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Simulation of the topological development of young eucalyptus using a stochastic model and sampling measurement strategy

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ABSTRACT

Tree crown architecture affects light interception, biomass production and mechanical stability. Crown architecture is largely determined by the topological development of the plant due to meristem activity. Modeling approaches can provide new insights into the dynamics of plant topology, but they are often hampered by experimental difficulties in data collection on complex trees with numerous internodes, especially in tropical tree species that present the additional difficulty of continuous growth with no marked cessation. Tree topological structure shows high variability resulting from genotypic and environmental factors in real stands. In this paper, a stochastic model was developed to describe the topological development of trees. In the model, growth and branching processes are driven by the respective probabilities of activity, rest or death of apical and lateral buds. Because of its mathematical formulation, the model inversion can be done analytically – which is rare – and parameter values can be estimated from experimental data. A new strategy was defined to sample measurements and applied to five eucalyptus trees. Incomplete systems were also defined for the case, common with trees, of incomplete datasets. After parameter estimation, simulation of random eucalyptus tree was presented. The model could describe tree topological development of eucalyptus reasonably well. This work offers a simple and practical method to describe the topological development of trees with continuous growth. It can realistically and flexibly describe the canopy topological development, and has the potential to be integrated with the process of biomass production and allocation for functional-structural plant modeling in the future.

Keywords: *Eucalyptus*; survival probability; mortality probability; rhythm ratio; random tree topological development

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1. Introduction

Canopy architecture is an important determinant of the height, light-capturing ability, dry matter production, and mechanical stability of trees (Hallé *et al.,* 1978; Kuuluvainen, 1992; Poorter *et al.,* 2006). The dynamic, multilevel and comprehensive approach is useful to quantitatively describing the components of crown architecture and helps to better explore the biological mechanisms of tree growth and productivity (Barthélémy and Caraglio, 2007). Tree crown architecture is commonly represented using decomposed components, geometrical and topological organization of these components (Godin, 2000). The topological development of the tree crown plays a major role in determining its final architecture. This topological development results from bud activity: buds either produce new organs, rest or die in response to environmental factors and internal regulators. To better understand these processes, adequate methods are necessary to analyze the tree topological development. Computer-based simulation and associated visualization tools facilitate the process of understanding tree topological development and have gained importance in recent decades (De Reffye and Houllier, 1997; Prusinkiewicz and Lindenmayer, 1990; Kurth, 1994). Models aim to accurately simulate the botanical structure and development of trees. They are based on botanical understanding of plant growth and form (Kurth, 1994; Birch *et al.,* 2003; Barthélémy and Caraglio, 2007). Numerous quantitative models of plant topological structure have been developed (Fisher and Honda, 1977; Ellison and Niklas, 1988; Hasenauer, 1997; Kang *et al.,* 2008; Loi and Cournede, 2008), and some of them have been successfully linked to ecophysiological models, leading to functional-structural plant models (De Reffye *et al.,* 1995; Perttunen *et al.,* 1998; Sievänen *et al.,* 2000; Yan *et al.,* 2004; Godin and Sinoquet, 2005; Cournede *et al.*, 2006; Kang *et al.,* 2008; Vos *et al.*, 2010; Wang *et al.,* 2011). Hasenauer (1997) employed a simple, deterministic model based on allometric relationships with stem dimensions to simulate plant topological structure. However, tree topological development is a complicated process resulting from stochastic branching, delay of growth, and morphological differentiation of axes (Barthélémy and Caraglio, 2007). Experimental observation showed that the pattern of internode appearance on axes is highly variable, even for branches of similar position and vigor (De Reffye *et al.,* 1995).

Tree topological structure shows high variability resulting from genotypic and environmental factors in real stands, thus stochastic models can more realistically describe tree topological development than deterministic ones. Models using stochastic processes apply different formalisms. Some examples have used automata for coffee and other trees (De Reffye, 1979; De Reffye *et al.,* 1991); a stochastic L-system (Prusinkiewicz and Lindenmayer, 1990; Kurth and Sloboda, 1997); a dual-scale automaton model with semi-Markov chain that allows the interactive generation of plant topological structure and development for pine and beech (Zhao *et al.* 2003); a hidden semi-Markov chain for apple (Costes *et al.,* 2008) and peach trees (Lopez *et al.*, 2008); and a flexible probability model producing the theoretical mean and variance of the number of organs in a plant structure for Scots pine (Kang *et al.,* 2008;

Wang *et al.,* 2010). Most of these works were applied to trees with simple structure, because complex trees are difficult to measure. In order to extend these stochastic models to complex trees with numerous internodes, a sampling strategy is necessary that reduces the experimental work.

In this paper, we focused on one part of crown architecture, the topological structure. We explored the feasibility of calibrating a stochastic model for eucalyptus, which presents the additional difficulty of a continuous growth with no marked endogenous cessation (De Reffye, 1979). Retrieving the growth trajectory of such a tree based on its analysis at a given stage is therefore extremely difficult, but it is not impossible.

Eucalyptus is an important and fast-growing tree species in South China. It has played a significant role in forestry, both economically and ecologically (Zhou, 2002), although there is continuing controversy about its ecological roles (Turnbull, 1999; Calder 1997; Yu *et al.,* 1999; Huang *et al.,* 2006). There is a growing awareness of the importance of the interaction between eucalyptus architecture and its physiological processes, especially water and nutrition. Building a functional-structural model of eucalyptus growth would help to better understand the contrasted effects of cultivating the species. A first step towards this goal is to analyze and model the topological structure development of eucalyptus. Therefore, the objective of our study was to use a stochastic model with the consideration of the stochastic behavior of the buds to describe the topological structure of eucalyptus. A major interest of this model is its exact mathematical inversion: thanks to the choice of relevant statistics to be computed, analytical expressions of the parameters can be derived. They can be used to estimate the parameter values values as functions of experimental data. A MATLAB program was developed to implement these formulas and to create stochastic tree topological structure from the model.

2. Materials and Methods

2.1 The architectural analysis: concepts and definitions

Our study was based on concepts developed in botanical studies of plant architecture (Barthélémy and Caraglio, 2007; Jaeger *et al.,* 1992; De Reffye, 1979) and functional-structural plant models such as GreenLab (Yan *et al.,* 2004). A *metamer*, the basic unit of plant structure, consists of an internode with axillary buds, leaves, and/or flowers. Metamers are the basic entities for modeling plant architectural development. The time between the appearances of two successive metamers of the trunk defines the time step of the model, hereafter called *growth cycle* (GC). The appearance of metamers is the result of the activity of buds. The activity of a given bud is characterized by an integer called *physiological age* (PA). This index has no unit and can be used to sort the different axes - or zones of axes - of any tree according to their botanical properties. The main trunk's PA is conventionally equal to 1, and the oldest PA corresponds to the ultimate state of differentiation for an axis: it is usually composed of short shoots without branches. For most trees, it is less

than five (e.g. Sabatier and Barthélémy, 1999). For instance, on eucalyptus trees, the PA can be generally set according to the branching order: the orthotropic trunk is PA 1, second-order plagiotropic branches are PA 2, and so on. The *chronological age* (CA) of a plant (or of an organ) is defined as the number of growth cycles it has survived. The position of a branch is determined by its *rank* (K) (Fig. 1), the number of metamers from the top of the bearing axis to the insertion point of the branch (i.e., basipetally). When two adjacent branches are both alive, they are called a *couple of branches*.
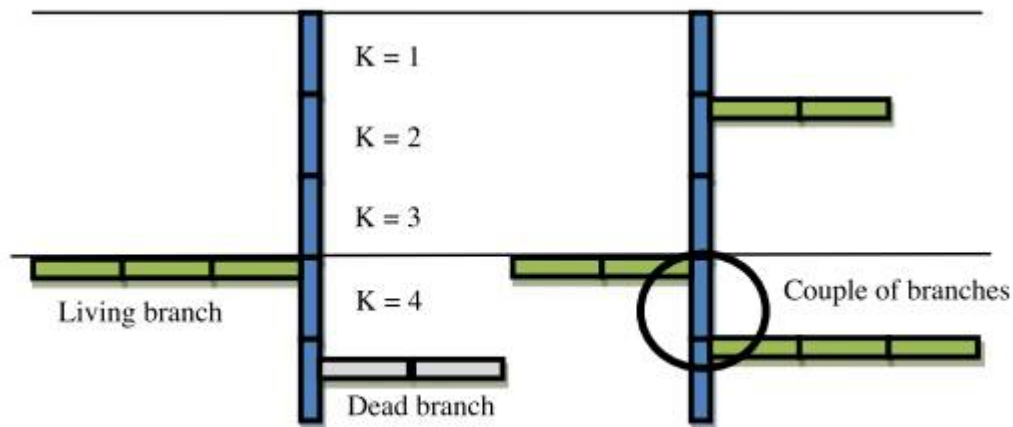
Fig. 1. Illustration of the simplified tree morphology.

2.2 The topological model

Here, we define the parameters used to determine the topological development of a generic tree.

The growth of a stem and branches results from the activity of the apical and lateral buds. A lateral bud at rank K produces a branch with a probability A_K. The average of all A_K values is defined as the branching probability A.

At each growth cycle, an apical bud can produce a metamer, rest, or die. Analyses of the complex patterns of axis development reveals that alternations of buds activity and pause phases can be generated by both stochastic and periodic processes. They can be distinguished given that the variance of the number of metamers along several axes is zero in the case of a purely periodic organogenesis. Periodic alternation corresponds to the case where the rhythm of branch organogenesis is different from that of the main stem. It is modeled by a parameter W, called the rhythm ratio, which is the ratio of the rate of metamer emission on branches to the rate of metamer emission on the trunk. For instance, if in a given period the bud of the main stem can undergo N_1 GCs, while the meristem of an axillary branch will undergo N_2 GCs, then we have $W=N_2/N_1$.

This periodicity of metamer emission is then subjected to random perturbations. If buds do not pause due to the rhythm ratio, they can produce a metamer with a probability P, which is assumed to be constant for each category of axis: P^m for the main stem, P^b for branches. Eventually, buds can die with probability $1-c_n$, where c_n is

the survival probability of buds at GC n.

This organogenesis model can be formalized using a stochastic F0L-System (Lindenmayer, 1968; Rozenberg and Salomaa, 1980; Smith, 1984; Prusinkiewicz and Lindenmayer, 1990), as introduced in Kang *et al.* (2007) and Loi and Cournède (2008) for branching processes indexed by the physiological age of metamers. Here, we use parametric F0L-Systems where the symbols of the alphabet can be associated with sets of parameters (see Hanan, 1992 for a formal definition) (Table 1). These parameters are used to include conditions in the production rules. Here, the alphabet consists of the set of metamers *t* (terminal symbols) and buds *s* (non-terminal symbols). For the sake of simplicity, we also add a terminal symbol *d* corresponding to a dead bud. The set of parameters consists of the physiological age {1, 2}, the chronological age *CA* and the rank *K*. The L-System rules are showed in Table 1.

Table 1
Rules of the stochastic F0L-System of the model

The development rules and their conditions of application	Probability values
r1: $s(1, CA, K) \rightarrow d$	$1 - c_n$
r2: $s(1, CA, K) \rightarrow s(1, CA + 1, K)$	$(1 - P^m) \cdot c_n$
r3: $s(1, CA, K) \rightarrow t(1, CA, K) \, s(1, 0, K + 1)$	$P^m \cdot (1 - A_K) \cdot c_n$
r4: $s(1, CA, K) \rightarrow t(1, CA, K) \, s(2, 0, 0) \, s(1, 0, K + 1)$	$P^m \cdot A_K \cdot c_n$
r5: $s(2, CA, K) \rightarrow d$	$1 - c_n$
r6: $s(2, CA, K):[W \cdot (CA - 1)] == [W \cdot CA] \rightarrow s(2, CA + 1, K)$	c_n
r7: $s(2, CA, K):[W \cdot (CA - 1)] \mathrel{!=} [W \cdot CA] \rightarrow s(2, 0, K)$	$(1 - P^b) \cdot c_n$
r8: $s(2, CA, K):[W \cdot (CA - 1)] \mathrel{!=} [W \cdot CA] \rightarrow t(2, CA, K) \, s(2, 0, k + 1)$	$P^b \cdot c_n$

Note: [ ] represents the integer part of the quantity in the square bracket. Parameters were explained in the part of Section 2.

These rules can be interpreted as follows:

A bud of physiological age 1 can die with probability $1 - c_n$ (rule r1). If it does not die, it can rest, with probability $1 - P^m$ (rule r2) or produce a metamer without or with an axillary bud of physiological age 2 (rules r3 and r4).

A bud of physiological age 2 can die with probability $1 - c_n$ (rule r5). If it lives, it can produce a metamer only at periodic times, determined by the rhythm ratio *W* (incorporated into rules r6-r8). At these times, the metamer actually appears with probability P^b (rule r8).

This model can be generalized to higher branching orders if needed.

2.3 Statistics of the topological model used for parameter estimation

2.3.1. Definitions

Parameter estimation for the organogenesis model is not straightforward, because the different stochastic processes intractably interact to generate the tree topology that can be observed *a posteriori*. We solved this problem by defining, for each branching

order, four statistics, X_K, V_K, v_K, and *F(K)* that can be analytically expressed as functions of the model parameters and that can be estimated using measurements on a population of individuals.

Let us consider the system formed by a main axis and its lateral branches. We note that X_K and V_K are the mean and variance, respectively, of the number of metamers on the branches at rank *K* in a basipetal ranking system (from apex to bottom). These values can be estimated if the dataset contains at least two branches at rank *K* and if they are still alive. We also introduce v_K, the average local variance of X_K for couples of branches at ranks *K* and *K+L* attached on a same stem, where *L* is the number of metamers between the adjacent branches forming a couple. It is based on the assumption that branches that appeared successively have similar characteristics and are driven by similar control variables. Thus they can be considered as repetitions of the same underlying random process. There must be at least one couple of branches which are still alive. Lastly, concerning branch mortality probability, *F(K)* is defined as the ratio between the number of dead branches and the total number of branches at rank *K*.

2.3.2 *Mathematical expression of the statistics: Complete system*

Owing to the stochastic laws of our organogenesis model, we can derive the theoretical expressions of these statistics as functions of the rhythm ratio, W_K and the probabilities of metamer emission on the main stem, P_K^m, and on the branches, P_K^b, at each rank *K* from the tip of the main stem:

$$
\begin{cases}
X_K = W_K \dfrac{P_K^b}{P_K^m} K \\[2ex]
V_K = W_K \dfrac{K}{P_K^m} P_K^b\left(1 - P_K^b\right) + \left(W_K P_K^b\right)^2 \dfrac{K\left(1 - P_K^b\right)}{P_K^{m\,2}} \\[2ex]
v_K = W_K P_K^b(1 - P_K^b) \dfrac{K + \dfrac{L}{2}}{P_K^m} + (W_K P_K^b)^2 \dfrac{L(1 - P_K^m)}{2\,P_K^{m\,2}} + (W_K P_K^b)^2 \dfrac{L^2}{2 P_K^{m\,2}}
\end{cases}
\tag{1}
$$

where *L* is the number of metamers between adjacent branches to be considered in the calculation of the local variance. For trees bearing several branches at each node (e.g. coffee or pine), the local variance can be defined as the variance in the number of metamers on each branch of a whorl. The case of eucalyptus is more complicated since each metamer bears at most only one branch. To overcome this limitation, it is assumed that couples of branches (i.e. *L=1*) can be treated the same as whorls of two branches. More branches could eventually be considered, but the variance would grow dramatically (so practically the formula should be used for *L=0* or *L=1* only). The proof of system (1) is presented in De Reffye (1981) and De Reffye (1988). This system can be analytically solved to obtain the parameters at each rank *K*:

9

$$
\begin{cases}
P_K^b = 1 - \dfrac{1}{X_K}\left(V_K - \dfrac{L}{2}\left(\dfrac{V_K}{K} + L\left(\dfrac{X_K}{K}\right)^2\right)\right) \\[4mm]
P_K^m = 1 - \dfrac{1}{X_K^2}\left(K\left(V_K - v_K + \dfrac{1}{2}\left(\dfrac{LX_K}{K}\right)^2\right) + \dfrac{LV_K}{2}\right) \\[4mm]
W_K = \dfrac{P_K^m}{P_K^b} \cdot \dfrac{X_K}{K}
\end{cases}
\tag{2}
$$

The parameters are then averaged over the range of selected ranks since they were assumed to be constant for each axis. Thus, if X_K, V_K and v_K are estimated for each rank K from the experimental data measured on N trees, it is possible to obtain the values of the hidden parameters driving the development. These estimations are obtained as follows:

$$
\begin{cases}
\hat{X}_K = \dfrac{1}{N}\sum_{i=1}^{N} X_{i,K} \\[4mm]
\hat{V}_K = \dfrac{1}{N-1}\sum_{i=1}^{N}\left(X_{i,K} - X_K\right)^2 \\[4mm]
\hat{v}_K = \dfrac{1}{2N}\sum_{i=1}^{N}\left(X_{i,K} - X_{i,K+L}\right)^2
\end{cases}
\tag{3}
$$

where $^\wedge$ denotes the variable estimation from the available experimental data, and $X_{i,K}$ is the number of metamers on the branch inserted at rank K from the top of the ith measured tree.

The next step is to analyze the random process of apical bud mortality. Let us denote $G(n)$ the expected proportion of dead branches among branches of CA n. This proportion depends on the probability of bud survival c_i at each GC i from 1 to n:

$$1 - G(n) = \prod_{i=1}^{n} c_i \tag{4}$$

(i.e. a branch of chronological age n is alive if its apical bud has survived at every GC of its life).

From this equation, we can recursively derive the expressions of c_n as follows:

$$
\begin{cases}
c_1 = 1 - G(1) \\[3mm]
c_n = \dfrac{1 - G(n)}{1 - G(n-1)} \qquad n > 1
\end{cases}
\tag{5}
$$

However, estimation of $G(n)$ from experimental data is not straightforward. Indeed, the measured variables can only be the proportion of dead branches at *rank K* from the top of the main stem, $F(K)$. Following De Reffye (1981) and De Reffye (1988), $F(K)$ is modeled by a Beta law function:

$$F(K) = \frac{\sum_{i=1}^{n} (\frac{i}{K_{max}})^{Ba}(1 - \frac{i}{K_{max}})^{Bb}}{\sum_{i=1}^{K_{max}} (\frac{i}{K_{max}})^{Ba}(1 - \frac{i}{K_{max}})^{Bb}} \qquad (6)$$

where the parameters B_a, B_b and K_{max} of this Beta law can be estimated with the least square method using data of the observed proportion of dead branches over the total number of measured branches at rank K along the N measured stems. Then, the ratio $F(K)$ has to be transformed according to the relationship between the chronological age of branches and their basipetal insertion rank along the main stem. As metamer appearance is subject to random processes, assessing the actual times when metamers of the main stem appeared can be done only because P^m was previously computed. The chronological age of metamers at rank K from top is distributed following a binomial negative law. Therefore, the expected value of metamer age at rank K from top is $n=K/P^m$. Assuming that the metamer age determines the age of its lateral branch, the proportion $\hat{G}(n)$ of dead branches of chronological age n is thus estimated as:

$$\hat{G}(n) = \hat{F}(n \cdot P^m) \qquad (7)$$

where $\hat{F}$ is the estimated value of F.

2.3.3 Incomplete systems

If no more than one branch was measured for each rank node, system (1) can not be used, because these formulas require computing variances. Nevertheless, we can get some information by making some relevant hypotheses. First we can always obtain the slope (R_K) of the number of internodes per branch with respect to its rank by a linear regression deduced from system (1):

$$X_K = R_K K = W_K \frac{P_K^b}{P_K^m} K \qquad (8)$$

Then, two different strategies can be adopted. The first is to assume that the growth probability of branches is the same as that of the trunk, that is $P_K^m = P_K^b$. Given this assumption, equation (8) becomes: $X_K = W_K \cdot K$. Thus it is possible to estimate the value of W_K from measurements of X_K. Variance v_K can not be computed because no couples of branches are present in the measured data. The variance V_K at rank K also can not be computed because there is only one sample. Therefore we introduce the global variance GV, which is defined as the sum of V_K for all ranks K. Its analytical expression is:

$$GV = \sum_{K=1}^{N} \left(W_K \frac{K}{P_K^m} P_K^b (1 - P_K^b) + (W_K P_K^b)^2 \frac{K(1 - P_K^m)}{P_K^{m2}} \right) \qquad (9)$$

And it can be estimated on the data by equation (10), because we have an estimate of R_K.

$$\hat{GV} \; = \; \sum_{K=1}^{N} \frac{(\hat{X}_K \; - \; \hat{R}_K \; \cdot \; K)^2}{N} \qquad (10)$$

Then $\hat{P}_K^b$ solves the equation:

$$\hat{P}_K^b \; = \; 1 \; - \; \frac{\sum_{K=1}^{N} \dfrac{\left(\hat{X}_K \; - \; \hat{R}_K \; \cdot \; K\right)^2}{N}}{\hat{R}_K\left(1 \; + \; \hat{R}_K\right)\sum_{K=1}^{N} K} \qquad (11)$$

We define this set of equations as Incomplete System 1.

The second strategy is to assume that the rhythm ratio, W_K, is equal to 1. Therefore, the slope of the linear regression of X_K with respect to K is the ratio $\dfrac{P_K^b}{P_K^m}$. Then we have:

$$GV \; = \; \sum_{K=1}^{N} \left(KR_K\left(1 \; - \; R_K P_K^m\right) \; + \; R_K^{\,2} K\left(1 \; - \; P_K^m\right) \right) \qquad (12)$$

And we get:

$$\hat{P}_K^m \; = \; \frac{\hat{R}_K(1 \; + \; \hat{R}_K)\sum_{K=1}^{N} K \; - \; \sum_{K=1}^{N} \dfrac{\left(\hat{X}_K \; - \; \hat{R}_K K\right)^2}{N}}{2\hat{R}_K K^2 \sum_{K=1}^{N} K} \qquad (13)$$

$$\hat{P}_K^b \; = \; \hat{R}_K \hat{P}_K^m \qquad (14)$$

This set of equations is called Incomplete System 2.

The program written in the MATLAB language is used for parameter estimation and tree topological structure simulation.

2.4 Site description and data

Data was collected at Zhanjiang (114°26'-115°38'E, 22°23'-23°30'N), Guangdong Province, China. Since there are numerous internodes for a eucalyptus tree (*Eucalyptus grandis* × *Eucalyptus urophylla*), a sampling protocol is designed to investigate the tree architecture. For each tree, diameter at breast height (1.3 m) was measured. The tree was then felled and total height, the total number of internodes and their corresponding locations (rank from top to bottom) and living status (alive or dead) were measured and recorded. The trunk was then divided into zones of 1 m in length denoted $Z_0(i)$ (Fig. 2). For each zone, two average branches ($Z_0(i)B_1(1)$, $Z_0(i)B_1(2)$) were selected and their internode number, length and diameter were measured. If the tree was very large, every other zone along the trunk was sampled for detailed measurements as described. For this study, three one-year-old and two two-year-old eucalyptus trees were destructively sampled (Table 2). A total of 35 branches

for one-year-old eucalyptus and 19 branches for two-year-old eucalyptus were measured, respectively.
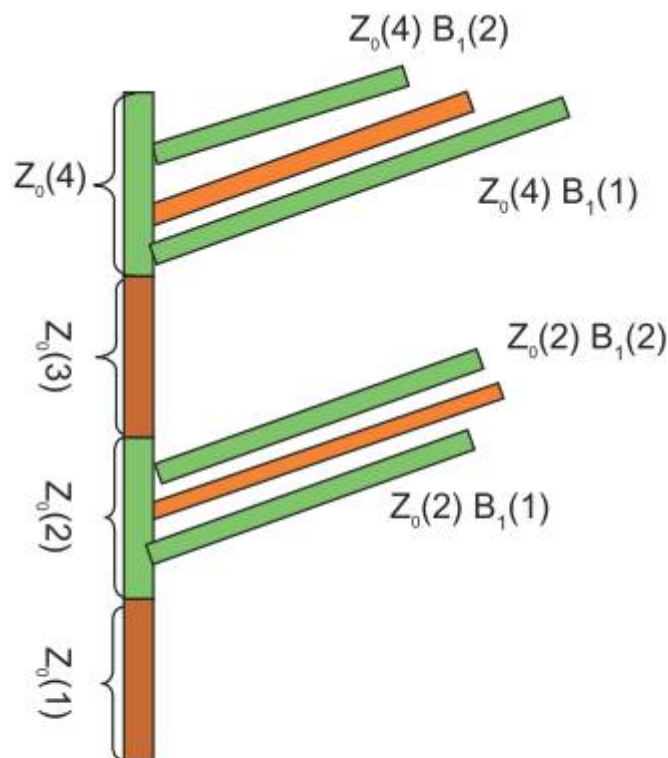
Fig. 2. Examples of zones and branches sampled for eucalyptus trees (green represents sampled zones and branches). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2
Descriptions of sampled *eucalyptus* trees.

Tree age	Tree height (m)				Diameter at breast height (cm)			
	Max	Min	Mean	SD	Max	Min	Mean	SD
1	6.8	6.0	6.4	0.40	5.5	4.4	5.0	0.45
2	11.0	8.4	9.7	1.30	8.7	8.4	8.6	0.15

3. Results

3.1 Estimation of parameters

Parameters fitted to the model described above based on measured data are listed in Table 3. Only main stem and first-order branches were considered here. When using the complete system, we found that the values of P^m and P^b were greater than 1 (Table 3), which is impossible. This may be due, as mentioned above, to the lack of repetition data for certain ranks. Thus, the complete system was not applicable in this case.

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Parameters	One-year-old *eucalyptus*			Two-year-old *eucalyptus*		
	Complete system	Incomplete system 1	Incomplete system 2	Complete system	Incomplete system 1	Incomplete system 2
P^m	3.35	0.55	0.82	2.86	0.72	0.78
P^b	1.00	0.55	0.41	1.01	0.72	0.68
W	1.99	0.50	1.00	3.01	0.88	1.00
A	1.00	1.00	1.00	1.00	1.00	1.00
Ba	5.62	5.62	5.62	23.84	23.84	23.84
Bb	1.95	1.95	1.95	31.02	31.02	31.02

Note: parameters were explained in the part of Section 2.

Using Incomplete Systems 1 and 2 produced different parameters. In both models, as expected, the growth of the main stem was found to be faster than that of branches. Both systems are plausible: in Incomplete System 1, the observed difference in growth speed can be explained by a deterministic rhythm ratio less than 1, while in Incomplete System 2, it is explained by a lower growth probability of branches compared to that of the main stem ($P^m > P^b$). It is interesting to note that the ratios P^b/P^m in Incomplete System 2 are 0.5 and 0.87 for the one-year-old and two-year-old trees, respectively. These values are approximately equal to the rhythm ratio values estimated in Incomplete System 1 (0.5 and 0.88, see Table 3). Thus, the parameter values estimated based on the two Incomplete Systems are consistent. That consistency is also shown by the fact that the values for P^m and P^b (which are equal) in Incomplete System 1 are in between the values of P^m and P^b in Incomplete System 2, as expected.

The estimated parameters of Incomplete System 2 allow us to compare the growth of one-year-old trees with the growth of the two-year-old trees. Older trees have a higher growth probability for branches than younger trees. However, the growth probability for the trunk gave contrary results. Younger trees had stronger apical dominance (height growth is faster relatively to lateral spread of the crown) than older ones, especially in eucalyptus (Graham *et al.*, 1998; Wilson, 2000), which could explain the apparent contradiction. The branching probability A is equal to 1, which indicates that lateral buds on main stems of both one-year-old and two-year-old eucalyptus trees have strong vitality at their first GC.

The results of fitting the number of internodes on branches to rank on trunk and the probability of dead branches at each rank are shown in Figures 3 and 4. The former showed a good linear relationship with the slope, R_K, which was equal to P_K^b / P_K^m here (Incomplete System 2). The coefficients of determination (R^2) are 0.59 and 0.82 for one-year-old trees and two-year-old trees, respectively. The latter followed a beta law as expected with the highest death probability at the base and the lowest at the top (Fig. 4). The dependency of branch mortality on rank is weak because of the sparsity of data in our study but it was shown in De Reffye (1981) and De Reffye (1988), that branch mortality meets beta distribution well for coffee trees. In an attempt of building a generic methodology, we therefore keep this function for our specific datasets. Note that it is necessary to use a continuous function since Equation 6 involves computing $F(K)$ at non-integer points.
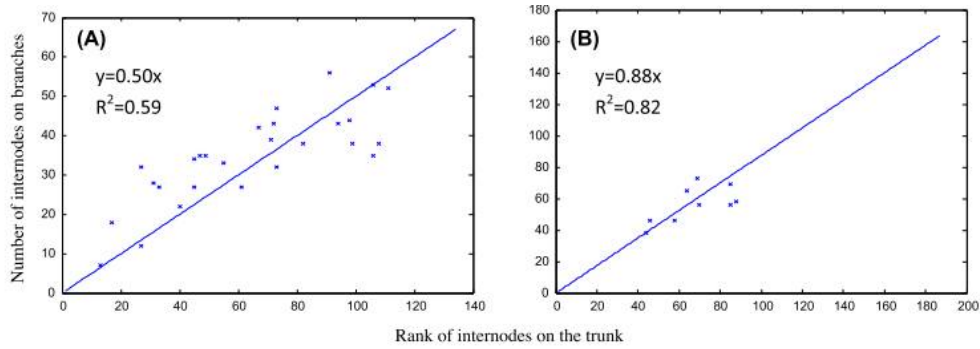
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Fig. 3. Fitting of relationships between the number of internodes on branches and the corresponding rank on the trunk (A: One-year-old tree, B: Two-year-old tree).
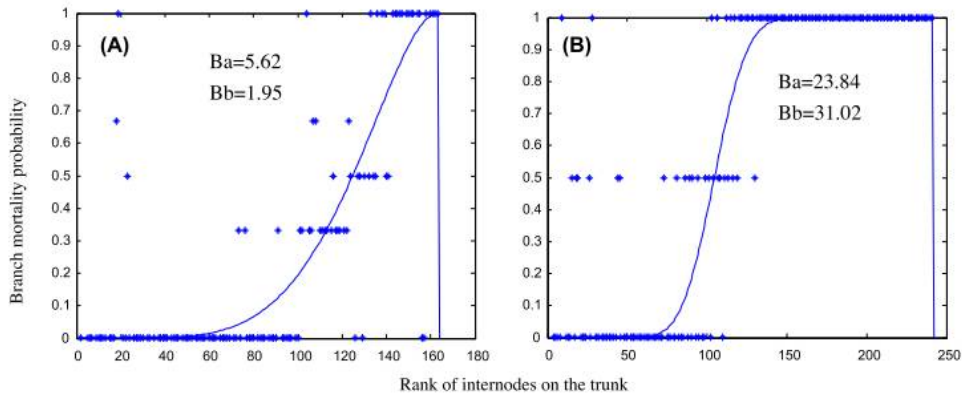

Fig. 4. Fitting of Beta distribution of branch mortality probability (Dots and Lines are the observed and simulated, respectively. A: one-year-old trees, B: two-year-old trees).

3.2 Simulation of random tree architecture

Using the parameters for Incomplete System 2, we can simulate random topological sturcture of eucalyptus trees with different ages. Here we present random tree architectures of one one-year-old eucalyptus and one two-year-old eucalyptus (Fig. 5 and Fig. 6, respectively). In our case, the branching probability A was equal to 1 based on observed data (Table 3). To illustrate the flexibility of our simulations, we could reset the branching probability A as 0.6, for example, with other parameters unchanged for the two-year-old eucalyptus above. When we did this, the stochastic morphologic structures changed as expected (Fig. 7).

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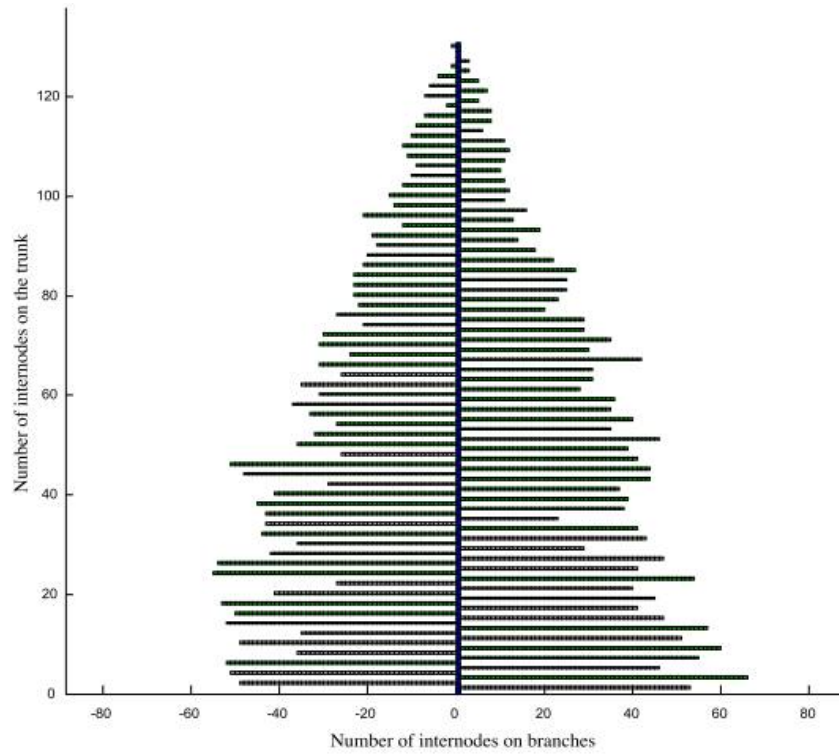
Fig. 5. Simulated stochastic topology of 1-year-old eucalyptus tree (green denotes alive branches, gray denotes dead branches). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
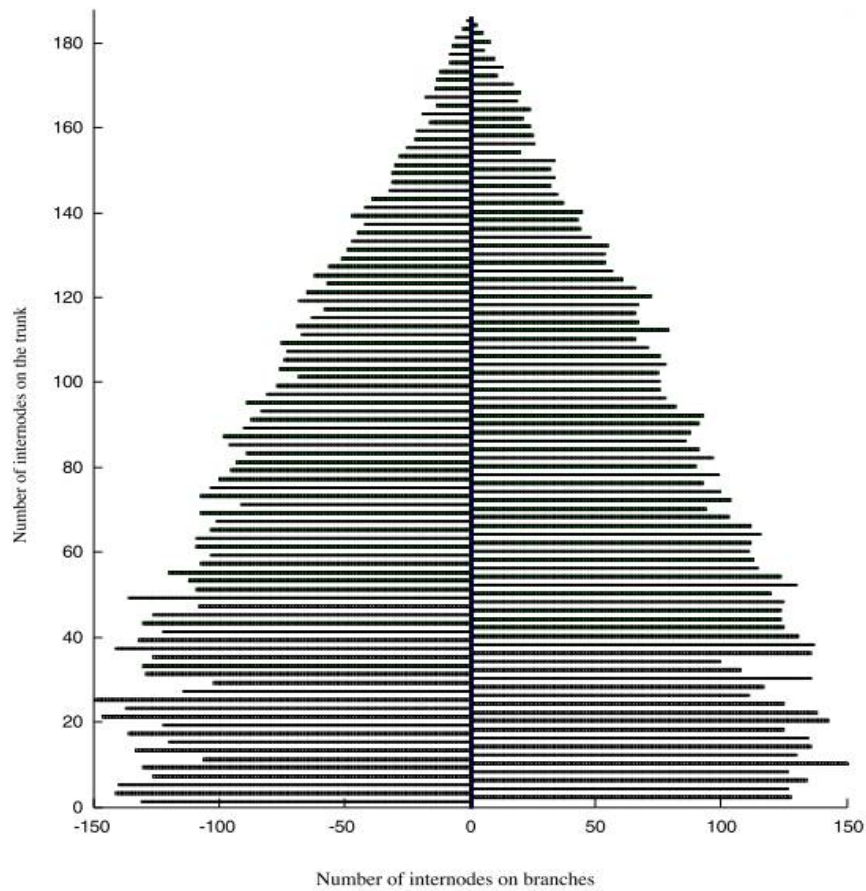
Fig. 6. Simulated stochastic topology of 2-year-old eucalyptus tree (green denotes alive branches, gray denotes dead branches). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Fig. 7. Simulated stochastic topology of 2-year-old eucalyptus tree ($A = 0.6$) (green denotes alive branches, gray denotes dead branches). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
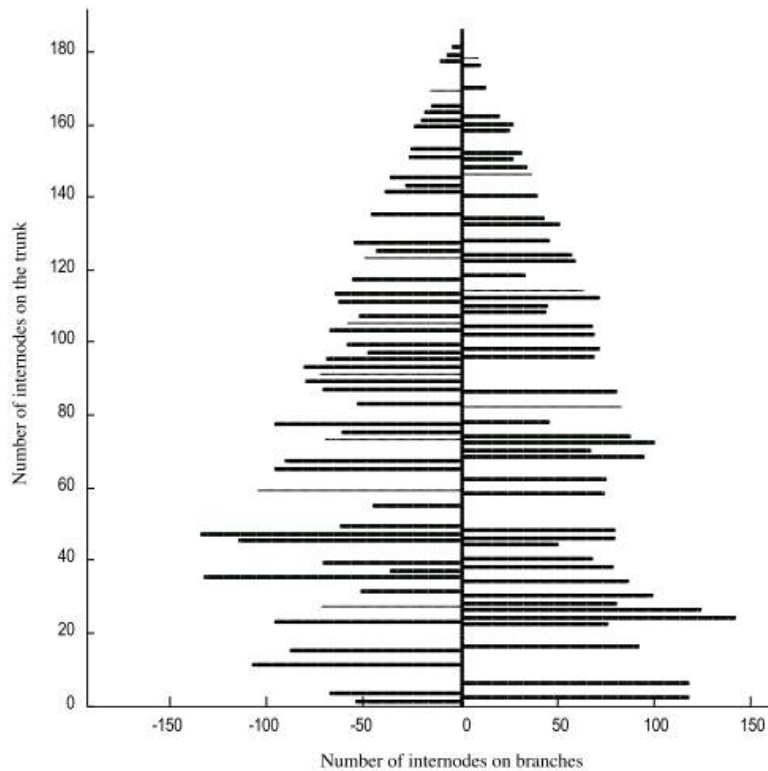
4. Discussion

The topological development of trees determines important ecological processes within forests, and describing tree topological development is an essential component of functional-structural plant modeling. Halle *et al.* (1978) established the basis of architectural analysis and distinguished some 23 'architectural tree models'. Topology structure was recorded at the time by different methods, for example the bracketed string notation L-system (Prusinkiewicz *et al.*, 1990) and the multiscale tree graphs (MTG) proposed by Godin and Caraglio (1998). MTG method allows one to specify plant topology at different scales and to incorporate temporal aspects. However, tree modeling presents big challenges due to the large amount of variation among individual structures and species, the difficulty of data measurement. Bud behavior results from both endogenous growth processes that are genetically programmed for each species as well as environmental influences on these growth processes (Barthélémy *et al.* 1989). A bud can die, become dormant, or become an internode, and the probability of each outcome varies with developmental stage. For trees grown in forest, long-term detailed follow-ups are impossible: past history and local environmental influences are thus completely unknown. In that context, stochastic modeling at least provides a descriptive analysis of tree growth. The choice of a stochastic approach seems relevant, even though very few biological processes can that be considered as "truly stochastic": it is nearly always possible to involve some causal relationships between processes by changing scale or by adding more control variables (micro-climate, animals, wind, etc). However stochastic models are good

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compromise and provide synthetic descriptions of tree growth when some knowledge is missing due either to some lack of biological knowledge about the growth processes or to the impossibility to have close information of every local micro-event, for example. .

A first work based on a similar methodology was initiated in Wang et al. (2007) where a stochastic model for the canopy architecture of young Mongolian Scots pine was developed and calibrated using mean and variance of the number of metamers. However, their model was specific to that tree species since it included only branching probability: bud dormancy or rhythm ratio were negligible for Mongolian Scots pine and not included in the model. Taking these processes into account greatly increased the complexity of the model of topological development and the difficulty to disentangle their influences in the observed topology. An adequate methodology had to be developed, based on the pioneer work of De Reffye (1981), and adapted to the specificities of eucalyptus and to the new strategy of measurement sampling that was designed for this study.

As a fast-growing tree species, eucalyptus display continuous growth of the trunk and branches, unlike species with rhythmic growth, like pine. Consequently, the model incorporates several parameters, including growth probability, branching probability, rhythm ratio and dead probability of branches. These parameters are obtained from well-chosen statistics on the number of internodes of branches, which can be analytically computed following the theory of stochastic processes. We measured parameters on one- and two-year old trees using a measurement protocol adapted to the numerous internodes of eucalyptus and simulated a random tree. Although we do not know the historical growth and environment, the model allows unraveling periodic metamer appearance (W in our model) from stochastic metamer appearance (P). The successful simulation suggests that we can realistically and flexibly describe tree architecture in terms of both botany and statistics.

The major achievements of this study were to consider the stochastic behavior of buds based on simplified sampling measurements, which are suitable for continuously growing trees and for large trees with numerous internodes. Although the model in the study has very few parameters (5 to describe a full crown), it can happen that the data are sparse and the number of couples of branches is not enough to assess the internal variance. So two incomplete systems were developed and the global variance was calculated. Compared with similar stochastic models in the literature (Kang *et al.,* 2008; Wang *et al.* 2010), ours deduced the values of probabilities of growth and bud survival, as well as the rhythm ratio, and is more suitable to big trees with numerous internodes like eucalyptus. Our approach offers a generic tool with uniform parameters and statistics, especially for the cases of insufficient datasets, which are a very common situation, rather than an exception, given the experimental difficulties to measure trees. We do not provide the error estimates of parameters in this study but this further statistical step should be made easier by the possibility to have exact theoretical expressions of the parameter values (since model inversion can be analytically solved, thanks to the choice of relevant statistics of experimental data).

In order to investigate the relationship between plant structural development and environment, both architectural and functional development should be taken into consideration in models. For example, the functional processes of plant growth are modeled using a source-sink approach in GreenLab. The parameters of tree topological development are essential for assessing the cumulative demands on the plant of the sink organs. The number of metamers produced in the plant's lifetime can be used to estimate total biomass production, which drives biomass allocation to organs according to sink strength. The impact of topology on plant functioning has been observed and explored by functional-structural plant models. Letort *et al.* (2009) theoretically analyzed the importance of topological development for plant functioning in the GreenLab model. The interaction between random structure and biomass partitioning was also explored in GreenLab model (Kang *et al.*, 2008; Wang *et al.*, 2011).

Tree biomass production is essentially determined by the balance between carbon gained through photosynthesis and that lost through respiration, and tree growth is the product of total biomass production minus losses of organs (branch mortality, for instance). In real forest stands, branch death is a stochastic process influenced by stand history and crown development, such as the timing of crown closure and the types and frequency of crown disturbances, which causes large fluctuations in the amount and accumulation rate of biomass in space and time (Grier and Logan, 1977). The topological development and biomass production of trees in a stand are largely stochastic rather than deterministic processes. Therefore, the stochastic approach for topological development used in this study is expected to be well reconciled with models of biomass production and allocation.

Plant architecture is the result of both genotypic and environmental effects, and the number of branches is strongly influenced by plant physiological activities (Buck-Sorlin and Bell, 2000). Here we only took the main axis and first-order branches into consideration. Other branches at different orders follow the same rule and will be tested in future work. The next step developing a complete model will be to integrate a functional component that includes biomass production and allocation into the topological development model to better understand the interaction between environment and the structural development of trees.

5. Conclusions

This work provides a new and simple method to describe the topological development of trees with continuous growth, like eucalyptus, using a stochastic model. The model can realistically and flexibly describe the canopy architecture, and it can be analytically inversed to estimate the parameter values from experimental data. A sampling protocol was designed to investigate the architectural patterns of eucalyptus. We could simulate tree development in order to obtain a random structure, and could define an average tree on which to assess branching and death patterns. The method considers the random behavior of buds and lays a foundation for the development of a functional-structural model of eucalyptus.

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