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Modelling Sugar maple development along its whole ontogeny: modelling hypotheses and calibration methodology

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Highlights: Relevant GreenLab model hypotheses can be used to model sugar maple development along its whole ontogeny. A dedicated methodology is presented for model calibration (from measurement to parameter calibration). It allows the modelling of long lived trees with highly complex structures.

Keywords: GreenLab model, Sink-source, Biomass partitioning, Factorization, Simulation, virtual plant, *Acer saccharrum* Marsh.

INTRODUCTION

Modelling tree development is a difficult task due to their long lifespan and complex crown structure. Traditionally in forestry, vertical complexity is represented by simple measures (e.g. Diameter at Breast Height (DBH), tree height) and the temporal scale is assessed by survey or ring and stem analysis. When more precise modelling is required (e.g. crown shape and branches sizes), plant architectural analysis provides a relevant framework to analyse and simulate tree structure development over time (Barthélémy & Caraglio 2007).

Dealing with long lifespan and spatial complexity is also an issue for computer simulations, mainly because as plants age, there is an exponential increase in the number of organs. For example, light interception simulation at the leaf level is often possible only on saplings (Perttunen *et al.* 2001).

The aim of this study is to provide a simple and accurate modelling approach for tree growth, architecture and biomass partitioning -across all ontogenetic stages- based on the GreenLab model (de Reffye & Hu 2003) and driven by tree scale constraints. GreenLab model presents desirable properties for tree modelling and simulation: (i) structure factorization based on botanical knowledge, (ii) possibility of doing simulation with or without tree geometrical reconstruction and (iii) data driven approach (hidden parameters estimation). We use Sugar maple (*Acer saccharrum* Marsh.) as a model species due to its ecological and economic importance in Eastern North-America temperate forests and the abundant existing ecophysiological knowledge of the species.

MODELLING HYPOTHESIS

Modelling scale

GreenLab is based on discrete time step modelling. In this study, each time step corresponds to a year and the structural unit is the annual shoot (i.e all organs produced by a single shoot apical meristem during a single year). Each time step is divided into two successive substeps: structure development (i.e. organogenesis), and organ functioning (i.e. assimilation and growth).

Structure development

Structure development is based on physiological age modelling assumptions (Barthélémy & Caraglio 2007): (i) each annual shoot produced by the tree can be labelled with a given Physiological Age (PA) and (ii) all annual shoots produced the same year and with the same PA behave the same way. This last property allows structure factorization that largely reduces computing limitations related to time and memory use. Structure development is modelled by a set of determinist (axes drift and base effect) and stochastic (branching and mortality) processes.

Branching and mortality rules were defined at PA scale. Branching corresponded to a square matrix with $n_{i,j}$ the average number of annual shoots of each PA j hold by an annual shoot of PA i. Mortality is modelled as a sigmoid function of axes age (i.e. age of the first annual shoot)

Axes drift (Barthélémy & Caraglio 2007) is modelled as a transition from a PA to another one along successive annual shoots of an axis.

Base effect (Barthélémy & Caraglio 2007) is modelled by constraining the number of internodes –and ultimately the number of lateral axis- produced by each PA with empirical ontogenetic rules.

Organ functioning

Biomass partitioning at each time step is based on sink-source equations:

$$q_i(t)=d_i(t)*Q(t-1)/ (\sum_i (d_i(t))+ Dwood(t)) \qquad (1)$$

with $q_i(t)$ increment of organ biomass at time t, $di(t)$ organ demand at time t, $Q(t-1)$ biomass assimilated by the tree at time t-1, $\sum_i (d_i(t))+Dwood(t)$ the total plant demand at time t that include plant demand for wood production ($Dwood(t)$). $Q(t=0)$ correspond to seed mass. Three different types of demands and allocations are considered: leaf demand, internode demand for primary growth and plant demand for secondary growth. The first two types only occur during the year of organ development and depend of annual shoots PA (i.e. one demand parameter per organ type and PA). Plant demand for secondary growth is proportional, with a parameter Pc, to the total leaf number. Internodes allocations to secondary growth are based on pipe model assumptions (surface section conservation).

Biomass assimilation is modelled as asymptotic function of leaf area:

$$Q(t)= 1/R * Sp\ (1-\exp(-k.Sf(t)/Sp)) \qquad (2)$$

with $Sf(t)$ the tree total leaf area at time t which is related to tree leaf biomass and Leaf Mass per Area ratio empirically calibrated (range from 40g.m-2 to 180g.m-2 along tree ontogeny), R a scaling factor, Sp the available surface for the tree (i.e. Sp/R correspond the maximal quantity of biomass the plant can assimilated per year given the environment and $Sf(t)/Sp$ to the LAI), k correspond to a calibration coefficient related to the efficiency of leaf displacement (i.e. self-shading).

CALIBRATION

Biological dataset (on AmapStudio)

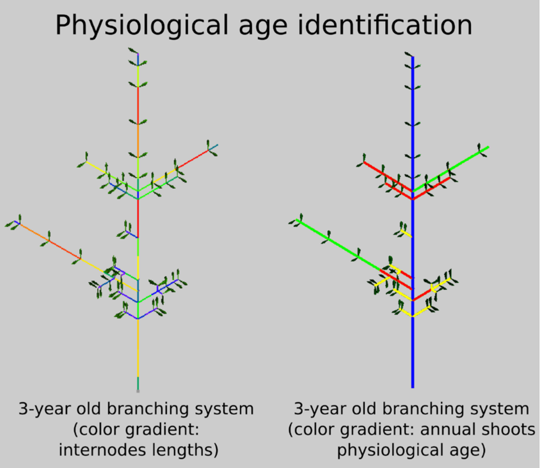
To minimize phenotypic variation driven by environmental factors, dominant or co-dominant trees of various sizes (from seedlings to 74cm of DBH) were identified in summer 2012. To do this, maple forest stands originating from clear cuts of contrasting ages (from 5 years to 34 years) were visited to obtain individuals ranging in size from seedling to 20 cm DBH. Larger individuals (up to 74 cm DBH) were sampled from uneven aged forest stands. Total sample consisted of 48 individuals.

In September after cessation of growth, the last 3-years of growth were sampled for the main stem, or for one of the main stems for reiterated trees. All the annuals shoots of these branching systems were labelled and the following traits were measured: topological location (following MTG formalism), annual shoot dry biomass, internodes lengths, leaf number, fresh leaf surface and leaf dry biomass.

Physiological age identification (on R)

A semi-automated algorithm was developed to perform PA labelling on measured annual shoots. The goal was to characterize a PA based on annual shoots morphological measurements (annual shoot length, number of leaves, average internodes length) and the estimated PA of its lateral axes. The initialization is made on the ultimate PA that can be recognized by the lack of any lateral axes development.

- Step 0: main stem annual shoots are associated with the first PA and were removed from following steps:
- Step 1: estimating a linear discriminant model on the occurrence of lateral axes on 2011 annuals shoots (unbranched vs. branched) based on morphological measurements.
- Step 2: predicting the PA of 2012 annual shoots: due to one-year delayed branching none of them already express branching.
- Redo step 1-2 with a supplementary group: unbranched 2011 annual shoots, branched 2011 annual shoots that hold ultimate PA axes (according to step 2 predictions) and other 2011 annual shoots.
- Redo step 1-2 with a supplementary group …


Physiological age identification

3-year old branching system (color gradient: internodes lengths)

3-year old branching system (color gradient: annual shoots physiological age)

Fig. 1: Physiological age identification based on morphological measurements. Left: Internodes colours correspond to their respective lengths (long internodes in red and short internodes in blue). **Right:** Annual shoots colours correspond to their physiological age (GreenLab color code convention).

The recursive algorithm is stopped when the “other 2011 annual shoots” contains too few annual shoots that can be recognized as main stem reiterations.

The R implementation of the algorithm takes as input a matrix of data at annual shoot scale that includes branching relationships between annual shoots. Data extraction was made with AmapStudio.

In our case, four PA were characterized (**Fig. 1**).

Branching, Mortality and ontogeny rules calibration (on R)

Based on PA identifications, branching rules were calibrated by the mean number of lateral axes of PA*j* hold by PA*i* 2011 annual shoots (i.e. a given annual shoot can hold different type of lateral axes simultaneously).

Mortality rules were estimated by making complement measurements on labelled trees. The proportion of dead lateral axes per PA was recorded, along 65 axes of various sizes. A two-parameter logistic curve was estimated per PA of lateral axes.

The ontogenetic changes of the number of internodes per annual shoots (i.e. ontogenetic rules) were described empirically with five control points with linear interpolation between each of them. As the real age of each tree remains unknown, the empirical functions were calibrated with tree DBH (or tree base diameter for smallest trees). Tree diameter was later converted to tree age based on ring width measurements.

Sink-source parameters calibration (on Matlab)

All parameters related to supply (R, Sp and k) and demand ($Q(t=0)$, Pc and leaves and stem demand per PA) computations were calibrated together. Data used correspond to the leaves and stem dry biomass per PA and per year (only the last for leaves) measured on the 48. Structure development rules were used to provide, for each time step, the number of annual shoots of each PA and each age. Gauss-Newton gradients were used for parameter estimations. Results of this analysis will be provided at the conference.

DISCUSSION AND PERSPECTIVES

In previous applications of GreenLab on trees, the development sub-model was by-passed thanks to an exhaustive topology description based on expert physiological age identification (e.g. Guo *et al.* 2012). To our knowledge, the current methodology is the first GreenLab application that allowed the stochastic development sub-model calibration (e.g. branching probabilities and branch mortality) for long-lived trees, which prevent any exhaustive measurements.

The physiological age identification algorithm appeared as an efficient way toward automation of the stochastic development sub-model calibration. An open question is to quantify the consistence of this algorithm with: botanical expertise, hidden Markov tree modelling (Durand *et al.* 2005) and other clustering methods (e.g. kmeans).

Based on accurate structure development and organ functioning calibration, several opportunities are possible: (i) tree growth simulation along 150 years; (ii) replacing ontogenetic rules by functional ones to get a feedback between structure complexity and environmental constraints and (iii) testing some pruning scenarios during simulations.

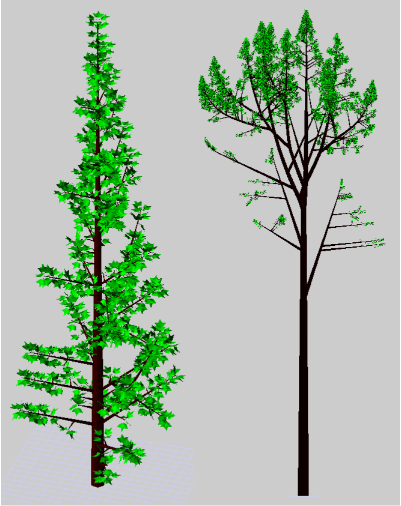


Fig. 2: The same virtual tree at two different time step. left: 15 years old; **right:** 90 years old (scales are not respected). Calibrated developmental parameters were used to calibrate AmapSim, thanks to AmapSim compatibility with developmental part of GreenLab. Visualisation was made in AmapStudio.

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