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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.

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 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 m^2 plots are visited annually, and all trees greater than 10 cm DBH are surveyed. Among other measurements related to tree health and performance, seed

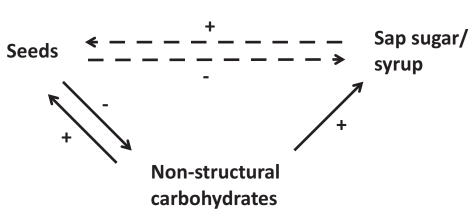

Fig. 1. Hypothesized relationships between seed production, non-structural carbohydrate stores, and sap sugar content or syrup production in sugar maple. Solid lines indicate direct effects; dashed lines indicate indirect effects. The resource budget model predicts mast years occur when resource levels 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.

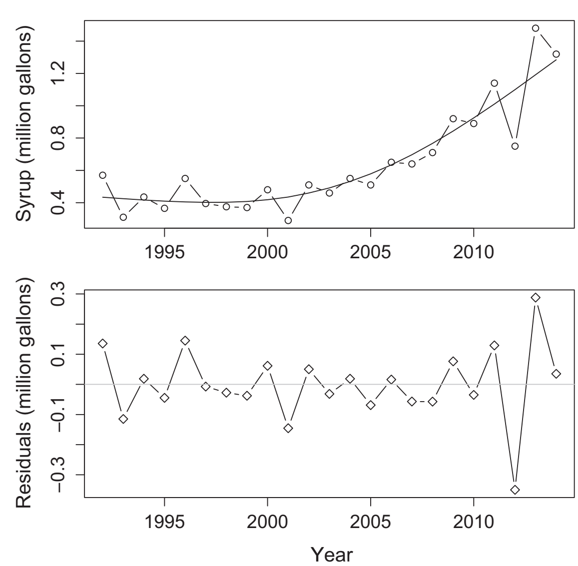

Fig. 2. Maple syrup production in Vermont from 1992 to 2014. Top panel shows the syrup production in millions of gallons as reported from annual surveys of maple syrup producers by the USDA National Agricultural Statistic Service. The trend line is a smooth spline fit to the data. The lower panel plots 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.