Drought Stress and Water Availability for Maple Sap Production: A Correction

David Moore, University of New Hampshire graduate student

I wrote an article that was published in the September 2020 issue of *Maple Syrup Digest* entitled "The Importance of Drought Stress and Water Availability for Maple Sap Production." Since I wrote that article, I have learned that the mechanism I described that causes sap flow to occur and pressure to develop in sugar maple stems during the winter dormant period is wrong. I apologize for the inaccuracies and wish to clear up my mistake by describing the mechanism correctly. I must especially apologize to Graf *et al*. for taking their explanation of this mechanism out of context (Graf *et al*., 2015). In addition that article, more information about sap flow and stem pressurization in sugar maples during winter dormancy can be found in articles written by Tyree (1995) and Cirelli *et al*. (2008). These three articles form the basis for the mechanism I describe in this follow-up article.

Sap flow and stem pressure in sugar maples during winter dormancy do indeed depend on the expansion and contraction of gas bubbles. These gas bubbles are primarily located in the libriform fibers of wood tissues, not in the xylem vessels. Though there are gas bubbles (embolisms) in the xylem vessels, these bubbles are not the dominant drivers of stem pressurization.

Four main types of xylem cells exist in sugar maple sapwood and are important in developing stem pressure (Fig. 1). Xylem vessels ('vessels') are long, relatively large-diameter, multicelled hydraulic conduits that are dead at maturity. Tracheids are shorter, single-celled hydraulic conduits that are smaller in diameter than vessels, and they are also dead at maturity. Ray parenchyma ('rays') are living cells in the sapwood that do not transport sap like vessels and tracheids do; instead, rays play a supporting role in sapwood function by being involved in plant defense, carbohydrate storage, and embolism repair. Libriform fibers ('fibers') are the thick-walled cells that provide structural support and are filled with air in sugar maples. Out of the four types of xylem cells, fibers comprise the bulk of sugar maple sapwood.

These four types of cells interact to provide sapwood with its functionality. Vessels, tracheids, and rays are all connected via pits, small openings in cell walls that allow for transport between cells. Fibers are not connected via pits to vessels, tracheids, or rays. Since cell walls are permeable to water and other small molecules (like fructose and glucose), but not to larger molecules (like sucrose), only water and small molecules can diffuse into fibers from vessels, tracheids, and rays. Sucrose and other larger molecules cannot.

When temperatures drop, the gas in fibers shrinks, and water from adjacent vessels diffuses through the cell wall to enters the space in the fibers formerly taken up by gas (Fig. 2). Since cell walls

are only permeable to small molecules, water can move into fibers from vessels, but sucrose is left behind. With a high concentration of sucrose in the vessels, water that moved into the fibers is osmotically attracted to the sweet sap in the vessels, but due to the decreased pressure in the fibers, water nonetheless moves into the fibers. Since water is being 'pulled' back into the vessels by this osmotic gradient, the water in the fibers isn't capable of dissolving the air in the fibers. When temperatures drop even more, the water in the fibers freezes and expands, compressing this gas even more. When temperatures rise again, this ice melts and is forced back into the vessels as the gas in the fibers expands (Fig. 2). As freezes and thaws occur, this process happens in many xylem cells simultaneously: during freezes, lots of water can be drawn into the tree to take up the space left by the shrinking gas bubbles, and during thaws, lots of pressure can be built up when these gas bubbles expand again. Accordingly, a freezing event is referred to as the 'uptake phase', and a thawing event is referred to as the 'exudation phase.' Tap holes in sugar maples act like localized pressure relief valves during thaws, and the weight of sap in the vessels above tap holes augments sap flow out of the tap hole generated by gas expansion.

Though there are undoubtedly air bubbles in the xylem vessels too, these bubbles do not play as prominent of a role in sap pressurization events. Air in the fibers does not dissolve in the water that enters these fibers during freezing events since this water is moving against the osmotic gradient – it is still chemically attracted to the sucrose on the other side of the cell wall, which prevents it from building up enough pressure to dissolve the air in the fibers. Air in the vessels, on the other hand, can dissolve readily in sap. The sap pressure that builds up during thaws pressurizes gas bubbles in xylem vessels and causes them to dissolve much more readily than they would in the absence of such a pressure build-up. Furthermore, gases, unlike solids, are more soluble in water at lower temperatures. When low temperatures and high pressures occur simultaneously in vessels, and when no osmotic gradient is present that would preclude water from dissolving gas, gas bubbles in vessels readily dissolve.

Correction continued on page 32

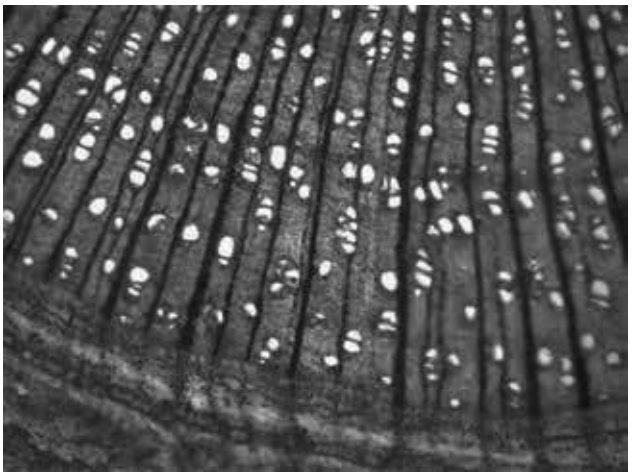

Figure 1. Sugar maple wood. The large pores are xylem vessels, which are responsible for most of the water transport in the tree. Micrograph by Mark Isselhardt, University of Vermont Extension maple specialist.

Correction: continued from page 31

Since fibers are air-filled in sugar maples during winter dormancy regardless of water availability during the previous growing season, this process is likely not driven by periods of drought during the growing season, as I suggested in my previous article. Fibers are, in other words, air-filled regardless of water availability; it is the air bubbles that form in vessels and tracheids that are brought about by periods of drought. Accordingly, sap pressurization during dormancy likely occurs similarly regardless of how droughty or wet the previous growing season was.

Again, I apologize for the inaccuracies from my article entitled "The Importance of Drought Stress and Water Availability for Maple Sap Production" in the September 2020 issue of *Maple Syrup Digest*.

Works Cited

Cirelli, D., R. Jagels, and M.T. Tyree. 2008. Toward an improved model of maple sap exudation: The location and role of osmotic barriers in sugar maple, butternut and white birch. Tree Physiol. 28:1145-1155.

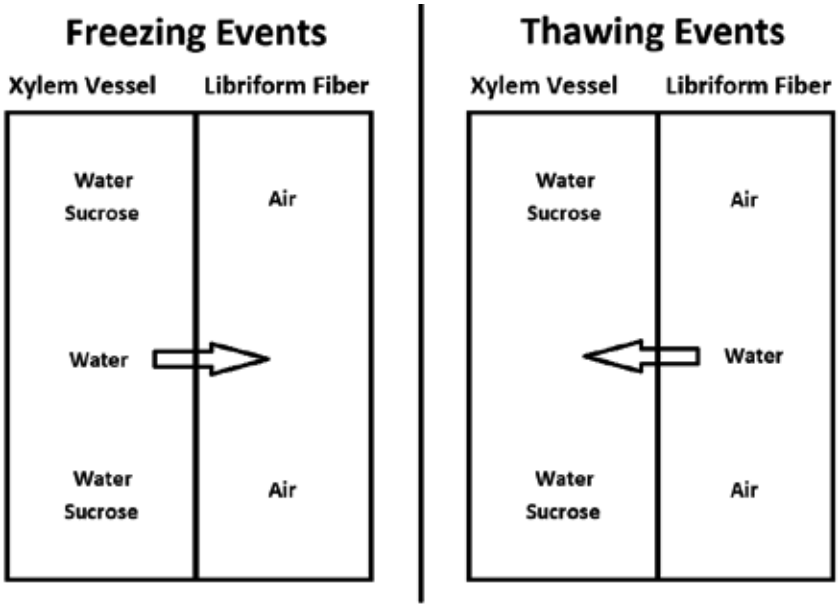

Figure 2. A diagram of water movement across xylem vessel-libriform fiber cell wall boundaries during winter dormancy. The cell wall separating vessels from fibers is permeable to water but not to sucrose. As temperature decreases and air in the fibers decreases in volume, water from vessels moves into fibers, but sucrose is left behind. During these temperature drops, water moves into fibers against the osmotic gradient. Ultimately, water freezes in fibers. As temperature increases and air in the fibers expands, water in the fibers melts and moves back into vessels. This movement follows pressure and osmotic gradients and can generate a significant amount of pressure in maple stems.

Graf, I., M. Ceseri, and J.M. Stockie. 2015. Multiscale model of a freeze-thaw process for tree sap exudation. Journal of the Royal Society Interface. 12:20150665.

Tyree, M.T. 1995. The Mechanism of Maple Sap Exudation. In: Terazawa, M., C.A. McLeod, and Y. Tamai. Proceedings of the 1st International Symposium on Sap Utilization (ISSU) in Bifuka '95, Bifuka, Hokkaido, Japan, April 10-12, 1995. Hokkaido University Press. Sapporo, Japan.

FDA Extends Labeling Compliance Deadlines for Small Producers

The U.S. Food and Drug Administration is announcing additional flexibility for manufacturers who need to comply with updated Nutrition and Supplement Facts label requirements by January 1, 2021. This upcoming compliance date applies to manufacturers with less than $10 million in annual food sales. Although the compliance date will remain in place, the FDA will not focus on enforcement actions during 2021 for these smaller food manufacturers. This additional flexibility includes manufacturers of packages and containers of single-ingredient sugars, regardless of the size of the manufacturer.

The FDA has heard from some manufacturers that more time may be needed to meet all of the requirements, especially during the COVID-19 pandemic.

The FDA provided the same flexibility for manufacturers with $10 million or more in annual sales, who were required to comply with the Nutrition and Supplement Facts label requirements by January 1, 2020, by indicating it would not focus on enforcement actions during 2020.

Mid-Winter Maple Classic 2021 Cancelled

After 25 years of in-person maple workshops and a trade show, the 2021 New York Winter Maple Conference has become the latest event to succumb to the COVID -19 virus. Also known as the Mid-Winter Maple Classic, the annual conference was scheduled to take place January 8 and 9, 2021 at the NYS Fairgrounds in Syracuse. It has now been officially cancelled.

While plans were underway, the host venue became unavailable. The NY State Fairgrounds have been closed to all indoor events since the start of the pandemic. Early in October, state fair management advised state maple association officers that they expect the building closure to continue into 2021 and therefore the state fairgrounds could not be planned for as the location for the Winter Classic.

NYSMPA explored other options, including a virtual conference, but the NYSMPA executive committee has concluded that there is no satisfactory substitute for the live event. NYSMPA President Tony VanGlad said: "The NYSMPA board decided not to have the Maple Classic this year, to ensure safety for the country's maple community. Stay healthy and here's hoping for a great maple crop this season!."