Examining the impact of seed production on sap sugar content

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Annual reports on the sugaring season are filled with references to the weather. Cold snaps and warm-ups alike are blamed for poor seasons, and a long season benefits from "good sugaring weather." Good weather for sap flow is well known to those who tap maple trees. Cold clear nights followed by warm sunny days cause the sap to flow, so those who tap trees are well advised to watch the weather during the tapping season. But sap flow is only part of what determines the total amount of syrup made (and how much money ends up in a syrup producer's pocket). New research suggests sugar makers may be advised to look to their trees' canopies as well as the weather forecast if they want to predict the tapping season.

Along with the volume of sap, how much sugar is in that sap is a major determining factor of how good a sugaring season is. With vacuum lines increasing sap volume and reverse osmosis machines taking out a large portion of the water with relatively low energy input, sap sugar content has received perhaps less emphasis than in the past, but it still matters. Sap with a sugar content of 3% will produce 50% more syrup than sap with 2% sugar, given an equivalent amount of sap. Sap sugar content can easily vary this much between trees, and even in the same tree in different years. Some of this variation between trees is due to genetics, and efforts to breed maples with sweeter sap have led to some success.[1,2] However, sugar maples grow slowly, and most sugarbush owners do not plant trees to tap. For the most part, you are stuck with what you have in the sugarbush already. Thinning the sugar bush to give trees more light, or fertilizing[3] may help to increase sap sugar content of individual trees, but is unlikely to influence the perhaps most enigmatic type of variation in sap sugar content: variation in the same trees from year-to-year.

In the October 2014 issue of *Maple Syrup Digest*, M. Isselhardt and colleagues described nonstructural carbohydrates (NSC), the energy stores of trees.[4] As they noted, some portion of the total NSC reserve of sugar maples makes it into a trees' sap, and can then be collected to make maple syrup. The balance in this "savings account" may vary between years and therefore account for variation in sap sugar content. But why does it vary, and why do trees have a savings account anyway? As the authors noted, trees use some of this reserve in the spring to fuel growth before leaves are on the trees, and may call upon their savings in times of need – defoliation by insects or frost, damage from wind or ice storm, or any number of other stressors. If a tree has recently been damaged, it may use this reserve to recover, and this is why many people will not tap damaged trees. Trees have another use for these NSC reserves that is often overlooked: making seeds.

Plants can put a tremendous amount of energy into reproduction. Agriculture is largely in the business of maximizing this investment – think of a champion pumpkin at the state fair. Forest trees invest less than agricultural crops and indeed most annual plants. They need to save energy for the next year and invest in woody growth. But maximizing reproduction over the lifetime of a tree, what biologists call "fitness," is a primary goal for a tree. Like all organisms, trees pass on their genes through reproduction, and the tree that makes the most seeds is most likely to pass on genes to the next generation. We can therefore expect trees to invest considerable resources in reproduction.

Sugar maples are a masting species. This means they don't produce large seed crops every year. Instead, big seed years are followed by years with little to no flowers and seeds. This in itself suggests that there is a cost to reproduction. Trees likely don't have the resources to invest in making seeds year after year without some trade-off with other plant functions, such as woody growth or defending against pests and pathogens. Theoretical ecologists have seized upon the observation that many plant species alternate high and low years of seed production to develop the resource budget model of masting.[5] The idea is that 'mast years' – big seed years – deplete stored resources (NSC), which plants then replenish during low flowering years. If this is true for sugar maples, it provides one reason why NSC, and hence the amount of sugar in sap, varies from year to year.

In addition to individual trees having a pattern of high and low seed years, groups of trees tend to all flower and produce seeds at the same time.

Sap: continued on page 17

Sap: continued from page 15

Indeed, my own observations, and data from across the northeastern U.S. and adjacent Canada[6-10] suggest a high degree of regional synchrony in seed production. Not only could masting provide an answer for variation in sap sugar for individual trees, but masting could influence syrup production regionally.

How does this ecological theory hold up in practice? In a recent study published in the peer-reviewed journal, *Forest Ecology and Management*, my co-author Elizabeth Crone of Tufts University and I analyzed data on seed and syrup production over 17 years in Vermont. The seed data were from 30 sugar maple stands throughout Vermont tracked by the Vermont Monitoring Cooperative. Every year, researchers visit each stand to measure tree growth, canopy condition, and other tree health metrics. They also observe whether or not the trees have seeds. The syrup data were from the National Agricultural Statistics Service, which sends out surveys to maple producers in the U.S. each year. While these data under-estimate syrup production since not every sugarmaker receives or returns a survey, the data do provide a good measure of the year-to-year variation in syrup production for entire states. Syrup production has increased over the past decade due to an increase in the number of taps, as well as the amount of sap collected per tap as more and more taps are put on vacuum. We wanted to remove this overall increase and only look at the year-to-year variation in syrup production. We therefore fit a trend line to the syrup production data, and then subtracted the yearly values from the overall trend. We used these values as the measure of year-to-year change in syrup production. We then compared these data to seed production in the previous year, since we expected seed production to deplete stored resources, leading to lower syrup production in the following year.

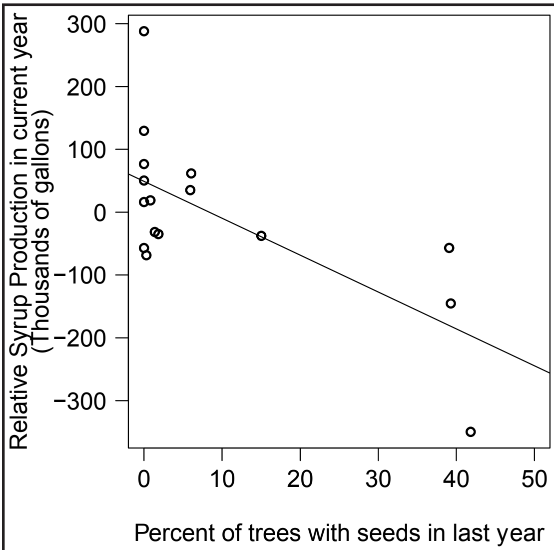

Figure 1. The relationship between maple syrup production and the percentage of trees making seeds in the previous year in Vermont. The y-axis shows the difference in annual syrup production from the overall (increasing) trend. Following mast years, when about 40% of sugar maple trees in plots monitored by the Vermont Monitoring Cooperative make seeds, syrup production is lower.

We found a surprisingly strong relationship between seed production and syrup production (Figure 1). Syrup production for Vermont was on average more than 200,000 gallons lower after a mast year that in other years, and 43% of the annual variation in syrup

Sap: continued on page 18

Sap: continued from page 17

production was explained by seed production alone.

What about the weather during the tapping season? We also tested if the monthly minimum and maximum temperatures from January through April could explain annual variation in syrup production, as had been seen in Quebec.[11] While average monthly temperatures are only coarsely related to the daily temperature fluctuations that cause sap to flow, a warm or cold season can affect the length of the season and how many days of sap flow there are, so it is not unreasonable to expect a relationship between monthly temperature and syrup production. However, in comparing different statistical models that only contained these temperature variables (but not seed production), the model that best accounted for the annual variation in syrup production was the model that didn't include any temperature variables at all. Hardly resounding support for temperature being important.

Does this mean climate is not important? No. When we included seed production along with the temperature variables in a single analysis, we found that maximum and minimum March, and maximum April temperatures helped explain variation in syrup production. Intuitively, this makes sense. March temperatures that are variable – cold nights and warm days – lead to the best sap flow, and a cold April lets the season hang on. These relationships are exactly the ones predicted by the data, but only after seed production in the previous year was accounted for. This model accounted for 79% of the annual variation in syrup production. In other words, about half the variation in syrup production was due to seeds and half to weather.

Can taking a look into the tree canopy in the fall help predict the next syrup season? This study suggests that it might be more effective than trying to predict the weather, and certainly easier.

Notes

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