

CHAPTER 10

MECHANISTIC MODELLING OF CARBON PARTITIONING

P.E.H. MINCHIN

ICG-III, Forschungszentrum Juelich, D52425 Juelich, Germany

Currently: HortResearch, Te Puke, New Zealand

Email: pminchin@hortresearch.co.nz

Abstract. Carbon partitioning between alternative sinks is the weak point of all plant growth models, being done using empirically based algorithms. While this approach is effective for simulations, it is unreliable for extrapolation to new conditions, and cannot provide mechanistic understanding of the processes involved. All long-distance carbohydrate transport and partitioning involves the phloem, hence partitioning must be a property of phloem physiology. However, no growth model utilizes the known phloem physiology. Relevant aspects of phloem physiology are discussed and used to produce a minimalist Münch-based flow model. This model provides a theoretical basis for an unambiguous definition of sink strength, with sink priority being an emergent property of the model. A method to extend this minimalist model is discussed.

INTRODUCTION

All plant growth models must have a method to partition carbohydrate between the sinks. While qualitative descriptions of partitioning are available, there is still no accepted mechanistic description (Wardlaw 1990; Marcelis 1993; Lacoite 2000; Le Roux et al. 2001). Plant growth models, therefore, use algorithms derived from observational data. While this is very effective for simulations within the range of the conditions associated with the observational data, this approach cannot be expected to be reliable outside of the calibration environment, and cannot provide information about the source of yield limitations.

DeJong (1999) pointed out that "... dry-matter partitioning does not direct the growth of the tree but is the result of the growth and development of the organs that make up the tree". So, all growth models can be accused of 'putting the cart before the horse'. To move outside the range of the calibration data sets to new locations and environments, in order to model alternative management practices and to gain insight into the plant processes that limit development and yield, mechanistic understanding of partitioning is essential.

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OVERVIEW OF CURRENT GROWTH MODELS

Marcelis and Heuvelink (this volume) classified modelling of carbon (C) partitioning into five categories of increasing complexity: 1) descriptive allometry; 2) functional equilibrium; 3) canonical modelling; 4) sink regulation; and 5) transport resistance (TR) models, where flow is driven by concentration gradients. The most mechanistic description of partitioning is the TR model. This paper elaborates on a TR model.

Respiratory needs have usually been handled independently from all other C-demands, by first removing this from the pool of available C and then distributing the remaining C between the sinks according to the rules of the model (Lacointe 2000). For example, Grossman and DeJong's PEACH model (1994) calculates the total C acquired during a time step, then removes the plant's entire maintenance respiration need from this pool. What remains (if any) is then partitioned between the plant organs according to rules based upon sink priority. This approach to respiration originates from the work of Crapo and Ketellapper (1981), who found that when a root was starved, maintenance respiration continued while growth respiration was reduced or stopped. This demonstrated a higher priority to maintenance, at the expense of growth respiration, but did not address transport of C to the root. Transport of C to the root cells, destined to either maintenance or growth, is via the same pathway, with allocation between these two forms of utilization occurring within the cells. Allocation between different utilization pathways may be determined by the different kinetics of alternative utilizations. Sink competition involves all the C used by that sink, including respiration.

Transport resistance model

The basis of the TR model, first formulated by Thornley (Thornley 1972; Thornley and Johnson 2000), is to put the solute flow J_s between the carbon source and sink proportional to the solute concentration differences ΔC . That is

$$J_s = \text{constant } \Delta C / R \quad (1)$$

with the resistance R involving the distance (L) between the source and sink. Assuming a similar TR description for nitrogen flow between root and shoot, with bi-substrate (C; N) growth kinetics, the well-known shoot:root balance follows Lacointe (Lacointe 2000 and references therein). The commonly observed distance effects, such as a source supplying the nearest available sink, are qualitatively explained by the resistance term. Thornley (1998) has put forward a strong argument that such a minimal TR model needs to be the starting point for all more complex transport models as it incorporates the "only two significant processes: transport and biochemical conversion".

However, this TR model does not reflect the physiological processes known to be occurring in phloem transport, with the source and sinks treated as bulk compartments described by average concentrations of transportable C, which do not reflect the concentrations within the sieve tubes (see below). These average

concentrations will be significantly lower than that of the sieve tubes. As the average tissue concentrations do not reflect those within the phloem transport system, the resistances required to give the observed flows will not reflect that of the phloem pathway. Also, equation 1 describes diffusive rather than mass flow processes, known to occur in long-distance phloem transport (see below), so this equation cannot be expected to describe sieve tube dynamics.

Attempts to assess the effects of the distance between source and sinks have generally led to the conclusion that the transport distance is not an important factor in limiting growth (Wardlaw 1990). Several authors have questioned the need to include transport resistance at all (e.g. Heuvelink 1995; 1996; Bancal and Soltani 2002). Heuvelink showed that the developing fruit of cucumber appears to be supplied from a common photosynthate source and transport resistance plays no role in partitioning between the fruit, and similarly for trusses of tomato fruit. Bancal and Soltani used a modified form of Minchin et al.'s (1993) model to argue that flow resistances are not important, but their model is flawed (see below) so their results need to be reassessed.

Mechanistic modelling by Hölttä et al. (2006) suggests that, with high loading rates, phloem transport may be inhibited by high sucrose concentration giving rise to high flow viscosity and hence high flow resistance. Lang (1978) argued that maximal flux within a bulk flow system occurs at sucrose concentrations of about 700 mM, remarkably similar to that found in phloem sap (Gould et al. 2004). Van Bel and Hafke (2005) showed that sieve pores of the sieve plates are often seen to be partially blocked; they suggest that unloading and reloading on either side of this partial blockage may be a mechanism to reduce the apparent flow resistance. Thompson and Zwieniecki (2005) suggested that unloading/reloading of potassium ions may have a role in reducing apparent flow resistance.

Work on flow resistance has involved small plants, and now needs to be reassessed on large plants (e.g., trees), where flow resistance is expected to play a bigger role.

Distribution of carbohydrate within plants is a major role of phloem transport, now generally agreed to function according to the mechanisms suggested by Ernst Münch in 1928. However, this mechanistic understanding has not been used in plant growth modelling (Minchin and Lacoïnte 2005).

BACK TO BASICS

I will outline important aspects of phloem physiology that I believe to be relevant to growth modelling. The current status of phloem physiology has been very well reviewed by Van Bel (2003). Münch proposed that phloem transport involves a semi-permeable-membrane-lined conduit linking the source and sink, now identified with the sieve tubes. At the source, phloem loading generates a high solute concentration within the sieve tubes with concomitant osmotic water flow generating a high hydrostatic pressure. At the sink, solute unloading results in a lower hydrostatic pressure. The resulting pressure gradient between source and sink drives bulk flow of phloem sap. Münch did not expand upon the details of phloem

loading or unloading. This has been an active area of research and is now believed to involve either active uptake by the phloem cells (probably the companion cells or possibly directly into the sieve tubes) from the apoplast, or by symplastic transport down a concentration gradient from the palisade cells, or a combination of these routes. Plants that transport sugars of the raffinose series are believed to generate a locally high solute concentration by symplastic transport (i.e. not involving crossing a membrane) of sucrose down its concentration gradient to the intermediary cells (a kind of companion cell) where the larger raffinose-series sugars are synthesized. Being large molecules these oligosaccharides are not able to diffuse back, and generate a hydrostatic pressure gradient that drives bulk flow (Turgeon and Ayre 2005). Many temperate-climate woody plants, including most of the tree species, are symplastic loaders (Turgeon and Medville 1998). While the specific details of generation of the sieve-tube pressure gradient is unlikely to be important to modelling plant growth, it is now accepted that phloem loading generates the driving force for bulk solution flow through the sieve tubes.

Phloem unloading into most tissues is thought to be symplastic, involving plasmodesmata linking cells within the sink region. Termination of symplastic flow is therefore not at the terminal sieve tubes but within the cells of the sink, with sink osmotic pressure being kept low by metabolism of the carbohydrate or conversion to less osmotically active forms (starch, fructans). There is growing agreement that the region of highest flow resistance is not within the transport phloem linking the source to sinks but is within the contiguous symplast of the sink cells (Gould et al. 2004). Within developing seeds, where the daughter tissue is symplastically isolated from the parent tissue, apoplastic transfer occurs between the generations, but phloem unloading into the seed coat is symplastic. Whatever the route, unloading kinetics are saturable.

Continuous and simultaneous leakage and reloading along the transport pathway have been demonstrated. (Minchin and Thorpe 1987; Thorpe and Minchin 1996; Van Bel 2003). Sieve-tube concentrations are high and biological membranes are not perfect, so it is not surprising that there is leakage into the surrounding apoplast. Reloading is essential if the conduit is not to lose its entire contents before delivery to terminal sinks. This leakage is probably essential in the maintenance of stem tissues, and is probably the route into the ray cells for storage and remobilization of carbohydrate within stems, trunks and roots of all plants. Transport phloem is symplastically isolated from the surrounding tissues (Van Bel 2003), a necessary step in maintaining high solute levels with the transport pathway, and giving leakage/reloading an important role in the controlled supply of carbohydrate for storage and subsequent remobilization. Plant species with symplastic phloem loading in the leaves have a higher potential for stem uptake of leaked photosynthate than found in species with apoplastic phloem loading in the leaves (Van Bel 1996). Van Bel has suggested that this may lead to symplastic loaders favouring lateral sinks over apical sinks, giving rise to differences in relative growth rates between lateral and terminal sinks and hence affecting architectural traits. A direct consequence of stem leakage and remobilization is a buffering of changes in sieve-tube content from changes in source supply and sink demand by decoupling these two processes (Thorpe et al. 2005; McQueen et al. 2005). When the stem pool is

depleted, this might be sensed by the storage cells within the stem to induce remobilization of storage pools.

Numerical modelling of Münch's basic hypothesis has demonstrated that, while this mechanism is able to account for both the observed mass flow rates and transport speeds observed in herbaceous species, files of sieve tubes longer than several meters are not able to support observed flow rates (Thompson and Holbrook 2003). Lang (1979) proposed that short files of contiguous sieve tubes, involving unloading from one with reloading into the next and thus acting as a relay, would overcome this problem. Van Bel and Hafke (2005) observed that, even within small plants, sieve plates linking adjacent sieve tubes can often be partially blocked and suggested unloading and reloading as a means to circumvent such a partial blockage. This suggestion combines the relay concept with transport phloem unloading/reloading. Numerical modelling incorporating transport phloem unloading/reloading has not been done, and is now badly needed to see if this significantly affects the dynamics of phloem transport. Recent detailed measurements of transport phloem dynamics within a bean stem shows increasing net unloading towards the shoot apex (Minchin unpublished), contrary to the numerical models.

All the detailed numerical work demonstrating feasibility of the Münch theory has been for a single source and single sink. However, no plant is so simple. To the author's knowledge the first Münch-based model involving two or more sinks was that of Minchin et al. (1993).

A MECHANISTIC MODEL OF CARBON TRANSPORT BASED UPON THE MÜNCH HYPOTHESIS OF PHLOEM TRANSPORT

A brief summary of the key points of the Minchin et al. (1993) model follows. This model is based upon a minimal set of assumptions similar to those proposed by Münch:

- the pathway of C flow is represented as a perfect non-permeable conduit, with flow described by Poiseuille's equation for laminar flow,
- at both source and sink, osmosis determines the local hydrostatic pressure described by a Van't Hoff equation, and
- sink unloading is non-linear and saturable, which for simplicity is described by a Michaelis-Menten equation.

With these hypotheses, a set of coupled non-linear equations for the flows can be written for any network of sources and sinks. Non-linearity of these equations forces one to use numerical methods for their solution, but it is this non-linearity that generates realistic carbon allocation.

With one source and one sink the flux of photosynthate F between source and sink is

$$F = s_0(s_0 - s_1)/\alpha \quad (2)$$

where s_0 is the source concentration, s_1 the sink concentration, and α a resistance term, incorporating solution viscosity and source–sink separation. At equilibrium, this flux must equal the Michaelis-Menten unloading, yielding an equation linking the Michaelis-Menten parameters v_m and k_m , with s_0 and s_1 , which can be solved for s_0 .

The important point of this model is that flow is proportional to the solute concentration gradient times the solute concentration at the source, so that flow is much more strongly affected by the source concentration than in the simple TR model, where flow is proportional to the concentration gradient alone.

It has been assumed that the conduit linking the source and sink is non-permeable, which allowed use of the Poiseuille law to relate pressure differences to flow. This is clearly not the case, but one purpose of models is to investigate what mechanistic detail is necessary to generate the observed phenomena. This involves reducing model detail to the bare essentials. Only by trial and error, does it become clear what processes are dominant. Also, solution viscosity depends upon the solute concentration, and when the solute is sucrose, viscosity can vary over a range of about 300% (Bancal and Soltani 2002; Thompson and Holbrook 2003). In our simplified model with a non-permeable conduit, solute concentration does not change within the conduit, so the flow resistance fully incorporates solution viscosity. Bancal and Soltani (2002) corrected for changes in flow resistance along the conduit, which would occur with a permeable conduit, but then Poiseuille's law is not valid. This law requires that the conduit is non-permeable and there is no concentration change within the conduit. This error in their modelling makes their final conclusions suspect.

In the original formulation, Minchin et al. (1993) used s_0 as a measure of carbohydrate supply. Bancal and Soltani (2002) pointed out that at equilibrium the rate of synthesis of photosynthate available for transport must match the calculated phloem flow rate and altered s_0 to match. This is a neat way to incorporate active phloem loading without a need to be explicit over details of the loading process – just that it generates the appropriate solute concentration to drive the required flow rate. Now, as supply varies, so do s_0 and the flow resistance. Bancal and Soltani incorporated this in their work, but unfortunately had an error in their model (see above), so their conclusions require reassessment.

Now we consider the more realistic example of one source and two sinks, coupled as shown in Figure 1 with the source leaf connected via a common resistance, representing the petiole, to two sinks, each with their separate resistances. Photosynthate is available at a rate F and loaded into the source region to give a local concentration s_0 and sink concentrations s_1 and s_2 . This configuration leads to two non-linear simultaneous equations requiring numerical solution, which in term is related to a specific rate of photosynthate supply F . See Bancal and Soltani (2002) for more detail.

Figure 1 illustrates the behaviour of this model with changing availability of photosynthate. The important point to note is that with declining s_0 , flow into both sinks falls and distribution between the sinks changes. That is, altering the supply of solute causes a change in partitioning of this solute between the two sinks. The sink

described by the larger v_m gets a reducing fraction of the available solute as the supply is reduced.

In the experimental literature there are many examples of reports that, after reducing the supply of available photosynthate, one sink receives a reduced fraction of the available supply, and this sink is said to have a lower priority than another which gets a greater fraction of the available supply. In the model, sink priority has appeared as a consequence of the interactions of the component parts; it was not part of the initial assumptions. So, sink priority is an emergent property of this model.

Experimentally, shading the shoot is known to result in increased shoot growth, relative to the root. Short-term measurements of labelled photosynthate distribution show that, within minutes of shading, the root gets a reduced fraction of the available photosynthate (Minchin and Thorpe 1996). Hence, in the model the sink with the larger v_m is the root, provided we assume that both shoot and root sinks are described by the same k_m . This seems reasonable as these two vegetative sinks probably have the same unloading process, and k_m being a binding constant is related to the nature of the carriers involved. This is a further potential source of difference between sink types, e.g., vegetative and reproductive, and needs to be investigated.

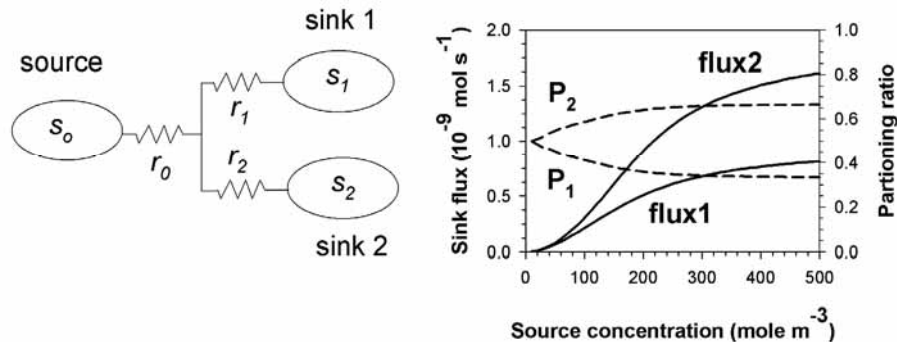


Figure 1. Left: Schematic of a 1-source, 2-sink model, with a common pathway resistance r_0 , and individual sink resistances r_1 and r_2 , respectively. Right: Plot of individual sink fluxes (flux1 and flux2, partitioning fractions P_1 and P_2), with varying source concentrations (s_0), for model parameter values: $r_0=1.0 \times 10^{13}$ mol m⁻⁶ s, and sinks (r , k_m , v_m) of $(1.0 \times 10^{13}$, 100, 1×10^{-9}) and $(1 \times 10^{13}$, 100, 2×10^{-9}) in units of k_m : mol m⁻³; v_m : mol s⁻¹

Having made this link between the model and the experimental plant we can now test the consequences. For example, v_m is expected to be associated with the amount of a specific sink. Experimentally we can reduce the root v_m by pruning or by lowering the temperature. If the root v_m is reduced to below that of the shoot then the root:shoot priority is predicted to be reversed. In fact, this is exactly what was found (Minchin and Thorpe 1996).

A further support for the model comes from experiments from other laboratories. Grusak and Lucas (1985) reported changes in partitioning between two developing

leaves of sugar beet in response to slow cooling of the petiole of the labelled source leaf. The model predicts a change in partitioning between alternative sinks when there is a change in the resistance of the common pathway (Minchin et al. 1993, Figure 7). Petiole cooling is expected to change, at least, the phloem sap viscosity, and possibly the sieve-plate resistance, so this explanation is consistent with the model. A change in solute supply rate may alter the flow resistance through a change in sap viscosity, so this could also be part of the shading response.

Within the phloem literature, especially associated with source–sink interactions, there is frequent use of the terms sink strength and priority. This simple model gives both of these terms a sound theoretical basis. Sink strength, defined as the potential import into a sink when supply is not limiting (Wareing and Patrick 1975) is represented by v_m , and sink priority can be quantitatively defined as the first differential of sink strength with respect to supply – that is, the rate of change of supply to a specific sink when the total available supply is altered by a small amount. Sink priority as a qualitative concept is well established, and summarized by the priority rank order (Wardlaw 1990):

seeds>fleshy fruit parts=shoot apices and leaves >cambium>roots>storage,

determined by pruning experiments. But, the term priority has frequently been misused. For example, it has often been said that a sink shows high priority because of high sink strength. Minchin and Thorpe (1996) have discussed this in detail.

What do we mean by the potential import into a sink? ^{14}C tracer studies show that on making more photosynthate available to a sink by reducing import into other sinks, that sink is not always able to utilize more photosynthate immediately (Farrar and Minchin 1991), but after several hours import does increase. So what do we take as the potential utilization rate? In the proposed model, v_m is the current potential rate of utilization and this appears to be under control of carbohydrate availability, which leads us to suggest that for a plant ‘in a steady state’, the v_m adjusts to make the associated sink appear to be near saturation (Minchin et al. 1993).

The importance of this model is not in its detail, but simply to show that a simple non-linear model based upon a few physiological mechanisms has a behaviour that parallels that of a real plant. Further work is now needed to investigate the process known to be functioning within the phloem but not incorporated within this model. Introduction of a semi-permeable conduit needs to be investigated, though this has been well treated in the continuum models of Christy and Ferrier (1973) and more recently by Thompson and Holbrook (2003). Unloading and reloading along the transport pathway is expected to have a greater effect and possibly alter the manifestation of resistance. Also, coupling to the nearby xylem system may be important (Hölttä et al. 2006).

Daudet et al. (2002) have shown a possible way to make these extensions. Their approach is based upon a description of the component parts in terms of discrete modules, each individual module with its own parameter values, allowing a large range of potential processes to be investigated. This approach could provide a mathematical tool to investigate the effect of specific mechanistic details upon predicted phloem dynamics for direct comparison with experimental results.

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