Theoretical Study and Numerical Simulation of a Stochastic Model for Plant Growth

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RÉSUMÉ. Le modèle GreenLab est un modèle de croissance des plantes combinant à la fois l'architecture et l'écophysiologie. Il s'appuie sur le fonctionnement d'un automate déterministe ou stochastique. Dans le cas stochastique, des plantes avec les mêmes paramètres endogènes peuvent avoir des architectures et des productions de biomasse très différentes. Afin de décrire les distributions stochastiques des variables du système, nous cherchons à déterminer leurs principaux moments. Nous présentons une méthode récursive pour le calcul de la moyenne et de la variance du nombre d'organes, et nous en déduisons la moyenne et la variance de la production de biomasse. Les résultats théoriques sont validés par une simulation de Monte-Carlo.

ABSTRACT. Recently, plant models combining both physiology and architecture have been attracting more and more attention. 'GreenLab' is such kind of functional-structural model, based on a deterministic or stochastic automaton. In the stochastic case, given the same parameters, the resulting plants can be notably different in terms of architecture and biomass production. To describe the stochastic distributions of the system variables, we need to evaluate their principal moments according to model parameters. We present a recursive method for computing the mean and variance of the number of organs and biomass production. These theoretical results are validated by comparing them with Monte Carlo simulations.

MOTS-CLÉS : Modèle de croissance de plantes, processus stochastique, simulation de Monte Carlo.

KEYWORDS: Plant growth model, stochastic process, Monte-Carlo simulation.

1. Introduction

Plant growth modelling has known in recent years a lot of significant improvements, particularly with the development of functional structural models (FSM), i.e. models describing both architecture and photosynthesis, see for example LIGNUM [3], AMAPHydro [5], and more recently GreenLab [4,8].

In fields or forests, similar plants in the same environmental conditions can have different growth processes. It is taken into account in various methods of plant simulation, see for example [6], in order to give a realistic effect for visualization. In GreenLab, organogenesis is modelled by a double-scale automaton, *cf.* [8]. It can be deterministic or stochastic, in order to represent more properly the natural variability of plants. Bud activity is thus described as a stochastic process. Analysis of model behaviour has been done in the deterministic case [7]. For the stochastic growth, it is possible to get statistical results with Monte-Carlo simulation, but it's inefficient. In this article is presented for the first time a method to determine analytically the mean and variance of the number of organs and biomass production according to parameters. First, GreenLab model is introduced and the stochastic bud behaviours are described. Then we present the method of recursive computation of mean and variance of the number of organs and for the biomass production. Examples are shown to help understanding.

2. GreenLab model

2.1. Organogenesis model

To generate plant architecture, a dual-scale automaton was designed, see [8] and Figure 1. There are two kinds of states, namely macrostates and microstates, which correspond to growth units and metamers. A growth unit (GU) is generated by a bud and is the part of an axis appearing during a growth cycle. It can contain N_f metamers. A metamer is a botanical unit composed of an internode, N_l leaves and N_B axillary buds. Thus, an axis is a succession of growth units, and we define a substructure as an axis with its branches. In the automaton, the botanical notion of physiological age (PA) is used to represent the organs differenciation. The PA of axillary buds are superior to that of the bearing axis and the different microstates in the same macrostate are distinguished by the PA of their buds. PA varies from 1, for the initial macrostate, to P_m , for the terminal one. We also define the chronological age (CA) of a botanical unit as the number of growth cycles since its appearance.

In the automaton, the number of repetitions of macrostates is N_s (for each PA).

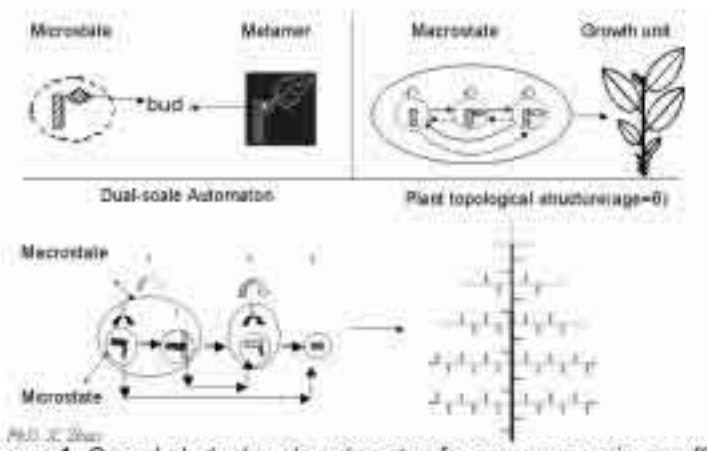


Figure 1. *GreenLab dual-scale automaton for organogenesis, see [8]*

2.2 Bud probabilities

In real plants, at each cycle, a bud may die, rest or grow. Thus, four kinds of probabilities are introduced to make the automaton stochastic:
1) Survival probability of terminal buds p_C, see Figure 2(a). If the terminal bud dies (×), the axis stops growing, and the resulting number of GU in the axis is a geometrical law;
2) Growth probability of terminal buds p_A, see Figure 2(b). If the bud survives, it can grow with probability p_A or rests with probability 1- p_A. If p_C =1, the resulting number of GU in the axis follows a binomial law of parameters N_E, p_A.
3) Probability of metamer appearance p_I, see Figure 2(c). The number of metamers per GU is random and follows a binomial law of parameters N_I, p_I;
4) Probability of growth of lateral buds p_B, see Figure 2(d).
These probabilities can have different values for each PA. Finally the numbers of internodes result from all of them, and thus follow compound distributions.

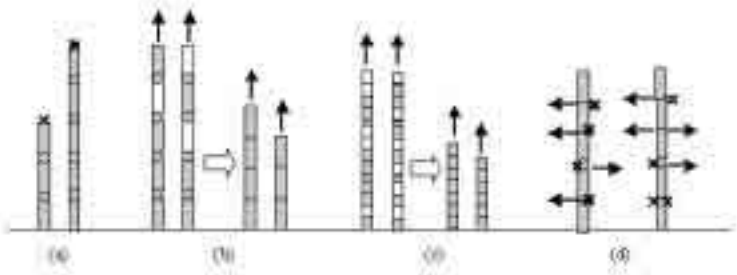


Figure 2 : probabilities

2.3 Photosynthesis model

The model describes the biomass production and its partitioning among organs at each growth cycle. If we suppose that leaves function for only one cycle (case of temperate trees), the recurrent equation of biomass production can be written in the following form:

$$Q(n) = E\frac{L(n)\,Q(n-1)}{A\,L(n) + B\,Q(n-1)} \qquad (1)$$

where $Q(n)$ is the biomass produced at growth cycle i, ($Q(0)$ being the seed), $L(n)$ is the number of functioning leaves, E is the environmental factor, A and B are parameters representing source-sink relationships, allometric rules and photosynthesis functioning in the plant. Details can be found in [7].

3. Mean and variance of the number of leaves

Since the number of leaves per metamer is a constant parameter, we only need to compute the number of metamers. The basic idea for the following computation is that each plant substructure is characterized by its CA and PA, and can be decomposed into a bearing axis and axillary substructures of superior PA. Naturally, the number of metamers in the structure is the sum of those from the bearing axis and from its substructures. This relationship can lead to a recursive computation method. We begin by the simplest structures with maximum PA (Pm), without branches, and end with the most complex one of PA=1, which represents the full plant structure.

3.1 Number of metamers in an axis

First, we recall an important result on compound stochastic processes, see [1] :

If a variable $Z=X_1+X_2+\ldots+X_Y$, where X_j ($1\leq j\leq Y$) are independent and identically distributed variables, Y is a random variable, then mean and variance of Z, M_Z and V_Z can be computed from that of X and Y :

$$\begin{cases} M_Z = M_X M_Y \\ V_Z = M_Y V_X + V_Y M_X^2 \end{cases} \qquad (2)$$

At every cycle, the terminal bud survives with a probability p_C. Thus, at cycle i, the probability that the bud still lives is p_C^i. Let X_i be the stochastic variable such that X_i=1 if at cycle i the bud still lives, X_i=0 otherwise. Then, we obviously get:

$M_i = p_i^i$ and $V_i = p_i^i(1-p_i^i)$,

and the covariance between X_i and X_j is:

$Cov(X_i, X_j) = p_i^j(1-p_i^j)\ (j>i)$

Let Y be the Bernoulli variable such that Y=1 if a living bud grows, then:

$M_Y = p_A$ and $V_Y = p_A(1-p_A)$

If Y=1, let v be the stochastic number of metamers in the GU. It follows a binomial law:

$M_v = N_v p_v$ and $V_v = N_v p_v(1-p_v)$

Considering that γ, the number of metamers produced by a living bud is 0 if Y=0 or v if Y=1, we get from the compound processes equations (2):

$M_\gamma = M_v M_Y$ and $V_\gamma = M_Y V_v + V_Y M_v^2$

Likewise, let μ_i be the number of new metamers created at cycle i. It is 0 if the bud dies, and γ otherwise. We get:

$M_{\mu_i} = M_\gamma M_{Y_i}$ and $V_{\mu_i} = M_\gamma V_{Y_i} + V_\gamma M_{Y_i}^2$

The covariances are:

$Cov(\mu_i, \mu_j) = M_\gamma^2 Cov(X_i, X_j)$

Finally, we can deduce μ, the total number of metamers in an axis of CA N, as the sum of all metamers created from cycle 1 to cycle n, where n=min(N, N_A), and we get:

$$M_\mu = \sum_{i=1}^{n} M_{\mu_i} = M_\gamma M_Y$$

$$V_\mu = \sum_{i=1}^{n} V_{\mu_i} + 2\sum_{i=1}^{n-1}\sum_{j=i+1}^{n} Cov(\mu_i, \mu_j) = V_\gamma M_Y^2 + M_\gamma V_Y M_Y \qquad (3)$$

with $M_Y = (M_1, \ldots, M_n)$, $V_Y = (V_1, \ldots, V_n)$,

$$M_1 = \begin{pmatrix} M_{X_1} \\ \vdots \\ M_{X_n} \end{pmatrix} = \begin{pmatrix} p_C^1 \\ \vdots \\ p_C^n \end{pmatrix} \quad , \quad V_X = \begin{pmatrix} p_C(1-p_C) & p_C^2(1-p_C) & \cdots & p_C^n(1-p_C) \\ p_C^2(1-p_C) & p_C^2(1-p_C^2) & \cdots & p_C^n(1-p_C^2) \\ \cdots & \cdots & \cdots & \cdots \\ p_C^n(1-p_C) & p_C^n(1-p_C^2) & \cdots & p_C^n(1-p_C^n) \end{pmatrix}$$

Note that this result is the multidimensional form of Equation (2).

3.2 Extension to branching structures

It is possible to generalize the results obtained for a single axis to the number of metamers of each PA in a substructure. Any structure can be decomposed into an axis and possible substructures. Let *S(k,m,N)* be the number of metamers of PA *m* in a structure of PA *k* and CA *N*. The case m=k corresponds to that of a single axis and has been solved in the previous section. If *m>k*, the counting process is recursive, and we have:

$$S(k,m,N) = \sum_{i=1}^{n(k)} X_i \sum_{j=k+1}^{P_m} \sum_{l=1}^{q_i(k,j)} S_j(j,m,N-i)$$

where $q_i(k,j)$ is the number of lateral substructures of PA *j* on an axis of PA *k* at cycle *i*, and $S_j(k,m,N-i)$ for $1 \le l \le q_i(k,j)$ are different realizations of the same stochastic variable.

Applying several times the compound processes equations (2) and in the same way of the previous section, we can prove that the mean and variance of *S(k,m,N)* are:

$$\begin{cases} M_{S(k,m,N)} = M_1 M_N \\ V_{S(k,m,N)} = V_1 M_X + M_1 V_N M_1 \end{cases} \quad (4)$$

where:

$$M_1 = \left[M_{s(1,m,0)} \quad \dots \quad M_{s(1,m,n-1)} \right] \quad , \quad V_1 = \left[V_{s(1,m,0)} \quad \dots \quad V_{s(1,m,n-1)} \right].$$

Thus, we have obtained a recursive way to compute the means and variances of the number of metamers for every substructure in the plant. In table(1) is shown the comparison between the theoretical results and those obtained by Monte-Carlo simulation (500 tests) on a stochastic plant with 4 different PA. The fitting is very good.

Mean					
PA	1	2	3	4	total
Formula	68.87	231.54	583.603	2109.45	2993.46
Simulation	68.77	240.66	599.28	2155.23	3063.94
Variance					
PA	1	2	3	4	total
Formula	226.04	3619.20	19337.19	236105.83	474455.49
Simulation	211.31	3463.19	19609.54	245223.26	484444.04

Table 1. *Mean and variance of the number of metamers*

4. Mean and variance of the biomass production

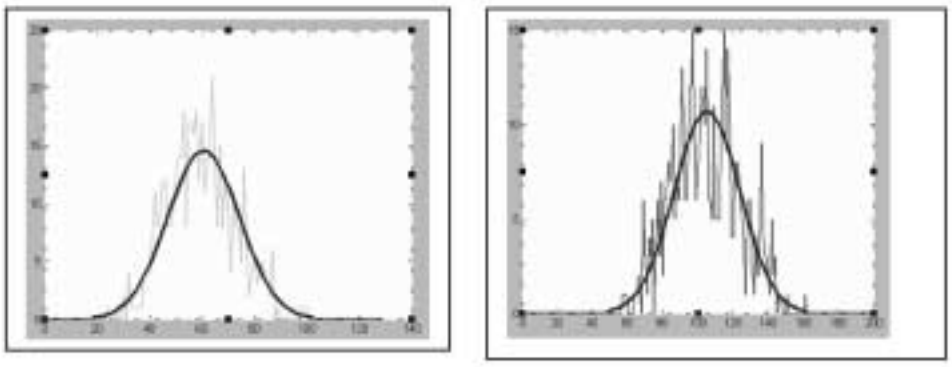
Equation (1) shows that if the organogenesis is stochastic, as the number of leaves varies, the biomass production will also be stochastic. In this section, thanks to differential statistics, we derive a direct way to compute approximated values of the mean and variance of the biomass production.

Let *X, Y, Z* be stochastic variables such that $Z=f(X,Y)$. If we know M_X, M_Y, V_X, V_Y and $Cov(X,Y)$, we can get approximated values of the moments of Z thanks to differential statistics:

$$M_Z \approx f(M_X, M_Y) + \frac{1}{2}\left(f''_{XX}(M_X, M_Y)V_X + f''_{YY}(M_X, M_Y)V_Y + 2f''_{XY}(M_X, M_Y)Cov(X,Y)\right)$$

$$V_Z = \left(f'_X(M_X, M_Y)\right)^2 V_X + \left(f'_Y(M_X, M_Y)\right)^2 V_Y + 2f'_X(M_X, M_Y)f'_Y(M_X, M_Y)Cov(X,Y)$$

From Equation (1), we know that $Q(n)$, the biomass production at cycle *n*, is a function of $L(n)$, the number of leaves at cycle n, and of $Q(n-1)$. Thus, we obtain a recurrent way of computing the mean and variance of the biomass production: if $M_{Q(n-1)}$ and $V_{Q(n-1)}$ are known, we compute $M_{L(n)}$ and $V_{L(n)}$ thanks to the method developed in section 3, we evaluate numerically the correlation between $L(n)$ and $Q(n-1)$ (in order to get $Cov(L(n),Q(n-1))$, and we deduce from the previous equations approximated values of $M_{Q(n)}$ and $V_{Q(n)}$. Actually, a theoretical expression of $Cov(L(n),Q(n-1))$ can be derived. It will be presented in a coming paper.



Leaves Distribution *Biomass Distribution*

Figure 3. *Comparison between theoretical distributions and simulations of the yields of a full stochastic plant*

In Figure 3, we show the numerical results obtained for a plant with 3 PA, with one metamer per GU, bearing up to 2 branches and p_C =0.9, p_A =0.8, p_B =0.5 for all PA. We suppose that the leaves and biomass distributions are gaussian as they are the results of numerous additive Bernoulli processes, and we compare the theoretical distributions obtained with the moments evaluated by our methods and the simulated distributions for 250 repetitions, at CA 20. The fitting is pretty good.

5. Conclusion

We have presented algorithmic methods to derive the mean and variance of a stochastic plant number of organs and biomass production. The results are synthetic and, for the first time, do not need a plant reconstruction, although they rely on the details of the architecture functioning. For most applications, these moments can be sufficient for the description of the yield, but the mathematical determination of the complete distributions for branching structures remains unsolved and is part of our current works.

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