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To cite this version:

Cédric Loi, Paul-Henry Cournède. A Markovian framework to formalize stochastic L-systems and application to models of plant development. [Research Report] RR-6830, INRIA. 2008, pp.24. inria-00359515

HAL Id: inria-00359515

https://inria.hal.science/inria-00359515v1

Submitted on 10 Feb 2009

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INSTITUT NATIONAL DE RECHERCHE EN INFORMATIQUE ET EN AUTOMATIQUE

Une approche Markovienne pour formaliser les L-systèmes stochastiques et application aux modèles de développement de plante

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N° 6830

Septembre 2008

Themes NUM et BIO

Rapport de recherche

ISSN 0249-6399 ISRN INRIA/RR--6830--FR+ENG

Une approche Markovienne pour formaliser les L-systèmes stochastiques et application aux modèles de développement de plante

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Thèmes NUM et BIO — Systèmes numériques et Systèmes biologiques
Projets Digiplante

Rapport de recherche n° 6830 — Septembre 2008 — 21 pages

Résumé : Ce document est un complément de l'article écrit par *Loi et Cournède* (DMTCS, 2008). Cet article établit la relation entre L-systèmes stochastiques et le modèle de développement GreenLab simplifié avec seulement branchement et différenciation. En écrivant la fonction génératrice correspondant à chaque phénomène et en les composant, nous obtenons l'espérance du nombre de métamères de tout type dans la plante entière. Dans ce rapport, nous rappelons brièvement les principaux résultats de l'article. En outre, nous montrons comment l'écriture de la fonction génératrice se généralise au cas où les unités de croissance peuvent contenir un nombre aléatoire de métamères. Nous obtenons également une équation récurrente permettant de calculer la variance du nombre de métamères de chaque type dans la plante. Enfin, nous illustrons les résultats au travers de simulations de Monte-Carlo sur quatre cas.

Mots-clés : L-système stochastique, processus de branchement multitype, phase-type, fonctions génératrices, développement végétal, modèles de croissance de plantes, GreenLab

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A Markovian framework to formalize stochastic L-systems and application to models of plant development

Abstract: This document is an extension of the article written by *Loi and Cournède* (DMTCS, 2008). This article shows the relationship between stochastic L-Systems and a simplified GreenLab growth model with only branching and differentiation. By writing the probability generating function corresponding to each phenomenon and by compounding them, we get the expected values of the numbers of metamers of each type in the whole plant. In this report, we recall the main results of this article. In addition, we show how to derive the generating function in the general case when growth units contain a random number of metamers. We also get a recursive equation to compute the variance of the numbers of metamers of each type in the plant. Finally, we illustrate the results throughout Monte-Carlo simulations in four cases.

Key-words: Stochastic L-system, multitype branching process, phase-type, generating functions, plant development, plant growth models, GreenLab

1 Introduction

When the smallest scale of interest is that of organs (and not cells), discrete models are generally used to simulate plant structural development. The parallel rewriting grammar introduced by Lindenmayer (1968) (called L-system) is particularly adapted to model the evolution of branching patterns. Thus, it properly describes models of plant development when the functionning (*i.e.* the production of biomass by photosynthesis) is not taken into account.

In Loi and Cournède (2008), the authors have studied the relationship between stochastic L-Systems and multi-type branching processes in order to compute the corresponding probability generating functions and the distribution moments of the number of organs. Concerning the organogenesis model, only branching and differentiation have been taken into account. In this report, we recall briefly the main results of the article. First, we introduce stochastic 0L-systems. In particular, we show that the definition of Prusinkiewicz and Lindenmayer (1990) is equivalent to that of Loi and Cournède (2008). Then, we explain how a stochastic grammar can be derived from the GreenLab growth model. We give the expression of the generating function of the branching process when growth units contain a random number of metamers and that of the differentiation process. By composing the L-systems associated to branching and differentiation, we get the generating function of the whole process and, as a consequence, we have recursive equations to compute the expected values and the variances of the numbers of metamers of each physiological age in the plant. In the last part, we illustrate the method on four test-cases (coffee tree, maize, a plant that mixes branching and differentiation and a plant with branching, differentiation and a random number of metamers per growth unit) and compare the theoretical results to those given by Monte-Carlo simulations.

2 Stochastic 0L-systems and generating functions

In this section, all the following sets are finite or countable. $V = \{v_1, v_2, \cdots, v_m\}$ denotes an alphabet, W the set of all words over V and W^+ the set of nonempty words over V. Let $\mathbf{1}$ be the empty word and "." be the concatenation operator. Then, $(W, ., \mathbf{1})$ is a noncommutative monoid.

2.1 Defining stochastic 0L-systems with transition matrices

We recall the definition of a stochastic 0L-system (Prusinkiewicz and Lindenmayer (1990)) :

Definition 2.1 (Stochastic 0L-system) *A stochastic 0L-system is a construct* $G = \langle V, \omega_a, P_r, \pi \rangle$ *where :*

- $\omega_a \in W^+$ *is called the* axiom. *It represents the structure initiating the growth.*
- $P_r \subset V \times W$ *is a finite* set of productions. *A production* $(s, \chi) \in P_r$ *is written as* $s \to \chi$ *and represents the evolution of the symbol* s *into* χ. s *is called a* predecessor.

– π *is called the* probability distribution. *It is a function from* P_r *into* $[0;1]$ *that maps the set of productions into the set of production probabilities. For instance,* $\pi(s,\chi)$ *gives the probability that* s *evolves into* χ. π *verifies the following equality :*

$$\forall s \in V, \qquad \sum_{(s,\chi)\in P_r} \pi(s,\chi) = 1.$$

For a given stochastic 0L-system, we can build a transition matrix based on the production rules :

Proposition 2.1 (Transition matrix associated to a stochastic 0L-system) *Let* $G = \langle V, \omega_a, P_r, \pi\rangle$ *be a stochastic 0L-system. Let* $\Pi = (\Pi_{x,y})$ *be the map from* V *to* W *such that :*

$$\forall (x,y) \in V \times W, \qquad \Pi_{x,y} = \pi(x,y)\mathbb{1}_{P_r}(x,y)$$

where $\mathbb{1}_{P_r}(x,y)$ *is equal to* 1 *if* $(x,y) \in P_r$ *and* 0 *otherwise. Then,* Π *is a transition matrix from* V *to* W. Π *is said to be the transition matrix associated to* G.

Π describes completely the production rules of G. Thus, the following definition of stochastic 0L-system is equivalent to that of Prusinkiewicz and Lindenmayer (1990) :

Definition 2.2 (Stochastic 0L-system with transition matrix) *A stochastic 0L-system is a construct* $G = \langle \omega_a, \Pi\rangle$ *where :*
- $\omega_a \in W^+$ *is called an axiom. It represents the structure initiating the growth.*
- Π *is a transition matrix from* V *to* W.

We can now define a more general class of L-systems called stochastic F0L-system, extending the classical definition of F0L-system (Rozenberg and Salomaa (1980), p. 89) to the stochastic case :

Definition 2.3 (Stochastic F0L-system) *A stochastic F0L-system is a construct* $G = \langle A, \pi\rangle$ *where :*
- A *is a finite nonempty subset of* V *(called the set of axioms of* G*).*
- *for every* $\omega_a \in A$, $G[\omega_a] = \langle \omega_a, \Pi\rangle$ *is a stochastic 0L-system (called component system of* G*).*

2.2 Generating function associated to a stochastic 0L-system

In this section, we use the Markov chain theory to define the generating function associated to a stochastic 0L-system. The following proposition has been proved in Loi and Cournède (2008) :

Proposition 2.2 *Let* $G = \langle A, \Pi\rangle$ *be a stochastic F0L-system. To every component system* $G[\omega_a] = \langle \omega_a, \Pi\rangle$ *there exists a Markov chain* $(F_n[\omega_a])_{n\in\mathbb{N}}$ *that represents the evolution of the structure starting with* ω_a *throughout* G.

Remark 1 : The Markov kernel associated to $(F_n[\omega_a])_{n\in\mathbb{N}}$ is the same for every component system $G[\omega_a] = \langle \omega_a, \Pi\rangle$. Thus, it is called the Markov kernel associated to G and it is denoted by $P = (P_{x,y})$ with $(x, y) \in W \times W$.

Remark 2 : Beside plant topological structures directly given by L-Systems, in order to compute plant functioning, the numbers of organs are crucial variables (see for example de Reffye et al. (2008)). To determine them, the order of symbols in words does not play any role, and we can consider the L-systems as commutative. Let R be an equivalence relation on W defined as follows : $w_1 R w_2 \Leftrightarrow$ there exists Π, a permutation on the symbol ranks, such that $\Pi(w_1) = w_2$. Let us denote the quotient set W/R by W^*. From now on, each word $w \in W$ will be assimilated to the ordered representative w^* of its equivalence class (*i.e.* wRw^* and $w^* = \prod_{i=1}^{m} {v_i}^{\alpha_i}$ for $(\alpha_1, \cdots, \alpha_m) \in \mathbb{N}^m$). W^* is isomorphic to $\mathbb{N}^m$. Let Υ be the canonical isomorphism from W^* into $\mathbb{N}^m$. For a word $w = \prod_{i=1}^{m} {v_i}^{\alpha_i}$ in W^*, we have $\Upsilon(w) = (\alpha_1, \cdots, \alpha_m)$. Let us denote by $\Upsilon_i(w)$ the i-th component of $\Upsilon(w)$ (*i.e.* $\Upsilon_i(w) = \alpha_i$). In the following, the transition matrix π is thus considered as a map from $V \times W^*$ into $\mathbb{R}$.

Because of their recursive properties, generating functions are powerful tools to analyse stochastic L-systems.

Let us now define the generating function associated to a stochastic 0L-system. Let $S = (s_1, \cdots, s_m) \in [0, 1]^m$.

Definition 2.4 (generating function associated to a stochastic 0L-system) *Let $G = \langle A, \pi\rangle$ be a stochastic F0L-system on $V = \{v_1, \cdots, v_m\}$. Let $G[\omega_a] = \langle \omega_a, \Pi\rangle$ be a component system of G and $(F_n[\omega_a])_{n\in\mathbb{N}}$ the corresponding Markov chain. For $n \in \mathbb{N}$, the generating function $\psi_n[\omega_a]$ of $F_n[\omega_a]$ is defined as follows :*

$$\psi_n[\omega_a](S) = \sum_{\chi\in W^*} P(F_n[\omega_a] = \chi) \prod_{i=1}^{m} s_i^{\Upsilon_i(\chi)}.$$

$\psi_1[\omega_a]$ is said to be the generating function associated to $G[\omega_a]$.

By using the classical composition of generating functions (Harris (1963)) for a multitype Galton-Watson branching process, we deduce directly the following theorem :

Theorem 2.3 *Let $G = \langle V, \pi\rangle$ be a stochastic F0L-system on $V = \{v_1, \cdots, v_m\}$. For all $v \in V$, let $G[v] = \langle v, \pi\rangle$ be a component system of G and and $(F_n[v])_{n\in\mathbb{N}}$ the corresponding Markov chain. For all $n \in \mathbb{N}$, let $\psi_n[v]$ be the generating function associated to $F_n[v]$. Then,*

$$\forall n \in \mathbb{N}, \forall \omega_a \in V, \qquad \psi_{n+1}[\omega_a](S) = \psi_1[\omega_a](\psi_n[v_1](S), \cdots, \psi_n[v_m](S))$$

2.3 Compound L-systems

Branching processes in biology can be very complex. It is easier to study them by breaking them up into several independent simpler processes. Therefore, the idea is to break up the total L-system into ìndependent L-systems with simpler production rules and then to compose them to get the whole system. Let us define the concept of compound L-systems :

Definition 2.5 (compound L-system) *Let $G = \langle V, \Pi \rangle$, $G^1 = \left\langle V, \Pi^1 \right\rangle$ and $G^2 = \left\langle V, \Pi^2 \right\rangle$ be stochastic L-systems on the same alphabet V. Let P, P^1 and P^2 be the Markov kernel associated respectively to G, G^1 and G^2. G is said to be the composition of G^1 by G^2 if $P = P^1.P^2$. We write $G = G^1 \circ G^2$.*

Then,we get an interesting result :

Proposition 2.4 *Let $G = \langle V, \Pi \rangle$, $G^1 = \left\langle V, \Pi^1 \right\rangle$ and $G^2 = \left\langle V, \Pi^2 \right\rangle$ be stochastic L-systems on the same alphabet V. For all $v \in V$, let $\psi_1[v]$, $\psi_1^1[v]$ and $\psi_1^2[v]$ be respectively the generating functions associated to $G[v]$, $G^1[v]$ and $G^2[v]$. If $G = G^1 \circ G^2$, then*

$$\forall S \in [0,1]^m, \forall \omega_a \in V, \qquad \psi_1[\omega_a](S) = \psi_1^1[\omega_a](\psi_1^2[v_1](S), \cdots, \psi_1^2[v_m](S))$$

Remark : Note that $G^1 \circ G^2 \neq G^2 \circ G^1$.

Compound L-systems are very useful if we want to compute moments associated to a complex branching process. Let G be the stochastic F0L-system associated to a complex branching process. By knowing the generating function of order n, we have access to the moments of the number of all types of individuals after n generations. The immediate way to get the generating function of order n is to use Theorem 2.3. By doing so, you only have to compute the generating function of order 1. However, in the case of a complex branching process, the probabilities are not always simple to compute. Thus, the idea is to break up G into K independent simpler L-systems such that $G = G^1 \circ G^2 \circ \cdots \circ G^K$. The transition matrices associated to G^1, ..., G^K are easy to compute and, therefore, we get immediatly their generating functions. Finally, we get the generating function of G by composing those of G^1, ..., G^K (cf Proposition 2.4).

3 Describing GreenLab organogenesis with stochastic F0L-system

The probability distributions and moments of the numbers of organs in plant structure are botanical data of interest. The need for an analytic computation of these distributions is crucial in stochastic functional-structural models in order to derive the distribution or the moments of biomass production (cf. Kang et al. (2008) for preliminary results). Stochastic F0L-systems are particularly adapted to model the evolution of branching patterns such as plant development. In the sequel, the aim is to apply the method developped in Section 2.3 to the GreenLab model of plant organogenesis.

3.1 Main botanical concepts

We recall some basic concepts about the GreenLab model of plant development (see de Reffye et al. (2003) for more details on the botanical modelling). GreenLab is a discrete time model whose time step is called *Growth Cycle*. Each plant is composed of a succession of elementary units called *metamers*. A *Growth Unit* is the set of metamers built by a bud during a growth cycle. The *Chronological Age* (CA) of a plant (or of an organ) is defined as the number of growth cycles it has existed for. Concerning the architecture of the plant, the axis can be listed into different categories depending on their morphological parameters. Thus, as explained in Barthélémy and Caraglio (2007), the concept of *Physiological Age* (PA) was introduced to represent the different types of axes. Let P be the maximal PA (in general, $P = 5$). It corresponds to the ultimate state of differentiation for an axis, it is usually short, without branches. The apical meristem or bud of an axis is thus characterized by the PA of the growth unit that it may produce and a metamer is characterized by its PA i (which is the PA of the growth unit that it belongs to). Moreover, along an axis, the morphological features of the growth unit may evolve with the age of the apical meristem. This process is described as the meristem sequence of differentiation by Barthélémy and Caraglio (2007), and corresponds to a transition to a superior PA of the meristem.

Since the number of potential metamers per growth unit and the number of potential axillary buds per metamer can be considered as a fixed botanical data, it is straightforward to deduce the whole plant structure from the population of buds. Moreover, we will often identify the meristem with the bud that it forms, for the sake of simplicity. Therefore, in the following, modelling plant development is equivalent to studying the dynamic evolution of the population of buds. It is mainly driven by the two botanical processes described above : branching resulting from the appearance of lateral buds in growth units and the differentiation sequence of meristems resulting in the change of PAs for terminal buds. As a consequence, at growth cycle n, a bud is characterized by 3 indices : its PA ϕ, the CA k of the axis (which is also the CA of the meristem) and the initial PA of the meristem β. It will be denoted by $b_{n,\phi}^{k,\beta}$. In the sequel, the two botanical processes will be referred to as *branching* and *differentiation*.

3.2 Stochastic F0L-systems in the GreenLab growth model

As shown in Kang et al. (2007) and Loi and Cournède (2008), GreenLab can be described by a stochastic F0L-system $G^{tot} = \langle V, \Pi^{tot} \rangle$. Let $N \in \mathbb{N}$ be the time during which we observe the growth of the plant. A bud $b_{n,\phi}^{k,\beta}$ is symbolized by $s_{\phi}^{k,\beta}$ and a metamer of PA j by m_j. V is the union of $\mathcal{S}=\{s_{\phi}^{k,\beta} : (\phi,\beta) \in \{0,\cdots,P\}^2, k \in \{1,\cdots,N\}\}$ and $\mathcal{M}=\{m_j : j \in \{1,\cdots,P\}\}$ where $\mathcal{S}$ is the set of buds (non terminal elements) and $\mathcal{M}$ is the set of metamers (terminal elements). A dead bud will be represented by the empty word $\mathbf{1}$.

The seed can be considered as the initial bud and is thus represented by $s_1^{0,1}$. We consider the component system $G^{tot}[s_1^{0,1}]$ and $(F_n^{tot}[s_1^{0,1}])_{n\in\mathbb{N}}$ the corresponding Markov chain. For $n \in \mathbb{N}$, $F_n^{tot}[s_1^{0,1}]$ is the random variable representing the possible realisations of a plant

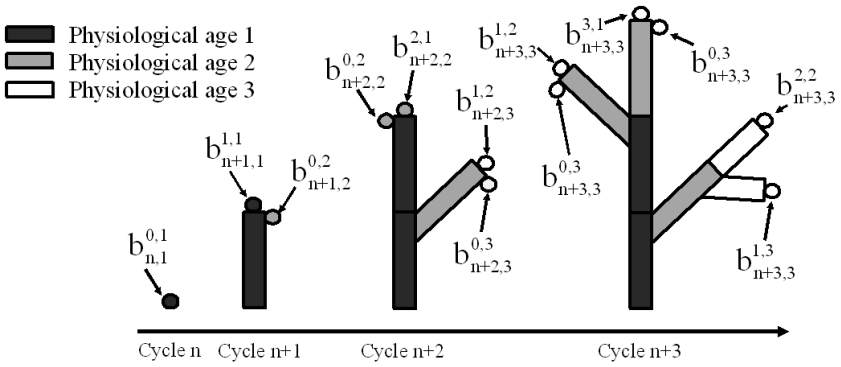

FIG. 1 – Example of deterministic development for a bud during 3 cycles. A bud of PA 1 gives a metamer of PA 1 bearing a lateral bud of PA 2 and a terminal bud of PA 1. A bud of PA 2 gives a metamer of PA 2 bearing a lateral bud of PA 3 and a terminal bud of PA 2. A bud of PA 3 gives a metamer of PA 3 and a terminal bud of PA 3. After two cycles, the terminal bud of an axis of PA 1 differentiates and its new PA is 2. After one cycle, the terminal bud of an axis of PA 2 differentiates and its new PA is 3.

after n growth cycles. Our objective is to determine the generating function associated to $F_n^{tot}[s_1^{0,1}]$. To do so, we will proceed as suggested at the end of Section 2.3. Thus, we only need to determine the generating function associated to $F_1^{tot}[s_1^{0,1}]$. GreenLab is a complex branching process. Therefore, the idea is to break up the whole system (branching + differentiation) into two elementary L-systems and study them separately. For each L-system, we write the corresponding generating function. Finally, we give the recursive equations for the generating functions derivating from G^{tot} by using Proposition 2.4.

3.2.1 Branching

The branching corresponds to the expansion of the architecture of the plant. Three different types of probabilities have been identified (de Reffye (1979)) :

- P_l : bud survival probability. At each growth cycle, a bud may stay alive with probability P_l or die with probability $(1 - P_l)$. It may depend on bud's PA and will thus be denoted by $P_l(i)$ for $1 \leq i \leq P$.
- P_a : bud activity probability. At each growth cycle, if a bud is alive, it may stay dormant with probability $(1 - P_a)$ or produce a new growth unit with probability P_a. P_a may also depend on bud's PA : $P_a(i)$ for $1 \leq i \leq P$.
- $P_{i,j}^b(k)$: production probabilities. If at a given growth cycle, a bud of PA i is active, $P_{i,j}^b(k)$ is the probability that the growth unit it develops into bears k axillary buds of PA j. Botanical constraints usually impose that $0 \leq k \leq B_{i,j}^{max}$ and $i \leq j$.

Let $G^{br} = \langle V, \Pi^{br} \rangle$ be the stochastic F0L-system associated to the branching process. For every component system $G^{br}[v]$ of G^{br}, the corresponding Markov chain is denoted $(F_n^{br}[v])_{n\in\mathbb{N}}$. Let $\psi_1^{br}[s_\phi^{k,\beta}](S,M)$ be the generating function associated to the component system $G^{br}[s_\phi^{k,\beta}]$. $S = \left(s_{\phi'}^{k',\beta'}\right)_{k',\beta',\phi'}$ and $M = (m_{\phi'})_{\phi'}$ are vectors respectively on $[0,1]^{(N+1)P^2}$ and $[0,1]^P$. The following theorem has been proved in Loi and Cournède (2008) :

Theorem 3.1 *The generating function associated to $G^{br}[s_\phi^{k,\beta}]$ is given by*

$$\psi_1^{br}[s_\phi^{k,\beta}](S,M) = 1 - P_l(\phi) + P_l(\phi)(1-P_a(\phi))s_\phi^{k+1,\beta} + P_l(\phi)P_a(\phi)m_\phi s_\phi^{k+1,\beta} \sum_{(j_\phi,\ldots,j_P)} \prod_{i=\phi}^{P} P_{\phi,i}^b(j_i)\left(s_i^{0,i}\right)^{j_i}.$$

We propose en extension of Theorem 3.1 including complex growth units. We recall that a growth unit is the set of metamers built by a bud during a growth cycle. In Theorem 3.1, the number of metamers per growth unit is constant and equal to 1. In the sequel, it will be a stochastic variable. In order to write the generating function in the general case, we have to refine the alphabet defined at the beginning of Section 3.2. In the sequel, a metamer will be described by two indexes. Let $m_{i,j}$ be the metamer of PA i that bears structures of PA j (*i.e.* when the metamer is created, it bears only lateral buds of PA j). Botanical constraints impose $i \leq j$. Let $\mathcal{M}'=\{m_{i,j} : (i,j) \in \{1,\cdots,P\}^2, i \leq j\}$ be the set of all metamers. Then, we have $V = \mathcal{S} \cup \mathcal{M}'$ where $\mathcal{S}$ is the set of all buds defined at the beginning of Section 3.2. We define a new type of development probability (after Kang et al. (2008)) :

- $\{P_{i,j}^m(k)\}_{k\in\{1,\ldots,M_{i,j}\}}$: probability distribution of the number of metamers $m_{i,j}$ in a growth unit of PA i. Botanical constraints usually impose that $0 \leq k \leq M_{i,j}^{max}$.

Thus, we can rewrite Theorem 3.1 in the case of growth units with a random number of metamers :

Theorem 3.2 *The generating function associated to $G^{br}[s_\phi^{k,\beta}]$ is given by*

$$\psi_1^{br}[s_\phi^{k,\beta}](S,M) = 1 - P_l(\phi) + P_l(\phi)(1-P_a(\phi))s_\phi^{k+1,\beta} + P_l(\phi)P_a(\phi)s_\phi^{k+1,\beta}\sum_{i=\phi}^{P}\left[\left(\sum_{q=0}^{M_{\phi,i}^{max}} P_{\phi,i}^m(q)\left[m_{\phi,i}\left(\sum_{j=0}^{B_{\phi,i}^{max}} P_{\phi,i}^b(j)\left(s_i^{0,i}\right)^j\right)\right]^q\right)\right]$$

Proof In order to get the generating function, we have to take the equation of Theorem 3.1. The last term of this equation corresponds to the case where the bud gives a new growth unit. We have to modify this term by taking into account all the possible PA of structures that may bear the growth unit. By doing so, we get Theorem 3.2.

3.2.2 Differentiation

The differentiation is the process corresponding to the change in PA of the apical bud changes along an axis. Two kinds of data are essential to describe the phenomenon :

- λ_i : inverses of average occupation times. During its sequence of differentiation, a meristem stays of PA i for an average period of $1/\lambda_i$.
- $q_{i,j}$: transition probabilities. When a meristem of PA i changes its PA, $q_{i,j}$ is the probability that its new PA equals j. Note that the botanical differentiation sequence imposes that $q_{i,j} = 0$ if $j \leq i$.

Let $G^{dif} = \langle V, \Pi^{dif} \rangle$ be the stochastic F0L-system associated to the differentiation process. For every component system $G^{dif}[v]$ of G^{dif}, the corresponding Markov chain is denoted $(F_n^{dif}[v])_{n\in\mathbb{N}}$. Let T_k^β be the random variable on $\mathbb{N}$ that represents the CA of an axis whose PA's apical bud is superior or equal to k for the first time given that the axis began with a bud of PA β.

Let $\psi_1^{dif}[s_\phi^{k,\beta}](S, M)$ be the generating function associated to the component system $G^{dif}[s_\phi^{k,\beta}]$. Let D be the event $\{T_\phi^\beta < k-1, T_{\phi+1}^\beta > k-1\}$. $S = \left(s_{\phi'}^{k',\beta'}\right)_{k',\beta',\phi'}$ is a vector on $[0,1]^{(N+1)P^2}$. The following theorem has been proved in Loi and Cournède (2008) :

Theorem 3.3 *The generating function associated to $G^{dif}[s_\phi^{k,\beta}]$ is given by :*

if $1 \leq k \leq N-1$,

$$\psi_1^{dif}[s_\phi^{k,\beta}](S) = P(T_{P+1}^\beta < k|D) + P(T_{\phi+1}^\beta > k|D)s_\phi^{k,\beta} + \sum_{i=1}^{P-\phi} P(T_{\phi+i}^\beta < k, T_{\phi+i+1}^\beta > k|D)s_{\phi+i}^{k,\beta}$$

and if $k = 0$,

$$\psi_1^{dif}[s_\beta^{0,\beta}](S) = s_\beta^{0,\beta}$$

As shown in Loi and Cournède (2008), all the probabilities of Theorem 3.3 can be given explicitely by using the properties of phase types distributions (see Neuts (1975) and Assaf et al. (1984)).

3.2.3 The complete model

In this section, we establish the recursion formulas for the generating functions derivating from the complete L-system $G^{tot} = \langle V, \Pi^{tot} \rangle$ defined at the beginning of Section 3.2.

The complete GreenLab development model mixes branching and differentiation. We assume that the priority is given to the branching process at each growth cycle. Then, each step of G^{tot} begins with a step of G^{br} and goes on with a step of G^{dif}. It is thus obvious that $G^{tot} = G^{br} \circ G^{dif}$. This result leads to the following theorem :

Theorem 3.4 *For all* $(\beta,\phi)\in\{1,\cdots,P\}^2$, $S=\left(s_{\phi'}^{k',\beta'}\right)_{k',\beta',\phi'}\in[0,1]^{(N+1)P^2}$ *and* $M=(m_{\phi'})_{\phi'}\in[0,1]^P$,

$$\forall n+k\leq N+1,\qquad \psi_{n+1}^{tot}[s_\phi^{k,\beta}](S,M)=\psi_1^{br}[s_\phi^{k,\beta}](\boldsymbol{\psi^{dif}}(\boldsymbol{\psi_n^{tot}}(S,M)),M)$$

with $\boldsymbol{\psi_n^{tot}}=\left(\psi_n^{tot}[s_\phi^{k,\beta}]\right)_{k,\beta,\phi}$ *and* $\boldsymbol{\psi^{dif}}=\left(\psi_1^{dif}[s_\phi^{k,\beta}]\right)_{k,\beta,\phi}$.

Setting $\psi_1^{tot}[s_\phi^{k,\beta}](S,M)=0$ for $k+n>N+1$ and $\boldsymbol{\psi^{br}}=\left(\psi_1^{br}[s_\phi^{k,\beta}]\right)_{k,\beta,\phi}$, we have :

Theorem 3.5 *For all* $n\leq N-1$, $\quad\boldsymbol{\psi_{n+1}^{tot}}(S,M)=\boldsymbol{\psi^{br}}(\boldsymbol{\psi^{dif}}(\boldsymbol{\psi_n^{tot}}(S,M)),M)$.

Let $m_j[s_\phi^{k,\beta},n]$ be the number of type j metamers in a structure initiated by $s_\phi^{k,\beta}$ after n growth cycles and let M_n be the matrix of size $(N+1)P^2$ by P whose j-th column vector is $\left(E\left[m_j[s_\phi^{k,\beta},n]\right]\right)_{k,\beta,\phi}$. Let e_k be the vector of size k with all its components set to 1. We deduce the fundamental recursion equation for the expectations of the numbers of organs on each type of structures. It is important to note that the first line of the matrix corresponds to those of the whole plant.

Theorem 3.6 *for* $N>0$,

$$M_{N+1}=\frac{\partial\boldsymbol{\psi^{br}}}{\partial S}(e_{(N+1)P^2},e_P)\frac{\partial\boldsymbol{\psi^{dif}}}{\partial S}(e_{(N+1)P^2},e_P)M_N+\frac{\partial\boldsymbol{\psi^{br}}}{\partial M}(e_{(N+1)P^2},e_P)$$

In the same way, we can give recursion formulas to get the variance. However, we cannot write a recursion formula that gives directly the variance like in Theorem 3.6 but we can write a method to get the variance. First, we have to determine $\frac{\partial^2\boldsymbol{\psi^{tot}}}{\partial M^2}(e_{(N+1)P^2},e_P)$. This is a tensor of dimension 3. The following proposition gives a recursion formula to get that tensor. The proof of Proposition 3.7 relies on basic properties of generating functions. The aim is to differentiate twice the equation of Theorem 3.4 with respect to S. To make the reading clearer, the entries of the functions are not written. In the following proposition, all entries are equal to $(e_{(N+1)P^2},e_P)$.

Proposition 3.7 *for* $N>0$,

$$\frac{\partial^2\boldsymbol{\psi_{N+1}^{tot}}}{\partial M^2}=2\frac{\partial^2\boldsymbol{\psi^{br}}}{\partial S\partial M}\frac{\partial\boldsymbol{\psi^{dif}}}{\partial S}\frac{\partial\boldsymbol{\psi_N^{tot}}}{\partial M}+\frac{\partial^2\boldsymbol{\psi^{br}}}{\partial S^2}\frac{\partial\boldsymbol{\psi^{dif}}}{\partial S}\frac{\partial\boldsymbol{\psi_N^{tot}}}{\partial M}\frac{\partial\boldsymbol{\psi^{dif}}}{\partial S}\frac{\partial\boldsymbol{\psi_N^{tot}}}{\partial M}+\frac{\partial\boldsymbol{\psi^{br}}}{\partial S}\frac{\partial\boldsymbol{\psi^{dif}}}{\partial S}\frac{\partial^2\boldsymbol{\psi_N^{tot}}}{\partial M^2}$$

Remark : Note that we manipulate tensors of dimension 3. The usual calculations on matrices can be easily extended to tensors of dimension 3.

Let D_N be the extracted matrix of $\frac{\partial^2\boldsymbol{\psi_N^{tot}}}{\partial M^2}$ such that :

$$\forall(i,j)\in\{1,\cdots,(N+1)P^2\}\times\{1,\cdots,P\},\qquad (D_N)_{i,j}=(\frac{\partial^2\boldsymbol{\psi_N^{tot}}}{\partial M^2})_{i,j,j}.$$

D_N is a matrix of size $(N+1)P^2$ by P. Let L_N be the matrix of size $(N+1)P^2$ by P whose components are the squares of the components of M_N (*i.e.* $(L_N)_{i,j} = ((M_N)_{i,j})^2$). Finally, let V_N be the matrix of size $(N+1)P^2$ by P such that the component $(V_N)_{i,j}$ represents the variance of the number of type j metamers of a structure that began with a type i bud after N growth cycles. Then, we have the following theorem :

Theorem 3.8 *for* $N > 0$,

$$V_N = D_N + M_N - L_N$$

4 Examples and numerical tests

In this section, we will illustrate and validate the result of Theorem 3.6 with four numerical examples, by comparing the theoretical equations to the results of Monte-Carlo simulations. The first one corresponds to a development model with branching and no differentiation. The second one involves differentiation for a single stem plant. The third numerical test combines both processes. Finally, the last model combines both processes and, in addition, the number of metamers per growth unit is random. For each test, we are interested in the whole plant, *i.e.* in a structure that begins with a bud $b_{0,1}^{0,1}$. Thus, we consider the component system $G_{tot}[s_1^{0,1}]$.

4.1 Branching

In this section, we focus on the example of coffee trees, plants with stochastic branching and no differentiation. They have two PAs (*i.e.* P=2). A metamer of PA 1 can bear a maximum of two lateral buds of PA 2 (*i.e.* $B_{1,2}^{max} = 2$). A metamer of PA 2 does not bear any lateral bud. At each growth cycle, there are three possible evolutions for a bud :

- case 1 : $F_1^{br}[s_\phi^{k,\phi}] = \mathbf{1}$ with $\phi \in \{1,2\}$, the bud dies.
- case 2 : $F_1^{br}[s_\phi^{k,\phi}] = s_\phi^{k+1,\phi}$ with $\phi \in \{1,2\}$, the bud is still alive but rests.
- case 3 : the bud is active. In that case, it produces a new metamer with lateral buds ($F_1^{br}[s_1^{k,1}] = m_1 s_1^{k+1,1}(s_2^{0,2})^j$ with $j \in \{1,2\}$) or not ($F_1^{br}[s_\phi^{k,\phi}] = m_\phi s_\phi^{k+1,\phi}$ with $\phi \in \{1,2\}$).

We apply Theorem 3.6 and Theorem 3.8 to the coffee tree case. That way, we get an analytical expression for the expectation and the variance of the number of each type of metamer. The following data are used for the simulation :

- $P_l(1) = 0.99$, $P_l(2) = 0.9$.
- $P_a(1) = 0.97$, $P_a(2) = 0.75$.
- $P_{1,2}^b(0) = 0.05$, $P_{1,2}^b(1) = 0.25$, $P_{1,2}^b(2) = 0.7$.

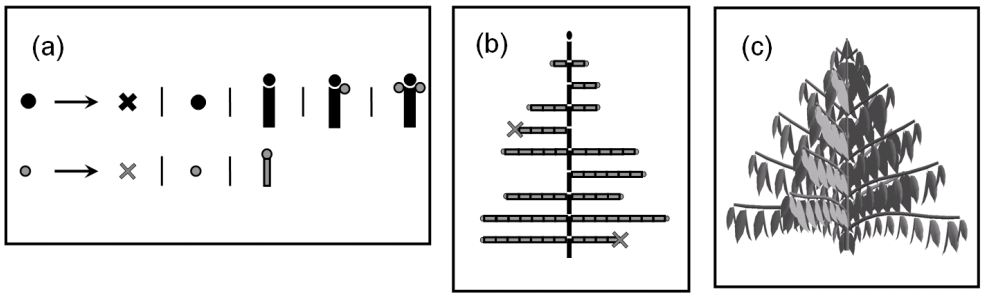

FIG. 2 – (a) Production rules of coffee trees : phytomers and buds of PA 1 are in black and those of PA 2 are in gray. The cross symbol represents dead buds. (b) An example of topology obtained after 10 growth cycles. (c) 3D representation.

We are interested in getting the theoretical expectations and variances of the numbers of metamers of physiological age 1 and 2 in the plant after N growth cycles. To do so, we have to determine respectively the coefficients of the first column of the matrix M_N and those of the matrix V_N. In a very similar way, we evaluate the theoretical variances of the numbers of metamers of physiological age 1 and 2. For each value of N, 50 000 stochastic simulations are carried out. Table 1 gives the results.

$N = 15$	
$M_{th}(1) = 13.4386$	$M_{th}(2) = 71.9330$
$M_{exp}(1) = 13.4428$	$M_{exp}(2) = 71.8159$
$V_{th}(1) = 10.4497$	$V_{th}(2) = 411.017$
$V_{exp}(1) = 10.4495$	$V_{exp}(2) = 409.0280$

$N = 50$	
$M_{th}(1) = 37.9313$	$M_{th}(2) = 351.1750$
$M_{exp}(1) = 37.9216$	$M_{exp}(2) = 350.9602$
$V_{th}(1) = 248.652$	$V_{th}(2) = 19953.1$
$V_{exp}(1) = 248.656$	$V_{exp}(2) = 19869.5$

TAB. 1 – Comparison of the theoretical and numerical expectations and variances of the numbers of metamers of physiological age ϕ (respectively $M_{th}(\phi)/V_{th}(\phi)$ and $M_{exp}(\phi)/V_{exp}(\phi)$) with $\phi = 1$ and $\phi = 2$ for the coffee tree.

As expected, there is a good agreement between the results of the MonteCarlo simulation and the theoretical compution.

4.2 Differentiation

In this section, we focus on the example of maize. This corresponds to a GreenLab model with differentiation and a very simple branching. We refer to Guo et al. (2006) for details on the topological model of maize. In standard cultivation conditions, maize is a mono-stem plant, that is to say without ramification. However, we can distinguish two types of metamers along the stem. The first ones are short and can potentially bear tillers. They are

followed by longer phytomers after meristem differentiation. Finally, the meristem ends up by flowering, which terminates the differentiation sequence and the stem development, see Figure 3. The two types of metamers are characterized by two different PAs ($P = 2$). We

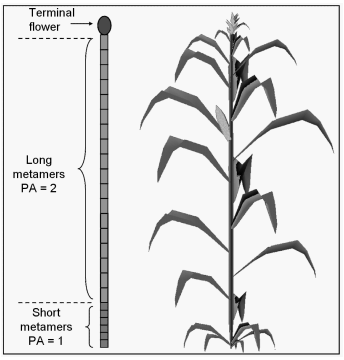

FIG. 3 – Differentiation sequence for maize and 3D representation.

assume that the terminal bud of an axis of CA $k = 0$ can not change its PA immediately. At each growth cycle, there are three possible evolutions for a bud through the differentiation process :

- case 1 : $F_1^{dif}[s_\phi^{k,1}] = s_\phi^{k,1}$ with $\phi \in \{1, 2\}$, the bud does not differentiate. The PA of the terminal bud remains the same.
- case 2 : $F_1^{dif}[s_1^{k,1}] = s_2^{k,1}$, the bud differentiates and is still alive. The PA of the terminal bud changes and is higher.
- case 3 : $F_1^{dif}[s_\phi^{k,1}] = \mathbf{1}$ with $\phi \in \{1, 2\}$, the bud differentiates and dies. The growth of the axis stops.

To get the full organogenesis model of maize, we need to combine the differentiation sequence with a simple branching process corresponding to axis elongation : $F_1^{dif}[s_\phi^{k,1}] = s_\phi^{k+1,1}$.

We apply Theorem 3.6 and Theorem 3.8 on the maize case. The following data are used for the simulation :

– $\lambda_1 = 1/7$, $\lambda_2 = 1/15$.
– $q_{1,2} = 0.98$.

As in Section 4.1, we are interested in getting the theoretical expectations and variances of the numbers of metamers of physiological age 1 and 2 in the plant after N growth cycles. For each value of N, 50 000 stochastic simulations are carried out. Table 2 gives the results.

$N = 15$	
$M_{th}(1) = 6.6306$	$M_{th}(2) = 5.8263$
$M_{exp}(1) = 6.6120$	$M_{exp}(2) = 5.8421$
$V_{th}(1) = 22.5827$	$V_{th}(2) = 21.0888$
$V_{exp}(1) = 22.5588$	$V_{exp}(2) = 21.0690$

$N = 50$	
$M_{th}(1) = 7.5060$	$M_{th}(2) = 13.6828$
$M_{exp}(1) = 7.5206$	$M_{exp}(2) = 13.7016$
$V_{th}(1) = 48.3288$	$V_{th}(2) = 148.8730$
$V_{exp}(1) = 48.8020$	$V_{exp}(2) = 148.9770$

TAB. 2 – Comparison of the theoretical and numerical expectations and variances of the numbers of metamers of physiological age ϕ (respectively $M_{th}(\phi)/V_{th}(\phi)$ and $M_{exp}(\phi)/V_{exp}(\phi)$) with $\phi = 1$ and $\phi = 2$ for maize.

Again, the results show the validity of the implementation of the theoretical computation.

4.3 The complete case

We apply Theorem 3.6 to a case that combines both complex branching and differentiation. The mixed model is easy to analyse. We have still three possibilities for the branching :

- case 1 : $F_1^{br}[s_\phi^{k,\phi}] = \mathbf{1}$ with $\phi \in \{1, 2\}$, the bud dies.
- case 2 : $F_1^{br}[s_\phi^{k,\phi}] = s_\phi^{k+1,\phi}$ with $\phi \in \{1, 2\}$, the bud is still alive but rests.
- case 3 : the bud is active. In that case, it produces a new metamer with lateral buds ($F_1^{br}[s_1^{k,1}] = m_1 s_1^{k+1,1}(s_2^{0,2})^j$ with $j \in \{1, 2\}$) or not ($F_1^{br}[s_\phi^{k,\phi}] = m_\phi s_\phi^{k+1,\phi}$ with $\phi \in \{1, 2\}$).

We have also three possibilities for the differentiation :

- case 1 : $F_1^{dif}[s_\phi^{k,1}] = s_\phi^{k,1}$ with $\phi \in \{1, 2\}$, the bud does not differentiate. The PA of the terminal bud remains the same.
- case 2 : $F_1^{dif}[s_1^{k,1}] = s_2^{k,1}$, the bud differentiates and is still alive. The PA of the terminal bud changes and is higher.
- case 3 : $F_1^{dif}[s_\phi^{k,1}] = \mathbf{1}$ with $\phi \in \{1, 2\}$, the bud differentiates and dies. The growth of the axis stops.

We apply the same method as in the two previous sections to get the expectations and the variances of the numbers of each type of metamer. The following data are used for the simulation :

- $P_l(1) = 0.99$, $P_l(2) = 0.9$.
- $P_a(1) = 0.97$, $P_a(2) = 0.75$.
- $P_{1,2}^b(0) = 0.25$, $P_{1,2}^b(1) = 0.75$, $P_{1,2}^b(2) = 0$.
- $\lambda_1 = 1/10$, $\lambda_2 = 1/5$.
- $q_{1,2} = 0.98$.

It could correspond to a herbaceous plant with a topology close to that of Arabidopsis or Rapeseed (see Christophe et al. (2008) for an application of the GreenLab model to Arabidopsis), see Figure 4. Table 3 gives the results for 50 000 simulations.

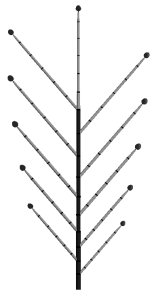

FIG. 4 – Topology of a plant with branching and differentiation processes (deterministic case). Phytomers of physiological age 1 are in black and those of physiological age 2 in gray. The differentiation sequence ends with flowering.

$N = 15$	
$M_{th}(1) = 7.4466$	$M_{th}(2) = 13.6313$
$M_{exp}(1) = 7.4423$	$M_{exp}(2) = 13.6388$
$V_{th}(1) = 24.7144$	$V_{th}(2) = 76.1223$
$V_{exp}(1) = 24.7159$	$V_{exp}(2) = 76.1401$

$N = 50$	
$M_{th}(1) = 9.1774$	$M_{th}(2) = 19.6512$
$M_{exp}(1) = 9.1951$	$M_{exp}(2) = 19.6616$
$V_{th}(1) = 74.3520$	$V_{th}(2) = 331.3130$
$V_{exp}(1) = 74.3167$	$V_{exp}(2) = 331.3630$

TAB. 3 – Comparison of the theoretical and numerical expectations and variances of the numbers of metamers of physiological age ϕ (respectively $M_{th}(\phi)/V_{th}(\phi)$ and $M_{exp}(\phi)/V_{exp}(\phi)$) with $\phi = 1$ and $\phi = 2$ for the mixed model.

Again, there is a good agreement between the theoretical and numerical results. It is interesting to compare the results of Table 1 and those of Table 3. The number of metamers is much lower in the mixed model. This is obviously due to the differentiation process. The population of buds dies much faster because of differentiation. This phenomenon highlights an interesting fact. In Section 4.1, we deal with a supercritical multitype branching process. In that case, the probability of extinction is not equal to 1 and the population of buds grows quickly. Considering the mixed model, the differentiation subdues the growth of buds. If there is no reiteration, we can prove that the probability of extinction is always equal to 1. It means that the growth is finite almost surely.

4.4 The complete case with complex growth units

In this section, we consider the same growth model as in Section 4.3 and, in addition, we have a random number of metamers per growth unit. The generating function for the development is that of Theorem 3.2. In the next simulation, growth units of physiological age 1 can have from one to three metamers and growth units of physiological age 2 can have one or two metamers. The results we can get are very similar to that of Figure 4 but with growth units of different lengths :

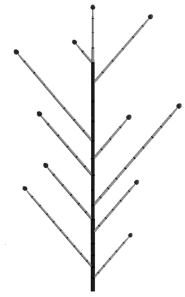

FIG. 5 – Mixed model with complex growth units

The following data are used :

- $P^m_{1,2}(1) = 0.20$, $P^m_{1,2}(2) = 0.35$, $P^m_{1,2}(3) = 0.45$.
- $P^m_{2,\cdot}(1) = 0.35$, $P^m_{2,\cdot}(2) = 0.65$.

Table 4 gives the results for 50 000 simulations.

$N = 15$	
$M_{th}(1) = 16.7548$	$M_{th}(2) = 22.4917$
$M_{exp}(1) = 16.7547$	$M_{exp}(2) = 22.5182$
$V_{th}(1) = 129.4920$	$V_{th}(2) = 210.3440$
$V_{exp}(1) = 129.5650$	$V_{exp}(2) = 211.5410$

$N = 50$	
$M_{th}(1) = 20.6491$	$M_{th}(2) = 32.4244$
$M_{exp}(1) = 20.6441$	$M_{exp}(2) = 32.3898$
$V_{th}(1) = 381.7990$	$V_{th}(2) = 906.4710$
$V_{exp}(1) = 380.6660$	$V_{exp}(2) = 904.4570$

TAB. 4 – Comparison of the theoretical and numerical expectations and variances of the numbers of metamers of physiological age ϕ (respectively $M_{th}(\phi)/V_{th}(\phi)$ and $M_{exp}(\phi)/V_{exp}(\phi)$) with $\phi = 1$ and $\phi = 2$ for the mixed model with complex growth units.

Again, there is a good agreement between the theoretical and numerical results.

5 Conclusion and discussion

While the interest of stochastic L-systems for plant growth simulation and visualization is broadly acknowledged, its full mathematical potential to characterize the probability distributions and moments of the numbers of organs in plant structure had not been taken advantage of. The need for an analytic computation of these distributions is crucial in stochastic functional-structural models in order to derive the distribution or the moments of biomass production (cf. Kang et al. (2008) for preliminary results). It has led us to clearly formalize the link between stochastic L-systems and multi-type branching processes, and thus to derive an inductive relationship to compute the associated generating functions. This framework was applied successfully to the GreenLab organogenesis model, by decomposing the development process into two botanical sub-processes, branching and meristem differentiation. For the latter, multivariate phase type random vectors were introduced to describe the stochastic sequence of meristem differentiation. From the inductive relationship on the generating functions of the numbers of organs, we can determine the inductive relationship giving the moments of the distributions.

In this report, some hypotheses concerning the modelling may be questionable. Using stochastic L-systems to represent the growth of plants imposes some constraints of orders. As a matter of fact, at each growth cycle, several physical phenomena are modelled (in this report, branching and differentiation). Thus, we have to organize these phenomena into a hierarchy (in this report, each growth cycle begins with a step of branching and then one of differentiation). When we deal with three or more phenomena, it may be difficult to organize them into a hierarchy without altering the meaning of the whole biological process.

The next step is the link of stochastic organogenesis and functioning models. It is possible to derive the approximate moments of biomass production thanks to differential statistics. An interesting issue concerns the modelling of the probability distributions governing organogenesis as functions of biomass production or growth rate (cf. Mathieu et al. (2006)). The stochastic processes resulting from these interactions between development and functioning should lead us to improve the proposed formalism.

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Éditeur
INRIA - Domaine de Voluceau - Rocquencourt, BP 105 - 78153 Le Chesnay Cedex (France)
http://www.inria.fr
ISSN 0249-6399