Exudation Pressure in Maple Trees: Comparing Simulations with Experiments

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Exudation is the process whereby certain trees such as maple, birch and walnut can generate a large positive pressure in stems or roots during months when the tree is leafless and mostly dormant and temperatures fluctuate above and below freezing. This exudation pressure is especially pronounced in sugar maple (Acer saccharum) and is what causes sap to flow from a tap hole so steadily and in such large quantities during the sap harvest season. For more than a century, numerous studies have attempted to explain the essential biophysical processes underlying sap exudation, but it was only in the series of papers [2,3,6,7,11] that the first complete mathematical model was developed. Apart from the mathematical results in these papers, this modelling work has also provided new insights into the detailed mechanisms that cause sugar maples to exude so profusely. A concise (math-light) overview of an earlier version of the model has already appeared in the Digest [5]. This article aims to provide an update on more recent modelling efforts in combination with experimental measurements from red/sugar maple trees at the University of Vermont Proctor Maple Research Center that validate the model results.

Background on Exudation

Past observations of sugar maple trees clearly demonstrate that stem pressure builds up during the sap harvest season over periods when temperatures oscillate above and below the freezing point, and specifically after freeze and thaw events. Tree physiologists proposed three mechanisms that could account for the build-up in pressure observed in maples [4,8]:

I. A purely physical freeze-thaw mechanism, in which gas trapped within certain sapwood cells is compressed as the sap freezes, while a subsequent thawing cycle releases the trapped gas to expand and repressurize the sap.

II. An osmotic process, in which semi-permeable cell membranes give rise to a sugar concentration difference that in turn induces an osmotic pressure.

III. A biological process, in which some temperature-induced response from living cells triggers a build-up in sap pressure.

Based on an extensive review of the literature, Améglio and co-authors concluded that “no existing single model explains all of the winter xylem pressure data” [1]. This

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suggested that either some combination of sap exudation mechanisms was required, or else some new explanation remained to be identified.

Milburn and O'Malley [8] were the first to propose a physical mechanism (based on i) which is closely tied to the special anatomical properties of maple sapwood. They were inspired by the observation that sapwood in deciduous trees like maple can be separated into two main cell types: vessels that are filled with sap; and (libriform) fibers that are filled with gas (see Figure 1a). During a freezing event, they hypothesized that liquid is drawn via a process called cryostatic suction from vessels into gas-filled fibers where it freezes, causing an ice layer to form on fiber walls that in turn compresses the gas trapped inside. When temperatures subsequently rise above freezing, this process reverses, releasing the trapped gas to re-pressurize the vessel sap.

A decade later, Tyree [9] argued that it is also essential to account for the selective permeability of the fiber/vessel wall, which contains pores so tiny that they permit water to pass through but prevent passage of sugar molecules. As a result, the liquid taken up by the fibers consists of pure water

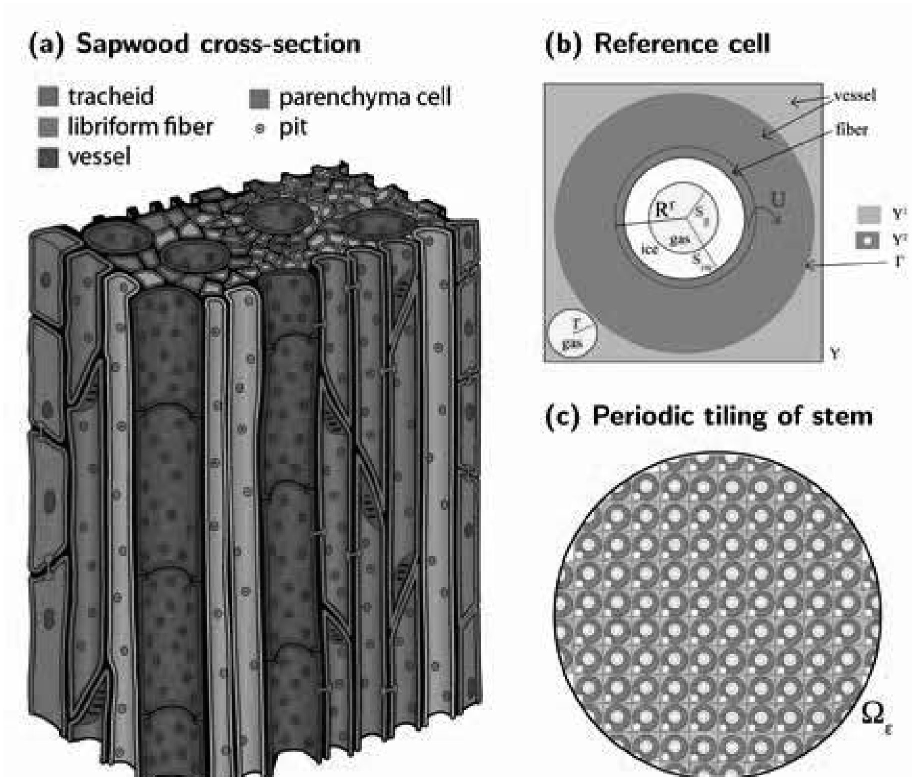

Figure 1. (a) Cut-away view of maple sapwood, showing vessels, surrounded by fibers. (b) Reference cell, showing a single vessel (with gas and liquid sap) and fiber (with ice layer enclosing trapped gas). (c) Stem cross-section tiled by copies of reference cell.

rather than sugary sap, which means that an osmotic pressure difference can be sustained between fiber and vessel (mechanism ii). Moreover, Tyree argued that the pressure in fibers/vessels can be high enough that dissolution of gas bubbles suspended in the sap must also be included (for a readable explanation of this process, refer to the short article by Tyree [10]). Despite these steps toward developing a working hypothesis for sap exudation, there has been no attempt until recently to formulate a set of mathematical equations that captures the physical processes behind this expanded Milburn-O'Malley mechanism.

Summary of the Mathematical Model

Sap exudation is a prototypical example of a multiscale problem, in the sense that different processes occur on widely differing spatial scales. All processes related to phase change and liquid/gas transport occur on the scale of microns and are largely determined by the cellular microstructure. Also, temperature differences on this microscopic scale are small enough that they can be approximated with a simple linear spatial dependence. In contrast, temperature variations on the macroscopic (or stem) scale are more complex, so that the full conservation equation for heat energy must be applied to properly capture release of latent heat during freeze/thaw cycles. Because of this separation in spatial scales, exudation is said to have an inherently "two-scale" nature, and the governing equations for processes on the micro- and macroscopic scales must be formulated separately.

Our mathematical model is therefore constructed in terms of three components:

1. *A microscale model for cellular processes*: which captures the Milburn-O'Malley freeze/thaw mechanism. This assumes a simplified "reference cell" in which a cylindrical fiber (with circular cross-section shown in Figure 1b) is surrounded by a reservoir of sap corresponding to the vessel. Gas is incorporated into both fiber and vessel as a circular bubble. Ice formation always begins in fibers because the freezing point of the pure water in the fibers is roughly 0.29°F (0.16oC) higher than that of the vessels (owing to sugar dissolved in the vessel sap).

2. *A macroscale model for stem temperature*: wherein transport of heat throughout the tree stem is driven by external variations in the ambient (air) temperature.

3. *Coupling between the micro- and macroscale models:* By tiling the stem with a periodic array of copies of the reference cell (see Figure 1c), the solution to the microscale problem can be averaged in a mathematically rigorous way to properly capture the contribution from latent heat of phase change to the stem temperature. This "careful averaging" procedure that couples the two scales comes is a practical application of results from homogenization theory [6,7].

The resulting mathematical problem consists of a nonlinear system of differential-algebraic equations, which have a "nice" structure that allows them to be implemented using standard solvers available in the Matlab® software package.

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Comparing maple experiments with numerical simulations

We now present a sample comparison between experimentally measured pressure and temperature data and corresponding numerical simulations of the sap exudation model. The experimental tree was a 14 inches (36 cm) DBH red maple [TP1] located in the sugarbush at the University of Vermont Proctor Maple Research Center in Underhill, Vermont. Air temperatures were measured using a type-T thermocouple located on the stem at a height of 4 feet (1.2 m). Pressure measurements were taken with an Omega PX-26-030GV pressure sensor connected to a standard nylon spout inserted into a tap hole with diameter 7/16 inch (1.1 cm) to a depth of 2 inches (5 cm). Both temperature and pressure sensors were measured with a Campbell Scientific 23X datalogger and data were recorded at 15 minute intervals.

Simulations are displayed along with measured data in Figure 2 as plots of temperature and measured/computed stem pressure versus time. The first thing to note is that most thawing events (at times when temperature rises above the melting point, T = 0°C) correspond to a spike or rapid increase in stem pressure for both simulations and experiments. Similarly, freezing events (when T falls below 0) are followed shortly after by a steep drop in pressure. The peak value of the pressure spikes is captured closely by the model, as is the gradual rate of decrease in pressure that follows each spike. There are a few exceptions such as the "weak" freeze/thaw events over the first seven days, but otherwise the correspondence is remarkably close. Similar results for other red and sugar maple trees are reported in the paper [11]. These results suggest that the model is capable of capturing the essential physical processes that underlie the build-up of exudation pressure in maple trees.

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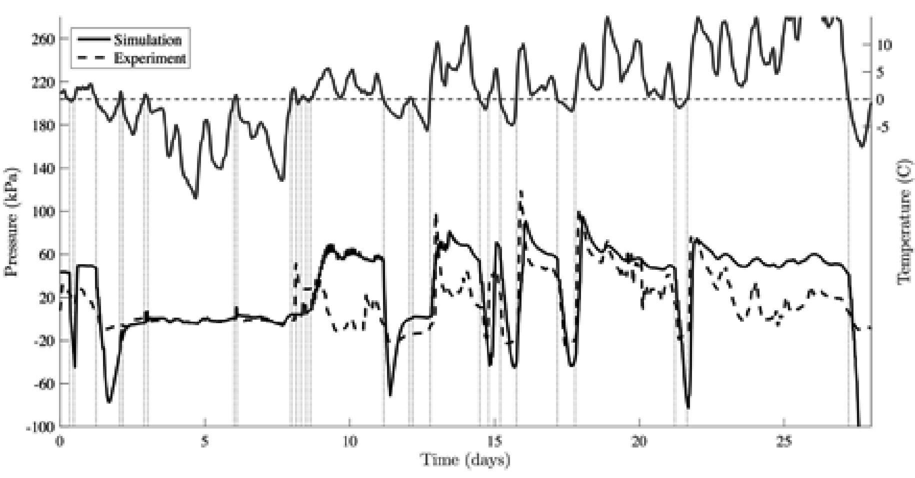

Figure 2. Comparison of experimental measurements and numerical simulations for a red maple tree, showing stem temperature (top) and pressure (bottom). Freeze and thaw events correspond to zero-crossings of the temperature and are highlighted with dotted vertical lines.

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Maple Trees Really Are Unique!

Besides our success in reproducing experimentally measured stem pressures, an important conclusion of this modelling study is pinpointing what precisely makes maples so unique among other tree species. In particular, the amazing ability of trees like red and sugar maple to exude sap derives from a unique combination of characteristics:

- High sap sugar content, which induces a freezing point depression of roughly 0.16°C within the sap that drives the entire pressure generation process.

- A wood cell anatomy with the special characteristic that libriform fibers are gas-filled and thus serve as a pressure storage reservoir.

- Selective permeability of the cell walls that separate fibers from vessels, which generates the osmotic pressure difference that in turn prevents gas bubbles suspended in the sap from completely dissolving.

Another insight relating specifically to the first point is that the phase change process driving sap exudation is restricted to a narrow thawing (or freezing) front that propagates into the stem on heating (or cooling), as pictured in Figure 3. This front consists of a very thin layer of sapwood cells at most 0.5 mm thick that is delineated by temperatures lying between -0.16°C and 0°C. The remainder of the stem is either in a fully thawed or fully frozen state, so that at any instant in time all of the real action behind sap exudation is taking place within this narrow circular band making up the freeze/thaw front region.

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Current and Future Work

Efforts to validate the model with additional field measurements are underway as part of an effort to better calibrate model parameters. This includes comparisons with experimental data from other tree species such as birch and walnut that are also known to generate positive stem pressures. We are also investigating how to incorporate the starch-sugar conversion process (known as hydrolysis) within our pressure generation model, which will capture seasonal variations in sugar content. In the long term, our hope is that these model improvements will help us to better answer practical questions of interest to the maple syrup industry such as: What is an optimal number and location of tap holes for a given tree? How does vacuum pressure affect sap content within the stem? Or what might be the effect on sap yield of shifts in seasonal temperatures from climate change?

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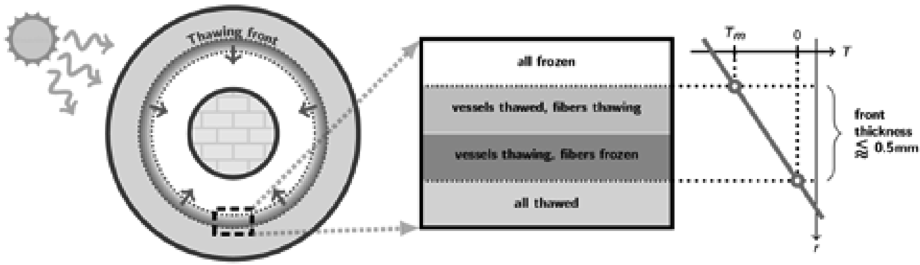

Figure 3. A thawing front driven by solar heating advances into the tree stem. The zoomed box depicts the transition from the inner region of sapwood in a completely frozen state to the outer thawed layer. This transition occurs over a thin annular ring that is determined by cells that have temperatures lying between the melting point of sap (Tm ≈ -0.16°C) and that for pure water (Tm = 0°C).

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