



Phloem transport in trees: A generic surface model



Damien Sellier*, Jonathan J. Harrington

Scion, Private Bag 3020, Rotorua 3046, New Zealand

ARTICLE INFO

Article history:

Available online 5 December 2013

Keywords:

Carbohydrate transport
Finite element analysis
Phloem
Pressure flow
Surface

ABSTRACT

Phloem transport is the process by which carbohydrates produced in the leaves are translocated throughout a plant. In trees, phloem transport determines the quantity of carbon locally available for radial growth. It is involved in the formation of stem shape and wood patterns. We present a model where the phloem is described as a three-dimensional surface with distributed carbohydrate unloading. Generic, simplified equations of transport for sap and carbohydrates are solved using finite element analysis. With that approach, complex shapes and material distributions can be simulated. We show that predicting sap movement for a branched architecture is easily handled with a surface representation. Numerical experiments predict that, in order to explain the translocation patterns observed in some gymnosperms, hydraulic conductivity must be at least 10^5 times greater along sieve cells than across them. Although the value remains to be confirmed by direct measurement, this result demonstrates how the model can be employed to study poorly documented phenomena such as the lateral component of phloem transport in trees. Finally, we discuss how trees can efficiently distribute carbohydrates over the stem surface to ensure a homogeneous cambial activity.

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1. Introduction

The phloem is the distribution network for carbohydrates in vascular plants. In most trees it is a thin layer located between the bark and the vascular cambium. The phloem forms a pathway that connects carbon sources to carbon sinks. Carbon is produced in the leaves by photosynthesis. Leaves are spatially distributed yet highly localised at one end of the pathway. In contrast, sinks are not only located at the other end but found everywhere in the plant. Although roots constitute a major sink, carbon is consumed everywhere in the symplasm for respiration and maintenance. In woody plants, secondary growth is an equally important carbon sink. The vascular cambium, where secondary growth takes place, is adjacent to the phloem and similarly distributed in the plant. Carbohydrate stores play a special role. At different times they are both sinks and sources. Stored carbohydrates can be significant sources at different stages of plant development, for instance to initiate new leaf growth in deciduous trees (Kozłowski, 1992). Storage pools can only release carbon for a limited time. Once depleted, stores must be filled again, thus becoming sinks. In order to tap and release into the globally available carbon, storage tissues are connected to the phloem and distributed throughout the plant. More than just a conduit, the phloem should be seen as an exchange surface.

A high degree of cellular specialisation ensures that phloem sap flows efficiently (van Bel, 2003). In angiosperms, sap moves through the sieve tubes. Sieve tubes are files of cells connected end-to-end by perforated sieve plates. Each cell in a file is referred to as a sieve-tube element or a sieve-tube member (Esau, 1965). The sieve-tube element is stripped of its internals to minimize the hydraulic resistance to transport. Each sieve-tube element is closely associated to a companion cell, which performs metabolic duties for both cells (Evert, 1977). Together, the sieve-tube element and the companion cell form the base functional unit for transport. A similar unit is found in the secondary phloem of conifers. It consists of a sieve element, the sieve cell, and an associated parenchymatic element, the albuminous cell (Evert, 1977). However, cell connectivity and structure differ between angiosperms and conifers. In conifers, the phloem structure is relatively simple and similar to that of the xylem (Esau, 1965), with sieve cells organised not in files but rather overlapping each other at their ends.

Münch (1930) first proposed that phloem sap movement is a pressure flow. Carbohydrates synthesised in the leaves are collected and loaded into the transport phloem. Different loading mechanisms exist in plants (Rennie and Turgeon, 2009) but, independently of the mechanism involved, loading results in a high solute concentration in the phloem that drives the water in by osmosis. The water intake leads to high turgor which pushes the sap down towards the roots. In the roots, osmotic potential and turgor are kept low as a result of solute removal and utilisation. A pressure gradient is thus maintained. Münch's hypothesis is interesting in that transport is passive. It is the by-product of phloem

* Corresponding author. Tel.: +64 73435709.

E-mail address: damien.sellier@scionresearch.com (D. Sellier).

loading and unloading and, while both those mechanisms may be active, the transport process itself requires no metabolic energy. Although the pressure-flow hypothesis is widely accepted as the base mechanism underlying phloem transport, it does not provide a good explanation for some aspects of phloem transport, for example the translocation rates measured in trees over long distance. Lang (1979) proposed a relay mechanism where solutes are actively transferred at the end of a file of sieve tubes into the next file in order to complement the pressure flow and to ensure solutes can move along the entire length of the pathway irrespectively of the distance to cover. An alternative theory is that of an osmoregulatory flow where pressure in the sieve tubes is biologically regulated by companion cells via exchanges with surrounding tissues, thus maximising the pressure flow efficiency (Thompson and Holbrook, 2003b; Thompson, 2006). In both cases, an active mechanism complements the pressure flow. Thus, the loading and unloading of solutes from sieve elements occurs not only to meet growth and metabolic requirements of the surrounding tissues, but also provides a way to control flow efficiency. In annual plants, pressures in the phloem can be quite high, up to 2.4 MPa (Fisher and Cash-Clark, 2000), *i.e.* more than 20 times atmospheric pressure. In trees however, pressures reach lower values, typically 0.6–1.4 MPa (Turgeon, 2010). Aside from providing a driving force, this pressurisation might play other roles. Thompson (2006) argued for pressure waves acting as a signalling mechanism. High pressure also deters most insects from feeding on the sucrose-rich liquid (Turgeon, 2010).

Because it is based on well studied physical processes, the pressure-flow hypothesis is attractive to model builders. It describes how phloem sap moves and not only the resulting carbohydrate distribution. With advances in microfluidics, the hypothesis can be directly evaluated using physical experiments (Jensen et al., 2011). Moreover, the hypothesis is generic as it applies to both herbaceous and woody plants. It also works across species with the proviso that phloem structure significantly differs between angiosperms and conifers (Evert, 1977). A recent study points towards a universality of Münch flow in seed plants, albeit with a lot of parametric variability across species (Jensen et al., 2012b). Over the last decade, numerous models of phloem transport have been developed. Thompson and Holbrook (2003b,a) carried out a comprehensive modelling study of single-solute pressure flow in a phloem described as a deformable, one-dimensional conduit. Lacoite and Minchin (2008) extended that approach to branched conduits. Some models relied on representing the loading zone, the transport zone, and the unloading zone as compartments with no explicit geometry. However, those models took into account other important aspects such as coupling phloem transport to xylem transport (Daudet et al., 2002) or coupling to growth activity (De Schepper and Steppe, 2010). Hölttä et al. (2006) introduced a model combining phloem and xylem transport processes with both pathways having an explicit length. Because the mathematical treatment of transport equations is not trivial, they are often solved numerically. Analytical solutions to the steady-state flow have also been documented (Pickard and Abraham-Shrauner, 2009; Jensen et al., 2011, 2012a).

Previous models of phloem transport only take the longitudinal direction of transport into account. That view is supported at the organism scale by the high length-to-diameter ratio usually observed in plants. It is also supported at the microscopic scale by the elongated nature of sieve elements through which phloem sap flows and, in angiosperms, by the arrangement of sieve tubes in files. It is mathematically convenient to simplify the transport equations to the one-dimensional case. Furthermore, it is computationally efficient to neglect transverse transport. Modelling a domain with a high dimensional ratio commonly implies setting the spatial resolution as a function of the smallest dimension.

However, for woody plants, modelling the phloem as a sequence of pipe elements presents several limitations. Firstly, in the longitudinal representation, carbohydrates at any point along a shoot or a root are uniformly available circumferentially. This is contrary to experimental evidence which shows that transport is laterally constrained. Carbohydrates produced by a branch are translocated in a narrow path on the stem's surface (Hansen and Beck, 1990; Kagawa et al., 2005, 2006). Only plant tissues located on that particular path can utilise the solutes. Circumferential variation also occurs with phloem pressure. Lee (1981) recorded a 0.4 MPa difference in pressure between the opposite sides of a *Fraxinus americana* trunk. Moreover, asymmetrical and non uniform growth patterns are abundant in trees. Those patterns include: anisotropic radial growth associated with the formation of reaction wood (Timell, 1986), mechano-regulation of cross-sectional shape in shoots and roots (Mattheck, 1998), nodal swelling at branch–stem junctions, and buttressing. Approximating plant axes as tubular elements is insufficient to predict carbohydrates distribution on those geometries, nor can it help to understand how such geometries emerge in the first place.

Secondly, in previous models, the direction of transport is taken to be that of the shoot while, in reality, the preferred flow direction is that of the sieve elements. In trees, these directions do not necessarily coincide. Carbohydrates can follow a helicoidal path downwards (Hansen and Beck, 1990) that is aligned with spiral grain (Kagawa et al., 2006). Because lateral transport is also limited, a root may be hydraulically connected with a branch on the opposite side of the stem. Furthermore, sieve cell orientation changes over time and so does the direction of translocation (Kagawa et al., 2005). As a result, phloem hydraulic connections on the stem's surface are continuously adjusted as the tree develops.

Understanding the carbohydrate pathway is critical in forestry to determine potential tree growth. It is known that higher photosynthetic production does not necessarily imply more sucrose into the phloem as it depends on the efficiency of phloem loading (Koerner et al., 1995). Similarly, when phloem loading rates increase, a higher availability of solutes for organ growth can only occur if transport does not become the limiting factor. The carbon supply also affects the quantity and properties of the wood laid by the vascular cambium locally. Variation in ring structure and wood properties in tree stems are principal factors impacting on processing and technological performance of wood products.

In order to accommodate the heterogeneity in the carbon supply to the cambium, we have developed a model of phloem transport designed specifically for trees. The phloem is modelled as a manifold. The orientation of sieve cells and the transverse movement of sap and solutes are explicitly taken into account. The present transport model is designed to interact with a model of individual tree growth based on the level set method, a computational technique used to simulate evolving interfaces (Sethian, 1999). In the growth model, the tree is also represented as an expanding surface (Sellier et al., 2011). Because of the focus on growth activity and wood formation, only steady-state transport equations are solved. We present two applications of the transport model that aim to emphasize the benefits of representing the phloem as a surface. In the first one, we show that the model can simulate phloem transport for a tree with a branched structure. In the second application, we investigate lateral transport in conifers by replicating *in silico* a pulse-labelled translocation experiment (Kagawa et al., 2006).

2. A surface model of phloem transport

2.1. Notation

We use matrix notation in this study. It is straightforward and allows equations describing multi-dimensional problems to be

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