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A Phloem Transport Model; A New Surface Evolver

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EXECUTIVE SUMMARY

An accurate modelling of wood formation involves understanding the processes by which photoassimilates are transported in the phloem tissue of trees. Knowing the local rates of growth at any point on the stem, another problem is to determine the global evolution of the stem shape in three dimensions.

FFR recognises that phloem transport is a physical process which partially explains wood anatomy and structure. Studies are under way to understand phloem transport with regard to tree physiology and also to understand how the distribution of sugars and auxin in the plant may affect wood quality.

This project addresses the development of a model to simulate tree carbon transport in trees. Carbon transport occurs passively through the phloem pathway. Accurate prediction of local photoassimilate concentration is critical to determine rates of wood production in the vascular cambium.

This project also covers the development of a new mathematical component. The component can simulate and display the evolution of tree shape during growth. This component can use radial expansion rates that are function of the local concentration of assimilates simulated by the carbon transport model.

A phloem transport model has been developed and is integrated in the *mechanobiology of wood formation* framework. This model is operational and allows simulation of carbon availability at any point of a tree stem.

A second-generation surface evolver has also been developed. It provides a sound basis to model more complex behaviour and also more realistic growth of the vascular cambium.

INTRODUCTION

While carrying out Milestone 2, issues were identified regarding the use of the Fast Marching Method (FMM) (Sethian 1995, 1999a) to evolve tree shape. On one hand, the FMM is a fast, efficient numerical approach to evolve interfaces that only grow outwards, which is the case of tree cambium. On the other hand, it is complex and mostly impractical to extract local interface quantities – e.g. curvature, normal direction to the interface – using the FMM. Such quantities may be needed to accurately define cambium development (i.e., anisotropic growth associated to Compression Wood). Hence the decision to develop a surface evolver that favours flexibility and relative ease of use over computational efficiency. After discussion with Mike Plank (UoC), the Level Set Method (Osher and Sethian 1988) was chosen for that purpose. We will see that, through the use of (i) adaptive numerical techniques and (ii) properties of tree growth, the surface evolver is made relatively efficient.

Another part of the present milestone has been to develop a model that simulates carbon allocation along a tree stem. Various approaches to modelling carbon allocation have been applied over the last decade. In the case of individual tree growth, it includes the use of empirical allocation coefficients; growth rules (including functional balance); sink-strength; transport resistance (see Lacointe 2000, Leroux *et al*. 2001 for reviews). The transport-resistance framework advocated by Thornley (1998) is the only mechanistic approach in that it relates to the Münch (1930)'s hypothesis according to which assimilates are transported by bulk flow from leaves to roots. Münch's hypothesis has been validated by experiments. Files of phloem cells (sieve tubes) longer than several meters are however not able to support observed flow rates (Thompson and Holbrook 2003), suggesting that a relay mechanism exists between short files (Lang 1979). Therefore, carbon transport is mostly a physical process, i.e., passive. In contrast, phloem loading/unloading is actively controlled.

In the current *mechanobiology of wood formation* modelling framework, carbon ecology is handled by the CABALA (CSIRO, Battaglia *et al*. 2004) component, which partitions the carbon available for growth between the main tree compartments (foliage, branches, stem, fine roots, coarse roots). The transport model that is presented is mainly focused on distributing the available biomass over the stem surface.

METHODS

Multi-compartment surface growth using the Level Set Method

The aim of the Level Set Method (LSM) is to track the motion of an interface as it evolves. The key principle is to embed the initial position of the interface as the zero level set of a higher-dimensional function φ. We can then link the evolution of this function to the propagation of the interface itself through a time-dependent initial value problem. At any time, the interface is given by the zero level set of the time-dependent level set function φ. The partial differential equation to evolve φ is given by Osher and Sethian 1988 as

$$\frac{d\phi}{dt} + F\left|\nabla \phi\right| = 0 \qquad (1)$$

given φ(x, t=0) and F an arbitrary evolution speed.

Main advantages of the level set perspective are that:

- topological changes in the evolving front are handled naturally,
- the solutions to equation (1) can be accurately approximated, and
- intrinsic geometric properties are easily determined and implemented.

The only disadvantage of the LSM is the computational cost associated with it. Indeed, LSM requires evaluating φ at over the entire computational domain – namely $O(N^3)$ operations in three dimensions, with N points in each dimension - every time step. However, the cost can be dramatically decreased by the use of adaptive strategies like the narrow band approach (Adalsteinsson and Sethian 1995) - the one retained here. The narrow band approach is to work only in a neighbourhood of the zero level set (i.e., near the studied interface) so that only the values of φ within the narrow band are updated and values of φ at other grid points are frozen. When the interface moves near the edge of the narrow band boundary, the calculation is stopped and a new narrow band is built around the current zero level set. This rebuilding process is known as re-initialisation. Typically, the Narrow Band method is ten times faster than the vanilla flavour of the LSM on a 160x160 grid (Sethian 1999b). Accuracy and speed-up of our implementation is presented in the results section.

As initially designed by Osher and Sethian 1988, the Level Set Method (LSM) applies to problems 'in which there is a clear distinction between an "inside" and an "outside"'. In first approach, it appears to be the case of trees with the vascular cambium being the growing interface, the xylem within and the phloem, bark and surrounding medium - air or soil - always remaining outside. This is a rather simplistic representation which, for instance, does not allow cambia of the stem and individual branches to have distinct developmental patterns. However the problem of simultaneously evolving several surface compartments is not naturally handled by the LSM and requires special attention. A solution is to recast the motion of the interface as the motion of one level set for each surface compartment (Sethian 1999b). The proposed technique has been applied to the case of triple points. It involves a low number of compartments and requires using an influence matrix to account for the interactions between each pair of compartments. Obviously, the case of tree growth is totally different from that of a triple point. Firstly, numerous compartments co-exist. The high number of compartments makes the problem computationally expensive because all points of the domain need to be evaluated at each time step as many times as there are compartments, and this in spite of the fact that all but one compartment will eventually reach one point. Secondly, using an influence matrix is unnecessary for tree growth, as compartments do not interact. Once a compartment has grown into a region, no other compartment can propagate into that region.

Growing a multi-compartment surface adapted to tree growth is readily achievable using Fast Marching (Plank *et al.,* 2007). Our implementation extends the latter to the level set framework.

The key aspects of our method are that:

- The update procedure is identical to the standard LSM implementation, but we use one narrow bad band for each surface compartment. Only the points within the narrow band attached to the currently evaluated compartment are taken into account to compute the derivatives and update φ values. In other terms, each narrow band carries its own level set function.
- Once all narrow bands have been updated, points that belong to at least two compartments are monitored for any sign change in φ values. If the minimum of all φ values is negative, it entails that point is now 'inside' one compartment. Therefore that particular point is removed from the other narrow bands since a property of tree growth is that no compartment can grow into another.

Biomass increase rate and growth speed

At each step of tree growth, CABALA outputs the current stem mass. However, the surface evolver requires a growth speed F, which corresponds to the length increment in the direction normal to the tree surface over a time step. The problem is to calculate F knowing the rate at which new volume is being occupied. F can be found from the following equation:

$$\frac{dV}{dt} = \int_{\Sigma(t)} F ds$$

where ds is an infinitesimal surface element.

If the speed F depends only on time F = F(t) then

$$\frac{dV}{dt} = F(t) \cdot S(t) \qquad (2)$$

The volume enlargement rate dV/dt is obtained by a) converting stem mass to stem volume using the basic density, and b) approximating the current time derivative of the volume using centred finite differences (4^{th} order). The current stem surface S(t) is calculated by extracting the current tree surface with a contourer routine.

Carbon transport model

As stated in the Introduction, the CABALA model already provides a partitioned carbon allocation. In this study, three different approaches were investigated to distribute carbon over the stem length:

(a) Uniform distribution: equation (2) is solved globally and resulting growth speed is applied to all points of the stem.

(b) Longitudinal distribution: all Growth Units receive the same amount of assimilates, then biomass is divided the outer perimeter of each growth unit. Therefore GUs with smaller sections have higher growth speed (but equal volume increments) than GUs with larger diameter.

(c) Pressler's law: the increment of cross-sectional area is proportional to the foliage area above the considered stem cross-section. This is the model used in Dave Pont's secondary growth model (Pont 2003).

All three approaches are empirical but propose an increasing realism. No circumferential variation in growth speed was considered.

RESULTS

Testing the Level Set Method

Table 1 shows the error on the predicted time of arrival of a growing interface at a fixed point. Approximation errors are consistent with the one expected (see Sethian 1999b p.142 for test cases). One can see that mesh size must be doubled to divide by two the error. It has also been observed that the time step has to be decreased to reach a threshold significantly lower than the Courant condition (CFL) to ensure the level set simulation remains “well-behaved”. Computational times were obtained on a computer equipped with an Intel(R) Pentium(R) M processor 1.73GHz.

Table 1: Summary of simulations of a growing sphere with a unity expansion speed using the level set method.

Grid dimensions	Error (ms)	CPU time (s)	Δt
21^3	35	10	0.9 CFL
41^3	17	192	0.8 CFL
81^3	n/a	> 3000	unstable at 0.7 CFL

Figures 1 and 2 show how the approximation varies in the case of time- and space-dependent growth speed. Results show that the level set method is fundamentally sound even when more complex growth speeds are used. They also highlight that particular care is required when choosing the time step and the mesh size in order to achieve maximum accuracy. This is linked to the fact that not only the level set update error but also the speed calculation itself is affected by those parameters.

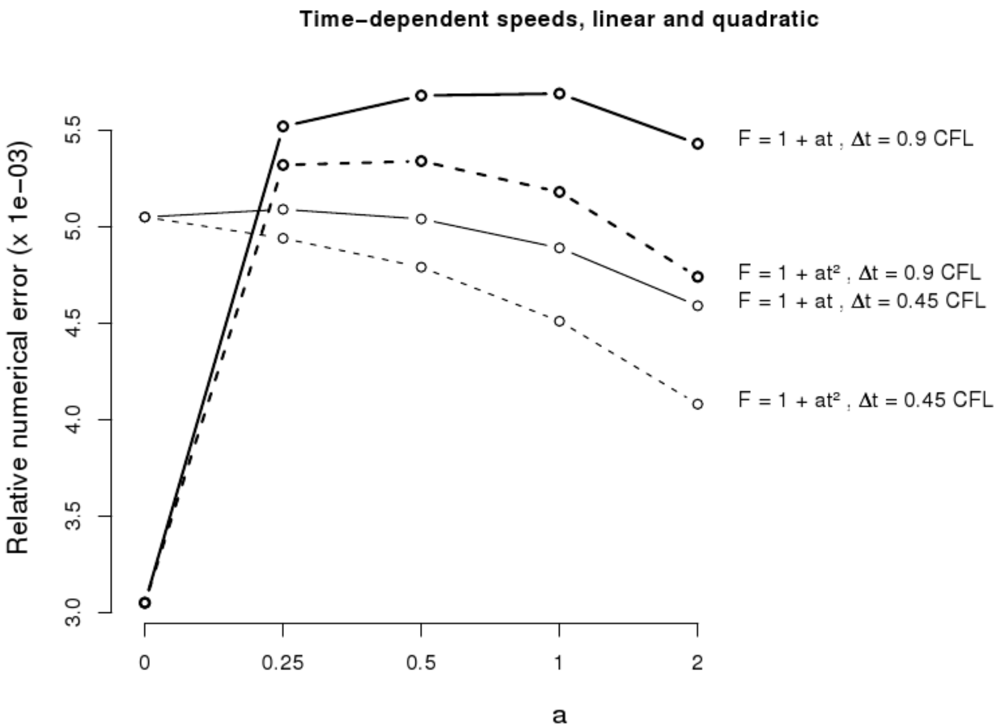

Figure 1: Simulating an expanding circle with time-dependent speeds. Numerical error as a function of the degree of dependence plotted for linear and quadratic laws.

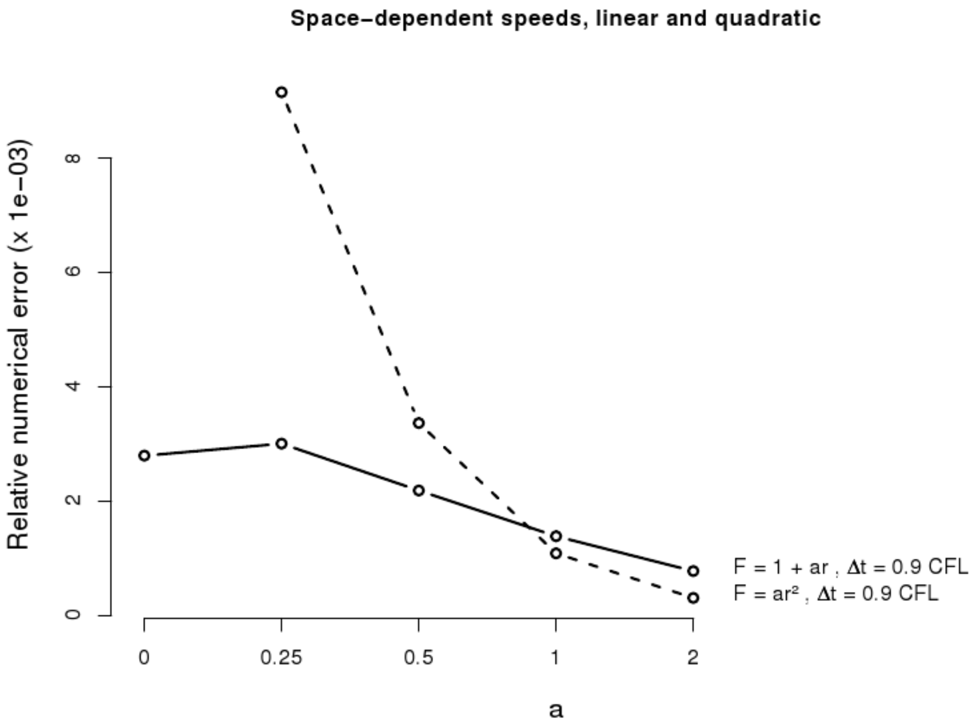

Figure 2: Simulating an expanding circle using space-dependent expansion speeds. Numerical error vs. degree of dependence to position.

Testing the narrow band approach

Table 2 shows results obtained with the narrow band level set method. Error values are similar to the non-adaptive LSM. Computational time speedups are significant being up to five times faster. Of particular interest, the larger the computational domain, the higher the speedup is. This demonstrates a good scalability of the narrow band approach. Additionally, those simulations were done using a constant growth speed. In such a case, speed doesn't need to be calculated at all points of the domain. Absolute speedups associated with the reduction of the computational domain can be expected to be higher for more realistic speed functions that depend on local variables and that must be evaluated at every point. Another aspect is that the width of the narrow band must be consciously chosen by the user to achieve optimal speed.

Table 2: Summary of simulation parameters and results using the Narrow Band Level Set Method.

Grid size	Error (ms)	CPU time (s) (re-initialisation/ LS update)	Narrow Band width (# cells)	Number of re-initialisation
21^3	34	8.3	7	13
21^3	34	7.7	13	5
41^3	17	62 (36/26)	7	27
41^3	17	67 (28/39)	13	10
81^3	9	602 (334/267)	7	55
81^3	9	675 (276/399)	13	21

Figure 3 shows a tree simulated with the multi-compartment approach described in the Methods section. The stem and every branch are different compartments: their growth speed is independent.

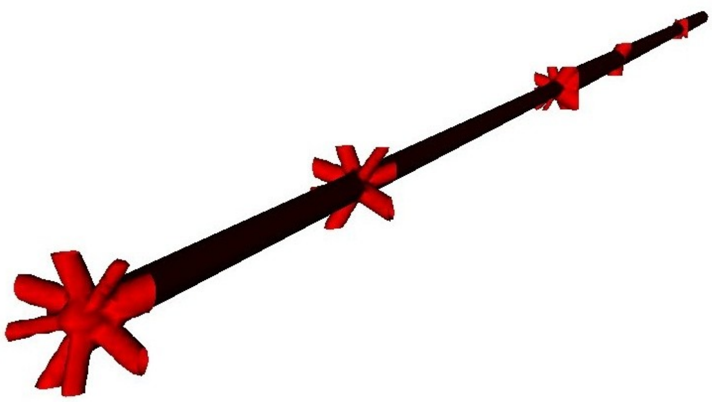

Figure 3: View from above of simulated 3-yr-old tree. Branches are truncated.

Comparing the different methods of allocation

Figure 4 shows the vertical profiles of stem diameter after 25 years of growth using three different allocation patterns. Only the profile obtained with Pressler's law depicts a realistic bi-linear tapering mode with a higher linear tapering in the crown and a lower tapering below the living tree crown. The other methods fail in that respect, with linear and parabolic tapering modes for uniform and longitudinal distributions, respectively. Since using Presser's law is satisfactory, it will be used in future simulations.

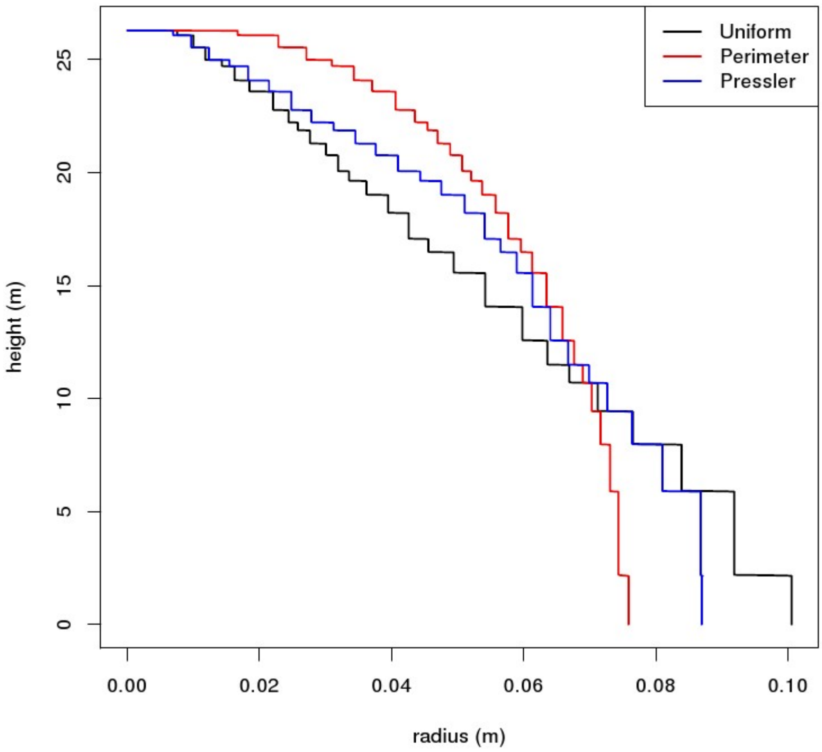

Figure 4: Stem contours in the vertical plane at age = 25 yrs using three different methods to allocate carbon. NB: Perimeter refers to the longitudinal distribution (see the Methods section).

Errors on total stem volume occurring during the simulations are shown in Figure 5. For a method notoriously famous for being numerically diffusive, results are surprisingly good. Re-evaluating tree stem surface at each level set iteration to determine the local growth speed was highly critical to maintain an error as small as such presented. The evaluation adds to the overall computational cost because the interface position must be explicitly extracted from the narrow band grid. It remains however the only option whenever accuracy is needed (Sethian 1999b).

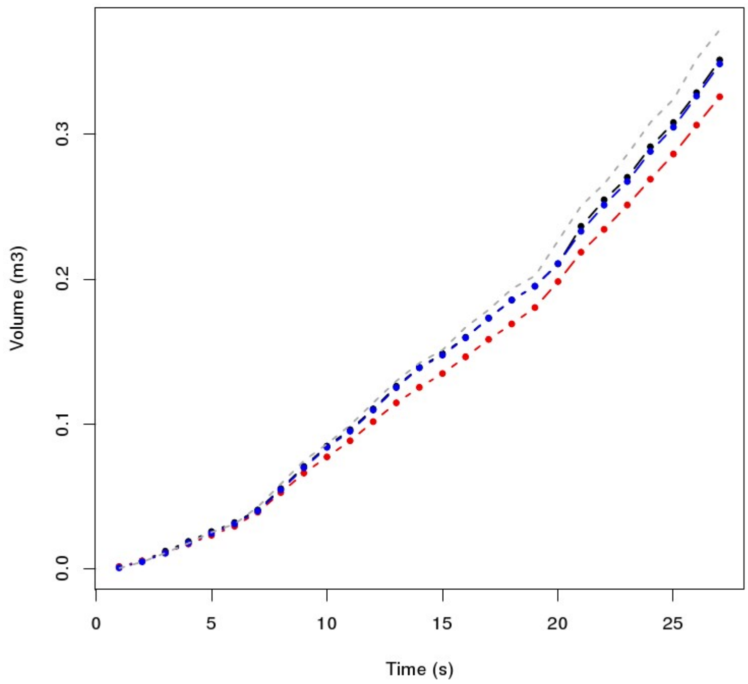

Figure 5: Numerical error on stem volume during growth simulation.

Colour legend refers to the three different methods of allocation of Figure 4. The grey dashed line is the reference volume given by the CABALA model.

CONCLUSION

A surface evolver of second generation has been developed. It provides a sound basis for other framework components to rely upon, in that it permits easy and accurate representation of complex growth speeds, a pre-requisite to model the activity and development of the vascular cambium. The evolver and its coupling to the CABALA component have been intensively tested to ensure an optimal trade-off between accuracy and computational efficiency was eventually reached. In parallel, a framework component has been developed to distribute biomass over the stem length. That component is based on Pressler's hypothesis that cross-sectional increases are proportional to the amount of foliage over the given stem section. Results have shown that realistic taper law can be simulated using that component. However, it is foreseeable that an improved phloem model based on the actual physical transport process will be developed in the future to replace the current, phenomenological one.

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