Parameter Identification of a Functional-Structural Tree Growth Model and Application to Beech Trees (*Fagus sylvatica*, Fagaceae)

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Introduction

Classical process-based forestry models usually rely on a very coarse description of tree architecture and thus are not sufficient to study specific processes in which plant geometry plays a key role. It has lead to the emergence of functional-structural models, simulating interactively the architectural development of trees and their physiological functioning (Sievanen *et al.* 2000, Prusinkiewicz 2004). However, due to the complexity of tree architecture, validation of such models remains a critical point. Indeed, although several models can provide a very fine description of the tree at organ scale, such a level of details is not easily available on real data: only global, aggregated or sampled measurements are reasonable to expect. Consequently, the model parameterization generally relies on the independent parameterization of the physiological processes involved (e.g. Perttunen *et al*., 2001). The model validation is often restricted to comparison of the model behaviour to general observation on real trees. Besides the problem of data collection, another obstacle limiting the calibration of complex topological structures is the speed of simulation. Any model inversion procedure relies on a large number of direct model simulations so a time-consuming simulation algorithm is not suitable for an efficient calibration. In this context, this paper presents and discusses a method to estimate the parameters of the functional-structural model GreenLab (Yan *et al*., 2004) dedicated to the special case of trees, or more generally to plants with a complex topological structure. The major idea is to adapt the model to a level of simplification in adequacy with the level of experimental data aggregation.

Materials and Methods

The GreenLab model simulates the architectural development and the dynamic allocation of biomass at organ level. Both processes are driven in parallel by a ratio of biomass supply (Q) and demand (D). For a detailed presentation, we refer to Yan *et al.* (2004) and Cournede *et al*., (2006). The topology of the plant is described using botanical observations, namely hierarchic organization and repetition phenomena in tree architecture (Barthélémy and Caraglio, 2007). The botanical concept of physiological age (PA) allows the structural factorization of the plant (*i.e.* the multi-scale decomposition of the plant into structural units that are computed only once and assembled to form the tree architecture). Thus, owing to a compact writing of the dynamical development equations (see Cournède *et al*., 2006), the computational time is reduced from exponential to quadratic time-dependence. At each growth cycle (one year for trees of temperate regions without polycyclism), the biomass produced by the leaves is allocated to buds and rings, according to their respective demands. The ring compartment is assumed to play a buffer role (not detailed here) so

that the simulated tree invests more in secondary growth if the conditions are favorable. Biomass allocation to the annual ring is computed for each internode according to the foliage surface above its position in the tree architecture, from an equation generalizing the often-limited Pressler law (Deleuze and Houllier, 2002). Bud demand depends on the tree architecture and on its potential ability to set up new metamers. Tree architectural plasticity is modeled by a feedback influence of photosynthesis on organogenesis. The number of metamers forming a new shoot depends on the biomass allocated to the bud, which is determined according to its potential demand and to the trophic competition state of the tree at the previous growth cycle. It can be modeled as a function of the ratio of available biomass to plant demand Q/D (Mathieu *et al*, 2004). For example, the number of new metamers from a bud of PA *i* and potentially bearing axillary buds of PA *k* is given by Equation (1):

$$M_{ik}(t) = \left\lfloor M_{ik}^1 + M_{ik}^2 \cdot \frac{Q}{D}(t) \right\rfloor \quad (1)$$

where $\lfloor x \rfloor$ represents the integer part of x and M_{ik}^1, M_{ik}^2 are parameters of the model. They can be estimated from sampled observations or estimated at any structure level by model inversion. As a consequence, it is possible to incorporate some species-specific general laws for the branching patterns, such as maximal branching order, maximal physiological age of axillary buds or the general structure of branching hierarchy. The remaining parameters are fitted to create an average structure with the same global demand at each growth cycle as the real one.

To test this method, three beech trees (*Fagus sylvatica*) were measured in May 2006 from a natural stand near Nancy (north-eastern France). The goal of the calibration was to find back the evolution of the main biomass compartments in the tree throughout its growth, with a particular focus on the main stem whose quality contributes to the determination of the yield. For each growth unit of the main stem, fresh mass, mean diameter and length were measured. At regular intervals, ring rays were recorded in 4 directions. For each branch of order 2, its length, basal diameter and total fresh weight were measured. They were classified into three categories of PA: short axes (short internodes, no branches) for PA 4, mean branches (bearing mainly axes of PA 4) for PA 3 and large complex branches for PA 2. The ratio of blade mass over wood mass and the specific leaf weight were estimated by sampling. The sink values (relative to blade sink of PA1 that is set to 1) were calculated from the ratio of new blade mass over new internode mass and averaged. These data were fitted with GreenLab using the non linear least square method, the simulated annealing algorithm and the particle swarm optimization implemented in the DigiPlant software (Ecole Centrale Paris).

Results and Discussion

For these first fitting results, one 21-year-old tree was considered. Four functional parameters and 15 topological parameters (driving the metamer and axis numbers for each PA-based category) remained to be fitted (results not shown). The parameter value found for biomass repartition to rings was similar to the one predicted by the Pressler law. The comparison between measured and fitted data is represented for compartment biomass on PA 2 branches (Fig. 1A). The hierarchical organization was set up following the simple rule that a growth unit of given PA can bear only branches of higher PA (e.g. each growth unit on the main stem consists of metamers possibly bearing either no branch and/or PA 4, PA 3 and/or PA 2 branches). The topological structure of the fitted tree is shown in Fig 1B. The numbers of axes are not the same than in the target tree but their demand is similar enough to reproduce the biomass allocation to each compartment and to each growth unit of the stem. The basal effect that can be observed on each substructure (the numbers of metamers and axes progressively increase) is dynamically generated by the model.
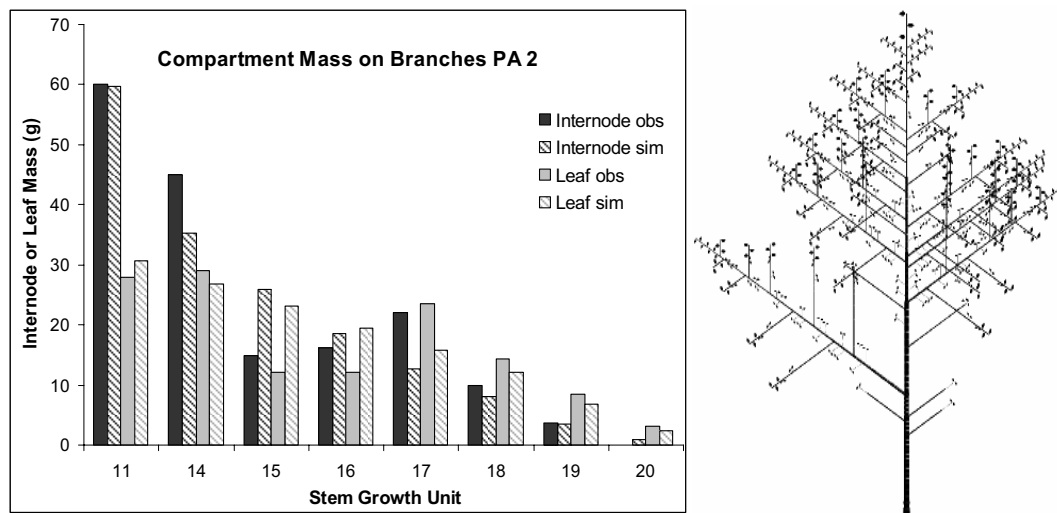
Fig. 1. Some fitting results : (A) graph of compartment biomass (leaf and internode) for substructures of PA 2 branched on the main stem ; (B) fitted tree topology (one grey scale for each PA). The number of branches and the number of metamers per growth unit are driven by the ratio of biomass supply over demand (Q/D).

The substructure factorization results in a natural simplification of the topology: it is no longer based on a detailed description of each branch growth, which would entail facing an inextricable variability. An exhaustive description of an individual tree is not useful if the objective is to determine general results about the interaction between a species and its environment, and transpose results to other individuals. For this reason, the GreenLab model focuses more on the average behavior of the plant and tries to define global rules from botanical observations. Although further study is needed, these first fitting results show that a tree with a simplified structure can reproduce the architectural and functional plasticity of a target tree growth when the branching structure is controlled by a dynamic feedback of its trophic state on its organogenesis processes.

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