A Mathematical Model for Maple Sap Exudation

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Physical Background.
Sap exudation refers to the process whereby sugar maple trees (*Acer saccharum*) are capable of generating significant stem pressure in a leafless state, something that occurs to a lesser extent in only a few other related species such as birch and walnut. This exudation pressure is what causes maple sap to flow from a taphole in sufficient quantities to be harvested and processed into syrup. Exudation has been studied for well over 100 years and has been the subject of many scientific studies, but there is as yet no definitive explanation for how such large pressures can be generated in the absence of transpiration (i.e., when no photosynthesis occurs to drive the flow of sap).

Observations clearly show that pressure rises during periods when temperatures oscillate about the freezing point and that significant pressure build-up happens only after several freeze-thaw cycles. Tree physiologists have proposed three mechanisms that could account for the elevated pressure observed in maple trees:

i. A purely physical freeze-thaw mechanism [8], in which gas is compressed in the sapwood cells as sap freezes, whereas thawing releases the trapped gas to expand and pressurize the sap.
ii. An osmotic process [5], in which semi-permeable membranes that separate cells in the sapwood restrict the transport of sugars, hence generating an osmotic pressure difference.
iii. A vitalistic process [7], in which some action of living cells initiates sap flow.

It has been demonstrated that none of these processes by itself is capable of generating the pressure levels observed in maple [1,9] and so some combination of the three effects must be responsible.

In 1984, Milburn and O'Malley [8] were the first to propose a plausible explanation (based on mechanism i only) that is clearly tied to observed microstructural properties of maple wood. They made use of the fact that the sapwood of deciduous trees like maple is separated into two primary cell types: *vessels* that are filled with sap; and *(libriform) fibers* that are filled with gas. During the freezing process, sap is drawn from the vessels into the fibers where it freezes on the inner surface of the fiber walls and thereby compresses the gas contained inside. When temperatures rise above freezing the process reverses, releasing the trapped gas that can then pressurize the vessel sap. Tyree [9] then recognized that it is essential to include mechanism ii in the form of a selectively permeable cell wall that separates vessels from fibers – this wall has pores small enough that it permits water to pass through but not sugar molecules, so that the frozen liquid in the fibers in fact consists of pure water. As a result, an additional osmotic pressure difference exists between the fiber and vessel, which is essential for boosting and maintaining the gas pressure at observed levels. They also noted the fact that at such high pressures, a portion of the gas will actually dissolve in the sap. A beautiful explanation for this process that also provides more details can be found in a short article by Tyree [10]. Although this freeze-thaw hypothesis has been well-accepted for the past 30 years, it is complicated enough that there has as yet been no attempt to develop a set of equations that governs the Milburn-O'Malley process. This is where the mathematics comes in.

Overview of the Mathematical Model.

Our initial aim was to develop a set of mathematical equations that capture the Milburn-O'Malley process at the cellular level. To this end, we focus on a single fiber and vessel as pictured in Figure 1, where we assume the cells both have the shape of circular cylinders. Gas is present in the form of a single bubble centered within each cell, while only the fiber contains ice owing to the fact that the freezing point in the vessel is lowered by the presence of sugar in the vessel sap. Because water is an incompressible fluid, gas is required in both fiber and vessel in order to permit exchange of pressure between them. We emphasize here that Milburn and O'Malley made no mention of gas in the vessel, and it was only during the development of our mathematical model that we were able to recognize the importance of including it.

We then proceeded to develop a consistent set of governing equations for the water, ice and gas phases in each cell based on the physical processes described in the previous section. Rather than repeating the equations here, we only summarize a few important features of the model and encourage the interested reader to consult the complete derivation in [3]:

- The key quantities in this model are the sizes of the gas, ice and water layers in the fiber and vessel (labeled s_{gi}, s_{iw} and r in Figure 1) as well as the corresponding phase temperatures. These quantities vary in space and time and their dynamics are described by a system of 7 nonlinear differential equations.
- Applying various other physical constraints related to volume conservation, osmotic pressure, capillary pressure and dissolved gases leads to a further 5 algebraic equations.

One other aspect missing from the Milburn-O'Malley process, which is necessary to generate a pressure build-up over multiple freeze-thaw cycles, is root pressure in the form of a root-water reservoir. This feature is consistent with recent experiments by

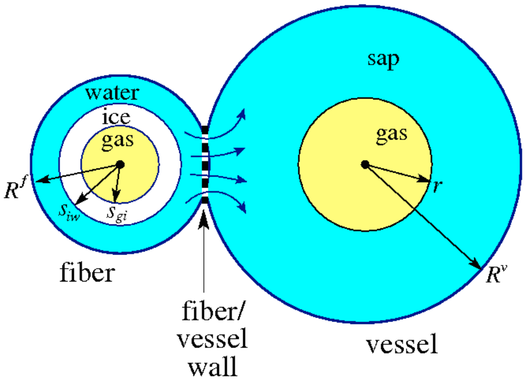

Figure 1: Layout of vessel and fiber cells in our mathematical model.

Perkins and van den Berg [2] on plantation-style stands of maple saplings.

Although there are a large number of physical parameters and unknowns, the equations have a “nice” mathematical structure that permits them to be solved using commonly-available numerical algorithms. In particular, we developed a software implementation that makes use of the solvers available in Matlab®.

Application to Maple Sap Exudation.

We provide here just a few examples of the typical numerical simulations that are possible using our cell-level model [3,4,6]. We start by taking an initially frozen state, corresponding to a typical morning during harvest season, and consider the thawing half of the freeze-thaw cycle by imposing a constant ambient temperature lying just above the melting point. The resulting dynamics of the pressure transfer from fiber to vessel is pictured in Figure 2(left). We observe that there is a rapid flow of melt-water (lasting roughly 1 minute) from fiber to vessel that drives a corresponding rise in the vessel pressure of approximately 130 kPa. The ice layer in the fiber melts over a longer time scale (10-15 minutes) after which only a slight re-adjustment in the pressure occurs.

Consider next a 3-day cycle of freezing and thawing, for which the numerical results are pictured in Figure 2(right). There is clearly a gradual build-up of pressure over the three days and we remark that this is only possible due to the uptake of root water during the freezing portion of the cycle. Furthermore, the magnitude of the pressure difference (100 kPa) is similar in size to what is observed in actual maple trees!

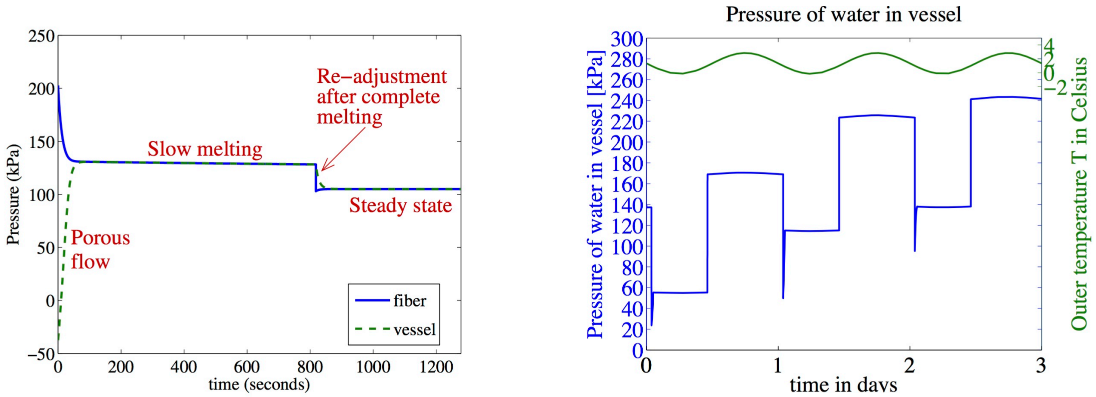

Figure 2. (Left) Vessel/fiber pressure over a single thaw cycle. (Right) Vessel pressure over multiple daily freeze/thaw cycles.

Future and On-going Work.

We plan to extend our sap exudation model in several ways. First and foremost, we need to “scale up” our equations from the cell level (or micro-scale) to a corresponding set of equations at the whole-tree level that is capable of capturing exudation on the macro-scale. For this purpose, we employ the mathematical technique of *periodic homogenization* for which we have already obtained partial results [6]. Our current efforts focus on validating our results through a careful comparison between numerical simulations of the homogenized model and experimental results from the literature.

Over the next several years, we plan to apply this model to investigate problems of more practical interest to the maple syrup industry as part of a NAMSC-funded project (2015-

2016). This includes answering such questions as: What is an optimal number and location of tap-holes for a given tree? What effect do environmental factors such as wind or snowcover have on sap exudation rate? How might changes in climate (e.g., temperature and snowfall patterns) affect sap yield? Answers to these and other questions are finally attainable now that we have a mathematical model in hand that captures the essential bio-physical processes going on in a maple tree.

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