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Résumé : Ce document est une étude comparative de quatre méthodes (chaînes de Markov, processus composés, décomposition en sous-structures et fonctions génératrices) permettant le calcul des distributions de probabilité associées aux processus de branchement homogènes. Bien que ces méthodes présentent toutes des intérêts, l'utilisation des fonctions génératrices s'avère la plus appropriée pour traiter ce genre de modèle probabiliste. Afin de pouvoir les comparer, chacune d'entre elles sera décrite dans un premier temps puis appliquée à un exemple de processus de branchement: l'évolution du nombre de bourgeons actifs pour un modèle de développement de plante particulier de type GreenLab.

Mots-clés : processus de branchement multitype, processus composé, fonction génératrice, développement plante, modèles de croissance de plantes, GreenLab

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Computing the moments of probability distributions for branching processes

Abstract: This document is a comparative study of four methods (Markov chains, compound processes, substructure factorization and generating functions) to compute the moments of probability distributions associated to homogeneous branching processes. Although all these methods have their own interests, the generating functions seem to be the most appropriate tools for this kind of probability model. In order to compare them, each method is first described and then applied to an example of multitype branching processes: the evolution of the number of active buds for a particular GreenLab plant growth model. Finally, the methods are listed according to their effectiveness.

Key-words: multitype branching process, compound process, generating function, plant development, plant growth models, GreenLab

1 Introduction

Branching processes were particularly studied in the sixties (Harris (1963)) and the seventies (Athreya and Ney (2004)). They are particularly used to model biological phenomena. They were first introduced to study the evolution of a population (Galton and Watson, 1874) and then applied in various biological areas such as botany or genetics. In this report we will focus only on homogeneous Galton-Watson branching processes. In that case, all individuals produce offspring independently of each other and of the past history of the process.

We have identified three general classes of methods to study this kind of probability model : the Markov chains, the compound processes and the generating functions. A specific method based on substructure factorization is also introduced and is proved very powerful for specific purposes. All of them share the same mathematical basis and give obviously the same results. However, the computations based on these methods can be more or less effective. The aim of this report is thus to highlight the benefits and the drawbacks of each method and then to study how and when to apply them.

These methods will be compared throughout a botanical example. The goal is to compute the expected value and the variance of the number of active buds for a plant during its growth. The model used to simulate plant development is the GreenLab model (see de Reffye and Hu (2003)). The GreenLab model is a functional-structural model, *i.e.* it combines the description of plant architecture at the organ level and that of biomass production and allocation. In this report, we will focus only on the development of the plant (*i.e.* the creation of new organs). This development is stochastic in the sense that the evolution of the architecture is given by a set of random variables. We will show that it corresponds to a multitype branching process.

This document first recall the concept of branching processes and draws a parallel between the GreenLab model and multitype branching processes. Then, each method is described in a general case and applied to the botanical example of the Leeuwenberg model with rest probabilities. At last, the methods are compared and listed with respect to their effectiveness.

2 Multitype branching processes

2.1 Definitions

Let us first recall the definition of a multitype branching process (Athreya and Ney (2004), Harris (1963), Mode (1971)). Let us consider a population with m types of individuals. Assume a type i individual produces children of all types according to a probability distribution $\{P_i(j) : j = (j_1, \cdots, j_m), j_i \in \mathbb{N}, 1 \leq i \leq m\}$. Assume all individuals produce offspring independently of each other and of the past history of the process. Let $B_{n,i}$ be the number of type i individuals in the n-th generation. Let $\{\xi_{n,i}^{(k)} : n \in \mathbb{N}^*, k \in \mathbb{N}, 1 \leq i \leq m\}$ be independant random vectors in $\mathbb{N}^m$ with $\xi_{n,i}^{(k)}$ having distribution $P_i(.)$.

Definition 2.1 (multitype Galton-Watson branching process) *If the vector* $B_n = (B_{n,1}, \cdots, B_{n,m})$ *of population sizes in the n-th generation evolves by the recursive relation*

$$B_{n+1} = \sum_{i=1}^{m} \sum_{k=1}^{B_{n,i}} \xi_{n,i}^{(k)}, \tag{1}$$

then $(B_n)_{n\in\mathbb{N}}$ *is a multitype Galton-Watson branching process.*

The j-th component of $\xi_{n,i}^{(k)}$ represents the number of type j individuals produced by the k-th type i individual in the n-th generation. The set $\{P_i(.)\}_{i\in\{1,\cdots,m\}}$ is called the offspring distribution.

An example of multitype branching process is the stochastic model of plant development GreenLab (see Section 2.2.1).

2.2 The GreenLab model for plant growth

2.2.1 Main botanical concepts

The GreenLab model of plant growth is a functional-structural model. The literature is already abundant on this generic model of plant growth (see de Reffye and Hu (2003), Yan et al. (2004), Cournède et al. (2008)), and we mainly focus in this section on the basic botanical concepts underlying GreenLab organogenesis model.

Plants based on the GreenLab model can be seen as a complex branching system whose architecture is a succession of elementary entities called metamers (or phytomers) (see for example Bell (1991)). A metamer is composed of an internode bearing organs : buds, leaves, flowers. When the growth is rhythmic, the plant grows by successive shoots of several metamers produced by buds. The appearance of these shoots defines the architectural Growth Cycle. A Growth Unit is the set of metamers built by a bud during a growth cycle. The Chronological Age of a plant (or of an organ) is defined as the number of growth cycles it has been existing 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 was introduced to represent the different types of axes. For instance, on coffee trees, there are two types : orthotropic trunk and plagiotropic branches. We need less than 5 physiological ages to describe the axis typology of most trees. The main trunk's physiological age is equal to 1 and the oldest physiological age corresponds to the ultimate state of differentiation for an axis, it is usually short, without branches.

In this report, we consider that the development of the plant is stochastic. A set of stochastic processes gives the evolution of the architecture (see Kang et al. (2007) and Kang et al. (2008) for more details). As far as the development of a bud is concerned, three kinds of probabilities are taken into account. The first one is the life probability P_l : for a given growth cycle, each bud survives with a probability P_l or dies with a probability $1 - P_l$. The

second one is the rest probability P_a : for a given growth cycle, even if a bud survives, it can rest with a probability $1 - P_a$. In that case, the bud is not active during the growh cycle but is still active for the next growth cycle. The last one is the probability of metamer appearance P_m. If a bud survives and does not rest, it gives a new growth unit containing M metamers where M follows a binomial law with parameters (P_m, B_m). B_m is the maximal number of metamers in a growth unit. All these stochastic processes can be summarized by the automaton of Figure 1.

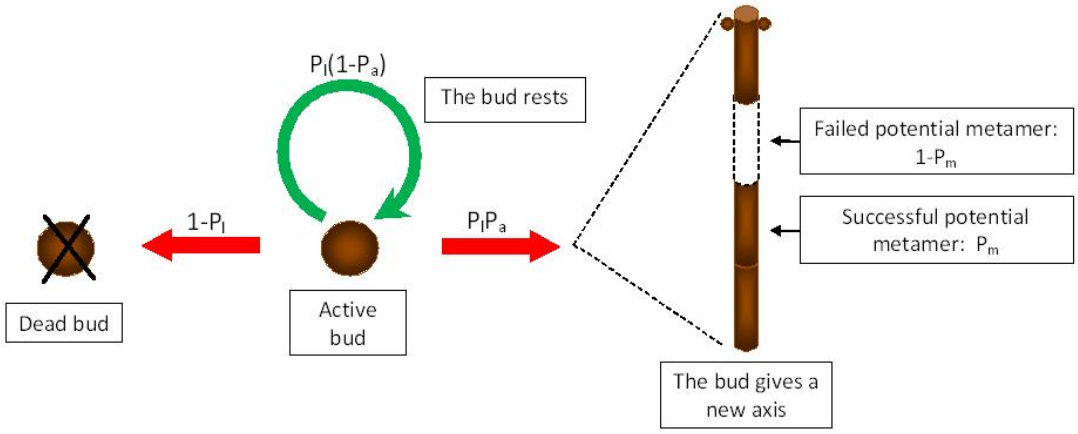

FIG. 1 – Stochastic automaton for the bud development

Given the type of GreenLab model used, these probabilities can depend on several parameters such as bud physiological age or plant chronological age.

2.2.2 Formalism

The stochastic model of GreeLab development can be formalized with the following stochastic L-system (Kang et al. (2007), Loi and Cournède (2008)) :

$$\mathcal{G} = \{\mathcal{V}, \mathcal{S}, \omega, \mathcal{P}_\nabla\}$$

where :

- V is the set of variables (i.e. symbols that can be replaced) : the set of active buds
- S is the set of constants (i.e. symbols that can not be replaced : the set of metamers
- ω is the initial state of the plant : a bud of physiological age 1

– P_r is the production rules (i.e. the set of rules that define how the variables can be replaced) : in this report, the evolution of a bud is given by a set of stochastic processes (see the previous automaton)

The population of buds is obviously described by a multitype branching process. Let m be the maximal physiological age. Let B_n be the random vector of size m ($B_n \in \mathbb{N}^m$) whose j-th component gives the number of active buds of physiological age j at growth cycle n. Let $\xi_{n,i}^{(k)}$ be the random vector of size m ($\xi_{n,i}^{(k)} \in \mathbb{N}^m$) whose j-th component represents the number of buds of physiological age j produced by the k-th bud of physiological age i at growth cycle n. Then, given buds reproduce independently from each other, the following equality holds :

$$B_{n+1} = \sum_{i=1}^{m} \sum_{k=1}^{B_{n,i}} \xi_{n,i}^{(k)}$$

As a consequence, $(B_n)_{n\in\mathbb{N}}$ is a multitype branching process. In the sequel, $B_{n,j}$ represents the number of active buds of physiological age j at growth cycle n. The study of the moments of the number of active buds is very interesting since the moments of the number of metamers is deduced straightforwardly. These last one are significant botanical data. As a matter of fact they give informations about the number of leaves or the number of fruits (characteristics of the metamers are considered fixed botanically). Hence, we get important information about the production of the plant.

2.2.3 A specific test case : the Leeuwenberg model with rest probabilities

The aim of this report is to describe and compare different methods to compute the moments of the number of individuals. In order to avoid big computations, the methods will be described for a 1-type branching process. However, we will explain how to extend these methods to multitype branching processes. All the methods introduced in this report are illustrated throughout a botanical example based on a particular botanical model : the Leeuwenberg type (Hallé et al. (1978)). The study of this kind of model is important because it is closely related to the theory of linear and binary trees. This model is simple but the aim is only to compare the methods. There is only one physiological age (i.e. one type). We consider a simplified stochastic model of development. Only the rest probability P_a is taken into account. In that case, one bud can give a metamer with two axial buds (with a probability P_a) or it can rest and remains a bud (with a probability $1 - P_a$) (cf figure 2)

Some occurrences of the stochastic model are represented in figure 3.

Let M_n be the total number of metamers at the beginning of growth cycle n, N_n the number of new metamers appeared at growth cycle n and B_n the number of buds at the beginning of growth cycle n. These variables are naturally related :

$$M_{n+1} = M_n + N_n \tag{2}$$

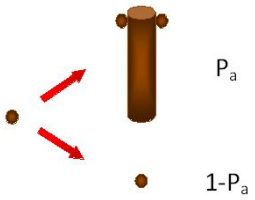

FIG. 2 – Stochastic automaton for the Leeuwenberg model with rest probabilities

FIG. 3 – Occurrences of the Leeuwenberg model with rest probabilities

$$B_{n+1} = B_n + N_n \tag{3}$$

By combining these two last equations, we get :

$$B_n = M_n + 1 \tag{4}$$

The initial state is a seed. Therefore, M_0 and B_0 are known :

$$M_0 = 0$$
$$B_0 = 1$$

Equation 4 proves that studying the number of metamers is equivalent to studying the number of active buds. Therefore, we will only compute the expected value and variance of the number of active buds B_n $(n > 0)$.

3 Computation with Markov chains

3.1 Main concepts

The aim of this method is to use the powerful properties of Markov chains. As a matter of facts we have seen in Section 2.1 that $(B_n)_{n\in\mathbb{N}}$ is a homogeneous Markov chain.

Let P be the transition matrix. Then :

$$\forall (i,j) \in \mathbb{N}^2, P_{i,j} = P\left(B_1 = j | B_0 = i\right)$$

If we denote $P^n = \prod_{i=1}^{n} P$, one of the basic properties of the Markov chains gives :

$$\forall (i,j) \in \mathbb{N}^2, P\left(B_N = j | B_0 = i\right) = (P^N)_{i,j}$$

Then, if the initial state is $B_0 = 1$, the expected value is easily computable :

$$E[B_N | B_0 = 1] = \sum_{i=1}^{\infty} i (P^N)_{1,i}$$

Let us remark that the previous sum is infinite but we will consider that it is convergent (the case when the sum is divergent is not biologically relevant). The following step consists in applying the Chapman-Kolmogorov equation :

$$\forall i \in \mathbb{N}, (P^N)_{1,i} = \sum_{j=1}^{\infty} (P^{N-1})_{1,j} (P^1)_{j,i}$$

Let us notice that this last equation is no more than a direct application of the law of total expectation. Thus, we get an inductive relationship between $E[B_N]$ and $E[B_{N-1}]$. Therefore, the last step is to solve it.

The computation of the variance is similar :

$$V[B_N | B_0 = 1] = \sum_{i=1}^{\infty} i^2 (P^N)_{1,i} - \left(\sum_{i=1}^{\infty} i (P^N)_{1,i} \right)^2$$

N.B. : The computation of the transition matrix becomes a lot more complex in the case of a multitype branching process. The idea is to compute each transition probability by breaking it up into the contributions of each type.

3.2 Example

3.2.1 Expected value

Let us first compute the transition matrix. We have to determine $P_{i,j} = P\left(B_1 = j | B_0 = i\right)$. Given the fact that we consider only rest probabilities, the number of new buds can only increase (i.e. $j \geq i$). Moreover, one bud can only give a maximum of two buds. Consequently, we have $j \leq 2i$. For $i \leq j \leq 2i$, let k be : $k = j - i$. Thus, the number of new buds is $j = i + k$. k can be seen as the number of old buds that will give two new buds. Therefore, k follows a binomial law of parameter (P, i). Then, $P_{i,j} = \binom{i}{k} P_a^k (1 - P_a)^{i-k} = \binom{i}{j-i} P_a^{j-i} (1 - P_a)^{2i-j}$. Therefore :

$$\forall (i,j) \in \mathbb{N}^2, \quad P_{i,j} = \begin{cases} \binom{i}{j-i} P_a^{j-i}(1-P_a)^{2i-j} & \text{if } i \leq j \leq 2i \\ 0 & \text{otherwise} \end{cases}$$

If we consider the Leeuwenberg model with rest probabilities, the maximal number of states is 2^N at growth cycle N. In that case, the computation of the expected value gives :

$$E[B_N|B_0=1] = \sum_{j=1}^{2^N} j(P^N)_{1,j} = \sum_{j=1}^{2^N} j \sum_{i=1}^{2^N} (P^{N-1})_{1,i}(P^1)_{i,j}$$

Since the sums are finite, they can be permuted :

$$E[B_N|B_0=1] = \sum_{i=1}^{2^N} (P^{N-1})_{1,i} \sum_{j=1}^{2^N} j(P^1)_{i,j} = \sum_{i=1}^{2^N} (P^{N-1})_{1,i} \sum_{j=i}^{2i} j \binom{i}{j-i} P_a^{j-i}(1-P_a)^{2i-j}$$

$$= \sum_{i=1}^{2^N} (P^{N-1})_{1,i} \sum_{j=0}^{i} (j+i) \binom{i}{j} P_a^j (1-P_a)^{i-j} = \sum_{i=1}^{2^N} (P^{N-1})_{1,i} \left[i \underbrace{\sum_{j=0}^{i} \binom{i}{j} P_a^j (1-P_a)^{i-j}}_{=1} + \underbrace{\sum_{j=0}^{i} j \binom{i}{j} P_a^j (1-P_a)^{i-j}}_{=iP_a} \right]$$

$$= (1+P_a) \sum_{i=1}^{2^N} i(P^{N-1})_{1,i} = (1+P_a) E[B_N|B_0=1]$$

And then :

$$E[B_{N+1}] = E[B_N](1+P_a) \tag{5}$$

We recognize a geometric sequence. The result follows :

$$\boxed{E[B_N] = (1+P_a)^N}$$

3.2.2 Variance

We use the same method :

$$V[B_N|B_0=1] = \sum_{i=1}^{2^N} i^2 (P^N)_{1,i} - \left(\sum_{i=1}^{2^N} i(P^N)_{1,i} \right)^2$$

Let us consider the first sum :

$$\sum_{j=1}^{2^N} j^2 (P^N)_{1,j} = \sum_{j=1}^{2^N} j^2 \sum_{i=1}^{2^N} (P^{N-1})_{1,i} (P^1)_{i,j} = \sum_{i=1}^{2^N} (P^{N-1})_{1,i} \sum_{j=1}^{2^N} j^2 (P^1)_{i,j}$$

$$= \sum_{i=1}^{2^N} (P^{N-1})_{1,i} \sum_{j=i}^{2i} j^2 \left(j \overset{i}{-} i \right) P_a^{j-i} (1-P_a)^{2i-j} = \sum_{i=1}^{2^N} (P^{N-1})_{1,i} \sum_{j=0}^{i} (j+i)^2 \binom{i}{j} P_a^j (1-P_a)^{i-j}$$

$$= \sum_{i=1}^{2^N} (P^{N-1})_{1,i} \left[i^2 \underbrace{\sum_{j=0}^{i} \binom{i}{j} P_a^j (1-P_a)^{i-j}}_{=1} + 2i \underbrace{\sum_{j=0}^{i} \binom{i}{j} j P_a^j (1-P_a)^{i-j}}_{=iP_a} + \underbrace{\sum_{j=0}^{i} \binom{i}{j} j^2 P_a^j (1-P_a)^{i-j}}_{=iP_a(1-P_a)} \right]$$

Then :

$$\sum_{j=1}^{2^N} j^2 (P^N)_{1,j} = (1+P_a)^2 \sum_{j=1}^{2^N} j^2 (P^{N-1})_{1,j} + 2P_a(1-P_a) \sum_{j=1}^{2^N} j (P^{N-1})_{1,j}$$

$$= (1+P_a)^2 V[B^{N-1}|B^0=1] + (1+P_a)^2 (E[B^{N-1}|B^0=1])^2 + 2P_a(1-P_a) E[B^{N-1}|B^0=1]$$

$$= (1+P_a)^2 V[B^{N-1}|B^0=1] + (1+P_a)^{2N} + 2P_a(1-P_a)(1+P_a)^{N-1}$$

Therefore :

$$V[B_{N+1}|B_0=1] = (1+P_a)^2 V[B^N|B^0=1] + 2P_a(1-P_a)(1+P_a)^N \tag{6}$$

This induction sequence can be solved. To do so, we have to consider the ration of two consecutive terms :

$$\frac{V[B_{N+1}] - (1+P_a)^2 V[B_N]}{V[B_N] - (1+P_a)^2 V[B_{N-1}]} = \frac{(1+P_a)^N P_a(1-P_a)}{(1+P_a)^{N-1} P_a(1-P_a)} = 1 + P_a$$

We get an induction sequence of order 2 :

$$V[B_{N+1}] = (1+P)(2+P)V[B_N] - (1+P)^3 V[B_{N-1}]$$

The roots of the characteristic polynomial are $1+P_a$ and $(1+P_a)^2$. Given the initial state, we get :

$$\boxed{V[B_N] = (1-P_a)(1+P_a)^{N-1}[(1+P_a)^N - 1]}$$

3.3 Conclusion

This method is the most classical one in the sense that all the mathematical methods used are elementary and well known. However, the computations are often long and contain technical difficulties. As a consequence, we have to develop new mathematical tools more appropriate to study branching processes based on compound processes and generating functions.

4 Computation with compound processes

4.1 Main concepts

This method is particularly well adapted to the computation of moments for a stochastic tree (see Sedgewick and Flajolet (1996) or Kang et al. (2008) for more details). Let $(X_n)_{n\in\mathbb{N}}$ be a sequence of real random variables and Y a discrete non-negative random variable. Let Z be a real random variable such as :

$$Z = \sum_{k=0}^{Y} X_k \overset{(not)}{=} Y \circ X$$

Then, the expected value of Z is given by :

$$E[Z] = E[X]E[Y] \tag{7}$$

and the variance of Z :

$$V[Z] = E[X]^2 V[Y] + V[X]E[Y]$$

A stochastic tree can be broken up into a set of compound processes. As a consequence, these formulas can be used. If we keep the notations of Section 2.1, $\xi_N^{(k)}$ represents the number of buds produced by the k-th bud at growth cycle N. Using the definition of a 1-type branching process :

$$B_{N+1} = \sum_{k=1}^{B_N} \xi_N^{(k)} = B_N \circ \xi_N$$

Then, we get :

$$E[B_{N+1}] = E[B_N]E[\xi_N] \tag{8}$$

and :

$$V[B_{N+1}] = E[\xi_N]^2 V[B_N] + V[\xi_N]E[B_N] \tag{9}$$

The last step consists in solving the previous inductive relationships.

N.B. : The extension to multitype branching processes is easy. Using the definition of a multitype branching processes (cf Section 2.1), we have :

$$B_{N+1} = \sum_{i=1}^{m} \sum_{k=1}^{B_{N,i}} \xi_{N,i}^{(k)} = \sum_{i=1}^{m} B_{N,i} \circ \xi_{N,i}$$

and then :

$$E[B_{N+1}] = \sum_{i=1}^{m} E[B_{N,i} \circ \xi_{N,i}] = \sum_{i=1}^{m} E[B_{N,i}] E[\xi_{N,i}]$$

A similar equation exists for the variance.

4.2 Example

4.2.1 Expected value

For the Leeuwenberg model with rest probabilities, each bud can give a new axis with a probability P_a or rest with a probability $1 - P_a$. Then, for a bud i, the number of children ξ_N is 1 with a probability $1 - P_a$ and 2 with a probability P_a. Consequently :

$$E[\xi_N] = 1 + P_a$$

Using Equation 8, we get :

$$E[B_{N+1}] = E[B_N] E[\xi_N] = E[B_N](1 + P_a)$$

This is the same induction as in Section 3.2.1 :

$$\boxed{E[B_N] = (1 + P_a)^N}$$

4.2.2 Variance

It is very easy to verify that :

$$V[\xi_N] = P_a(1 - P_a)$$

Using Equation 9, we have :

$$V[B_{N+1}] = E[\xi_N]^2 V[B_N] + V[\xi_N] E[B_N]$$

And then :

$$V[B_{N+1}] = V[B_N](1 + P_a)^2 + (1 + P_a)^N P_a(1 - P_a)$$

This is the same induction as in Section 3.2.2. Again, the result is :

$$\boxed{V[B_N] = (1 - P_a)(1 + P_a)^{N-1}[(1 + P_a)^N - 1]}$$

4.3 Conclusion

This method is very easy to use (even in the case of multitype branching processes). The formulas are simple to write and we get the results quickly. Compound processes are well adapted to biological applications because the equations have a real physical sense. Just by looking at them, we understand completely how the structures are organized.

5 Computation with generating functions

5.1 Main concepts

Generating fucntions are well known in probability theory for their useful properties. The moments of a stochastic distribution can be easily computed by differentiating one or several times its probability generating function. The generating function ψ of a discrete random variable X is given by :

$$\psi_X(z) = E[z^X] = \sum_k P(X = k)z^k$$

with $z \in [0, 1]$. Thus, the expected value E and the variance V are given very easily by :

$$\begin{array}{l} E[X] = \psi'_X(1) \\ V[X] = \psi''_X(1) + \psi'_X(1) - \psi'^2_X(1) \end{array} \tag{10}$$

Intuitively, the generating function represents the sum of all possible realisations of the random variable X weighted by their occurrence probabilities. Given that, we can extend the notion of generating function to a stochastic tree. Let ψ_N be the generating function of order N for a stochastic tree. Thus, ψ_N represents the sum of all possible occurrences associated to a tree weighted by their occurrence probability after N growth cycles. Thus it is possible to get an inductive relationship between ψ_N and ψ_{N-1} :

$$\psi_{N+1}(s) = \psi_N(\psi_1(s)) = \psi_1(\psi_N(s)) \tag{11}$$

This last equation is fundamental. It is not easy to give an explicit expression for a generating function of order N except for $N = 1$. The aim is to write the generating function of order 1 and then to use Equation 11. By differentiating once or twice the previous equation, we get an inductive relationship for $E[B_N]$ and $V[B_N]$ to solve.

N.B : The extension of this method to a multitype branching process is easy. Let us defined first ψ^j_N, the generating function of order N for a type j individual. ψ^j_N is a generating function of order N whose first individual is of type j. If we keep the notations of paragraph 2.1 then m is the number of different types of individuals. In that case, ψ^j_N becomes a function of m variables and the previous method remains the same by replacing all derivatives by partial derivatives with respect to the j-th variable.

The reader can find more details about the basic properties of generating functions in Harris (1963).

5.2 Example

5.2.1 Expected value

Before using Equation 11, $\psi_1(s)$ must be determined. The initial state is a bud s. After one growth cycle, either the bud rests (and remains s with probability $1 - P_a$) or it gives a metamer m with two lateral buds s^2 (s becomes ms^2 with probability P_a). As a consequence, the generating function of order 1 for the Leeuwenberg model with rest probabilities is given by :

$$\psi_1(s) = (1 - P_a)s + P_a s^2$$

If we combine this with Equation 11, we get :

$$\psi_{N+1}(s) = (1 - P_a)\psi_N(s) + P_a \psi_N(s)^2$$

Differentiating this equation and taking $s = 1$, we get an induction for $E[B^N]$:

$$\psi'_{N+1}(1) = (1 + P_a)\psi'_N(1)$$

i.e. :

$$E[B_{N+1}] = (1 + P_a)E[B_N]$$

and :

$$\boxed{E[B_N] = (1 + P_a)^N}$$

5.2.2 Variance

The method used for the computation of the variance is quite similar. This time, Equation 11 has to be differentiated twice :

$$\psi''_{N+1}(s) = (1 - P_a)\psi''_N(s) + 2P_a \left(\psi'_N(s)\right)^2 + 2P_a \psi''_N(s)\psi_N(s)$$

The variance is given by :

$$V[B_{N+1}] = \psi''_{N+1}(1) + \psi'_{N+1}(1) - \psi'^2_{N+1}(1)$$

And combining the two last equations :

$$V[B_{N+1}] = (1 - P_a)\psi''_N(1) + 2P_a \left(\psi'_N(1)\right)^2 + 2P_a \psi''_N(1) + (1 + P_a)\psi'_N(1) - (1 + P_a)^2 \psi'^2_N(1)$$

$V[B_{N+1}] = (1+P_a)(\psi''_N(1)+\psi'_N(1)-\psi'^2_N(1))+P_a(1-P_a)\psi'^2_N(1) = (1+P_a)V[B_N]+P(1-P_a)E[B_N]^2$

This induction is different from the previous one (cf Section 4.2.2) but the roots of the characteristic polynomial are the same.

Finally :

$$V[B_{N+1}] = (1+P_a)V[B_N] + P_a(1-P_a)(1+P_a)^{2N} \tag{12}$$

Here is an interesting result. The induction relationship of Equation 12 is different from induction 6. However, the characteristic polynomial of the sequence remains the same and we get obviously the same result :

$$\boxed{V[B_N] = (1-P_a)(1+P_a)^{N-1}[(1+P_a)^N - 1]}$$

5.3 Conclusion

This method is very effective and is very closed to the compound processes. However, using generating functions becomes very powerful with L-systems. The stochastic L-systems describing plant development can be seen as a multitype branching process, and the generating function is easily deduced in the same way (see Kang et al. (2007)). It represents the sum of all possible words weighted by their probabilities of occurrence (Loi and Cournède (2008)). The following is the same. We can have the moments by differentiating the generating function. The advantage is a very simple and intuitive use. Let us take for instance the Leeuwenberg model with rest probabilities. After one growth cycle, either the bud rests (and remains s with probability $1-P_a$) or it gives a metamer m with two lateral buds s^2 (s becomes ms^2 with probability P_a). As a consequence, the generating function of order 1 coupled with L-systems is given by :

$$\psi_1(s) = (1-P_a)s + P_a m s^2$$

The difference is the appearence of the letter "m" in the equation. If we combine this with Equation 11 we get :

$$\psi_{N+1}(s) = (1-P_a)\psi_N(s) + P_a m \psi_N(s)^2$$

If we differentiate this equation with respect to s and then take $(s,m) = (1,1)$, we get the same inductive relationship as in paragraph 5.2.1. The interesting result is that if we differentiate the previous equation with respect to m and then take $(s,m) = (1,1)$, we get immediatly an inductive relationship for the expected value of M_n (*i.e.* the number of metamers at growth cycle n). This method is very attractive because it is very simple to write the generating function of order 1 coupled with L-systems (the only task is to write the structure of the tree with words and then to weight them by their probabilities of occurrence). An important application is that we can have all the distributions for all the elements of the plant.

6 Computation based on plant structural factorization

6.1 Main concepts

The L-system associated to GreenLab plant development can be factorized (cf Smith (1984), de Reffye et al. (2003), Cournède et al. (2006)).

Let us define the notion of substructure. Let us consider an individual at cycle N. If we take this individual and its entire line of descent after M cycles then we have a substructure of age $M+1$: S_{M+1}. Keeping the same notation as in paragraph 2.1, we have the substructure formula :

$$S_{N+1} = (S_N)^{\xi_N} \tag{13}$$

Let $\mathcal{W}$ be the set of all possible occurrences for a substructure and let ϕ be the morphism of $\mathcal{W}$ into $\mathbb{R}$ which gives to a substructure S_N the expected value of the number of individuals in S_N. Then, we have :

$$\phi(S_{N+1}) = E[\xi_N]\phi(S_N) \tag{14}$$

We get an inductive relationship to solve.

N.B. : In the case of a multitype branching process, the method is similar. Let $S_{N,j}$ be the substructure initiated by a type j individual after $N+1$ growth cycles. Then, in the case of a m-type branching process :

$$S_{N+1,j} = (S_{N,1})^{\xi_{1,j}} (S_{N,2})^{\xi_{2,j}} ... (S_{N,m})^{\xi_{1,m}} \tag{15}$$

Let $\mathcal{W}$ be the set of all possible occurrences for a substructure and let ϕ_J be the morphism of $\mathcal{W}$ into $\mathbb{R}$ which associates to a substructure S_N the expected value of the number of individuals of type J in S_N. Let $\xi^i_{N,j}$ be the number of children of type i produced by an individual of type j at generation N. Then :

$$\phi_J(S_{N+1,j}) = E[\xi^1_{N,j}]\phi_J(S_{N,1}) + E[\xi^2_{N,j}]\phi_J(S_{N,2}) + ... + E[\xi^m_{N,j}]\phi_J(S_{N,m})$$

6.2 Example

6.2.1 Expected value

Let ϕ be the morphism of $\mathcal{W}$ into $\mathbb{R}$ which gives to a substructure S_N the expected value of the number of active buds in S_N. Using Equation 14, we get :

$$\phi(S_{N+1}) = E[\xi_N]\phi(S_N) = (1+P_a)\phi(S_N)$$

i.e. :

$$E[B_{N+1}] = (1+P_a)E[B_N]$$

And then :

$$\boxed{E[B_N] = (1 + P_a)^N}$$

6.2.2 Variance

The computation of the variance thanks to a morphism is not possible because the variance is not linear.

6.3 Conclusion

The principle of this method is quite similar with that of the generating functions. It is an interesting way to use the substructures formula. However, the use of a morphism becomes impossible when we deal with nonlinear computations and, in that case, this method is not adapted.

7 Comparison of the methods and conclusions

The Markov chain theory leads to complex computations and the method using the substructures formula is not adapted to nonlinear computations (such as the computation of the variance). Compound processes and generating functions are more appropriate to study branching processes. As a matter of fact, the equations are very simple to write and easy to understand even for somebody without a wide mathematical background. Generating functions are particularly well adapted to branching processes in botany because they can be directly deduced from the L-system describing plant development. By doing so, we can get in a simple way the distributions of all kinds of elements in plants (metamers, buds, fruits, ...).

Compound processes and generating functions can be adapted to inhomogeneous branching processes (the probabilities are functions of the generation). However, it becomes almost impossible to get explicit equations for the expected value and the variance as in the case of the Leeuwenberg model with rest probabilities. In that case, we have to compute them numerically.

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