

Experimental and computational comparison of freeze–thaw-induced pressure generation in red and sugar maple

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Sap exudation is the process whereby trees such as sugar (*Acer saccharum* Marsh.) and red maple (*Acer rubrum* L.) generate unusually high positive stem pressure in response to repeated cycles of freeze and thaw. This elevated xylem pressure permits the sap to be harvested over a period of several weeks and hence is a major factor in the viability of the maple syrup industry. The extensive literature on sap exudation documents competing hypotheses regarding the physical and biological mechanisms that drive positive pressure generation in maple, but to date, relatively little effort has been expended on devising mathematical models for the exudation process. In this paper, we utilize an existing model of Graf et al. (J Roy Soc Interface 12:20150665, 2015) that describes heat and mass transport within the multiphase gas–liquid–ice mixture in the porous xylem tissue. The model captures the inherent multiscale nature of xylem transport by including phase change and osmotic transport in wood cells on the microscale, which is coupled to heat transport through the tree stem on the macroscale. A parametric study based on simulations with synthetic temperature data identifies the model parameters that have greatest impact on stem pressure build-up. Measured daily temperature fluctuations are then used as model inputs and the resulting simulated pressures are compared directly with experimental measurements taken from mature red and sugar maple stems during the sap harvest season. The results demonstrate that our multiscale freeze–thaw model reproduces realistic exudation behavior, thereby providing novel insights into the specific physical mechanisms that dominate positive pressure generation in maple trees.

Keywords: exudation, freeze–thaw mechanism, periodic homogenization, positive pressure, red and sugar maple, xylem transport.

Introduction

Sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.) and several other *Acer* species have a remarkable ability to generate positive xylem (or sapwood) pressure in response to freeze–thaw cycles, during a season when the tree is leafless and mostly dormant. The resulting exudation pressure can persist on and off for weeks or even months, which allows maple sap to be harvested in sufficient quantities that it is an economically viable agricultural product in northeastern North America. A few other tree species such as black walnut (*Juglans nigra*), butternut (*Juglans cinerea*) and white birch (*Betula papyrifera*) are likewise capable of generating elevated positive stem pressures, but none to such a high degree as maple. It is well known that the presence of dissolved sugar (2% or more by mass) in the sap of these species plays an important role in the accumulation of stem pressure during the freeze–thaw process (Marvin 1968), but the precise causes of sap exudation have proven difficult to pinpoint. Indeed, exudation has been studied extensively for over 150 years, during which time researchers have attributed it to a wide variety of physical and biological mechanisms, including osmosis (Wiegand 1906); thermal expansion of gas, water and wood (Sachs 1860, Merwin and Lyon 1909, Marvin 1949); active processes in living cells (Johnson 1945,

Marvin 1958); and enhanced sap uptake due to ice crystal formation (Stevens and Eggert 1945).

A major advance in the understanding of exudation was achieved by Milburn and O'Malley (1984), whose experimental observations inspired them to propose a purely physical hypothesis for maple sap exudation based on a freeze–thaw mechanism that incorporates distinctive features of the cellular structure of maple wood. More specifically, their model focused on two classes of cells in the maple xylem: libriform fibers that are filled with gas and are considered to play mainly a structural role; and vessels and tracheids that are mostly liquid-filled and constitute the primary pathways for sap transport. Milburn and O'Malley's breakthrough came from recognizing that during a freezing cycle, sap is drawn into the normally gas-filled fibers in the form of ice crystals that freeze on the interior surface of fiber walls thereby compressing the gas trapped within. This freeze-induced sap uptake is driven by an ice–water surface tension, which was already suggested by Stevens and Eggert (1945) to operate in sugar maple trees and is analogous to the phenomenon of 'cryostatic suction' that has been used to explain frost heave and ice lens formation in soils (Fowler and Krantz 1994). During a subsequent thaw, the stored pressure is then released into the vessel sap. This model explains the variations in xylem

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pressure due to transfer of liquid during a sequence of freeze–thaw events; however, it remains incomplete because it fails to explain the essential role of dissolved sugars which are known to play a major role in exudation.

This gap in understanding was addressed by several authors (Tyree 1983, Johnson et al. 1987, Johnson and Tyree 1992) who recognized that one consequence of the sugar content in sap is to suppress the natural tendency in gas–liquid suspensions for gas bubbles to dissolve at high pressure. Tyree (1995) then proposed a modification of the Milburn–O'Malley model that incorporates two additional physical effects: expansion, contraction and dissolution of gas bubbles in response to pressure variations in the suspending fluid; and existence of an osmotic potential due to differences in solute concentration engendered by the selectively permeable nature of certain cell walls in maple xylem. In particular, Tyree argued that the lignified cell wall separating the fiber and vessel permits water and small solutes to pass but impedes larger molecules such as sucrose that make up the bulk of solutes in maple sap. This gives rise to a significant osmotic potential between vessels (containing high-sucrose sap) and surrounding fibers (containing pure water). Tyree then demonstrated that this osmotic potential is sufficient to stabilize gas bubbles over long enough time periods to sustain a realistic exudation pressure, and the role of the selectively permeable fiber/vessel walls in osmosis was later confirmed experimentally by Cirelli et al. (2008). An extensive review of the current literature on positive stem pressure and its causes can be found in the paper by Schenk et al. (2021).

Despite these advances in understanding of physical mechanisms behind pressure generation in sugar maple and related species, significant controversy remains in the literature over the causes of exudation. For example, Améglio et al. (2001) argued that ‘no existing single model explains all of the winter xylem pressure data’, supported by experiments suggesting that biological processes in living wood cells are necessary for exudation. These differences in opinion have been exacerbated by the lack of a mathematical description for the exudation process. Indeed, around the time that Milburn and O'Malley developed their model, Tyree (1983) commented that ‘there is insufficient quantitative information to set up a system of physical equations to describe the model’. Some efforts have since been made to formulate equations governing certain aspects of the relevant physics, such as the diffusion model for embolism recovery developed by Yang and Tyree (1992) that captures the gas transport and dissolution processes similar to that which occurs in exudation.

However, it was only in a series of papers (Ceseri and Stockie 2013, 2014, Graf and Stockie 2014, Graf et al. 2015) that a concerted attempt was made to devise a complete mathematical model of the essential physical mechanism behind the freeze–thaw process of Milburn and O'Malley (1984), modified to include the influence of gas bubbles and osmotic pressure (Tyree 1995, Cirelli et al. 2008). The model is based on a system of nonlinear diffusion equations for the cellular scale freeze–thaw process that incorporate sap phase change, compression and dissolution of gas bubbles, and osmosis (Ceseri and Stockie 2013, 2014), and captures the pressure exchange between fibers and vessels during a single freeze–thaw cycle. This cellular-level model was then coupled with a macroscale heat transport equation obtained by a multi-scale averaging process known as periodic homogenization

(Graf et al. 2015). Numerical simulations yielded realistic pressure oscillations as well as a build-up in exudation pressure over multiple freeze–thaw cycles. These homogenized model simulations were then compared with laboratory experiments on black walnut trees subjected to an imposed periodic variation in temperature (Améglio et al. 2001) and exhibited excellent qualitative agreement. A recent paper by Reid et al. (2020) compared experimental measurements of maple stem temperatures with solutions to a simpler but closely related model of heat transfer only, further demonstrating the effectiveness of this class of models in predicting realistic stem temperatures.

Our main aim in this paper is to further validate the model of Graf et al. (2015) using experimental measurements consisting of temperature and pressure time-series sampled over a period of roughly 40 days from red and sugar maple trees located at the University of Vermont Proctor Maple Research Center in Underhill, VT, USA. Having such a highly resolved dataset provides an ideal opportunity to validate the time-dependent model for maple sap exudation under actual field conditions.

After describing the experimental procedures used to collect field measurements on maple trees in Materials and methods, we present the multiscale sap exudation model including the primary simplifying assumptions and supplying sufficient details to elucidate the essential physical processes underlying the model. The comparison of experimental and numerical results in Results and Discussion begins with a parameter sensitivity analysis for a model tree subjected to a synthetic (smoothly varying) ambient temperature, which aims to determine best estimates for parameters used in our simulations of real maple trees. We then perform a sequence of simulations using actual data that feature rapid variations in temperature and pressure, and significant levels of measurement noise. A detailed comparison is then drawn between stem pressures from simulations and experiments in order to validate our hypothesis that a multiscale model based solely on physical transport processes is capable of reproducing realistic exudation pressures in maple trees subjected to repeated cycles of freeze and thaw.

Materials and methods

Field experiments

Measurements were taken during the spring sap flow season over the years 2005–10 in several mature sugar maple and red maple trees ranging in size from 14 to 61 cm DBH (diameter at breast height). The trees were located 180 m within the experimental sugarbush to the southeast of the laboratory of the University of Vermont Proctor Maple Research Center in Underhill, VT, at ~425-m elevation, latitude 44.5254, longitude -72.8660. Type-T (24-gauge) thermocouples were used to measure the following: air temperature at heights of 1.2 and 16.5 m; branch temperature measured in the center of a hole drilled in a canopy branch at 16.5-m height, and within the tapping zone at 1.2-m height and 5-cm depth; and soil temperature at depths of 0 cm (surface) and 30 cm. Pressure measurements were made by drilling a standard 1.1-cm diameter, 5-cm deep taphole and inserting a black nylon maple spout in an inverted position. A tube leading from the spout was filled with water and connected to an Omega PX-26-030GV pressure sensor (with $\pm 1\%$ accuracy).



Figure 1. Photograph of a taphole containing a black nylon spout that is connected by plastic tubing to an Omega PX-26-030GV pressure sensor. Additional wires leading to thermocouples are also shown.

Both thermocouples and pressure sensors were wired to a Campbell Scientific 21X datalogger and measurements were stored at 15-min intervals. A photograph showing the taphole and wired connections is given in [Figure 1](#). Stem temperature and pressure were measured on both north and south sides of the tree and were often very divergent. Sap flow was measured from a taphole in a nearby tree of similar size using a standard maple spout connected via tubing to a collection chamber. Data were downloaded from the datalogger as comma-separated values and stored in Excel files for analysis.

Mathematical model

Background on xylem structure in maple

Before presenting the mathematical model for the freeze-thaw process governing sap exudation, we begin by briefly summarizing the physical and structural characteristics of maple xylem that play an essential role in sap transport and exudation (more detail is provided in [Tyree and Zimmermann \(2002\)](#)). The xylem in hardwood trees such as maple is built primarily of rigid and nearly cylindrical structures that consist of the hollowed-out walls of dead wood cells. Sapwood has a regular and quasi-periodic microstructure shown in [Figure 2a](#) that consists of regularly spaced vessels interspersed with much more abundant tracheids and (libriform) fibers having a smaller diameter. Vessels are the primary water-conducting conduits in sapwood, and each is divided lengthwise into vessel elements that are connected end-to-end via perforation plates, thereby forming long capillary tubes. Vessel walls are interspersed with cavities called pits that connect cells hydraulically through pit membranes as long as the pits in adjacent cells align or ‘pair up’. Tracheids are intermediate in size between vessels and fibers and are also connected through paired pits with neighboring vessels and other tracheids. Since both vessels and tracheids are mostly sap-filled, they serve as the primary conduits for xylem sap transport. Fibers on the other hand are known to contain mostly gas ([Milburn and O’Malley 1984](#)) and their walls demonstrate a relative lack of pitting. As a result, they are usually regarded to have negligible impact on sap transport and instead serve a structural function. The lignified fiber walls have nonetheless been found to contain micropores (much smaller than those in pit membranes) which are selectively permeable, in the sense that they allow water and small solutes to pass but inhibit the passage of larger molecules such as sucrose ([Cirelli et al. 2008](#)).

Microscale model for the thawing process

We next describe our model for the essential processes governing sap exudation on the microscopic (cellular) scale which include: heat transport; phase change due to freezing and thawing; expansion, contraction and dissolution of gas; and porous flow through paired pit membranes and selectively permeable micropores in the fiber–vessel wall. Our ultimate goal is to model repeated freeze–thaw cycles in response to ambient temperature variations as depicted in [Figure 3](#), where a thawing (or freezing) front propagates into the tree stem and separates regions of the sapwood that are frozen from those that are thawed. The front actually comprises a thin annular section of sapwood that exists in a mixed state containing water/sap in both liquid and ice phases. We focus our attention on equations for the thawing process only and refer the interested reader to [Graf et al. \(2015\)](#) for the modifications required to capture all other possible freeze–thaw stages.

In order that our model remains tractable, we make a number of simplifying assumptions.

- (i) Vertical variations due to gravity and height-dependence are neglected, so that we can focus on a 2D horizontal cross-section through a circular tree stem. We also assume a constant stem diameter because there was no noticeable change in the stem cross-section during the period that measurements were taken.
- (ii) At the cellular level, we consider only the contribution of vessels and fibers to exudation. Tracheids are not treated separately but rather lumped together with vessels. Other sapwood components (such as ray cells) are ignored but are acknowledged as the source of sucrose in the vessel lumens.
- (iii) Sapwood has a uniform, periodic microstructure consisting of cylindrical vessels and fibers, both having constant lengths (L^v , L^f) and radii (R^v , R^f). Then, we can reasonably restrict our attention to a horizontal slice through a single vessel element and adjacent fiber as pictured in [Figure 2b](#).
- (iv) Each vessel is in contact with N fibers on average (see [Figure 2b](#)) so that the influence of multiple fibers can be incorporated by simply multiplying by a factor of N the contribution from the single fiber being modeled.
- (v) Because the fiber and vessel cross-sections are circular (from assumption 3.2), we assume radial symmetry and take all microscopic variables to depend on a radial coordinate y that passes through the line joining the centers of the fiber and vessel.
- (vi) Gas is also present in the vessels, which is consistent with observations showing that exuding maple sap contains suspended gas bubbles ([Wiegand 1906](#), [Marvin and Greene 1959](#), [Perkins and Berg 2009](#)). We are also guided by the observation of [Milburn and O’Malley \(1984\)](#) that both sap and xylem tissue are essentially incompressible at the pressures typically experienced during maple sap exudation. Consequently, gas bubbles suspended in the vessel sap provide a convenient mechanism to facilitate pressure exchange between fiber and vessel. As the sap pressure periodically rises and falls through the freeze–thaw cycles, a portion of the gas may dissolve within the sap if the local pressure is high enough.
- (vii) Gas, liquid and ice within the fiber and vessel exist as distinct layers arranged as concentric annuli shown in

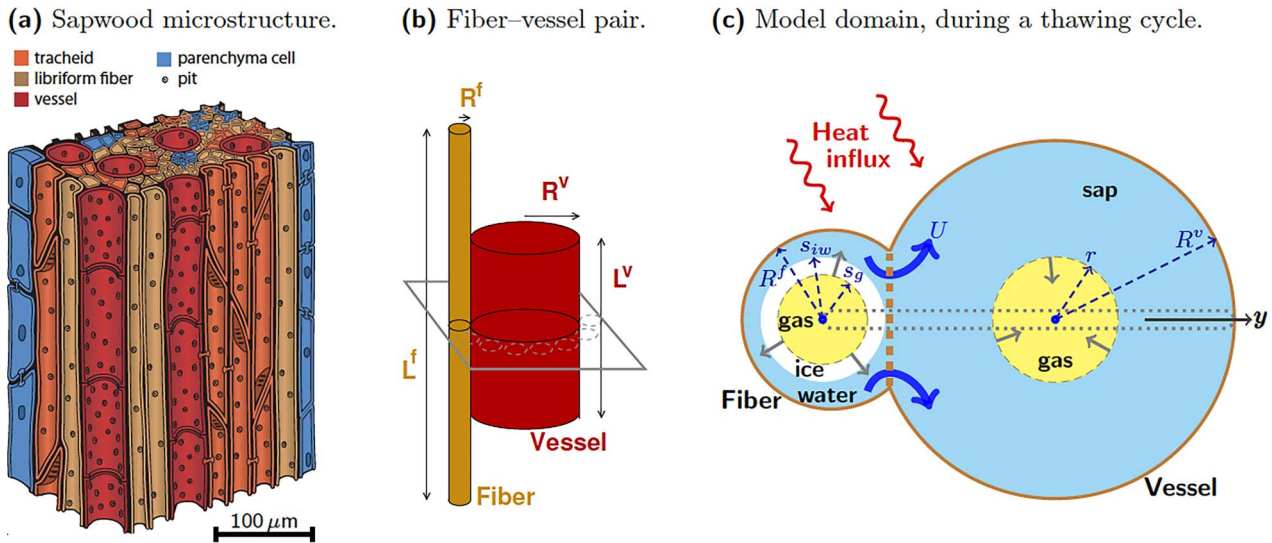


Figure 2. Sapwood microstructure and the idealized 2D model geometry. (a) A microscopic cut-away view of the sapwood within a typical hardwood tree, depicting the vessels and (libriform) fibers that are central to the model. Tracheids are connected hydraulically to neighboring vessels via paired pits, which is why they are ‘lumped together’ in our model with vessels. Note that fiber walls also contain pits, but they are unpaired and hence unconnected to adjacent vessels or tracheids. (b) A single fiber–vessel pair showing the main geometric parameters. The horizontal cutting plane highlights the planar cross-section corresponding to the 2D model geometry in panel (c). The dashed circles represent the N copies of the fiber that are incorporated into the equations through a simple multiplier N . (c) The 2D model geometry depicting a thawing scenario. A thawing fiber of radius R^f (containing nested layers of gas, ice and liquid water) is located adjacent to a thawed vessel of radius R^v (containing gas and liquid sap). As the fiber ice layer thaws, the fiber gas bubble expands and forces melt-water through the porous wall into the vessel at a rate U , thereby compressing the vessel gas and increasing the vessel sap pressure.

Figure 2c. This assumption is made for mathematical convenience since it permits the geometry to be captured by a single radial coordinate. This is also consistent with Milburn and O’Malley (1984) who conjectured that ice accumulates on the inner fiber wall due to cryostatic suction from previous freezing cycles to encase a central gas bubble and that during a thawing cycle, any liquid melt-water collects in a layer between the ice and the wall. When it comes to the vessels, experimental observations suggest that bubbles form asymmetrically at nucleation sites along the inside of the vessel lumen (Zwieniecki and Holbrook 2000, Brodersen et al. 2010); however, the precise location of these bubbles is unimportant for the purposes of our model because the influence of the gas appears only as a volume fraction in the model equations.

- (viii) The temperature in the gas and ice layers is assumed to be constant and equal to that of the adjacent liquid. Furthermore, during any freeze or thaw cycle, the temperatures of the gas/ice layers in the fiber remain constant at the critical temperature (or freezing point) of water, denoted T_c . This is justified because the fiber radius is roughly 6 times smaller than in the vessel, and the thermal diffusivities for gas and ice (1.9×10^{-5} and $1.5 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$) are at least an order of magnitude larger than that for water ($1.4 \times 10^{-7} \text{ m}^2 \text{ s}^{-1}$) (Tyree and Zimmermann 2002).
- (ix) Any liquid entering the fiber from the vessel must have a negligible sucrose content owing to the selective permeability of the fiber–vessel wall (Cirelli et al. 2008).
- (x) Liquid water is present within the soil even under freezing conditions and tree roots passively transport water throughout the entire freeze–thaw cycle, both of which are supported by observations (Marvin 1958, Robitaille

et al. 1995, Sorkin 2014). However, we do recognize that the upper few centimeters of soil may remain frozen.

Based on the above assumptions, we now present the governing equations for the thawing cycle of the exudation process during which vessels are completely thawed, whereas the fibers are in a partially frozen state (depicted in Figure 2c and corresponding to stage (iv) in Figure 3). The model equations are essentially the same as those presented in Graf et al. (2015), and complete details of the derivation can be found there and in Ceseri and Stockie (2013). The physical state of the various phases (liquid, ice, gas) within a given vessel and fiber pair can be described by the following six time-dependent functions.

- $s_g(t)$: fiber gas bubble radius, measured from the center of the fiber,
- $s_{iw}(t)$: radius of the fiber ice–water interface,
- $r(t)$: vessel gas bubble radius,
- $U(t)$: total volume of melt-water that flows through the porous fiber–vessel wall, measured positive from fiber to vessel,
- $U_r(t)$: total volume of water influx from the roots,
- $\mathcal{T}(y, t)$: temperature in the vessel sap, which also depends on the radial coordinate y with origin at the vessel center so that $r(t) \leq y \leq R^v$ (recall that temperature is taken to be constant elsewhere in the fiber and vessel).

We will now state equations for the first five unknowns, leaving the microscale heat equation for \mathcal{T} to the next section. First of all, an algebraic equation for conservation of volume can be derived that relates the thickness of various layers within the fiber and balances with any melt-water exiting into the vessel (U). After exploiting the circular symmetry in the

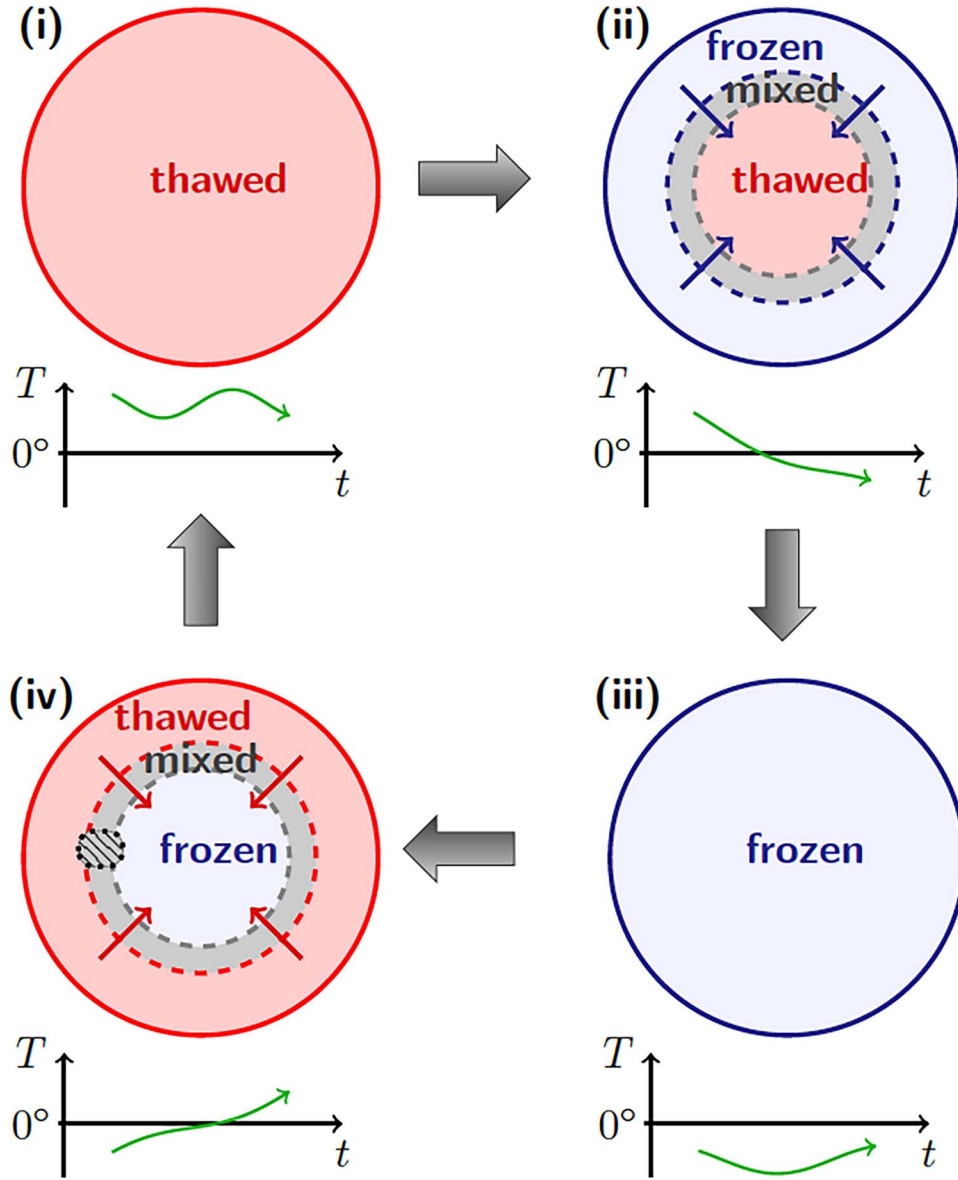


Figure 3. The freeze–thaw process within a circular tree stem cycles between four main stages (i \rightarrow ii \rightarrow iii \rightarrow iv \rightarrow i \rightarrow ...) as ambient temperature T cycles below and above the freezing point: (i) completely thawed (with $T > 0$); (ii) partially frozen ($T \searrow 0$), with a freezing front advancing radially inward to the center of the stem; (iii) completely frozen ($T < 0$); (iv) partially thawed ($T \nearrow 0$), with a thawing front advancing radially inward. The freezing/thawing fronts in (ii, iv) are thin annular regions (shaded, and in reality much thinner than depicted here) wherein the liquid is in a ‘mixed’ state; that is, the water in the fibers is freezing/frozen and the sap in the vessels thawing/thawed. The thawing front circled on the left of (iv) is magnified in Figure 2c to the cellular scale, which depicts an individual vessel and an adjacent fiber in a partially thawed state.

fiber, this volume constraint is differentiated in time to obtain

$$\partial_t s_g = -\frac{(\rho_w - \rho_i)s_{iw}\partial_t s_{iw}}{\rho_i s_g} + \frac{\rho_w \partial_t U}{2\pi L^f \rho_i s_g}, \quad (1)$$

where ρ_w and ρ_i are the water and ice densities, respectively. Note that this equation is an ordinary differential equation (ODE) for the variable $s_g(t)$. A similar volume conservation equation governs the vessel gas bubble radius $r(t)$

$$\partial_t r = -\frac{N\partial_t U + \partial_t U_r}{2\pi L^v r}, \quad (2)$$

which involves an additional term arising from root water U drawn into the xylem vessel network. Note that the $\partial_t U$

term is multiplied here by N , which is the average number of fibers connected to each vessel. The dynamics of the ice–water interface s_{iw} is governed by a phase change process that obeys the Stefan condition

$$\partial_t s_{iw} = -\frac{k_w/\rho_w}{E_w - E_i} \partial_n T + \frac{\partial_t U}{2\pi L^f s_{iw}}, \quad (3)$$

where k_w is the thermal conductivity of water, $(E_w - E_i)$ is the latent heat and $\partial_n T \equiv \nabla_y T \cdot \vec{n}$ denotes the normal heat flux.

The two remaining equations are obtained by applying Darcy’s law for flow in porous media. The liquid flux through the porous fiber–vessel wall obeys

$$\partial_t U = -\frac{\mathcal{L}A_{iv}}{N} (p_w^v - p_w^f - C_s \mathcal{R}T(R^v, t) + p_{ice}), \quad (4)$$

where $\mathcal{A}_v = 2\pi R^v L^v$ is the surface area of the fiber–vessel wall and \mathcal{L} is its hydraulic conductivity. The term in parentheses represents a balance at the fiber–vessel wall between four pressures: vessel and fiber liquid pressures, $p_w^v(t)$ and $p_w^f(t)$; osmotic pressure deriving from the sap sugar concentration C_s ; and cryostatic suction p_{ice} which is an ice–water surface tension that is zero under thawing conditions, but nonzero when the fiber is completely frozen and the adjacent vessel contains liquid sap. A second application of Darcy’s law at the root gives the volume flux of root water as

$$\partial_t U_r = -\mathcal{L}_r \mathcal{A}_r (p_w^v - \Psi_s), \quad (5)$$

where \mathcal{L}_r is the root hydraulic conductivity and \mathcal{A}_r is the root area (per vessel). The pressure balance here is expressed in terms of a difference between water potentials in the soil (Ψ_s) and xylem (p_w^v , our vessel sap pressure). With this in mind, the conductivity \mathcal{L}_r should actually be viewed as an effective parameter that accounts for the various conductivities along the water path through roots, xylem and vessel.

The only quantities in the above equations that remain to be specified are the liquid pressures p_w^v and p_w^f within the vessel and fiber. In the vessel, the sap pressure satisfies

$$p_g^v(t) = \frac{\varrho_g^v(t) \mathcal{R} T_c}{M_g} - \frac{2\sigma_{gw}}{r(t)}, \quad (6)$$

which represents a balance between gas pressure (from the ideal gas law) and surface tension at the gas bubble interface (from the Young–Laplace equation). Here, $\varrho_g^v(t)$ is the vessel gas density and σ_{gw} is the gas–liquid surface tension. The gas density is related to the volumes $V_w^v(t)$ and $V_g^v(t)$ of the vessel sap and gas regions by

$$\varrho_g^v(t) = \left(\frac{V_g^v(0) + \mathcal{H} V_w^v(0)}{V_g^v(t) + \mathcal{H} V_w^v(t)} \right) \varrho_g^v(0), \quad (7)$$

which accounts for gas dissolving in the sap via terms involving Henry’s constant \mathcal{H} . Finally, the cell volume quantities are determined by simple geometric constraints

$$V_g^v(t) = \pi L^v r(t)^2 \quad \text{and} \quad V_w^v(t) = \pi L^v \left((R^v)^2 - r(t)^2 \right). \quad (8)$$

An analogous set of equations govern the fiber water pressure $p_w^f(t)$ but are not included here.

Recall that the ODEs Eqs (1) to (5) along with the algebraic constraints Eqs (6) to (8) describe the dynamics within the fiber and vessel during a thawing cycle only, when a fiber in the midst of thawing lies adjacent to a vessel that is completely thawed. There are five additional cases corresponding to the various stages of freeze–thaw within the fiber and vessel, and each case leads to a modification of the governing equations detailed in Graf et al. (2015).

Homogenized two-scale model for heat transport

To complete the model description, we must derive two additional equations describing heat transport: the first capturing microscale effects that arise from phase change within the fibers and vessels; and the second governing macroscale effects

throughout the xylem that are driven by ambient temperature variations. However, the temperatures on the two scales are tightly coupled so that extra care must be taken to properly account for the transfer of heat energy between the micro- and macro-scales. For this purpose, we apply the method of periodic homogenization or two-scale convergence (Allaire 1992), which posits that in a material such as sapwood having a clear separation of scales, the detailed microscale dynamics can be represented by a simpler problem defined on a reference cell \mathcal{Y} . For reasons of simplicity, \mathcal{Y} is typically assumed to have radial symmetry, which is not the case for the microscale geometry in Figure 2c; nevertheless, we can still define a modified reference cell that has the requisite symmetry. Because the essential freeze–thaw processes that govern pressure generation occur within fibers, we choose a fiber-centric coordinate system with radial variable y , in which the fiber is placed in the middle of a square reference cell having side length ε (see Figure 4a). Since the vessel is so much larger than the fiber, it appears simply as a sap reservoir from the fiber perspective. Consequently, we consider the vessel as the region of the reference cell lying outside the fiber, as depicted in Figure 4a (which in some sense ‘turns the vessel inside-out’). In order that this modified reference cell remains consistent with the original fiber–vessel geometry in Figure 2c, we impose a simple volume constraint

$$\pi (R^v)^2 + \pi (R^f)^2 N = \varepsilon^2, \quad (9)$$

which ensures that each reference cell captures the net influence of one vessel and N adjacent fibers. Although Figure 4a depicts the vessel gas as a circular region in the lower left corner, the gas is not strictly assigned to any physical location, otherwise the radial symmetry would be broken. Instead, it is represented in terms of the radius r of the equivalent gas bubble along with the fraction of gas in dissolved form. As a result, the equations from the previous section remain identical despite this apparent change in reference cell geometry.

Next, we exploit the regular, quasi-periodic microstructure of sapwood and view the stem as being constructed of a periodic array of reference cells as pictured in Figure 4b. The macroscopic domain \mathcal{X} is the 2D stem cross-section, which is an annular cylinder having outer radius $x = R_{tree}$ and inner radius $x = R_{sap}$ (bounding the non-conductive heartwood). Our aim is now to derive two equations for heat transport: one on the reference cell that incorporates local variations in temperature due to freeze–thaw processes occurring in a given reference cell at location $x \in \mathcal{X}$ and a second equation capturing macroscopic heat transport throughout \mathcal{X} in response to ambient temperature fluctuations, combined with the local effects. The main objective of the periodic homogenization process is to derive appropriate heat transport coefficients for the macroscale heat equation that incorporate the effects of the microscale by averaging the solution of the reference cell problem \mathcal{Y} appropriately. Note that the size ε of the reference cell plays a dual role in homogenization: it can be considered as a physical dimension, but it must also be viewed asymptotically in the limit as $\varepsilon \rightarrow 0$ to obtain the averaged effect of the microscale freeze–thaw process on the macroscale.

We now summarize the essential aspects of the periodic homogenization procedure, for which complete mathematical details are provided in Konrad et al. (2017). For technical

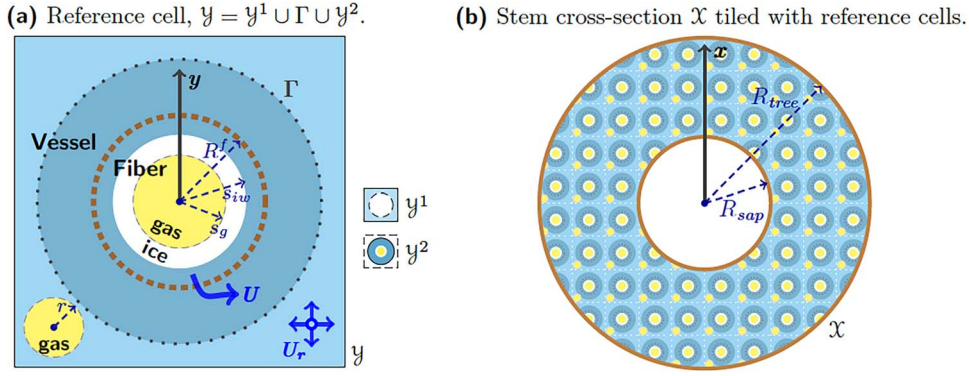


Figure 4. (a) The reference cell \mathcal{Y} containing a fiber located at the center (the brown dashed line is the fiber wall) outside of which lies the vessel. For the purposes of the periodic homogenization process, an artificial boundary Γ (outer dotted circle) is introduced that separates \mathcal{Y} into two sub-regions: \mathcal{Y}^2 , a fiber–vessel overlap region where heat diffusion is slow (shaded in medium blue) and \mathcal{Y}^1 , the outer portion of the vessel region where diffusion is relatively fast (light blue). A gas bubble of radius r is depicted in the lower left corner, and the root water source U_r in the lower right. (b) An annular sapwood cross-section is tiled periodically with copies of the reference cell from (a). Mature trees contain a non-conducting heartwood region extending out to radius $x = R_{sap}$, whereas younger saplings may have no heartwood ($R_{sap} = 0$).

reasons, the reference cell \mathcal{Y} is separated into two sub-regions (\mathcal{Y}^2 and \mathcal{Y}^1) pictured in Figure 4a, where \mathcal{Y}^2 refers to the fiber plus the inner portion of the vessel where heat diffuses slowly, whereas \mathcal{Y}^1 is the remaining outer portion of the vessel where diffusion is fast compared with \mathcal{Y}^2 . The curve Γ is an artificial boundary separating \mathcal{Y}^1 from \mathcal{Y}^2 so that $\mathcal{Y}(x, t) = \mathcal{Y}^1 \cup \Gamma \cup \mathcal{Y}^2(x, t)$. Note that an implicit time and space dependence appears in \mathcal{Y}^2 (and hence also \mathcal{Y}) owing to the motion of phase boundaries that alters the geometry of \mathcal{Y} depending on the specific location x (although our notation will often omit this dependence). Our aim is then to derive two heat diffusion equations, one for $\mathcal{T}(x, y, t)$ on the microscale domain $\mathcal{Y}^2 \times \mathcal{X}$ and the other for $T(y, t)$ on the macroscale domain \mathcal{X} .

The governing equations are stated in a mixed temperature–enthalpy formulation in order to properly capture phase transitions. To this end, we define $T(x, t)$ and $E(x, t)$ as the macroscale temperature and enthalpy variables, which are both constant inside \mathcal{Y}^1 and thus depend only on the macroscale spatial coordinate x . The corresponding microscale variables on $\mathcal{Y}^2(x, t)$ are $\mathcal{T}(x, y, t)$ and $\mathcal{E}(x, y, t)$, which vary at each point in the macroscopic domain as well as the microscale y . We impose the usual temperature–enthalpy relationship on both $T = \omega(E)$ and $\mathcal{T} = \omega(\mathcal{E})$, where

$$\omega(E) = \begin{cases} \frac{E}{c_i}, & \text{if } E < E_i - \delta_i, \\ T_c - \frac{2E - E_i - E_w}{2c_\infty}, & \text{if } E_i - \delta_i \leq E \leq E_w + \delta_w, \\ T_c + \frac{E - E_w}{c_w}, & \text{if } E_w + \delta_w < E, \end{cases} \quad (10)$$

captures implicitly the change in phase that occurs at the critical (freezing) temperature T_c . This ω is a piecewise function consisting of two linear segments with slopes c_i^{-1} in ice and c_w^{-1} in liquid, connected by a steep layer with slope c_∞^{-1} (where $c_\infty \approx 10^7$). The constants c_w and c_i refer to the specific heat capacities of water and ice, while $\delta_i = \frac{c_i(E_w - E_i)}{2(c_\infty - c_i)}$ and $\delta_w = \frac{c_w(E_w - E_i)}{2(c_\infty - c_w)}$ are chosen to ensure that $\omega(E)$ is continuous.

Heat transport within the liquid-filled subregion \mathcal{Y}^2 is governed by the heat equation

$$c_w \partial_t \mathcal{T} - \partial_y (D(\mathcal{E}) \partial_y \mathcal{T}) = 0 \quad \text{in } \mathcal{Y}^2(x, t) \times \mathcal{X}, \quad (11)$$

where D is a thermal diffusion coefficient that is also a given piecewise linear function of enthalpy (Visintin 1996)

$$D(\mathcal{E}) = \begin{cases} \frac{k_i}{\varrho_i}, & \text{if } \mathcal{E} < E_i, \\ \frac{k_i}{\varrho_i} + \frac{\mathcal{E} - E_i}{E_w - E_i} \left(\frac{k_w}{\varrho_w} - \frac{k_i}{\varrho_i} \right), & \text{if } E_i \leq \mathcal{E} \leq E_w, \\ \frac{k_w}{\varrho_w}, & \text{if } E_w < \mathcal{E}. \end{cases} \quad (12)$$

The partial differential Eq. (11) requires boundary conditions on the inner ($\partial \mathcal{Y}^2$) and outer (Γ) boundaries of \mathcal{Y}^2 , which are

$$\mathcal{T} = T_c \quad \text{on } \partial \mathcal{Y}^2(x, t) \times \mathcal{X} \quad (\text{phase-change boundary}), \quad (13)$$

$$\mathcal{T} = T \quad \text{on } \Gamma \times \mathcal{X} \quad (\text{coupling to macro-temperature}). \quad (14)$$

The homogenization procedure that we apply next to obtain a macroscale heat equation is more complicated and requires first taking $y = x/\varepsilon$ in the microscale problem and then expanding the solution asymptotically as $\varepsilon \rightarrow 0$, which is referred to as the two-scale limiting process. The governing equation is written in an integral (weak) formulation, but after approximating the resulting integral terms in the $\varepsilon \rightarrow 0$ limit, one obtains the following strong formulation of the limit problem:

$$\partial_t E - \partial_x \left(\Pi D(E) \partial_x T \right) = \frac{1}{|\mathcal{Y}^1|} \int_{\Gamma} D(\mathcal{E}) \partial_n \mathcal{T} dS \quad \text{in } \mathcal{X}. \quad (15)$$

Note that this is an alternate form of the heat diffusion equation, written in a mixed temperature–enthalpy form that implicitly captures parameter discontinuities across phase interfaces. There are two new terms appearing in Eq. (15) via the homogenization process that are critically important in properly capturing the influence of the microscale problems on the macroscale.

- The homogenized diffusion operator contains an extra constant factor Π , which is a purely geometric quantity

consisting of a 2×2 matrix with entries

$$\Pi_{ij} = \frac{1}{|\mathcal{Y}^1|} \int_{\mathcal{Y}^1} (\delta_{ij} + \partial_y \mu_i) dy. \quad (16)$$

Here, δ_{ij} is the Kronecker delta symbol and $\mu_i(y)$ are solutions to simple elliptic PDE problems on the reference cell \mathcal{Y}^1 (Allaire 1992).

- The source term on the right-hand side is a surface integral over the artificial boundary Γ of the microscopic heat flux.

It is important to recognize here that the temperature–enthalpy relationship $T = \omega(E)$ in Eq. (10) involves the critical temperature, T_c . Within the fiber (which contains pure water), we take $T_c = 0^\circ\text{C}$, but in the macroscale problem, T_c must be replaced with

$$T_{c,\text{sap}} = T_c - \frac{K_b C_s}{\rho_w}, \quad (17)$$

where $K_b = 1.853$ is the cryoscopic (or Blagden’s) constant. This accounts for the freezing point depression or freezing point depression (FPD) that arises due to dissolved solutes (primarily sugar) in the vessel sap. Finally, the partial differential equation or PDE (Eq. (15)) is supplemented with the boundary condition

$$T = T_a(t) \quad \text{on } \partial\mathcal{X}, \quad (18)$$

which sets the outer stem surface temperature equal to a given ambient air temperature and is what ultimately drives the freeze–thaw process. Complete details of the homogenization procedure can be found in Konrad et al. (2017), and we also refer the interested reader to the work of Chavarría-Krauser and Ptashnyk (2013) who applied periodic homogenization to a related problem involving osmotic transport in non-woody plants.

The parameter values appearing in these equations are taken mostly from previous work (Graf et al. 2015, Konrad et al. 2017) that focused on comparisons to experimental data from black walnut. These parameters are summarized in Table 1, with a few small adjustments for red/sugar maple as indicated. The ‘base case’ is indicated that there corresponds to a sugar maple sapling with a diameter of 14 cm that has sap sugar content of 3% by mass.

Numerical solution algorithm

The exudation model equations consist of five ODEs (Eqs (1) to (5)) for the microscale variables along with two PDEs (Eq. (11)) and (Eq. (15)) for temperature. We apply the method-of-lines to discretize the temperature equations by first approximating all spatial derivatives using a finite volume approach, which yields a large coupled system of time-dependent ODEs. The macroscale variable x is discretized at n_x equally spaced points, with n_x chosen between 25 and 50 (depending on tree size) so that the grid spacing $\Delta x = (R_{\text{tree}} - R_{\text{sap}})/n_x$ is less than 0.3 cm, which we find is sufficient in practice to resolve the freezing and thawing fronts. For the microscale problem, we obtain satisfactory accuracy with a relatively coarse grid having $n_y = 6$ points.

Assembling the semi-discrete equations for temperature together with the remaining ODEs and algebraic constraints within each reference cell at location x yields a coupled differential–algebraic system that is integrated in time using the stiff

solver ode15s in MATLAB (2020). We note that a stiff solver is required for this problem because of the widely disparate time scales arising from the disparate dynamics on the cellular level and within the tree stem. The strong coupling between micro- and macroscale temperatures is handled by applying a split-step time discretization: first, the microscale equations for $s_g, s_{iw}, r, U, U_r, \mathcal{T}$ in the reference cell at each discrete point are advanced in time while holding the macroscale temperature T constant; following that, T is advanced in time by holding other variables constant. More details related to implementation of the multiscale algorithm can be found in Graf et al. (2015).

Results

Experimental data and temperature smoothing

Based on the experiments described in Materials and methods, we have chosen to focus our attention on two red maple trees (which we label R1 and R2 for convenience) and one sugar maple (labeled S1). A more detailed description of these experiments that emphasizes the temperature measurements can be found in Wilmot (2006). Air temperature data for all three trees are displayed in Figure 5 (left) over periods of 33 days (R1, R2) and 45 days (S1). These samples were singled out for comparison with numerical simulations because the air temperature in each case features several pronounced freeze–thaw cycles during the measurement period. Note that the temperature plot for sugar maple in Figure 5b–i includes a second curve (red, dashed) showing the soil temperature at 30-cm depth which for most of the 45-day period remains positive, even during times when the air temperature is below zero. This provides strong evidence in support of the earlier assumption(x) 3.2 that liquid water is available for root uptake or water extrusion even under freezing conditions. Water can be extruded from roots to soil if the sum of hydrostatic pressure (ρgh) and stem pressure exceeds the osmotic pressure of sugar and solutes in the xylem of minor roots.

Although these air temperature measurements have an inherent large-scale oscillation that varies roughly on a daily period, the two zoomed-in views in Figure 5a and b–i show that there are also significant fluctuations from one 15-min time interval to the next. These rapid changes are likely due to a combination of local temperature variability and measurement errors and are a major distinguishing feature that sets these field measurements apart from others obtained under carefully controlled laboratory conditions. Indeed, just such an experiment on black walnut trees (Améglio et al. 2001) was used to validate a previous incarnation of our multiscale model (Graf et al. 2015) where the input temperatures were specified as a given smoothly varying function of time. Consequently, our measurements for red/sugar maple provide an excellent opportunity to validate the model under more realistic conditions.

Because our exudation model is based on differential equations that expect the ambient temperature $T_a(t)$ in Eq. (18) to vary continuously in time, we need to impose some regularization to smooth the raw temperature data. To this end, we apply a simple weighted-average smoothing procedure in which each temperature value is averaged with its two neighboring points using weights $[\frac{1}{4}, \frac{1}{2}, \frac{1}{4}]$, with this procedure being repeated 10 times. The smoothed temperature is displayed as a solid curve along with the raw data in the two zoomed plots in Figure 5a and b–i, from which it is clear

Table 1. Model parameters used in the base case simulations are taken from [Graf et al. \(2015\)](#), unless otherwise indicated. Modifications to parameters R_{tree} , R_{sap} , γ_s for comparison with the red/sugar maple experiments are detailed in the text.

Symbol	Description	Values	Units
<i>Variables (functions of time t and space x or y):</i>			
s_{iw}, s_g	Fiber interface locations		m
r	Fessel bubble radius		m
U	Water transferred from fiber to vessel		m ³
U_r	Root water uptake		m ³
\mathcal{T}, T	Temperature		°C
p	Pressure (relative to atmospheric)		Pa
ρ	Density		kg m ⁻³
V	Dolume		m ³
<i>(Subscripts: i, w, g for ice, water/sap, gas; superscripts: f, v for fiber, vessel)</i>			
<i>Tree physiological parameters:</i>			
\mathcal{A}_{fv}	Surface area of fiber–vessel wall	6.28×10^{-8}	m ²
\mathcal{A}_r	Root area per vessel = $\mathcal{A}_{tree}(R^v/R_{tree})^2$	1.14×10^{-6}	m ²
ε	Dide length of reference cell, Eq. (9)	4.33×10^{-5}	m
L^f	Length of fiber	1.0×10^{-3}	m
L^v	Length of vessel element	5.0×10^{-4}	m
\mathcal{L}	Hydraulic conductivity of fiber–vessel wall	5.54×10^{-13}	m s ⁻¹ Pa ⁻¹
\mathcal{L}_r	Root hydraulic conductivity (Steudle and Peterson 1998)	2.7×10^{-16}	m s ⁻¹ Pa ⁻¹
N	Number of fibers per vessel	16	–
R^f	Inside radius of fiber	3.5×10^{-6}	m
R^v	Inside radius of vessel	2.0×10^{-5}	m
<i>Physical constants:</i>			
\mathcal{H}	Henry’s constant for air dissolved in water	0.0274	–
K_b	Cryoscopic (Blagden) constant	1.853	kg °C mol ⁻¹
M_g	Molar mass of gas (air)	0.029	kg mol ⁻¹
M_s	Molar mass of sugar (sucrose)	0.3423	kg mol ⁻¹
\mathcal{R}	Universal gas constant	8.314	J °C ⁻¹ mol ⁻¹
<i>Water phase properties:</i>			
c_i, c_w	Specific heat capacity	<i>Ice</i> <i>Water</i> 2100 4180	J °C ⁻¹ kg ⁻¹
E_i, E_w	Enthalpy at T_c	574 907	kJ kg ⁻¹
k_i, k_w	Thermal conductivity	2.22 0.556	W m ⁻¹ °C ⁻¹
ρ_i, ρ_w	Density	917 1000	kg m ⁻³
σ_{iw}, σ_{gw}	Surface tension (Fowler and Krantz 1994)	0.033 0.076	N m ⁻¹
c_∞	Enthalpy regularization parameter, Eq. (10)	1.0×10^7	J °C ⁻¹ kg ⁻¹
<i>Base case parameters:</i>			
R_{tree}	Tree stem radius	0.07	m
R_{sap}	Sapwood/heartwood boundary	0	m
θ	Heartwood fraction = R_{sap}/R_{tree}	0	–
γ_s	Sap sugar content (mass fraction)	0.03	–
\mathcal{A}_{tree}	Total root area (Day and Harris 2007)	14	m ²
C_s	Sap sugar concentration = $\gamma_s \rho_w / M_s$	87.6	mol m ⁻³
$T_{c,sap}$	FPD = $-K_b C_s / \rho_w$	–0.162	°C
Ψ_s	Soil water potential = $p_w^v(0)$	2.03×10^5	Pa

that this procedure eliminates many irregularities without sacrificing much detail. There is of course a risk that genuine fine-scale variations in temperature are suppressed, but we have observed that reducing the number of smoothing steps has no appreciable effect on the model simulations. This is consistent with the section Numerical simulations of red and sugar maple, which shows that exudation behavior is dominated by the location of temperature zero-crossings and influenced much less by variations in $T_a(t)$ away from zero.

Parameter sensitivity study

To study the relative importance of various geometric and physical properties on the sap exudation process, we identify a base case using the parameters listed in Table 1 and then vary certain parameters relative to these base values. Our chosen

base case represents a young sapling with $R_{tree} = 0.07$ m and $R_{sap} = 0$ that has not yet developed any heartwood, and we use our best estimates for the remaining parameters. To mimic a repeated sequence of diurnal freeze–thaw events, we impose a simple sinusoidally varying ambient temperature, $T_a(t) = 5 - 15 \sin(2\pi t/86400)$, that oscillates between -10 and $+20$ °C over a time interval of 5 days. This is admittedly an extreme range of temperatures, but it does ensure that the entire stem is able to freeze and thaw completely during each cycle. Results of the parameter sensitivity study are presented in [Figure 6](#) as plots of root water uptake U_r and stem-averaged pressure $\bar{p} = \frac{1}{|A|} \int_A p_w^v dA$, where $|A|$ is the area of the annular-shaped sapwood region. This averaged pressure is a better representation than any specific point value for what is measured by a pressure gauge inserted into a taphole.

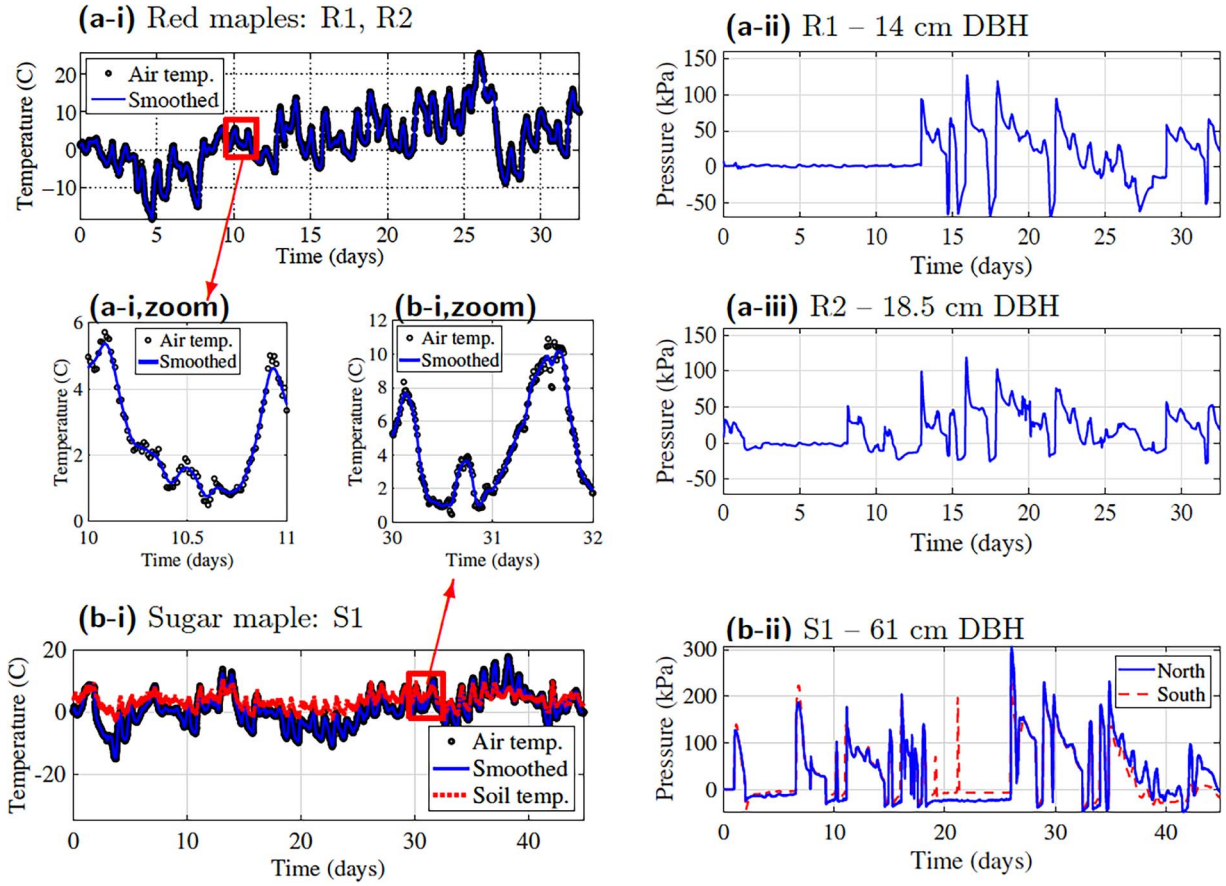


Figure 5. (Left, a-i and b-i) Measured air temperatures are plotted for two red maple trees (R1, R2) and one sugar maple (S1) from the UVM experiments. The temperature plot for sugar maple in (b-i) also includes values of soil temperature (at 30-cm depth), which remain mostly above 0 °C, hence supporting the assumption that liquid water is present even when air temperatures are below freezing. The raw temperature data (points) are regularized by applying a simple weighted-average smoothing—the resulting smoothed data are shown alongside the original temperatures in the zoomed views (a-i,zoom, b-i,zoom). (Right, a-ii, a-iii and b-ii) Corresponding pressure data for the three trees. An extra set of pressure measurements is included in the sugar maple plot (b-ii) to illustrate the impact of taking measurements on the north/south sides of the stem.

The results plotted in Figure 6 focus on variations in four key model parameters and how they affect the behavior of pressure and root uptake.

- (i) Stem radius (R_{tree}), which is the primary geometric parameter that distinguishes between the mature trees in this study and younger saplings. Values of R_{tree} are selected between 5 and 30 cm which covers the range of tree sizes in the experiment discussed in Materials and methods and the corresponding \bar{p} and U_r solution curves are shown in Figure 6a. Note that the curve corresponding to the base case ($R_{tree} = 0.07$) is always drawn as a solid blue line and is highlighted in the legend with a '*'.
- (ii) Heartwood fraction ($\theta = R_{sap}/R_{tree}$), which is zero for young saplings but can be significantly larger in mature trees. The red/sugar maples considered in this study are from a well-established area of the forest in which trees typically have 25–50% of their basal area taken up by heartwood (with lower fractions in smaller trees and higher fractions in larger trees). Most of these trees have been tapped annually for maple collection over a period of 50–60 years, which generates a column of non-conductive wood that extend above and below each year's taphole (typically by a distance of ± 0.25 m).

Therefore, while there is undoubtedly some heartwood in these trees, there is also considerable non-conductive wood within the tapping band as a result of tapping history. We therefore chose values of heartwood fraction within the range $\theta \in [0, 0.7]$, which is consistent with the measurements of Duchesne et al. (2016) who found a maximum value of $\theta \approx 0.45$ while also allowing for even higher values such as those reported by Baral et al. (2017).

- (iii) Total root area ($A_{tree} = A_r(R_{tree}/R^v)^2$), which is related to the root area per vessel (A_r) by scaling proportionally to cross-sectional area. Because values of A_{tree} for red maple have been reported to lie in the range 10.4–18.6 m² (Day and Harris 2007), we choose a value of $A_{tree} = 14$ for the base case that lies near the middle of this range; scaling by the area ratio yields a corresponding root area per vessel of $A_r = A_{tree}(R^v/R_{tree})^2 \approx 1.14 \times 10^{-6}$ m². For the sensitivity results shown in Figure 6c, we have actually selected a wider range of $A_{tree} \in [1, 100]$.
- (iv) Sap sugar content by mass (γ_s), which is related to sugar concentration by $\gamma_s = C_s M_s / Q_w$, where M_s the molar mass of sugar. High sugar content is an important feature distinguishing maples from other species that exude sap. Sugar maple sap contains roughly 3% sugar on average during the sap harvest season (Laroche et al. 1998) but

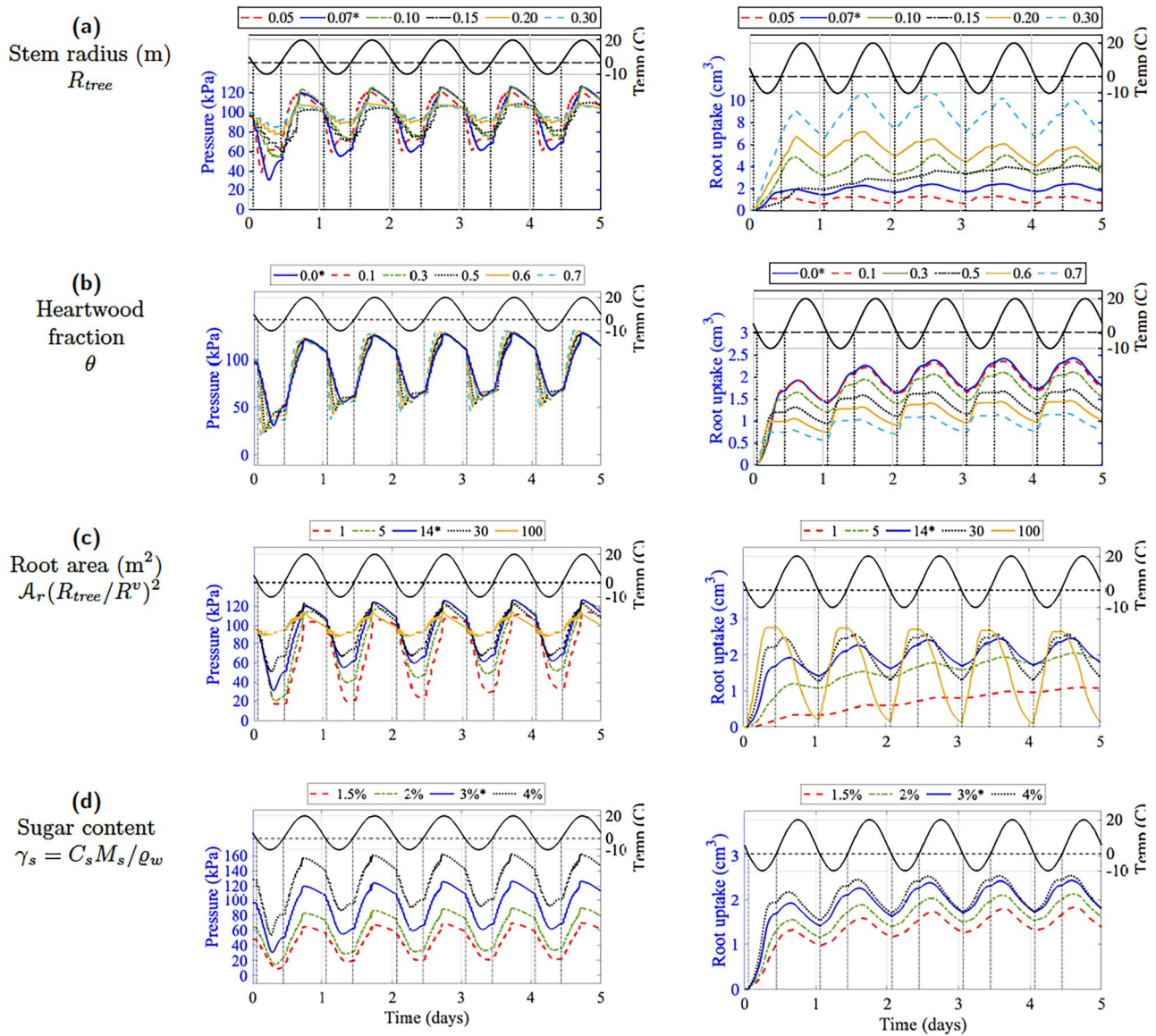


Figure 6. Parameter sensitivity study showing the effects on stem-averaged pressure (\bar{p}) and root water uptake (U_r) due to variations in four parameters: (a) stem radius, (b) heartwood fraction, (c) total root area and (d) sap sugar content. In each plot, the parameter value from the base case is highlighted in the legend with a '*' and the corresponding curve is drawn with a solid line. The dotted vertical lines indicate freeze and thaw events, which are times when the ambient temperature crosses zero.

can be as high as 5% in some trees (Jones and Alli 1987). On the other hand, red maples tend to have a lower sugar content that is closer to 2% on average. Sugar content also varies significantly between seasons, between trees and also throughout a given season (starting a bit low, rising for the first quarter to third of the season, then steadily dropping toward the end). We have therefore chosen a representative value of 3% ($\gamma_s = 0.03$) for the base case along with several other values selected from the range 1.5–4.0% as depicted in Figure 6d.

This parameter sensitivity study is partly based on results from Zarrinderakht (2017), which includes additional results not reported here.

Numerical simulations of red and sugar maple

We next apply the MATLAB code to simulate the three trees singled out earlier, taking the smoothed temperature curves depicted in Figures 5a and b-i as input for the ambient

temperature $T_a(t)$. Two simulations are performed for red maple trees (R1, R2) with stem radii $R_{tree} = 7$ and 9.25 cm, both consisting entirely of sapwood ($R_{sap} = 0$) since they are relatively young trees. The sugar content for these trees is set to 1.8% which is a representative value for mid-to-late season, but otherwise, all model parameters are the same as the base case in Table 1. The equations were integrated over a period of 27 days, which covers the majority of freeze-thaw events occurring in the air temperature measurements. The resulting plots of simulated average pressure \bar{p} are displayed in Figure 7a and b alongside the corresponding experimental measurements. The smoothed temperature data are shown at the top of each plot, with dotted vertical lines drawn at each time when $T_a(t)$ crosses 0°C for an easy identification of freeze and thaw events.

One sugar maple simulation (S1) is performed with ambient temperature $T_a(t)$ taken equal to the smoothed temperature from Figure 5b-i and stem radius set to $R_{tree} = 30.5$ cm.

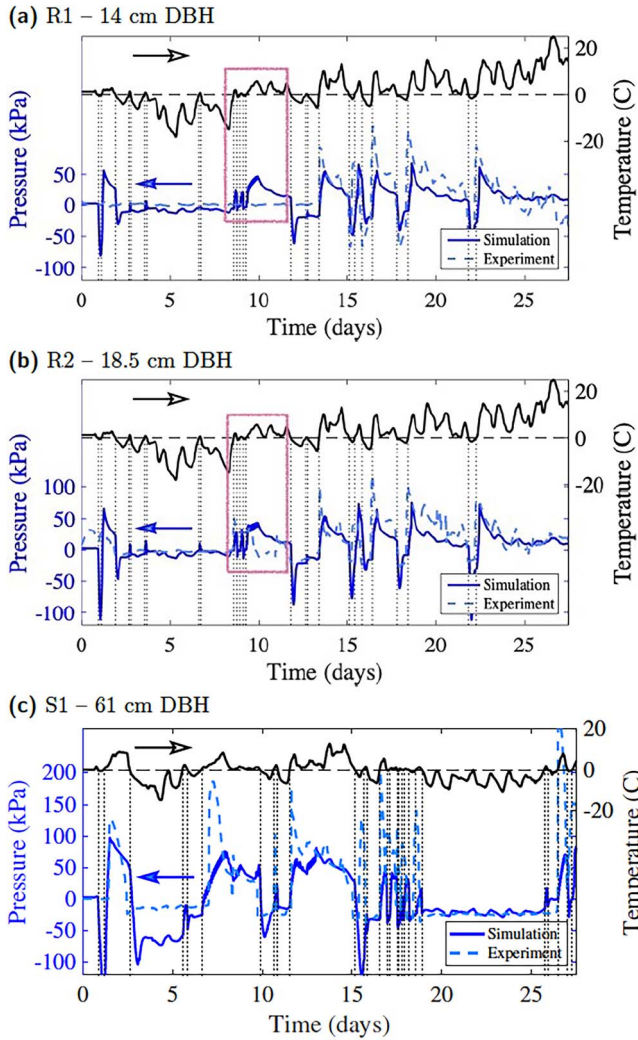


Figure 7. Comparison of stem pressure from experiments (solid blue lines) and simulations (dashed lines) for red maple (a, b) and sugar maple trees (c). The smoothed temperature data are also displayed on the top set of axes, and each freeze–thaw event is highlighted with a vertical dotted line (at each time where temperature crosses 0 °C) so that these events are easily connected with corresponding pressure spikes. A ‘weak thaw’ event is highlighted inside a box in the R1, R2 simulations (a, b).

Because this is a more mature tree than the red maples, we assume that the heartwood extends half-way through the stem and take $\theta = \frac{1}{2}$. The resulting pressure curves are displayed in Figure 7c, with the experimental pressure taken from the north-side sensor measurements (refer to Figure 5b-ii).

Discussion

Thaw events trigger pressure spikes

Based on the experimental measurements of pressure in the right-hand plots of Figure 5 (right), a characteristic feature of all three trees is the spikes or rapid increases in pressure that occur at certain discrete times. By viewing these plots alongside the corresponding temperature curves from Figure 5 (left), it is clear that the spikes coincide with times that thaw events occur, which is when the temperature increases past the freezing point (this correspondence is much more clearly seen in the plots appearing later in Figure 7). After thawing, and for as long as the temperature remains above zero, each spike

is followed by a period of gradually falling pressure where the rate of decrease appears fairly consistent between thawing events. This behavior is consistent with other experimental pressure measurements in maple and related species (Tyree 1983, Cortes and Sinclair 1985, Améglio et al. 2001, Ewers et al. 2001). The timing, amplitude and decay of these pressure spikes will form the main points of comparison when we discuss the numerical simulations shortly.

It is also worth noting that for the sugar maple only, we have provided two pressure curves (see Figure 5b-ii) that correspond to measurements taken from two sensors located opposite each other on the north and south sides of the stem. The measured pressure variations are qualitatively very similar, especially as regards the timing and height of the pressure spikes and their subsequent decay. A notable exception is the two spikes recorded by the south sensor around Day 20 that do not have matching spikes in the north side data. Because these two spikes correspond to especially weak thaw events (‘weak’ in the sense that temperature exceeds zero for only a brief time interval), it is likely that they are not experienced as thawing events around the entire tree stem. For this reason, we have chosen to use the north-side pressure data for comparison with the S1 simulation.

Xylem pressure is most sensitive to R_{tree} and γ_s

The parameter sensitivity study in Figure 6 will guide our choice of parameter values for use in the experimental comparisons in the next section, as well as pinpointing those parameters that have the greatest impact on the model solution and hence are most important to estimate accurately. We begin by comparing the qualitative features of the solutions in Figure 6a for different stem radius, R_{tree} . In all cases, we observe that average stem pressure \bar{p} behaves similar to the experiments in that it exhibits a steep increase whenever temperature increases past the freezing point. This is followed by a gradual decline, while the temperature remains positive, but as soon as temperature falls below zero, there is a similarly steep drop in pressure, after which the cycle repeats. The amplitude of the pressure oscillations decreases for larger radius trees, which is consistent with there being a larger sapwood area to freeze and hence a correspondingly larger water uptake. The pressure is affected significantly by changes in R_{tree} in that the amplitude of pressure oscillations decreases with increased R_{tree} ; however, the time-averaged pressure (which sits midway between the pressure minima/maxima) is relatively insensitive to changes in radius. This contrasts with the relatively huge increase in root water uptake for higher values of R_{tree} , but again, these larger trees have a proportionally greater volume to freeze and over which to distribute the stored pressure.

The simulations in Figure 6b correspond to different values of the heartwood fraction θ between 0 and 0.7. Clearly, both the shape of the pressure oscillations and the exudation pressure build-up are relatively insensitive to heartwood ratio. The root water uptake curves shift downward as θ increases, but this is simply a geometric effect due to the corresponding decrease in sapwood area. Among the two geometric parameters (R_{tree} and θ), the solution is clearly most sensitive to stem radius, which is fortunate since θ is difficult to measure (non-destructively) in a live tree.

The root area A_{tree} that controls root water flux can be estimated from data in the literature, but it still remains the most uncertain parameter in our model. When increasing A_{tree} over two orders of magnitude (from 1 to 100), Figure 6c shows that

the amplitude of the stem pressure oscillations increases significantly owing to a drop in the minimum pressure, whereas the peak pressures remain approximately the same. However, over the narrower range of values $A_{\text{tree}} \in [10.4, 18.6]$ reported by Day and Harris (2007) for red maples, the differences in stem pressure are relatively small.

The final parameter we consider is sap sugar concentration for which Figure 6d shows that increasing γ_s within the range $[0.015, 0.04]$ has the greatest impact on increasing stem pressure compared with the other three parameters. This supports our earlier remarks regarding the essential role played by sugar in terms of generating a local differential between freeze/thaw in fibers and vessels (due to FPD), which permits ice to accumulate in fibers at the same time as the sap in neighboring vessels remains in the liquid state. Increasing γ_s therefore permits additional ice accumulation in fibers through cryostatic suction which is also reflected in a corresponding increase in root water uptake with γ_s . It is worth recalling that sap sugar also induces an osmotic contribution to pressure through Eq. (4), but we have clearly demonstrated in previous work (Graf et al. 2015) that osmosis is eclipsed in importance by the effect of FPD. Finally, because sap sugar content is so easy to measure, it is especially important that any similar experimental study of sap pressure and temperature also includes measurements of γ_s in order that the model can be properly calibrated.

Multiscale model reproduces realistic pressure variations

We begin by discussing the results in Figure 7a and b that compare experimental and numerical results for the two red maples R1 and R2. The measurements are dominated by pressure spikes appearing at times $t \approx 13, 15, 16, 18, 22$ days that coincide with similar spikes in simulations. Each spike is clearly matched with a thaw event in which air temperature increases past the critical temperature. The simulated peak pressure for some spikes does not reach the same peak value as in experiments but the correspondence is nonetheless excellent, not to mention that the pressure minima following subsequent freeze events are captured very closely. The simulations also show that each spike is followed by a relaxation period during which the pressure gradually decays at a rate that is similar to that seen in the measured data.

During the initial 13 days on the other hand, the match between red maple simulations and experiments is not nearly as close. The measured R1 data in Figure 7a show that the pressure remains essentially constant at zero, whereas the simulation exhibits significant pressure fluctuations in response to freeze–thaw events, most notably on Days 2 and 9. Deviations are also present with R2, although the match is slightly better because the pressure sensor captures some small fluctuations between Days 1–2 and 8–11. One possible explanation for these discrepancies is that the thaw events for times $t < 13$ days are weaker in that temperature increases only slightly above 0°C before either falling below freezing again or hovering near zero, which may be causing the stem to remain more deeply frozen. These ‘weak thaw’ events seem to be captured more readily by the model computations, although the computed pressure does exhibit a more gradual increase instead of the sharp spike seen at the onset of other thaw events; this behavior is especially apparent for the thaw event highlighted in Figure 7a and b during Days 9–11.

The observations of low pressure/flow earlier in the season may also be attributed to the fact that trees tend to be very well-buffered to temperature on the north side due to reduced sun exposure (Reid et al. 2020) (recalling that our comparison is based on north-side sensor data). Furthermore, higher accumulations of snow near the base of the stem may also limit the root water uptake. In either case, it is well known that several repeated cycles of freeze and thaw are typically required before pressure and flow rates can ramp up to higher values.

Next, we shift to the comparison depicted in Figure 7c for the sugar maple S1, which shows that the timing of pressure spikes and the subsequent relaxation rate from simulations both exhibit a reasonable match with experiments, although the simulated pressure peak values are significantly lower. We have as yet no definitive explanation for this discrepancy, but it may be at least partly due to our pressure average \bar{p} , which is integrated all the way to the heartwood boundary and so includes portions of the xylem that may be more deeply frozen and lower the average. Finally, we single out the thaw event on Day 7 during which the simulated pressure builds up much more gradually than in the experimental data, which is again analogous to what we observed for the weak thaw events in trees R1 and R2.

Essential mechanisms governing sap exudation

These comparisons between experiments and simulations demonstrate that a purely physical model is capable of capturing both qualitatively and quantitatively the essential features of sap transport and pressure generation observed in actual maple trees undergoing exudation. Furthermore, we have clearly identified four mechanisms that are essential for generating stem pressure build-up.

- (i) The distinctive cellular structure of maple sapwood which is made up of libriform fibers containing mostly gas that are connected hydraulically through selectively permeable walls to sap-filled vessels. This structure has two very important consequences: first, it provides a mechanism for fiber–vessel pressure exchange via compression of gas in the fibers; and second, the selectively permeable nature of the fiber–vessel wall ensures that any liquid drawn into the fiber (through cryostatic suction) contains no sucrose.
- (ii) The sugar content of sap affects the freeze–thaw-induced pressure generation in maple xylem in two major ways. First, dissolved sugar in the vessels induces a significant osmotic potential between fiber and vessel, which extends the range of pressures over which gas bubbles persist in sap. A second and more critical contribution to exudation is the FPD of roughly 0.16°C in the vessel sap relative to pure water (assuming a 3% sugar content). This is what allows the fibers to accumulate a frozen pure-ice layer, while the sugary sap in neighboring vessels remains thawed because of the FPD. The combination of these two effects is clearly evident in the comparison of pressure variations from the sensitivity study pictured in Figure 6a.
- (iii) A clear separation of spatial scales that exists between freeze–thaw processes on the microscopic (cellular) scale and heat transport on the macroscopic (tree) scale. Specifically, the FPD may appear to be insignificant on the macroscale on which freezing/thawing fronts

propagate through the tree stem, but it dominates on the cellular scale by permitting thawed vessels to co-exist adjacent to partially frozen fibers.

- (iv) An available supply of soil water in the liquid phase (even under freezing conditions) is the key to generating a build-up in exudation pressure over multiple freeze–thaw cycles via accumulation of ice within the fibers. Although this feature is not specific to trees that exude, the availability of significant soil water under sub-zero conditions has recently been confirmed in experiments on maple saplings.

Each of these distinguishing features has been recognized in other studies of maple or related species; however, this is the first time that they have all been linked together to construct a complete quantitative model for the exudation process that also provides a reasonable match with experimental measurements. This is a minimally complete model in the sense that leaving out any of these four effects from the governing equations results in a failure of the model tree stem to accumulate exudation pressures that are consistent with actual trees. It is important to recognize that these fundamental insights we have gained into the physical mechanisms driving the sap exudation process were only possible by developing a detailed mathematical model and performing careful parametric studies of the resulting numerical simulations.

Opportunities for future research

The results presented in this paper and the mathematical model on which they are based open up several opportunities for future research in the study of exudation and sap flow in maple and other species.

- First of all, our sensitivity study singles out two parameters—sap sugar content and root surface area—for which accurate estimates are required in order to properly calibrate the model. Because the root surface area has not been accurately measured yet for maple trees, this suggests at least one opportunity for future experimental studies.
- The 2D stem model can be extended in a straightforward fashion to a more realistic 3D axisymmetric stem geometry by stacking a sequence of 2D cross-sections in the vertical direction and then coupling sap flux and temperature between adjacent sections. We could then incorporate the effect of changes in gravitational potential with height, while at the same time, obtaining a more realistic representation of how soil water from the roots is drawn by cryostatic suction to higher elevations in the tree.
- With such a 3D model in hand, we could also easily incorporate the variation of sap sugar content with height that has been observed by Milburn and Zimmermann (1986). It would then be natural to incorporate the temporal dynamics of the starch conversion process wherein living xylem cells release sugar into the vessels in response to temperature variations (Améglio et al. 2001, Wong et al. 2003).
- Some authors have argued that hysteresis and supercooling play an important role in the freeze–thaw events that occur during the sap exudation process (Tyree 1983, Bozonnet et al. 2023). These effects would be relatively straightforward to incorporate into our model but would have to be validated through careful comparisons with experiments on maple or other tree species (Robson and Petty 1987, Neuner et al. 2010, Charrier et al. 2015).

- Several studies suggest that the ability of trees to exude sap is can be attributed at least partially to root-level processes, in addition to the stem processes, we have considered here (Kramer and Boyer 1995, Westhoff et al. 2008, Hölttä et al. 2018). A modelling study of root pressure generation would thus form a very interesting avenue for future research, especially in species such as birch which are thought to be dominated by root pressure.
- Finally, there are fascinating connections to explore between sap exudation and freeze-induced embolism, motivated by studies that have demonstrated a close relationship between embolism recovery and positive pressures in xylem (Sperry et al. 1988, Hölttä et al. 2018, Schenk et al. 2021).

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Authors' contributions

Study conception and design (J.M.S.); mathematical model development (I.K., J.M.S.); algorithm implementation and numerical simulations (I.K., M.Z., J.M.S.); experimental design and data collection (T.R.W., T.D.P., A.K.v.d.B.); data analysis, synthesis and interpretation (M.Z., T.D.P., A.K.v.d.B., J.M.S.); manuscript writing and revision (all authors).

Data availability statement

The experimental data and the Matlab source code used to perform the numerical simulations in this paper can be obtained from the corresponding author upon request.

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