Mathematical analysis explains transpiration-driven sap flow in coniferous trees

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The exact science of tree sap transport has puzzled plant physiologists for many years. Sap's migration throughout tree trunks and branches is linked heavily to transpiration, the movement and subsequent evaporation of moisture from plants. As carbon dioxide diffuses inward from the air to plant leaves, a vapor pressure deficit between the leaf interior and surrounding atmosphere causes evaporation. This generates tension within leaf cell walls that is then transmitted via sap to tracheids—conductive hollow wood cells with vertical grooves that comprise the trunk, stem, and branches of trees and are collectively called sapwood. The resulting negative sap pressure draws water from roots to leaves, sometimes to heights of over 300 feet.

Tracheids are the primary conductive elements in coniferous trees, and resemble tubes with small holes (or pits) that connect them both vertically and radially. Substances travelling in the radial direction must pass through many of these pits; thus, radial travel is more difficult than vertical travel. As a result, hydraulic conductivity is highly anisotropic (direction-dependent) and liquid movement is easier in the vertical direction.

In an article publishing this week in the *SIAM Journal of Applied Mathematics*, Bebart M. Janbek and John M. Stockie present a multidimensional porous medium model that measures sap flow within a tree stem. "I became interested in tree sap flow about seven years ago when I started studying the freeze-thaw mechanism that governs exudation—a fancy name for oozing—of maple sap from sugar maple trees during harvest season in late winter," Stockie said. "I grew up in Ontario and visited sugar bushes as a child, so I was thrilled by the opportunity to apply mathematical techniques to the study of the iconic sugar maple." His work with Janbek expands upon an existing one-dimensional model, and notably includes a nonlinear parabolic partial differential equation (PDE) with a transpiration source term.

Researchers frequently use mathematical models to study the flow of sap within conductive sapwood. Electric circuit analogy and porous medium models—which model sap flow quite well due to the simple, repeating microstructure of sapwood—are both popular approaches. Unfortunately, most PDE-based porous models are one-dimensional, thus ignoring the radial variations within plant stems that make sapwood anisotropic.

The authors' extended multidimensional model of a tree trunk records radial velocity and allows for the study of radial flow patterns within the stem. It also includes a more realistic tapered axisymmetric stem geometry. In this geometry, an outer layer of conducting sapwood—containing both liquid sap and air— surrounds a core region of non-conducting heartwood (the dense, inner part of a tree trunk) that is resistant to flow. An imposed transpiration flux along the outer surface drives the flow of water from the roots through the stem and branches to the leaves or needles.

"The main advantage of this model is that it captures radial variations through the stem," Stockie said. "This is important when studying effects of geometry, which lead to significant differences between very young trees, which are cylindrical columns of conducting sapwood, and more mature trees, where a 'dead' sapwood core means that flow is constrained to a thin annular-shaped layer. One-dimensional models can only capture transport between roots and branches in an averaged sense, and cannot distinguish radial flows or geometric effects."

Janbek and Stockie employ realistic coefficient functions fit to experimental data on Norway spruce, a conifer native to Northern, Eastern, and Central Europe. However, they note that their model is not limited to any particular tree species. "We choose the Norway spruce for three main reasons," Janbek said. "First, there is a great deal of experimental data available that can be compared to results from our original one-dimensional porous medium model. Secondly, the stem anatomy in conifers like spruce is much simpler, and so we were much more confident in applying our model. Finally, Norway spruce grows in temperate regions where there is sufficient rainfall to ensure that our key assumption of a well-hydrated tree is valid; this spares us the extra complications arising from formation of embolisms (air bubbles) under very dry conditions."

As with most spruce trees, the Norway spruce's stem resembles a circular cylinder that tapers from base to crown. Because its branches occur densely and consistently throughout the entire trunk and stem, the authors can postulate the transpiration flux as a complimentary distribution in the axial direction and include a sap outflow with a subsequent flux boundary condition. They then conduct asymptotic analysis.

"The asymptotic analysis helped us reduce the number of model parameters to a manageable set of dimensionless parameters that allows us to interpret results on tree hydraulics in a meaningful way," Janbek said. "We can capture many essential observations, like the finite speed at which disturbances travel through the stem or the effect of high anisotropy on radial variations in sap flow." Janbek and Stockie validate their findings via a numerical method with a cell-centered finite volume approximation, which confirms the accuracy of their analysis for a large range of saturations.

"Our asymptotic results provide new insights into various flow regimes that occur in tree hydraulics and how this behavior depends on easily-measured physical parameters," Stockie said. "One interesting and somewhat surprising result is that the stem aspect ratio has a much greater influence on sap transport than the degree of anisotropy in the hydraulic permeability, which is often emphasized in other studies. We also derived approximate formulas describing how certain flow variables depend on parameters, which could provide tree physiologists with new opportunities for experimental studies."

The authors' findings enable future study of additional model parameters and inverse problems related to transpiration functions. Future work includes a plan to extend the model to a more general nonsymmetric, three-dimensional geometry to yield a solution with angular variations, and to account for a more complicated branching distribution along the stem. These types of expansions would allow Janbek and Stockie to examine the interplay between transpiration and embolism formation under more extreme conditions. "There are many interesting questions that can be studied using such a model, such as 'what happens when a tap-hole is drilled into the stem of a maple tree, thus breaking radial symmetry?'" Stockie said. "Or, 'how can we explain the known correspondence between temperature fluctuations and small expansion/contraction in stem diameter, and how does this affect sap transport?' The long-term goal of our research is to develop a comprehensive model for tree sap flow that incorporates a whole array of physical and biological mechanisms taking place over multiple spatial scales."

More information: Janbek, B.M., & Stockie, J.M. (2018). Asymptotic and Numerical Analysis of a Porous Medium Model for Transpiration-driven Sap Flow in Trees. *SIAM J. Appl. Math*. (to be published).

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