



Maple syrup production declines following masting



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ABSTRACT

Maple syrup is a non-timber forest resource, for which yield depends strongly on natural processes. Past research has heavily emphasized the role of weather and climate in determining sap flow, and the relationship between sap flow and syrup yield. However, syrup yield depends on sap sugar content, as well as sap flow. Although sap sugar content varies widely among years, less is known about the causes of this variation. Drawing on ecological theories for causes of mast-seeding in trees, we hypothesized that a trees' carbohydrate stores would fluctuate through time in concert with seed production, and that this fluctuation would affect sap sugar and syrup yield. We evaluated weather variables and past seed production as possible causes of inter-annual variation in maple syrup yield in Vermont, USA. Past seed production was strongly correlated with current syrup yield, suggesting that carbohydrate costs of reproduction affect stores. Climate variables were also important for syrup yield, but were only statistically significant predictors after accounting for variation in seed production. Seed production occurs several months before syrup production, and can be used as a way to forecast expected syrup yields, and prepare harvest plans accordingly.

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1. Introduction

Maple syrup is a non-timber forest resource for which yield depends strongly on natural processes, as well as management. Sugar maple (*Acer saccharum* Marsh.) xylem sap is collected in the late winter and early spring (generally late-January through April, depending on the geographic location) when the daily temperature range spans the freezing point of water (Skinner et al., 2010). The diurnal freeze thaw cycle, with above freezing temperatures during the day and below freezing temperatures at night, causes sap flow (Tyree, 1983; Johnson and Tyree, 1992; Tyree and Zimmermann, 2002; Cirelli et al., 2008; Ceseri and Stockie, 2013) during the season when trees convert starch to sugar in the xylem (Marvin et al., 1971; Milburn and Zimmermann, 1986; Wong et al., 2003), which becomes incorporated into the sap (Sauter et al., 1973; Johnson et al., 1987).

Past studies have established a relationship between sap flow or syrup yield and weather variables. Daily sap flow is positively correlated with temperature (Kim and Leech, 1985), although sap flow decreases over time if night-time temperatures do not fall below freezing (Cortes and Sinclair, 1985). Very cold nights can impede sap flow the following day, because several hours of above-freezing temperatures may be necessary for the xylem to thaw (Cortes and

Sinclair, 1985). On annual scales, sap and syrup yield are correlated with the number of days during the tapping season when temperatures cross 0 °C, as well as maximum temperature, snow cover, and winter precipitation (Plamondon and Bernier, 1980; Pothier, 1995). At regional scales in Quebec, 4 monthly temperature variables explained 84% of variation in maple syrup yield (Duchesne et al., 2009).

However, sap flow volume only partially determines syrup yield and profitability. Sap sugar content determines the amount of syrup that can be produced from a given volume of sap. Sugar maple sap averages 2–3% sugar, but varies considerably within years, among trees, and among years. This variation appears to reflect a complex array causes, and remains poorly understood. Most research on sap sugar to date has focused on differences among trees. For example, trees tend to maintain their relative ranking of sweetness among years, even though sugar content varies from year to year (Taylor, 1956; Marvin et al., 1967). Variation in sap sugar among trees has a genetic component (Gabriel, 1972; Kriebel, 1989, 1990); trees with more and larger xylem rays have higher sap sugar content (Morselli et al., 1978). Sap sugar content is also related to tree health and site quality (Morrow, 1955; Gabriel and Seegrist, 1977; Noland et al., 2006), although significant aspects of this variability remain to be explained (Wilmot et al., 1995; Larochelle et al., 1998). Variation among years has received relatively little attention, even though this type of variation can be considerable (Larochelle et al., 1998) and has the potential to impact syrup yields at larger scales, particularly if sap sugar

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varies in concert among trees. The only study that we could find about inter-annual variation in sap sugar (Pothier, 1995) correlated sugar content with weather variables, and found a positive correlation between sap sugar content and the number of days during the tapping season that temperatures cross 0 °C.

Theoretical models of mast-seeding suggest an additional cause of inter-annual variation in sap sugar content. Mast seeding is highly variable and synchronous reproduction across plant populations (Kelly and Sork, 2002). The resource budget model (Isagi et al., 1997; Satake and Iwasa, 2000) posits that masting trees flower only after reaching a threshold of resource stores. High seed production in turn depletes resources, and it takes one or more years for trees to gain enough resources to flower again. Sugar maple is a mast seeding tree with intervals between high seed years of between 2 and 5 years (Graber and Leak, 1992; Garrett and Graber, 1995; Houle, 1999; Cleavitt et al., 2011; Jensen et al., 2012; Graignic et al., 2014). Like many temperate masting tree species, sugar maple flowers in the spring before leaf flush, meaning that stored nonstructural carbohydrates (NSC) are most likely the only source of carbon during flowering. If the resource budget model applies to sugar maples, then NSC would cue flowering, and, in high-flowering years, NSC would be depleted after seed production. Following on this line of reasoning, if sugar in xylem sap also reflects the available pool of stored NSC, sap sugar should be depleted after a year of heavy seed production (Fig. 1). This leads to the hypothesis that seed production in sugar maple should be negatively correlated with sap sugar content in the following year. Because masting is by definition a population-level phenomena, masting could affect sap sugar content and hence syrup yield across large areas (Fig. 1).

We used 17 years of monitoring data on syrup and seed production from Vermont to evaluate the relationship between seeds and syrup. We hypothesized that: (1) costs of reproduction (flower and seed production) related to masting would lead to lower syrup yields in the year following a masting event; and (2) masting would be positively correlated with syrup production in the same year (Fig. 1). We then compared the effect of masting on syrup production to the well established relationship between climate and syrup production, to see whether having knowledge of seed production in the previous year could improve sugar season forecasts for producers.

2. Methods

2.1. Data

Sugar maples are native to northeastern North America. Maple sap is commonly harvested from scattered trees on individual farms, and occasionally from trees planted in plantations. Sap is

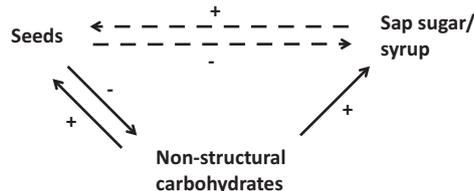


Fig. 1. Hypothesized relationships between seed production, non-structural carbohydrate stores, and sap sugar content or syrup production in sugar maple. Solid lines indicate direct effects; dashed lines indicate indirect effects. The resource budget model predicts mast years occur when resource levels are high, and that masting depletes resource stores. We hypothesize sap sugar content is a function of non-structural carbohydrate stores. This leads to an indirect reciprocal relationship between seeds and syrup production where seed production should be high in years of high sap sugar content, and masting should lead to lower syrup production in the following year.

collected in the late-winter (generally mid-February through mid-April in the study area) to produce maple syrup. Trees flower in May, and leaf out a few weeks after flowering. Seeds mature over the course of the growing season and fall from the trees in autumn. Our study focused on data from Vermont, USA. We chose Vermont because of the availability of overlapping time series of syrup and seed production.

We compiled data on sugar maple seed production, maple syrup production, and weather in Vermont from publicly available sources. From these data, we obtained overlapping time series of syrup and weather for 16 years, relating seed production from 1998 to 2013 to syrup production from 1999 to 2014.

Data for maple syrup production came from the United States Department of Agriculture National Agricultural Statistics Service annual surveys of maple syrup producers (National Agricultural Statistics Service, 2014). Data on maple syrup production measured in gallons is available since 1992, but analyses included data for Vermont from 1999 through 2014 to match the time span of the seeding time series (see next paragraph). Maple syrup production has increased since the early 2000s due to increased tapping effort, which includes both increasing the number of taps and the amount of sap collected per tap (Farrell and Chabot, 2011). In Vermont, the number of taps increased monotonically, and nearly linearly ($F_{1,13} = 32.81$, $P = 0.011$, adjusted $r^2 = 0.89$) from 2010 to 2014 (the only years these data were available). Yield, the number of gallons of syrup produced per tap, also increased from 2001 to 2014, and was highly correlated with syrup production ($r = 0.91$, $p < 0.0001$). To remove the effects of increased effort, we detrended the time series by fitting a smooth spline to the data, and using the residuals in further analyses (Fig. 2).

Data on sugar maple seed production came from the Vermont Monitoring Cooperative (Lund et al., 2013). In 1988, monitoring plots were established in 30 sugar maple stands throughout Vermont to assess tree health as part of the North American Maple Project (NAMP). Seed production was assessed annually at these sites starting in 1998. At each site, five 400 m² plots are visited annually, and all trees greater than 10 cm DBH are surveyed. Among other measurements related to tree health and performance, seed

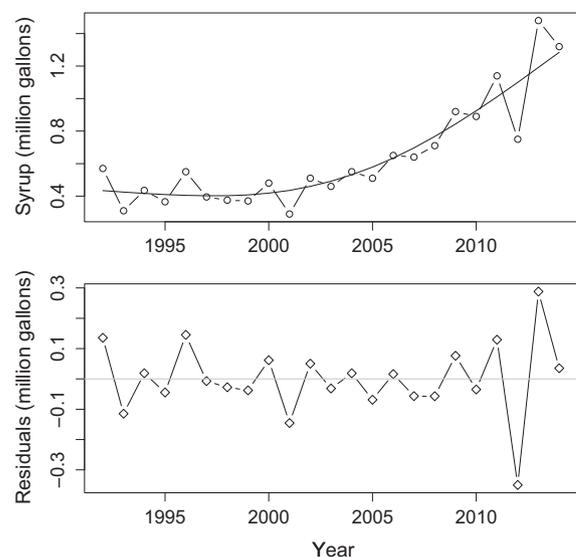


Fig. 2. Maple syrup production in Vermont from 1992 to 2014. Top panel shows the syrup production in millions of gallons as reported from annual surveys of maple syrup producers by the USDA National Agricultural Statistic Service. The trend line is a smooth spline fit to the data. The lower panel plots the residuals of the spline fit. These residuals were used in analyses comparing seed production and monthly climate as predictors of annual variation in syrup production.

production of individual sugar maples is recorded on a three point scale: none, light to moderate, and heavy (Vermont Monitoring Cooperative, 2007). To construct an index of site level seed production, we first designated a subset of mature trees that produced seeds at some point during the time series, and then excluded sites that had fewer than 5 mature trees. This resulted in a data set containing 685 trees in 28 sites (6–39 trees per site, mean = 24.5 trees). We then calculated the proportion of trees seeding in each year from this reduced set (Fig. 3). We also calculated the proportion of trees with heavy seed production in each year; this was highly correlated with the proportion of trees seeding in each year (Pearson's $r = 0.98$). Unsurprisingly, results using the proportion of masting trees as a predictor were qualitatively similar to those using the proportion of trees seeding. Therefore, we do not discuss these analyses further in this manuscript.

We used monthly climate variables (minimum and maximum temperature, and total precipitation) from the PRISM Climate Group at Oregon State University (PRISM Climate Group, 2014) for 1999–2014. Monthly maximum and minimum temperatures and total precipitation are interpolated on a 4 km grid from nearby climate stations. We used data for pixels that included the 28 NAMP sites with seed data, and then calculated state-level average monthly minimum and maximum monthly temperatures, and average total winter (October–April) precipitation for each year. Maximum and minimum monthly temperatures of individual months were correlated (Pearson's r between 0.81 and 0.96), but much less so among months (Pearson's $r < 0.52$ for all comparisons). None of the climate variables were strongly correlated with past seed production (Pearson's $r < 0.35$ in all cases). Therefore, we can clearly discriminate effects of these weather variables from those of seed production, even though we cannot clearly attribute weather effects to one of two correlated weather variables (see discussion).

2.2. Analysis

We used multiple linear regression models to evaluate factors that predict syrup production. We compared models with (1) only weather variables as predictors and (2) only seeds in the previous fall as a predictor, and (3) models with weather and seeds as predictors. Prior to fitting these models, we rescaled the predictor variables by centering each predictor and dividing by two standard deviations to aid in model convergence and make it possible to compare effect sizes of specific predictors (Gelman, 2008). After fitting each full model we used functions in the R package MuMIn (Barton, 2014) to run a suite of models with all possible combinations of the fixed effects and calculate model AICc values and

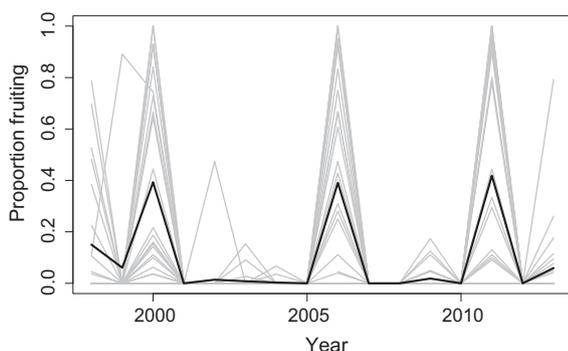


Fig. 3. Proportion of trees observed to have seeds from 1998 to 2013 in 28 sites throughout Vermont surveyed by the Vermont Monitoring Cooperative as part of the North American Maple Project. Gray lines show individual sites, while the black line shows the statewide trend.

weights. We choose the best models that used seeds only, weather only, and seeds plus weather predictors as the one with the lowest AICc value in each group and then compared these three models to each other, again using AICc. AICc is a more conservative version of AIC that accounts for small sample size (Burnham and Anderson, 2002). For the models with the lowest AICc in each group we visually confirmed that the distribution of residuals was unimodal and symmetric. We then used model averaging to estimate shrinkage-adjusted coefficients and Relative Importance values from the models with the lowest AICc scores ($dAICc < 4$). We calculated jackknife confidence intervals for model parameters by sequentially removing one year of data and repeating the analysis. All analyses were done in R version 3.1.0 (R Core Team, 2014).

In addition, we tested the hypotheses that seeding would be positively correlated with syrup production in the same year. We modeled seed production as a binomial process (logistic regression), with trees either having seeds in a given year or not, as a function of detrended syrup production in the same year.

3. Results

Models with only weather variables as predictors poorly predicted syrup production. The full model with monthly minimum and maximum January through April temperatures and total winter precipitation had an R^2 of 0.75, but an adjusted R^2 of 0.37, an overall P -value of 0.21 and only one statistically significant ($P < 0.05$) predictor, maximum March temperature (Table 1A). Across all possible models including only climate variables, the intercept only (null) model had the lowest AICc (Table 2). These results were also supported by the jackknife analysis, in which single years of data were sequentially removed, all possible models were fitted to the reduced data, and these models were ranked using AICc. In only two of the reduced datasets did a model other than the intercept only model have the lowest AICc. In both, maximum and minimum March temperatures were included. The null model had a similar AICc value ($dAICc$ of 0.12 and 2.01, respectively), indicating that it fit the data nearly as well. A model averaging analysis confirmed that no single climate variable was a significant predictor at the $P = 0.05$ -level (Table 1A). Relative importance values ranged between 0.05 and 0.34; no single predictor was included in a majority of the best models ($dAICc < 4$). The most commonly included variable was maximum March temperature.

In contrast to weak relationships with climate alone, syrup production was strongly negatively associated with the proportion of trees seeding in the previous year (equation: $\text{syrup} = 0.04901 - 0.58715 * \text{seeds}_{t-1}$, $F_{1,13} = 12.349$, $P = 0.0034$, adjusted $R^2 = 0.4307$; Fig. 4a). The full model containing seeds and all climate predictors explained most of the variance in syrup production (multiple $R^2 = 0.98$, adjusted $R^2 = 0.94$, $P = 0.001$). Proportion of trees with seeds in the previous year, minimum and maximum January, March, and April temperatures, and maximum February temperature were all significant predictors at $P < 0.05$ (Table 1B). However, the combination of predictors with the lowest AICc was a model that included only proportion of trees with seeds, minimum and maximum March temperatures, and maximum April temperature (Table 2). This model explained 79% of the variation in syrup production (Table 2). Only two other models had a $dAICc$ of less than 4, both of which also contained proportion of trees with seeds and maximum April temperature. One of the models also contained minimum April temperature. With model averaging, proportion of trees with seeds and maximum April temperature were significant predictors at $P < 0.05$, and minimum and maximum March temperatures had marginal support (Table 1B). Jackknifing showed that the proportion of trees with seeds and maximum April temperature were strong predictors regardless of the dataset used; both had high relative importance

Table 1
Model coefficients and Wald statistics for the full model and model-averaged coefficients including (A) monthly weather variables and (B) weather variables and seeding frequency to predict annual syrup production. Statistically significant predictors are identified in italics.

	Full model			Model averaging (with shrinkage)					P-value	Relative importance
	Estimate	SE	t value	P-value	Estimate	SE	SE (adj)	z value		
A. Model with weather predictors only										
(Intercept)	-0.15	0.12	-1.20	0.28	-0.02	0.14	0.15	0.14	0.89	
<i>T_{min,Jan}</i>	-2.21	1.68	-1.32	0.24	-0.03	0.13	0.14	0.20	0.84	0.09
<i>T_{max,Jan}</i>	1.24	1.53	0.81	0.45	-0.03	0.13	0.13	0.21	0.83	0.10
<i>T_{min,Feb}</i>	0.79	1.03	0.77	0.47	-0.01	0.10	0.11	0.13	0.90	0.06
<i>T_{max,Feb}</i>	-0.61	0.48	-1.27	0.25	-0.03	0.15	0.16	0.22	0.83	0.10
<i>T_{min,Mar}</i>	1.57	0.75	2.09	0.08	0.23	0.55	0.57	0.41	0.68	0.27
<i>T_{max,Mar}</i>	-2.07	0.57	-3.62	0.01	-0.32	0.60	0.61	0.53	0.60	0.34
<i>T_{min,Apr}</i>	1.59	0.76	2.09	0.08	-0.003	0.07	0.08	0.04	0.97	0.05
<i>T_{max,Apr}</i>	-1.28	0.58	-2.22	0.07	-0.01	0.08	0.09	0.12	0.90	0.06
<i>P_{Oct-Apr}</i>	-0.10	0.43	-0.22	0.83	0.01	0.08	0.08	0.11	0.91	0.05
B. Model with seed frequency and weather predictors										
(Intercept)	-0.06	0.04	-1.56	0.18	0.02	0.07	0.08	0.28	0.78	
<i>T_{min,Jan}</i>	-1.90	0.53	-3.59	0.02	-	-	-	-	-	-
<i>T_{max,Jan}</i>	1.41	0.48	2.93	0.03	-	-	-	-	-	-
<i>T_{min,Feb}</i>	0.51	0.32	1.57	0.18	-	-	-	-	-	-
<i>T_{max,Feb}</i>	-0.61	0.15	-4.04	0.01	-	-	-	-	-	-
<i>T_{min,Mar}</i>	1.27	0.24	5.30	0.003	0.86	0.45	0.47	1.84	0.07	0.86
<i>T_{max,Mar}</i>	-1.47	0.20	-7.44	0.0007	-0.93	0.47	0.49	1.92	0.05	0.86
<i>T_{min,Apr}</i>	1.03	0.25	4.14	0.009	0.04	0.15	0.16	0.27	0.78	0.11
<i>T_{max,Apr}</i>	-1.13	0.18	-6.22	0.002	-0.63	0.19	0.21	3.06	0.002	1.00
<i>P_{Oct-Apr}</i>	-0.16	0.14	-1.14	0.30	-	-	-	-	-	-
<i>Seeds_{t-1}</i>	-0.71	0.10	-7.45	0.0007	-0.85	0.15	0.17	4.93	<0.001	1.00

Table 2
AICc table comparing models for syrup production using only proportion of trees seeding in the previous year, only monthly climate variables, or seeds and climate as predictors. Values shown are for the model with the lowest AICc in each model group.

Model category	Predictors retained in final model	K	Log-likelihood	ΔAICc	ωAICc	Adj R ²
Seeds only	Seeds _{t-1}	3	-7.6	6.4	0.0393	0.43
Climate only	(none)	2	-12.6	13.4	0.0012	0.00
Seeds + Climate	Seeds _{t-1} , <i>T_{min,Mar}</i> , <i>T_{max,Mar}</i> , <i>T_{max,Apr}</i>	6	2.3	0.0	0.9596	0.79

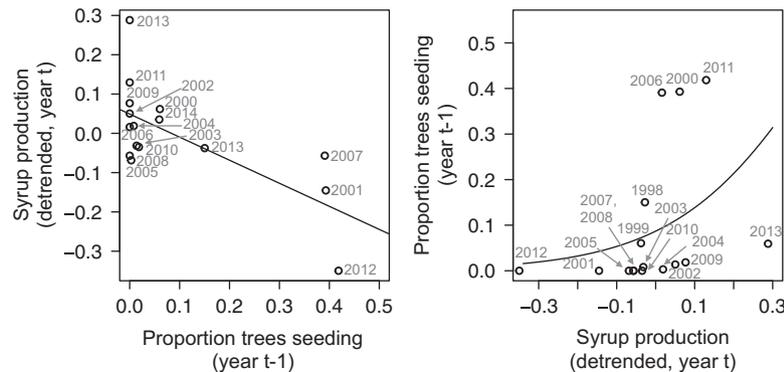


Fig. 4. The relationship between syrup production and mast seeding in Vermont. (a) Syrup production as a function of the proportion of trees producing seeds in the previous year. The line shows the linear regression fit to the data. (b) The proportion of trees seeding as a function of syrup production in the same year. The line shows the logistic regression fit to the data.

values and a large magnitude coefficients across subsets of data. Minimum and maximum March temperatures also were strong predictors with the full dataset, but were more sensitive to removing years of data, with larger jackknifed confidence intervals for coefficients and relative importance values (Fig. 5).

The relationships above are consistent with expectations from the resource budget model (Fig. 1). This model predicts that seed production reduces nonstructural carbohydrate stores and hence lowers sap sugar content and syrup production in the following year. The resource budget model also predicts a positive relationship between resources and seed production in the same year (Fig. 1). Consistent with this expectation, seed production and

syrup production in the same year were positively correlated (logistic regression: $\beta = 5.42$, $SE = 0.27$, $X^2 = 377.17$, $df = 1$, $P < 0.0001$; Fig. 4b). However, this model explained only 5% of the variance in the proportion of trees producing seeds (Efron's R-squared = 0.05; Efron 1978).

4. Discussion

Seed production was significantly and negatively correlated with syrup production in the following year. Unlike weather variables, which mainly influence syrup yield through sap flow volume (Cortes and Sinclair, 1985; Kim and Leech, 1985; Skinner et al.,

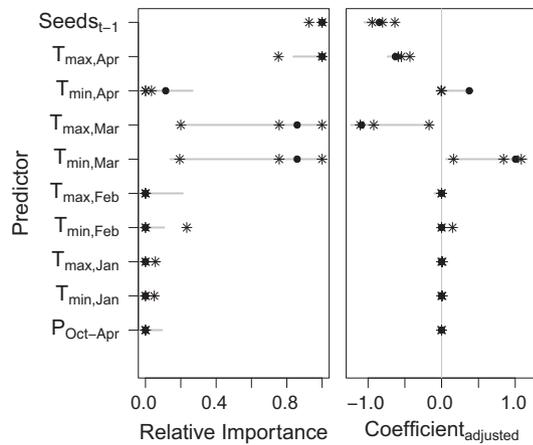


Fig. 5. Results of the model averaging analysis of the full model containing seeds and climate variables as predictors of syrup production. The left panel shows the sum of model weights for the models with a $dAICc < 4$ that contained each predictor. The right panel shows the estimated coefficients for each predictor, adjusted for shrinkage. Filled circles show the value obtained when modeling the full dataset, while grey lines (non-mast years) and asterisks (mast years) show the range of values for a jackknife analysis where each year was sequentially removed and the dataset reanalyzed.

2010), we hypothesize that seed production affects syrup yield via sap sugar content. Since both sap volume and sugar content contribute to total syrup yield, we expect both to play a role. Indeed, the combination of monthly weather variables and past seed production explained more variation in syrup production than either seeds or weather alone. What is perhaps surprising is that patterns of seed production better explained inter-annual variability in maple syrup production than did climate variables. These climate variables were found to be important predictors of sap flow and syrup yield in previous studies (Pothier, 1995; Duchesne et al., 2009). This highlights the importance of sap sugar content for syrup yield (Marvin et al., 1967; Gabriel and Seegrist, 1977).

In the past, explaining variability in sap sugar content among sites and years has met with limited success (Wilmot et al., 1995; Laroche et al., 1998). The resource budget model supplies a novel explanation for inter-annual variability in sap sugar content. Lower syrup yields observed following mast years are consistent with seed production depleting tree carbohydrate stores, and with these same stores being the source for sugar in xylem sap (Fig. 1). This cost of reproduction acts at the individual tree-level. Masting species reproduce synchronously, sometimes over areas that encompass hundreds to thousands of square kilometers (Koenig and Knops, 1998; Koenig, 1999). The resource budget model hypothesizes that this is because resource dynamics are also correlated over large areas (Satake and Iwasa, 2002). While our study is not an explicit test of this model, it supports it in the sense that synchronous reproduction (masting) is correlated with one measure of resource dynamics (syrup yield) over a similar geographic area. Reciprocal feedbacks of resources on seeds, suggested by theory, are also supported by the observation that seed production tends to be higher in years of high syrup yields (Fig. 4). Monitoring whole plant resources has proved a barrier to testing the resource budget model generally (but see Crone et al., 2009), especially in trees. These results suggest that in sugar maple whole tree resource stores can be tracked via monitoring of sap sugar. Data on seeds and sap sugar from individual trees could be a way a forward to test the model more rigorously in sugar maple.

The relationship between seeds and syrup suggests potential for forecasting syrup yields, which would be valuable for producers. Profit for syrup producers depends on total production, the value of that production, and the cost per unit of production. To produce

commercial maple syrup, sap is concentrated from 2–3% to 66% sugar by weight (Heiligmann et al., 2006). Traditionally, this was accomplished by boiling off the excess water, an energy intensive process. Therefore, the cost per unit of production was strongly linked to sap sugar content. Reverse osmosis, which removes up to 75% of the water prior to boiling (Underwood and Willits, 1969; Heiligmann et al., 2006), has lowered the cost per unit of production. The industry has therefore focused on ways to increase sap production, via increasing the number of taps and greater utilization of vacuum pumping systems that increase the yield of sap per tap (Kelley and Staats, 1989; van den Berg et al., 2012). This has led to higher syrup production (Fig. 2). However, inter-annual variation in production still occurs, which is commonly attributed to the vagaries of weather (i.e. National Agricultural Statistics Service, 2013). Our study suggests that seed production may play at least as large a role as weather in determining total yield over large geographic areas. This information could be used to predict sap sugar content and syrup production several months in advance, since seeds mature over the course of the previous summer. This would be useful for individual producers and others involved in the syrup industry.

While our analysis supports a role for masting in driving inter-annual variability in syrup production, it does not discount a role for weather. Models including past seed production and three monthly climate variables had a lower $AICc$ than the model with past seed production alone. While the monthly climate variables are correlated, and this precludes definitive identification of the most important climate variables for syrup production, the low correlation between past seed production and the climate variables tested supports partitioning variance among seed production and climate, suggesting a role for each. These relationships were derived from data aggregated at the scale of an entire state. We hope these patterns observed at broad scales will encourage studies at finer scales. For instance, past site-level studies support a role for climate variables not tested in this analysis (i.e. number of days temperature crosses freezing, Plamondon and Bernier, 1980; Pothier, 1995) for determining sap yield. It is also possible that some unmeasured weather variable is a driver of both seed and syrup production, leading to the shared correlation; because the correlation is between seed production in fall and syrup in the following spring, such a shared driver would probably need to be something that occurs before seed production, and also affects sap >6 months later. Further site-level studies are needed to understand the relative importance of mechanistic weather drivers and resource dynamics related to reproduction for syrup production, as well as the causal link between masting and syrup yield.

Maple syrup is a natural resource for which harvest depends on natural processes, as well as human activities. In forest ecology, we often think of these natural processes as being primarily environmental drivers of plant performance. The role of masting on syrup yields highlights a second kind of ecological process: resource allocation within individual plants, leading to effects of past performance on current yield. Our results show that both kinds of ecological processes are important for maple sugar yields, but the advantage of understanding the importance of plant life-history is that it provides some predictive power about yields in the near future.

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