

Mechanistic modelling of carbon allocation among sinks

A generalised Münch model for branched architectures

André Lacointe⁽¹⁾ and Peter Minchin⁽²⁾

⁽¹⁾UMR (INRA - Université B. Pascal) PIAF, INRA, Site de Crouel,
234 avenue du Brézet, F-63039 Clermont-Ferrand Cedex 2, France

⁽²⁾ The Horticultural and Food Research Institute of New Zealand Ltd., 412 No. 1 Rd., RD2
Te Puke, New Zealand

lacointe@clermont.inra.fr , pminchin@hortresearch.co.nz

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Introduction

Partitioning of carbohydrate between competing sites is fundamental to all plant development, growth, and eventually yield. Carbohydrate is synthesised in the mature leaves and distributed by the phloem vasculature to sites of utilisation. The mechanism currently believed to drive phloem transport was proposed by Münch in 1928 and only recently generally accepted. However, the processes determining how much goes to each competing sink are still unknown. Models of plant growth that integrate knowledge of the individual processes still rely upon empirical algorithms to describe carbon (C) partitioning, which is a major bottleneck to allow truly predictive modelling, especially in changing conditions (Lacointe 2000, Minchin and Lacointe 2005), and can only be solved through mechanistic understanding.

Mechanistic models: phloem transport v. C allocation

To date, all mechanistic modelling of phloem transport, i.e. pressure-driven mass flow, has involved simple flow geometries (Thompson and Holbrook 2003, and references therein; Hölttä et al. 2006), as realistic geometries make the mathematics intractable. As a result, these attempts could not address spatial allocation among sinks, although they successfully simulated a number of quantitative properties of phloem transport. On the other hand, Minchin et al. (1993) developed a mechanistic model, based upon a simplified version of Münch's hypothesis, which successfully mimicked C flows to two competing sinks, suggesting that sink priority is an emergent property of osmotically driven mass flow. That is, sink priority is a property of the entire system, not any single component. Recently, the same minimal Münch model of osmotically generated pressure driven phloem flow through a resistive non-leaky transport pathway, has been incorporated into the functional-structural tree model L-PEACH (Allen et al., 2005) which can handle a realistic complex branched architecture. However, this minimal model ignores most of the known physiology of conduction tissues, including ubiquitous lateral transfers between both sap systems. As a result, the importance of these to the overall function and partitioning of phloem flow is still unclear.

A generalised Münch model for realistic architectures

A few years ago, Daudet et al. (2002) introduced the modular approach to handle realistic geometries in an extended Münch model that quantitatively described the coupled water/C fluxes through the double xylem/phloem pathway. Beside its ability to represent any branched architecture, the modular concept allowed explicit descriptions of local C and water exchange properties as well as C metabolism at an arbitrary level of detail (i.e. the size of elemental modules), thus allowing a realistic description of the local source/sink functions throughout the architecture and eventually a mechanistic description of C allocation among organs. However,

because of its implementation based on the electronic circuit simulation software SPICE, the original version was hardly user-friendly, and above all could not be easily interfaced with other process modules in an integrated structural-functional model. To overcome these limitations, the generalised Münch model has recently been transcribed into the C++ computer language.

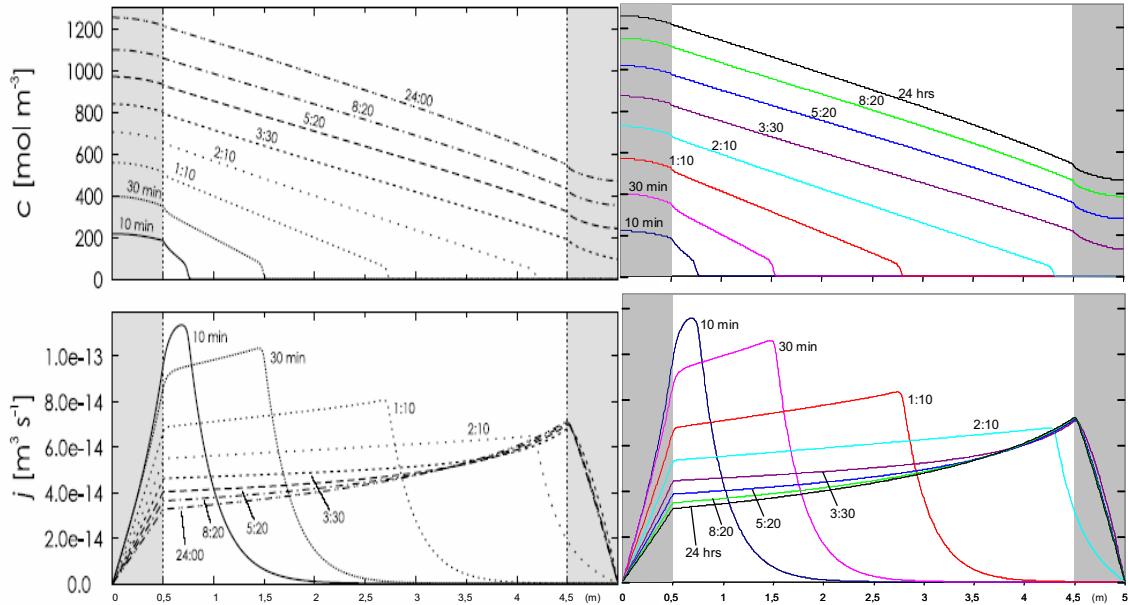


Fig. 1. Münch model: standard continuous approach (Thompson and Holbrook 2003, to the left) v. modular approach (to the right) : simulation of dynamic profiles of concentration and axial water fluxes along an ideal 5-metre-long sieve tube with a 50-cm-long uniform loading area and a 50-cm-long uniform unloading area at either end. On this simple, unbranched architecture, both approaches yield quasi-identical results; however, contrary to the continuous approach, the modular approach can handle realistic, branched architectures and complex loading/unloading patterns.

Current version of the model

Beside its ability to interact with other processes, the generalised Münch model has been significantly improved in 2 aspects: (1) entering the architecture configuration and source-sink properties is much more straightforward, by just editing a few lines in the code; (2) the mathematical solving capacities, now allowing a significantly larger number of elemental (branched or not) modules to be included in the architecture ($N > 1000$). It has been validated by comparison with the current reference for the Münch model (Thompson and Holbrook 2003), in the simple, unbranched configuration that the continuous approach can handle (Fig. 1). This comparison further demonstrated the flexibility and extensibility of our modular approach, as a few refined biophysical details (e.g. viscosity changes with concentration, or non-zero specific sugar volume) that were not originally present in the SPICE version (Daudet et al. 2002) had to be included in the model.

At the current stage of development this model describes a static (non-growing) architecture, but the same approach is easily extended to a developing architecture by inclusion into any modular FSPM that allows deriving parameters and state variables of the new modular elements from those of pre-existing elements. Accordingly, it will be implemented into the model PIAF-1 (Lacointe and Donès, 2007) as a mechanistic module for water and C fluxes.

This presentation will further show how the generalised Münch model can account for sink priority in a simple branched configuration: 1 source / 2 sinks, i.e. the original configuration of Minchin et al. (1993) but including more relevant physiological processes, especially xylem/phloem interactions in relation to loading/unloading properties.

References

- Allen MT, Prusinkiewicz P, DeJong TM 2005. Using L-systems for modelling source-sink interactions, architecture and physiology of growing trees: the L-PEACH model. *New Phytologist* 166(3): 869-880.
- Daudet F.A, Lacointe A., Gaudillère J.P., Cruiziat P. 2002. Generalized Münch coupling between sugar and water fluxes for modelling carbon allocation as affected by water status. *Journal of Theoretical Biology* 21: 481–498.
- Hölttä T., Vesala T., Sevanto S., Perämäki M., Nikinmaa E., 2006. Modeling xylem and phloem water flows in trees according to cohesion theory and Munch hypothesis. *Trees* 20: 67-78.
- Lacointe A., 2000. Carbon allocation among tree organs: A review of basic processes and representations in functional-structural tree models. *Annals of Forest Science* 57, 521-533.
- Lacointe A., Donès N., 2007. Functional –structural modelling using the generic tool PIAF-1 : a simulation example on young walnut. This workshop, oral presentation.
- Minchin PEH, Thorpe MR, Farrar JF., 1993. A simple mechanistic model of phloem transport which explains sink priority. *Journal of Experimental Botany* 44: 947–955.
- Minchin P.E.H., Lacointe A., 2005. New understanding on phloem physiology and possible consequences for modelling long-distance carbon transport. *New Phytologist* 166: 771–779.
- Münch E, 1928. Versuche über den Saftkreislauf. *Deutsche botanische Gesellschaft* 45, 340-356.
- Thompson MV, Holbrook NM., 2003. Application of a single-solute non-steady-state phloem model to the study of long-distance assimilate transport. *Journal of Theoretical Biology* 220: 419–455.