



A Model of Phloem Transport

Summary

In IFS Objective 2 *Mechanobiology of wood formation*, we are developing a simulation framework to integrate and improve our knowledge of the mechanisms of wood formation. The purpose of this project is to obtain a better understanding of the drivers of growth rate and wood property patterns.

In this milestone, we developed a new software component for the simulation framework. The component is a computer model simulating the transport of photoassimilates (sugars and other compounds) within a tree. The model replaces an empirical relationship previously in use to simulate carbon allocation. The new model actually describes the process by which sugars are transported, not just the resulting allocation. In that respect, the new model satisfies the philosophy of Objective 2 which is to investigate causal relationships. The model can be used across species as it is based on an hypothesis widely accepted for all higher plants. Unlike the old model, carbon flow around branches can be simulated, and the effect of grain orientation is taken into account.

The new component allows the local carbon supply to be predicted at any point on a tree stem, which is essential to determine the rate at which wood is being laid. It is a major step towards the integration of a radial growth model in the IFS Objective 2 modelling framework. Such integration is the missing link between simulating wood formation rate and properties at a fine spatial scale and simulating growth of a whole tree. It is an important step for a better assessment of the resource quality.

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Objective

The purpose of this milestone was to upgrade the transport capability in the IFS Objective 2 modelling framework. There are two main transport pathways in trees: the phloem and the xylem. The xylem is the wood and this is where water and nutrients transit from the soil to the leaves. Sugars and other organic solutes produced by photosynthesis travel in the opposite direction, i.e. downwards, through the phloem. In our previous modelling approach, carbon was allocated using an empirical relationship between foliage distribution and diameter growth. While that relationship implicitly acknowledges that assimilates are produced in the leaves and that transport is distance dependent, it does not explain how sugars are transported, and nor does it account for the geometry and properties of the physical pathway where the transport occurs. The old component has been replaced by a new one able to predict sugar concentration at any point on the tree stem surface in a mechanistic manner. The new approach is biologically more realistic and in agreement with Objective 2's focus on cause-effect relationships. It also allows more complex cases to be simulated.

The Phloem: A Pathway for Carbon

The phloem is a tissue found in vascular plants whose function is to transport carbohydrates. The phloem is a layer located at the periphery of woody shoots and roots, just under the bark. Van Bel¹ calls the phloem a 'miracle of ingenuity', hinting thereby at its complexity. Much of the complexity derives from a high degree of specialisation to ensure sap flows efficiently. For instance, the main functional unit in the phloem is not one cell but a cooperative tandem: a sieve element that is a tube optimised for fluid motion and a companion cell that performs metabolic duties for both. An uninterrupted file of sieve elements can go the whole length of a plant, up to a hundred meters in the case of trees. This aspect points to the multi-scale nature of phloem transport or, as Thompson² puts it, 'the long and the short of it.' Fisher³ describes the phloem as 'pigs feeding at a long trough' or in other words, the phloem is the distribution network from which growing tissues ('sinks') get their building material ('sugars'). The phloem is also a 'high-pressure manifold'³ with sap pressure reaching values ten times the atmospheric pressure. Pressurization is assumed to be the driving force behind sap flow (see next section). Alternative theories exist, stating that pressure either plays a



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signalling role², or that pressure deters insects from feeding on the sap (imagine trying to drink from a fire extinguisher). In spite of the extensive work done on it, phloem transport is an active area of research and to this day remains 'a puzzle'⁴.

Münch's Hypothesis

Münch⁵ proposed that sap movement in the phloem is a pressure flow. Sugar concentration is high at the leaves where solutes are being synthesised and loaded into the phloem. Water is sucked into the conduit by osmosis. The water intake leads to high turgor pressure which pushes the sap down the phloem towards the roots. Solute are transported along with the sap. The mechanism proposed by Münch is interesting because it is theoretically passive: no metabolic energy is required. In practice however, it has been suggested that loading and unloading occur along the conduit and that the flow is actively regulated². That alternative theory is an osmoregulatory flow where the amount of pressure is biologically controlled by the companion cells via exchanges with surrounding tissues. The main weakness with Münch's hypothesis is that it does not accurately explain transport over long distances. Despite that, the hypothesis is the most widely accepted theory on how phloem transport occurs.

Modelling State-of-the-art

The need for mechanistic transport modelling has been asserted by Thornley⁶ as the minimal framework to describe plant growth dynamics. Yet in spite of his recommendation, few individual tree growth models describe carbon transport as a process⁷. When they do, they use a transport-resistance approach which has been criticised for not really describing transport as a flow⁸. On the other hand, models that are only used for studying the phloem all describe carbon translocation as a pressure flow.

The sap flow in the xylem is physically simpler than the phloem sap flow as the former is uncomplicated by the effect of organic solutes. Yet Zimmermann⁹ already noted that models of "sap ascent have become so mathematical that they are not read by many plant anatomists." This aspect is much worse in the case of the phloem, which leads to complicated mathematical treatments. So there is a clear gap in how accurately phloem transport is modelled

depending on whether that model is single-purpose or a part of a growth model.

In the past decade, models of phloem transport have been proposed, each introducing new features at the time:

- Daudet *et al.*¹⁰: xylem and phloem flows are coupled; foliage, stem, roots are compartments.
- Thompson and Holbrook¹¹: phloem flow in a conduit with explicit dimensions and deformable boundaries.
- Hölttä *et al.*¹²: xylem and phloem flows are coupled; stem has explicit length.
- Lacoïnte and Minchin¹³: phloem flow in a branched architecture.
- De Schepper and Steppe¹⁴: xylem and phloem flows are coupled; no explicit length (compartments); accounts for irreversible growth; can predict response to girdling.

IFS Objective 2's Carbon Transport Component

The new component developed to simulate carbon transport describes sap as a pressure flow. Flow equations are derived from conservation of water mass and solute mass over a control volume. Using simplifying assumptions, we reduce the system of equations to a diffusion-like system. The analogy of diffusion is common in engineering to describe the behaviour of groundwater flows, and this is by and large what we reduce the sap flow to. So far, daily fluctuations in sap flow are neglected, an approach that is consistent with the time scale of growth. The component is built on top of Abaqus (SIMULIA, Providence RI, USA) and Calculix (www.dhondt.de) Finite Element software. After a simulation, the component returns sugar concentration and sap pressure at any point of the tree surface and at any time. The simulated data can be used to drive a model of radial growth rate. This would result in a tree growth model that can predict wood structure with a very high resolution.

The phloem transport component introduces new features with respect to previous models:

1. Circumference of shoots is an explicit dimension; the phloem is represented as an actual manifold and not a pipe.
2. The impact of fibre orientation on translocation is taken into account.



- The possibility exists to distribute the unloading of sugars over the entire tree surface rather than just at the roots' end.

Application

To demonstrate the new component, it is applied to a simple test case. We consider a stem section with fixed values of sucrose content at both extremities. Concentration is high at the top ($c = 400 \text{ mol m}^{-3}$) and low at the bottom ($c = 100 \text{ mol m}^{-3}$). A circular region representing a branch insertion is created on the stem surface. Sucrose concentration is very high in the branch ($c = 500 \text{ mol m}^{-3}$). The distribution of sap pressure resulting from those conditions is shown in Figure 1.

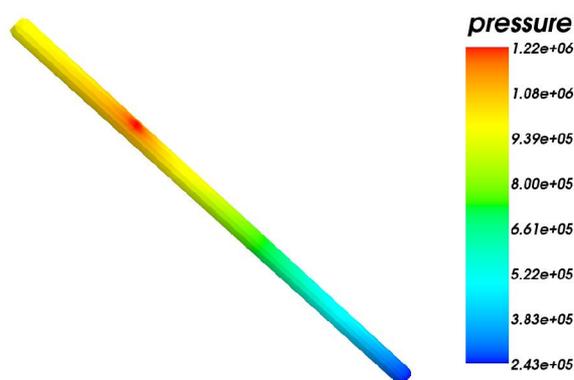


Figure 1: Distribution of phloem sap pressure (Pa, $10^5 \text{ Pa} = 1 \text{ atm}$) on a tree stem section.

The perturbation of the overall pattern caused by branch presence is limited to branch vicinity. Hydraulic conductivity in the direction of the fibres is in agreement with those found in the literature, suggesting that the impact caused by the presence of a branch on the supply of carbon to the cambium is quite local. The major uncertainty in this simulation is the degree of lateral transport. Lateral conductivity was arbitrarily fixed as a tenth of the longitudinal. Knowledge regarding the matter is scarce; we are aware only of Kagawa *et al.*¹⁵'s study on carbon translocation in Siberian larch trees. Their study shows that carbohydrates are transported along the grain direction and no evidence for lateral movement has been observed. It will be interesting in the future, after the model has been coupled to radial growth, to see what sets of carbon transport parameters yield realistic shapes for radiata pine trees

Conclusions

In order to better understand patterns of wood variation within stems we are developing a stem formation simulation framework. In this work we have reviewed the state-of-the art in regard to phloem transport.

Amazingly, after several hundred years of research into plant physiology, there is still a degree of uncertainty about the fundamental mechanisms involved in transport of photoassimilates (sugars and carbon) within the phloem. However, the so-called Münch hypothesis is still the most widely accepted explanation.

Based on Münch's hypothesis we have developed a computer model that simulates the phloem transport process. This model predicts carbon supply at any point in a stem and it can help determine the rate at which wood is laid down. It improves over the model previously employed within the simulation framework by replacing empirical relationships with causal mechanisms.

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