and ray cell abundance in Acer saccharum. Can. J. Bot. 55 (20), 2559-2564.
- Gregory, R.A., 1982. Release of Sap Sugar and Control of Sap Pressure, Section I: Sugar Maple Research; Sap Production, Processing, and Marketing of Maple Syrup. USDA Forest Service Technical report, NE-72.
- Horsley, S.B., Long, R.P., Bailey, S.W., Hallett, R.A., Hall, T.J., 2000. Factors associated with the decline disease of sugar maple on the Allegheny Plateau. Can. J. For. Res. 30, 1365-1378.
- Horsley, S.B., Long, R.P., Bailey, S.W., Hallett, R.A., Wargo, P.M., 2002. Health of eastern North American sugar maple forest and factors affecting decline. North. J. Appl. Forestry 19 (1), 34-44.
- Juice, S.M., Fahey, T.J., Siccama, T.G., Driscoll, C.T., Denny, E.G., Eagar, C., Cleavitt, N.L., Minocha, R., Richardson, A.D., 2006. Response of sugar maple to calcium addition to northern hardwood forest. Ecology 87 (5), 1267-1280.
- Kolb, T.E., McCormick, L.H., 1993. Etiology of sugar maple decline in four Pennsylvania stands. Can. J. For. Res. 23, 2395-2402.
- Kriebel, H.B., 1961 Fertilization Increases Sap Sweetness in Sugar Bush. Ohio Farm and Home Research, November-December, 92-93.
- Laing, F.M., Howard, D.B., 1990. Sap sweetness consistency vs. growth rates in
- young sugar maples. North. J. Appl. For. Res. 7 (1), 5–9. Larochelle, F., Forget, E., Rainville, A., Bousque, J., 1997. Sources of temporal variation in sap sugar content in a mature sugar maple (*Acer saccharum*) plantation. For. Ecol. Manage. 106, 307-313.
- LaValley, P.E., 1969. Studies of Fast Methods of Growing Trees. North. Logger and Timber Processor March, 24-25.
- Leech, R.H., Kim, Y.T., 1990. Methods to investigate fertilization as a means to improve growth and sugar yield of sugar maples. Commun. Soil Sci. Plant Anal. 1 (17&18), 2029-2051.

- Liu, X., Ellsworth, D.S., Tyree, M.T., 1997. Leaf nutrition and photosynthetic performance of sugar maple (Acer saccharum) in stands with contrasting health conditions. Tree Phys. 17, 169-178.
- Long, R.P., Horsley, S.B., Hallett, R.A., Bailey, S.W., 2009. Sugar maple growth in relation to nutrition and stress in the northeastern United States. Ecol. Appl. 19 (6), 1454-1466.
- Long, R.P., Horsley, S.B., Hall, T.J., 2011. Long-term impact of liming on growth and vigor of northern hardwoods. Can. J. For. Res. 41, 1295-1307.
- Marvin, J.W., Morselli, M., Mathes, M.C., 1971. Rapid low temperature hydrolysis of starch to sugars in maple stems and in maple tissue cultures. Cryobiology 8, 339-344.
- Marvin, J.W., 1958. The physiology of maple sap flow. In: Thimmann, K.V. (Ed.), The Physiology of Forest Trees. Ronald Press, N.Y..
- Miller, I., Lachance, D., Burkman, W.G., Allen, D.C., 1991 North American Sugar Maple Decline Project: Organization and Field Methods. Northeastern Forest Experiment Forest Station; General Technical Report NE-154.
- Moore, J.D., Houle, D., 2013. Soil and sugar maple response to 8 years of NH4NO3 additions in a base-poor northern hardwood forest. For. Ecol. Manage. 310, 167-172.
- Moore, J.D., Ouimet, R., 2010. Effects of two Ca fertilizer types on sugar maple vitality. Can. J. For. Res. 40, 1985-1992.
- Moore, H.R., Anderson, W.R., Baker, R.H., 1951. Ohio maple syrup: some factors influencing production. Ohio Agric. Exp. Bull. 718, 1-53.
- Moore, J.D., Ouimet, R., Duchesne, L., 2012. Soil and sugar maple response 15 years after dolomitic lime application. For. Ecol. Manage. 281, 130-139.
- Morrow, R.R., 1955. Influence of tree crowns on maple sap production. Cornell Univ. Agric. Exp. StnBull. 916, 5-30.
- Morselli, M.F., Marvin, J.W., Laing, F.M., 1978. Image-analyzing computer in plant science: more and larger vascular rays in sugar maples of high sap and sugar yields. Can. J. Bot. 56, 983-986.
- Naples, B.K., Fisk, M.C., 2010. Belowground insights into nutrient limitation in northern hardwood forests. Biogeochemistry 97 (2-3), 109-121.
- Noland, T.L., McVey, G., Chapeskie, D., 2006. Ice storm and fertilization effects on root starch, sap productivity and sweetness, diameter growth, and tap hole closure in sugar maple stands of eastern Ontario. Ontario For. Res.: Inst. For. Res. Note, 68.
- Paré, D., Bernier, B., 1989. Origin of the phosphorus deficiency observed in declining sugar maple stands in the Quebec Appalachians. Can. J. For. Res. 19, 24-34. http://dx.doi.org/10.1139/x89-004.
- Perkins, T.D., van den Berg, A.K., 2009. Maple syrup-production, consumption, chemistry, and sensory characteristics. Adv. Food Nutr. 56, 101-143.
- Safford, L.O., 1973. Fertilization Increases Diameter Growth of Birch-Beech-Maple Trees in New Hampshire. USDA Forest Service Research Note. NE-182, 1-4.
- Schaberg, P.G., Perkins, T.D., McNulty, S.G., 1997. Effects of chronic low-level N additions on foliar elemental concentrations. Can. J. For. Res. 27, 1622–1629.
- Schaberg, P.G., Tilley, J.W., Hawley, D.H., Bailey, S.W., 2006. Associations of calcium and aluminum with the growth and health of sugar maple trees in Vermont. For. Ecol. Manage. 223, 159-169.
- Smith, M.L., Martin, M.E., 2001. A plot-based method for rapid estimation of forest canopy chemistry. Can. J. For. Res. 31, 549-555.
- Statistics Canada. 2013, November 8. Table 001-0008: Production and farm value of maple products. Government of Canada. <http://www5.statcan.gc.ca/ cansim/a26?lang=eng&retrLang=eng&id=0010008&pattern=maple&tabMode= dataTable&srchLan=-1&p1=1&p2=-1> (accessed 19.03.14).
- Sullivan, T.J., Lawrence, G.B., Bailey, S.W., McDonnell, T.C., Beier, C.M., Weathers, K.C., McPherson, G.T., Bishop, D.A., 2013. Effects of acidic deposition and soil acidification on sugar maple trees in the Adirondack Mountains, New York. Environ. Sci. Technol. 47, 12687–12694.
- Taylor, F.H., 1956. Variation in Sugar Content of Maple Sap. Univ. Vermont State Agric. Coll., Bull. 587.
- Thomas, R.Q., Canham, C.D., Weathers, K.C., Goodale, C.L., 2010. Increased tree carbon storage in response to nitrogen deposition in the US. Nat. Geosci. 3, 13-17.
- Tyree, M.T., 1983. Maple sap uptake, exudation, and pressure changes correlated with freezing exotherms and thawing endotherms. Plant Phys. 73, 277-285.
- Vadeboncoeur, M.A., 2010. Meta-analysis of fertilization experiments indicates multiple limiting nutrients in northeastern deciduous forests. Can. J. For. Res. 40 (9), 1766-1780,
- Watterston, K.G., Leaf, A.L., Engelken, J.H., 1963. Effect of N, P, and K fertilization on yield and sugar content of sap of sugar maple trees. Soil Sci. Soc. Am. J. 27 (2), 236-238.
- Whitney, G.G., Upmeyer, M.M., 2004. Sweet trees, sour circumstances: the long search for sustainability in the North American maple products industry. For. Ecol. Manage. 200, 313-333.
- Wilde, S.A., Corey, R.B., Iyer, J.G., Voigt, G.K., 1979. Soil and plant analysis for tree culture. Oxford and IBH Publishing Company, New Delhi, India, pp. 224.
- Wilmot, T., Perkins, T., 2004. Fertilizing a Sugar Bush. Proctor Maple Research Center, University of Vermont.
- Wilmot, T.R., Brett, P.W., Tyree, M.T., 1995. Vigor and nutrition vs. sap sugar concentration in sugar maple. North. J. Appl. For. Res. 12, 156-162.
- Yawney, H.W., Walters, R.S., 1973. Special Forest Crops and Fertilization. Forest Fertilization Symposium Proceedings: USDA Forest Service General Technical Report NE-3, 122-131.