

Research: Trees

Does sugar removal impact trees?**A complex question to answer.**

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When a discussion about maple sugaring turns to modern, high vacuum sap collection or climate change one question arises frequently, does tapping injure maple trees? Unfortunately, that simple question can't be answered easily. Two main issues relate to the sustainability of maple sugaring; tree wounding and sugar removal. In other words, does a tapped maple tree grow more wood than is compartmentalized (functionally "removed" by the tree's normal wound response process) each year and/or does sap collection take more sugar from the tree than can be readily replaced through photosynthesis? These two issues, although separate in some respects, are inextricably intertwined. At the University of Vermont Proctor Maple Research Center, one component of a recently initiated, comprehensive re-examination of tapping guidelines is a long-term study focusing on the growth aspect of this question (funded by the Chittenden County Maple Sugarmakers Association and the Vermont Agricultural Experiment Station). The goal of this 5-10 year study is to determine whether gravity or high-vacuum sap collection impacts stem growth compared to untapped trees. This article will therefore leave the question of tree growth and wounding for another time and focus instead on issues related to sugar removal.

Sugar maples, like all trees, convert solar energy into chemical energy (sugar) through the process of photosynthesis. Trees allocate some of that energy to nonstructural carbohydrates (NSC), essentially soluble sugars and starch. Soluble sugars, such as sucrose, are the "active" form of NSC, which are used for various physiological functions such as growth, reproduction, cold tolerance, defense, and respiration.¹ Any excess NSC is stored as starch, which is the primary reserve compound for trees.

The balance of soluble sugars and starch is dynamic throughout the year and fluctuates depending on whether the tree is actively growing, dormant, or in the transition between these two states. Allocation to storage has historically been considered a passive process; trees put more into storage when production of NSC exceeds the immediate demand.² Wood NSC concentration has largely been assumed to be an indicator of tree health (i.e. trees with higher wood NSC concentrations must be comparatively healthier than individuals with lower concentrations).³ Questions remain, however, whether or not this model is too simplistic and fails to fully capture how trees balance the current needs for NSC with potential future needs. Some evidence suggests that allocation of NSC to storage may

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even be in direct competition to allocation to growth.⁴ If this is the case, then higher NSC concentrations might actually be an indicator of tree stress. Some recent work suggests that rather than a simple, single pool of storage NSC, there may be both fast and slow cycling NSC pools (Figure 1).⁵ Fast cycling NSC pools may be used first (think of this as a checking account that is used to pay daily expenses). Under this model, reserves from slow cycling pools (more like a long-term savings account) are only used if needed, such as when photosynthesis or NSC in fast pools are insufficient to cover immediate needs.⁶

Other questions about the production and use of NSC in trees also remain unanswered. For example, it is not known how much allocation of NSC to growth comes at the expense of other critical functions such as establishment of cold hardiness and resistance to decay. Additionally, it remains unknown how much of the reserve NSC stored within the tree are truly available for use. It is possible for a tree to

die with a sizeable portion of its NSC untouched. Given these gaps in even our basic understanding of tree carbon relations, it should come as no surprise that the state of the science as it relates to how NSC removal in maples during the sugaring season impacts tree health is nearly completely lacking.

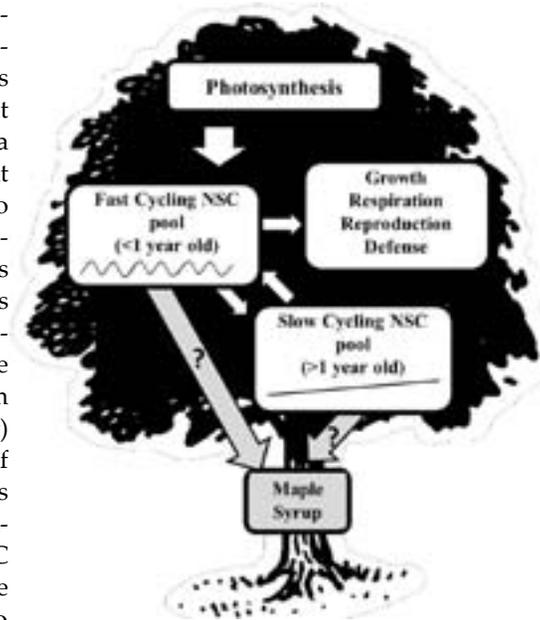


Figure 1: Movement of nonstructural carbohydrates (NSC) in sugar maples tapped for syrup production. Fast cycling NSC pool (<1 year old) experiences wide annual fluctuations related to metabolic demand for critical processes. Slow cycling NSC pool (>1 year old) represents stored NSC and accumulates proportionally with tree growth. Question marks illustrate gaps in knowledge as to which pool (or what mix of pools) contributes the NSC to maple syrup production. Adapted from Richardson et al. 2013.

It is important to understand that when NSC is removed during sugaring (in the form of sucrose-enriched xylem sap) is at the end of the dormant period. Trees have used stored NSC to maintain living tissue during the winter and need to mobilize additional NSC to fuel the growth of the stem, roots, and a new canopy of leaves. The size of the pool of stored NSC can therefore be considered a fixed quantity until after the time of bud break. After that time, even partially-expanded leaves can become net producers of NSC.⁷ That is not to say that this early period of growth is not critical, just to say that there is a finite length of time where NSC pools are

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drawn from without replenishment. It is estimated that mature trees contain enough NSC to reflush the canopy of leaves several times.⁸ This apparent abundance of NSC may in fact be part of trees long term survival strategy when faced with catastrophic but rare stresses (fire, ice storm, etc.).⁹

Equally important to understand is that as a tree grows its storage capacity also grows. This can best be illustrated in early work by University of Vermont maple researcher J. L. Hills, who estimated that sugaring (gravity sap extraction of around 2.75 lbs. syrup/tap) removed somewhere between 4-9% of a small trees total NSC.¹⁰ Hills multiplied the concentration of starch and sugars in a portion of wood by the allometric volume of a small tree (around 8" diameter) to estimate the tree's to-

tal available NSC. This percentage [of NSC removed] drops dramatically as trees get larger in size. Conversely, the percentage would be larger if modern equipment and practices are used, up to 20% of the small tree's total reserves. However, Hill's calculation assumed all NSC present throughout the entire tree was available to the sugarmaker or to the tree itself. Without knowing how much of the NSC is available to both sugarmaker and tree alike, the answer to the question of sustainability will include some uncertainty. Given the lack of clear and convincing evidence to the contrary it is reasonable to assume that even high vacuum sap extraction does not remove enough NSC to be considered an acute stress to the tree as long as tapping guidelines are adhered to and an otherwise healthy tree does not face additional stresses such including

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a fully suppressed canopy, prolonged drought or repeated defoliation. To what degree the annual removal of NSC by maple producers, perhaps in combination with other stresses (chronic or acute), could impact the overall health of trees will also remain unknown for the time being.

Notes

¹Kozlowski, T.T. 1992. Carbohydrate Sources and Sinks in Woody Plants. *The Botanical Review* 58: 109-184.

²Chapin FS, Schulze ED, Mooney HA. 1990. The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics* 21: 423-447.

³Körner, C., Asshoff, R., Bignucolo, O., Hättenschwiler, S., Keel, S., Peláez-Riedl, S., Pepin, S., Siegwolf, R. and Zotz, G. 2005 Carbon Flux and Growth in Mature Deciduous Forest Trees Exposed to Elevated CO₂. *Science* 26: 309 (5739), 1360-1362.

⁴Silpi, U., Lacoite, A., Kasempap, P., Thanysawanyangura, S., Chantuma, P., Gohet, E., Musigamart, N., Clement, A., Ameglio, T. and Thaler, P. 2007. Carbohydrate reserves as a competing sink: evidence from tapping rubber trees. *Tree Physiology* 27: 881-889.

⁵Richardson AD, Carbone MS, Keenan TF, Czimeczik CI, Hollinger DY, Murakami P, Schaberg PG, Xu XM. 2013. Seasonal dynamics and age of stemwood nonstructural carbohydrates in temperate forest trees. *New Phytologist* 197: 850-861.

⁶Carbone, Mariah S.; Czimeczik, Claudia I.; Keenan, Trevor F.; et al. 2013 Age, allocation and availability of nonstructural carbon in mature red maple trees. *New Phytologist* 200:4. Pg. 1145-1155

⁷Keel, S.G. and Schädel 2010. Expanding leaves of mature deciduous forest trees rapidly become autotrophic. *Tree Physiology* 30: 1253-1259.

⁸Hoch G, Richter A, Korner C. 2003. Non-structural carbon compounds in temperate forest trees. *Plant, Cell & Environment* 26: 1067-1081.

⁹Sala A, Woodruff DR, Meinzer FC. 2012. Carbon dynamics in trees: feast or famine? *Tree Physiology* 32: 764-775.

¹⁰Hills, J. L. 1904 Vermont Agricultural Experiment Station Bulletin 104, The Maple Sap Flow. Pg. 219 Burlington: Vermont Agricultural Experiment Station.