Sap Flow and Heat Transport in Trees

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4th International Conference on Porous Media
and its Applications in Science, Engineering and Industry

Potsdam, Germany

June 21, 2012

Acknowledgments

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(summer students)

Funding was provided by:

North American Maple Syrup Council Research Fund

MITACS Network of Centres of Excellence

Natural Sciences and Engineering Research Council

Outline

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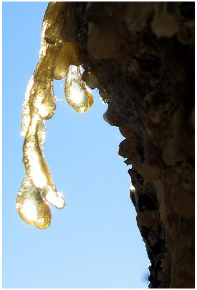
1. Physical background
   - Tree physiology and sap flow
   - Maple sap
2. Macro-model: Sap flow
   - 1D model of Chuang et al.
   - Extension to 2D
3. Macro-model: Heat transport
4. Micro-model: Freeze/thaw dynamics in sapwood

What is tree sap?

- Tree sap is mostly water plus small amounts of sugars, minerals and nutrients.
- Water content of sap in deciduous trees (e.g., sugar maple) can be 98% or higher.
- In conifers, higher solute concentration lowers the freezing point.

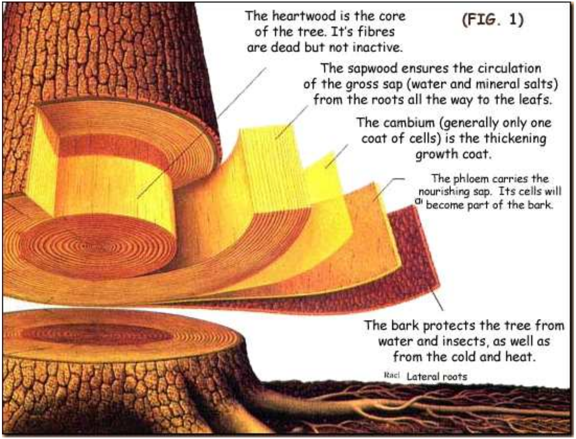
Maple sap



Pine sap

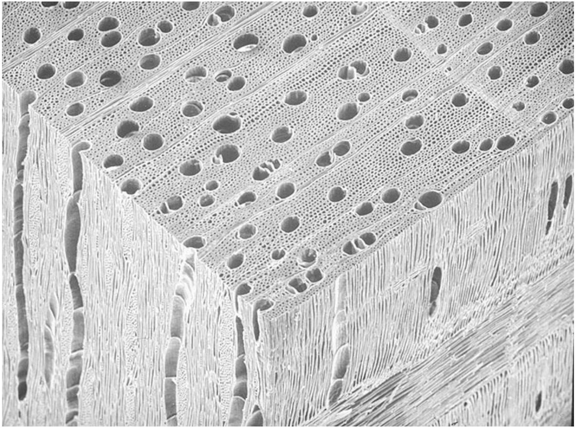
Tree physiology

- Tree wood is classified into several well-defined functional layers.
- Sapwood (*xylem*) and inner bark (*phloem*) both play a central role in sap transport.



Porous structure of wood

- Wood is made of rigid cellulose fibers.
- Fibers transport water like capillary tubes.
- Transport properties are strongly anisotropic.



Sugar maple, `http://www.swst.org/teach/set2/struct1.html`.

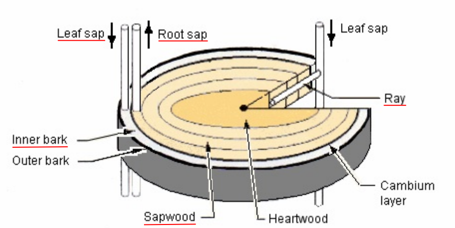
Sap hydraulics

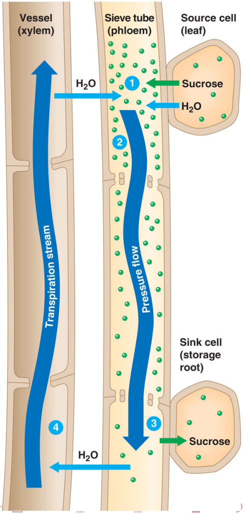
1. Sapwood (*xylem*): carries water and nutrients upward from the roots to the leaves.

2. Photosynthesis: occurs in leaves, driving the "transpiration stream":

$$\underset{\text{(air)}}{6CO_2} + \underset{\text{(roots)}}{6H_2O} + \underset{\text{(sun)}}{\text{energy}} \longrightarrow \underset{\text{(glucose)}}{C_6H_{12}O_6} + \underset{\text{(air)}}{6O_2}$$

3. Inner bark (*phloem*): carries sugars from leaves back to growing parts of the tree.





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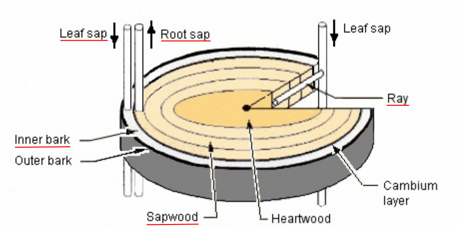

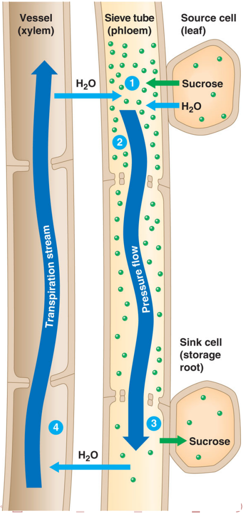

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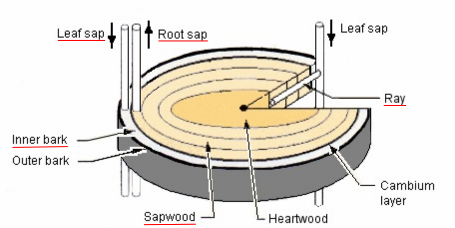
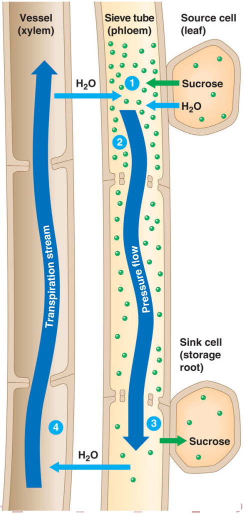




Seasonal variations in deciduous trees

Annual growth cycle for deciduous trees in northern climates:

- Summer/Fall:
  - Photosynthesis generates sugars.
  - Sugars are consumed to support growth in cambium layer.
  - Enzymes convert excess sugars to starch, which is stored in roots, sapwood and ray cells.
- Winter:
  - Hormones and enzymes prepare the tree for its dormant phase.
- Spring:
  - **Maple sap harvest season**.
  - Stored starches are conveted back to sugars and used to initiate new growth of leaves and blossoms.
  - Photosynthesis begins and the cycle repeats.

Current state of sap flow modelling

- The vast majority of existing sap flow models employ an electrical circuit analogy:

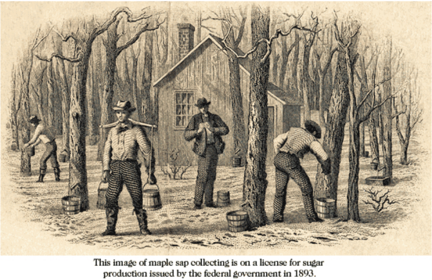
current	voltage	$(\text{resistance})^{-1}$	charge
$\Downarrow$	$\Downarrow$	$\Downarrow$	$\Downarrow$
sap flux	pressure	hydraulic conductivity	saturation

  - **Advantage:** simple and easy to understand, few fitting parameters.
  - **Disadvantage:** saturation can be negative (non-physical), lacking in detailed physics, parameters are difficult to determine.

  Refs: Cowan (1965), Phillips et al. (1997)
- A few physically-based models treat the tree as a porous medium: Aumann & Ford (2002), Chuang et al. (2006).
- Otherwise, the state of tree modelling is relatively immature.

Maple sap

- Maple syrup is a traditional agricultural product in Canada and USA.
- Most maple sap comes from the sugar maple (*Acer saccharum*).
- Other trees such as black maple and birch also yield edible sap, but in much smaller amounts.



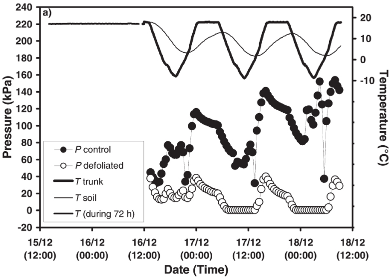
Vermont (1893)

Onset of maple sap exudation in spring

Observations:

- Maple sap begins to exude in late February or early March.
- Temperatures must be above 0°C during the day and below 0°C at night to generate exudation pressures.
- In winter and early spring, there is no transpiration and no inflow from roots.

Améglio et al. (2001)



Question:

So what causes sap exudation ?

The controversy over exudation

Several competing theories attempt to account for pressure that drives maple sap flow during harvest season:

1. Purely physical process: (Milburn & O'Malley, 1984)
   - Gas is compressed in xylem/root cells as sap freezes.
   - Thawing sap allows gas to expand, generating pressure.
2. Osmotic process: (Cirelli et al., 2008)
   - Osmotic pressure is generated by semi-permeable membranes that prevent sugars in xylem vessels from diffusing into surrounding cells.
3. "Vitalistic" process: (Johnson, 1945)
   - Some action of living cells initiates sap flow.

> *"No existing single model explains all of the winter xylem pressure data. A simple osmotic model accounts for the modest positive xylem pressures that occur at low, non-freezing temperatures. However, one or more physical models may be needed to account for the enhanced xylem pressures that occur during and after freeze-thaw events."*
> *—Améglio et al. (2001).*

Our objective

Our main objective is to develop a series of macro- and microscopic mathematical models for ...

1. Transpiration-driven flow in xylem (macro)
2. Heat transport in tree trunk (macro)
3. Exudation driven by thawing and osmosis in xylem (micro)
4. "Scale up" micro-scale processes from step 3, and couple with macro-scale models from steps 1–2 (multi-scale)

This talk: focuses on models 1–2 at the tree scale.

Ultimate goal: to develop a whole-tree simulation tool that ...

- Aids our understanding of sap transport in (maple) trees.
- Captures processes occurring at multiple scales.
- Permits studies of climate change effects on sap flow, optimal harvesting strategies, etc.

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Outline

General model of transpiration-driven sap flow

During summer:

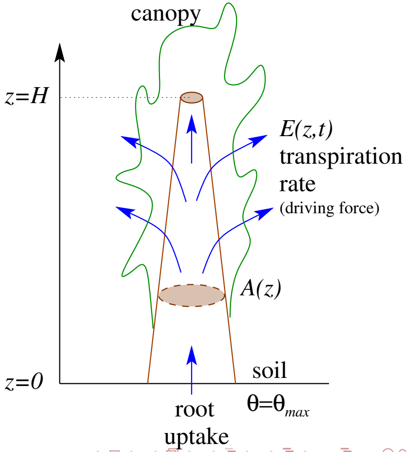
- Only 5–10% of total water flowing within a tree is actually used in photosynthesis.
- The remainder is transpired (evaporated) from leaves, to generate pressure gradients required to overcome gravity.
- Sap flow rates can be 1000 L/day or more!

1D sap flow model: Assumptions

(with Kevin Lorimer and Bebart Janbek)

Begin with the model of Chuang et al. (2006):

- Based on data from Norway spruce (conifer).
- Sap flow is driven by transpiration (summer months).
- Simplify in/outflow effects at roots and branches, treating them as source terms or BCs.
- All flow is vertical (1D).



Governing equations

Saturation or liquid volume fraction $\theta(z, t)$ obeys Richards' equation:

$$\frac{\partial \theta}{\partial t} - \frac{1}{A}\frac{\partial}{\partial z}\left(KA + \frac{KA}{C}\frac{\partial \theta}{\partial z}\right) = Q$$

where

$$\begin{aligned} A(z) &= \text{trunk cross-sectional area } [\mathrm{m}^2] \\ K(\theta) &= \text{hydraulic conductivity } [\mathrm{m/s}] \\ C(\theta) &= \text{hydraulic capacitance } [\mathrm{m}^{-1}] \\ Q(z,t) &= \text{transpiration sink term } [\mathrm{s}^{-1}] \end{aligned}$$

Governing equations (2)

- $Q(z,t)$ encompasses transpiration flux due to branches distributed along the trunk:

$$Q(z,t) = -\frac{\ell(z)\, E(z,t)}{\rho\, A(z)}$$

where

$$\begin{aligned} \rho &= \text{sap density } [\mathrm{kg/m^3}] \\ \ell(z) &= \text{local leaf area density } [\mathrm{m}] \\ E(z,t) &= \text{transpiration flux density } [\mathrm{kg/m^2\,s}] \\ &= E_o(z)\,\sin(t/\tau) \end{aligned}$$

- Boundary conditions:

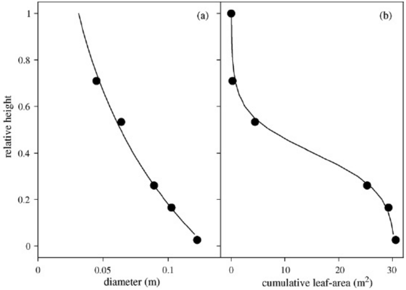
Roots are saturated at $z = 0$: $\quad \theta = \theta_{max}$

No flux out of crown at $z = H$: $\quad -KA\left(1 + \frac{1}{C}\frac{\partial\theta}{\partial z}\right) = 0$

Solution algorithm

- Use a cell-centered finite volume discretization in space.
- Integrate the resulting ODEs in time using Matlab's `ode15s`.
- Parameters:

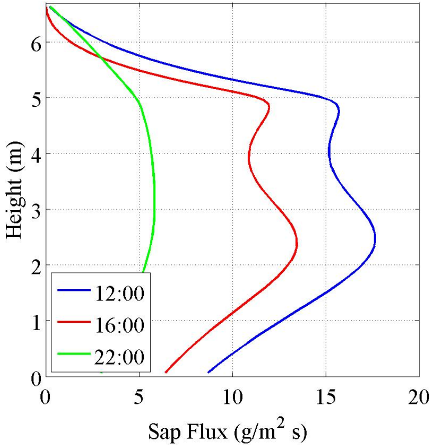
$$H = 6.7$$
$$\theta_{max} = 0.5735$$
$$A(z) = 0.013e^{-2.84z/H}$$
$$\ell(z) = (91.9/H)\,\mathrm{sech}^2(6z/H - 2.4)$$
$$E_o(z) = \text{(a rough fit to very noisy data)}$$



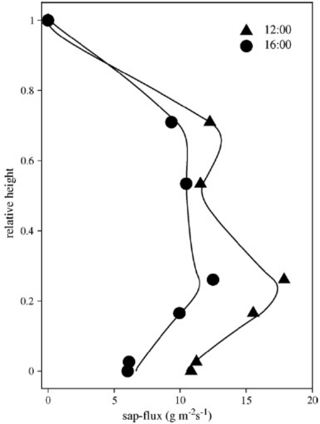
Chuang et al. (2006)

Numerical results in 1D

Our computed results



Chuang's experiments (points) and simulations (lines)



Extension to 2D

- Trunk is axially symmetric: coordinates (r, z)
- Permeability is anisotropic: $K_r \ll K_z$.
- Trunk is tapered with

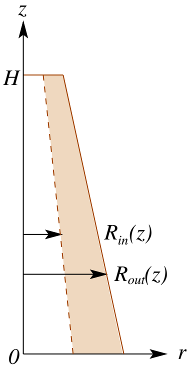
$$\begin{aligned} \text{heartwood (no flow):} \quad & 0 \leqslant r \leqslant R_{in}(z) \\ \text{sapwood (xylem):} \quad & R_{in} \leqslant r \leqslant R_{out}(z) \end{aligned}$$

- Governing equation becomes

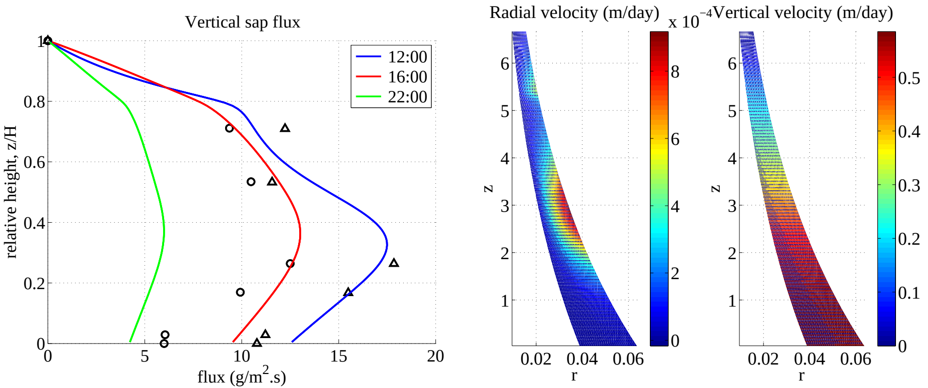
$$\frac{\partial \theta}{\partial t} - \frac{\partial K_z}{\partial z} - \frac{1}{r}\frac{\partial}{\partial r}\left(r\frac{K_r}{C}\frac{\partial \theta}{\partial r}\right) - \frac{\partial}{\partial z}\left(\frac{K_z}{C}\frac{\partial \theta}{\partial z}\right) = 0$$

- Source term (Q) moved to a boundary condition:

$$\frac{K_r}{C}\frac{\partial \theta}{\partial r} = -\frac{\ell(z)E(z,t)}{2\pi\rho R_{out}(z)} \qquad \text{at } r = R_{out}(z).$$

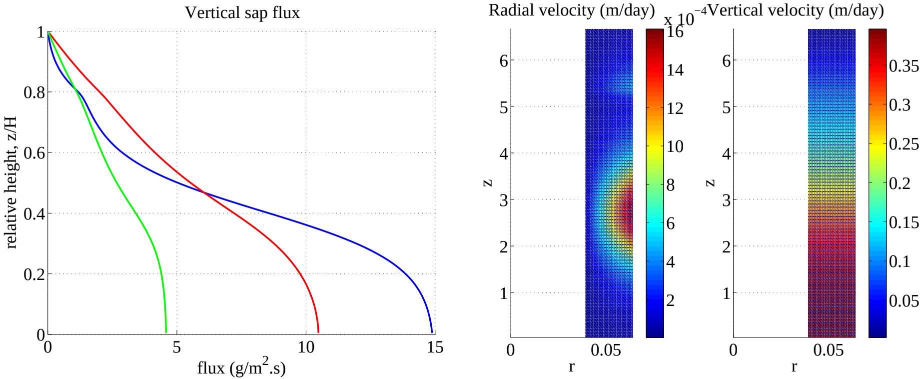


Numerical results in 2D



Match with experimental results is reasonable considering uncertainty in parameters.

Numerical results: Constant radius

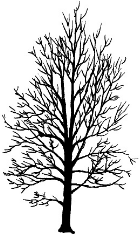


A tapered trunk is necessary to generate the “double-peak” in flux seen in Chuang’s experiments.

Summary: Sap flow

- Our 2D simulations reproduce behaviour from Chuang's experiments and computations (for Norway spruce).
- We still need data to estimate parameters $E(z,t)$, $\ell(z)$, ... for deciduous trees.

Norway spruce



Sugar maple

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Model for heat transport

(work with Bebart Janbek)

- Heat transport in a tree trunk involves:
  - Diffusion in whole trunk.
  - Convection in xylem (via sap).
  - Convective heat transfer between bark and air.
  - Radiative heat transfer with the surroundings.
  - Solar heating.
  - Coupling through θ- and T-dependent parameters (e.g., thermal conductivity, sap density).
- We begin with the model of Potter & Andresen (2002) and add thermal convection BUT neglect coupling with sap flow (for now).

Note: Existing models for heat transport in trees focus almost exclusively on capturing heat damage from forest fires.

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Governing equations

Temperature T obeys the convection–diffusion equation:

$$\rho c_p \left(\frac{\partial T}{\partial t} + \underbrace{\vec{u} \cdot \nabla T}_{\textit{convection}} \right) = \underbrace{\nabla \cdot (k \nabla T)}_{\textit{diffusion}}$$

where
$$\begin{aligned} \vec{u} &= \text{sap velocity} \approx 6 \times 10^{-5} \text{ m/s} \\ \rho &= \text{wood density} = 650 \text{ kg/m}^2 \\ c_p &= \text{specific heat} = 2000 \text{ J/kg °K} \\ k &= \text{thermal conductivity} = 0.5 \text{ W/m °K} \end{aligned}$$

Boundary conditions

Boundary condition at the outer surface of the trunk, $r = R(z)$:

$$-k\frac{\partial T}{\partial r} = \underbrace{h(T - T_a)}_{\textit{convection}} + \underbrace{(1-\alpha)S}_{\textit{solar heating}} + \underbrace{\sigma(T^4 - T_a^4)}_{\textit{radiation}}$$

with

$$\begin{aligned} T_a &= \text{ambient temperature} \\ h &= \text{convective heat transfer coefficient} = 0.2\ \text{W/m}^2\,{}^\circ\text{K} \\ \alpha &= \text{albedo} = 0.2 \\ S &= \text{solar heating term} = 1368\ \text{W/m}^2 \\ \sigma &= \text{Stefan-Boltzmann constant} = 5.67 \times 10^{-8}\ \text{W/m}^2\,{}^\circ\text{K}^4 \end{aligned}$$

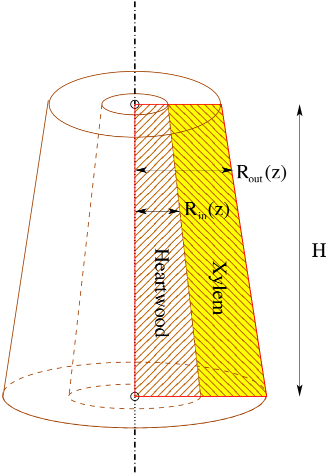
Note: Both $T_a(t)$ and $S(t)$ vary on a daily cycle.

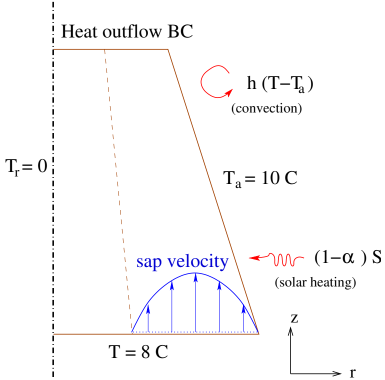
Assumptions

- Tree trunk is cylindrical and axially-symmetric $\Longrightarrow \quad T(r, z, t)$
- Sap flow is driven by transpiration, with $u \approx 6 \times 10^{-5}$ m/s (based on 1000 L/day).
- Radiation effects are negligible.

Geometry and boundary conditions

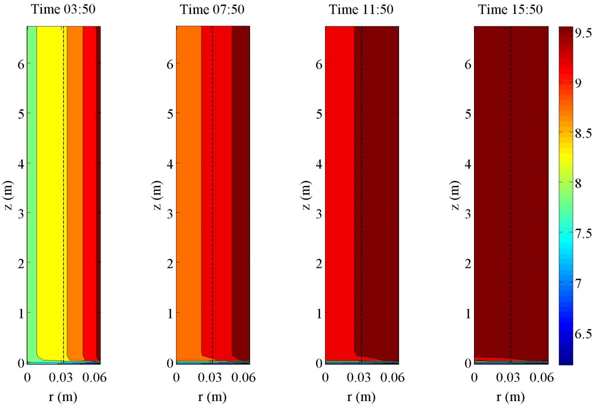
Cylindrical trunk section (axial symmetry) $\Longrightarrow$ Simple 2D domain (coordinates r, z)





Results: Effect of sap velocity

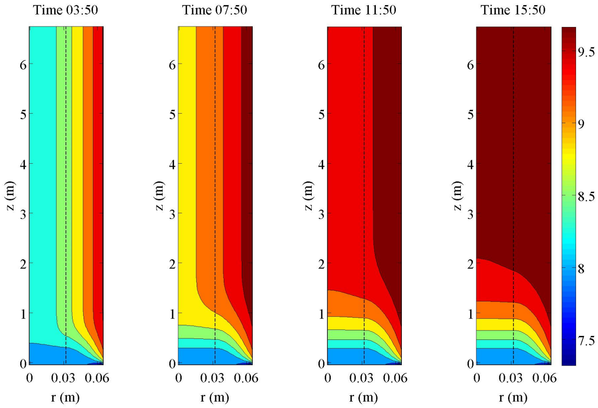
Assume rectangular geometry, no solar heating ($S = 0$), $u_z = 0$ m/s:



Constant steady state reached in roughly 14 hours.

Results: Effect of sap velocity

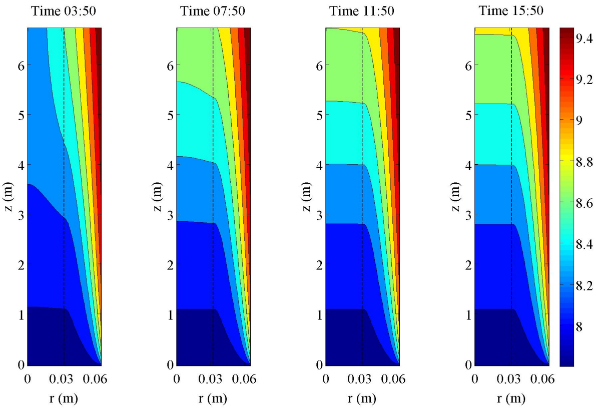
Use peak velocity profile from sap flow simulations
(max $u_z \sim 6 \times 10^{-5}$ m/s):



Convective transport doesn't influence the top boundary.
Effect of the radial outflow on heat flux are negligible.

Results: Effect of sap velocity

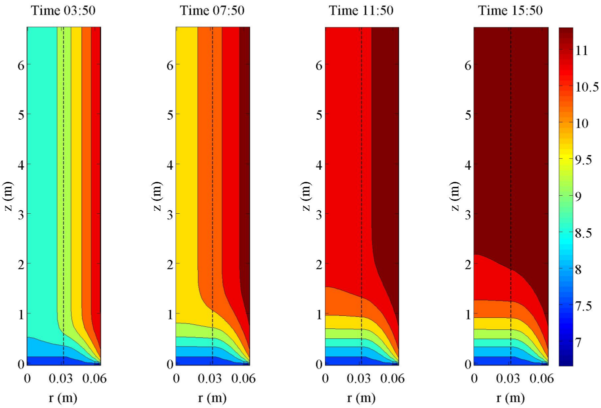
Increase velocity (max $u_z \sim 6 \times 10^{-4}$ m/s):



Top boundary "feels" root temperature.
Steady state reached in roughly half the time.

Results: Add solar heating

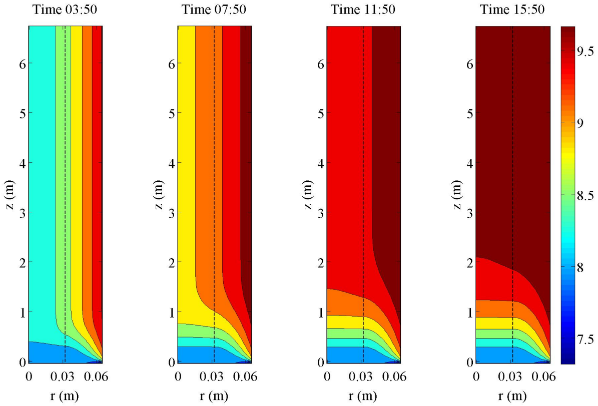
Introduce solar heating term $S = 1368$ W/m^2 (constant) with $\max u \sim 6 \times 10^{-5}$ m/s:



Temperature increases, but distribution remains the same.

Results: Add solar heating

Compare to $S = 0$ results:



Summary: Heat transport

- We implemented an existing model for heat transport in the tree trunk (Potter & Andresen, 2002).
- A parametric study of heat transport indicates that ...
  - Sap flow has a minor effect on temperature distribution, concentrated near the roots.
  - Solar heat flux introduces an upward "shift" in temperature.
- It is straightforward to implement:
  - Vertical variation in radius.
  - Daily fluctuations in ambient temperature T_a and solar flux S.
  - One-way coupling via the actual computed sap flow velocity.
- During the growing season, temperature variations have minimal effect on sap transport coefficients $\Longrightarrow$ the primary influence of temperature on sap flow is due to thawing of frozen sap in spring ...

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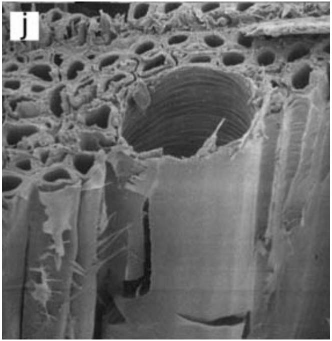
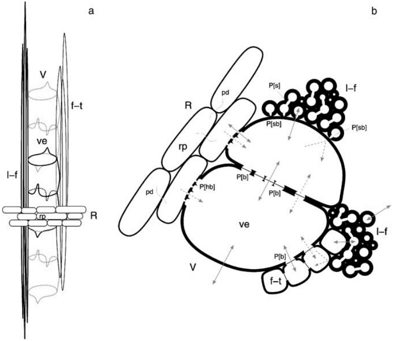
4. Micro-model: Freeze/thaw dynamics in sapwood

Milburn–O'Malley hypothesis

- Milburn & O'Malley (1984) proposed a physical mechanism explaining the effect of freeze/thaw on sap exudation.
- Main hypotheses:
  - Fibers (small) are gas-filled and xylem vessels (large) remain sap-filled, supported by experiments of Wiegand (1906).
  - Freezing starts in fibers, not vessels.



Fibers surround vessels

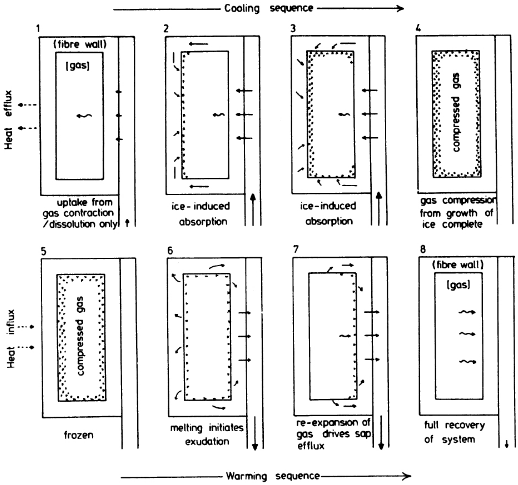


Fibers (l–f), Vessels (v)

Milburn–O'Malley hypothesis: Freezing in fall

- As temperature drops, ice forms on inner walls of the fiber.
- Ice formation drives absorption from the vessel.
- Ice growth compresses gas trapped in the fiber.

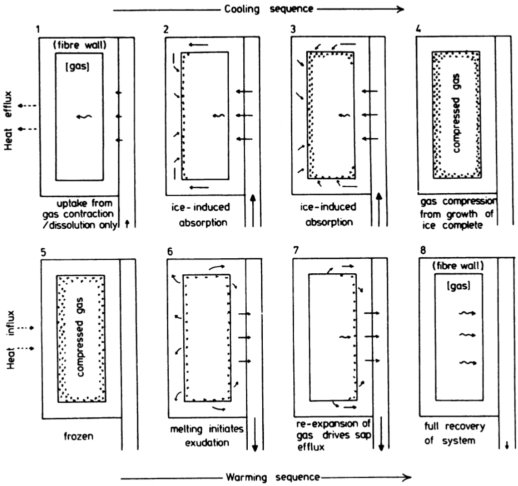
Fall



Milburn–O'Malley: Thawing in spring

- As temperature rises, the process runs in reverse.
- Compressed air generates a positive pressure in the vessels as sap flow is restarted.

Spring



Milburn–O'Malley hypothesis (cont'd)

- Problem with the Milburn–O'Malley hypothesis:
  - At such high pressures, gas should dissolve entirely in the sap after just a few hours!
  - To sustain these pressures, some other mechanism is required.
- Other researchers have suggested incorporating osmosis or other effects.

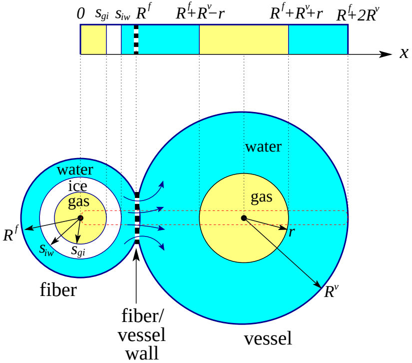
> *"There is insufficient quantitative information to set up a system of physical equations to describe the model predicted in Figure 8. There is no theoretical basis upon which to predict whether O'Malley's model will explain the effect of the rate of freezing on the time course of sap flow rate or pressure change."*
> *—Tyree (1983).*

- No attempt has been made (yet) to model the Milburn–O'Malley process!

Model for sap freeze/thaw in xylem

We developed a mathematical model for generation of stem pressure in early spring as frozen sap begins to thaw:

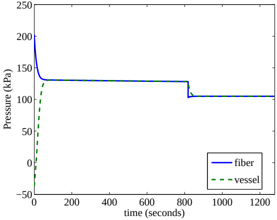
- Focus on one vessel, one fiber.
- Three-phase: gas, water, ice.
- Ice in fiber thaws in response to external heat source.
- Melt-water is driven through porous fiber/vessel wall.
- Vessel gas bubble is in turn compressed.
- Bubbles dissolve/cavitate in response to pressure changes.



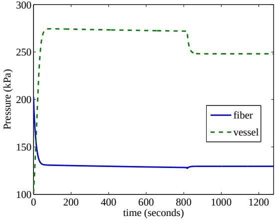
Details in: M. Ceseri & JMS: "A mathematical model of sap exudation in maple trees governed by ice melting, gas dissolution and osmosis", submitted.

Numerical results: Large vessel bubble

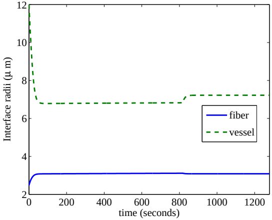
Water pressures



Gas pressures



Gas bubble radii

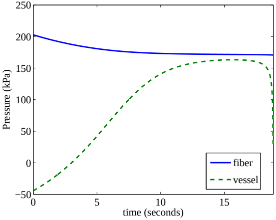


- As expected, there is a transfer of water pressure from fiber to vessel.
- Fiber and vessel equilibrate over time.
- Increase in vessel pressure ($\Delta P \approx$ 60–80 kPa, leaving out osmosis) is close to what's observed in maple trees.
- Gas dissolution occurs over the same time scale seen in experiments (roughly 2–4 hours).

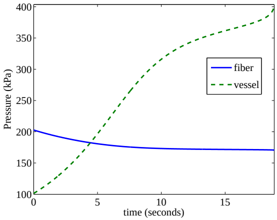
Numerical results: Small vessel bubble

For a more typical value of vessel bubble radius . . .

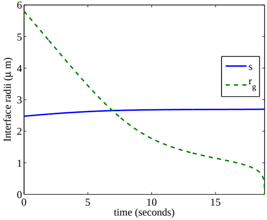
Water pressures



Gas pressures



Gas bubble radii



. . . the vessel bubble collapses, which may be connected with embolism recovery!

Conclusions

We have derived:

- Macroscopic models for sap flow and heat transfer in a tree trunk that incorporate daily fluctuations in parameters.
- A microscopic model for sap exudation during thawing.

All reproduce qualitative (and some quantitative) behaviours observed in experiments.

On-going and future work

- Extend sap flow model for sugar maple in spring thaw conditions.
- "Up-scale" the cell-level freeze/thaw model to obtain T-dependent transport coefficients.
- Fully couple the sap flow and heat transport models.
- Peform detailed comparisons with experiments on sap exudation and embolism recovery.
- Investigate effects of climate changes on sap flow, optimal harvesting strategies, etc.

Thank-you!

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