Invited Talk. Relevant Qualitative and Quantitative Choices for Building an Efficient Dynamic Plant Growth Model: GreenLab Case

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Abstract

A systematic study of plant growth modeling is a real challenge for researchers and scientists because multidisciplinary aspects have to be integrated. Through a mathematical formalism, a plant functional-structural model needs to be developed based on knowledge from botany, agronomy, forestry, eco-physiology and computer sciences. Specialists in each discipline have proposed variety models, but most of these models are limited within their own field. It is well recognized that the malfunctioning and the limitations of these models are due to their mono-disciplinary aspects applied. A dialog between the various scientific domains involved in plant modeling is not obvious. It needs to choose, simplify and adapt the relevant knowledge from each other that is necessary and sufficient to build a plant functional-structural model. This needs also to define a right level of observations. Each notion is simplify, but the interactions between them give new theoretical results and applications. Several questions are discussed in this work. How botany gives keys to organize the multi-level information inside the plant topological structure and eventually speed up the growth computing? What kind of mathematical formalism is needed to introduce powerful tools of automatic control into plant modelling? The goal of this paper is to propose simple choices, from both biological and mathematical viewpoints, and adapt them to build an efficient dynamical model. With this model, it is possible to insure optimisation and control that are needed in agronomy.

Keywords: plant growth, modeling, dynamic process, botany, agronomy, mathematics, relevant study

1 Introduction

Modeling plant growth and plant architecture is a challenge due to multidisciplinary components involved. Botany, agronomy, eco-physiology and computer-sciences for their own needs have endeavoured to success in this task in their particular domains. Many researchers have tried to build a minimum but general plant description that is sufficient to

enable them to perform their specific models at the best level they can. The results are quite unbalanced between the disciplinary fields, and strong limitations in the model functioning can occur most often because the interactions with other field knowledge are ignored. Thus there are models for mechanics (tree stability), physiology (light interception or biomass production and partitioning) and for computer graphics images [1]. Besides numerous papers in this domain, several interesting reviewing [2-5] have been carried out, that underline the main results on the subject.

The Process Based Models (PBM) in [2] concern the plant functioning in related to the physical environment. Therefore, biomass acquisition and its partitioning are the main goal of study. The plant is divided into crude compartments (leaves, branches, roots) as global sources and sinks, and the growth is continuous. The span of observation is usually short (from less than one hour to a day) so that physiologists are able to track the mechanisms of photosynthesis and water transpiration due to various stresses (light, temperature, water). Even hormonal actions are studied [6]. PBMs can be adapted to the plant structure once it is digitalized, to assess with more accuracy the effect of architecture in light interception and water transpiration. Owing to the use of a short time unit, the computational cost in simulation of the photosynthesis using EDP algorithm is quite expensive even for a simple plant architecture. Moreover, no feedback is generated between a static architecture and a kinetic functioning.

The Geometric Models (GMs) in [3] concern the 3D plant architecture construction. The background of these models is related to mathematics and computer sciences. The idea is to build complex trees using simple rules but processed by powerful algorithms. Upon the skill of the operator, some pure mathematical algorithms as fractals, binary trees, particles systems, can give birth to pretty shapes of plants. Other algorithms integrate botanical knowledge, simple for herbaceous (L-systems Grammars [7]) or sophisticated for trees (AMAP [8]). The temporal period for the plant construction is longer for GM than for PBM. The growth is discretised and relies on the delay of a Growth Unit (GU) that is a set of metamers built within the same continuous growth period, (from several days for shrubs to one year for temperate trees). The 3D generated architecture can be quite enormous for big trees by composing of millions of internodes and leaves. Here the detail levels are the organs. They do not play any role in the growth but only dress the plant structure. It is obvious that the computation will be at least proportional to the number of organs. The plant is not calculated but simulated step by step. No validation of the numerical results is available since this is not necessary for computer graphics needs.

The Functional-Structural Models (FSMs) in [4] endeavour to merge the both approaches. The goal is to control the whole plant development in its organogenesis and photosynthesis. The organs play their true roles as sources and sinks, and have interaction between the architecture and the functioning during the plant development. The models in [9] are in fact much closer to GM, because the organs do not play any roles as sinks. The photosynthesis is computed but does not participate to the plant organs construction.

More sophisticated models are true FSMs as Cotton [10], Lignum (pine tree) [11], or AMAPhydro [12]. The first two are specialized for a given plant with a solid physiology but with a crude geometry, meanwhile the last one is generic with a detailed architecture combined to a crude physiology based on transpiration.

The main risk of the existing FSMs is to add the respective drawbacks of GMs and PBMs, *i.e.* to deal with a huge number of spatial entities with a short period of time. Sievanen [4] underlines four points necessary for FSMs. The Plant is made of an idealized elementary

unit (IEU) (the GU in botany) that is repeated numerous times in the tree topological structure. This IEU is defined for its homogeneous botanical structure and functioning. Moreover, the author stresses to take account of the local environment effects and to integrate the exchanges between the neighbouring IEU on the whole tree structures.

The drawbacks of both existing PMs and GMs are due to their added heavy topological structures and heavy time consuming. Therefore, no forest stand functioning can be contemplated by them. The reliability of such a complex system has to be analysed seriously.

The purpose of this paper is to propose a new simple level for plant modelling in which there is a good balance in the knowledge taken from each involved different domain and that could be sufficient for numerous applications. Of course each domain has to simplify, adapt its scientific field, and eventually make relevant choices for this purpose. But the expected results are important. We could bring out for the first time well balanced interactions and feedback between plant architecture and plant functioning in respect to environmental factors. The model should indicate how to range from the single plant structure functioning to the field one. Moreover each scientific field could discover new unexpected applications that allow a breakthrough in its own domain. The proposed method needs to rely more on a mathematical formalism than on simulation techniques.

2 Some Considerations about Plant Architecture and Plant Functioning

2.1 Some general observations

Upon the goal we attempt to reach, the spatial and temporal scales must be compatible. Here we are concerned by the yield at the level of the plant architecture. Organs have sizes, weights and they are made mainly of dry matter (DM) and water roughly in the proportions 20% and 80% respectively. Other elements, such as N,P,K, participate mainly to the plant functioning but not to the plant constitution. Physiological models always deal with dry-matter that is computed from photosynthesis. But in the reality except for the seeds, the yield relies often on the fresh matter (FM). Marcellis et al. [2] point out:

"*Many horticultural product are characterized by a low DM content* (<5%) ... *many of these products are sold by fresh weight.... An error of more than* 25% *in predict fresh weight can arise when a constant DM is assumed. The relationship between growth in fresh matter and DM, is still poorly understood....*"

To study the architecture development, it is more relevant to rely on the fresh biomass. If necessary, the costs of the DM fabrication and of the respiration, can be assessed. Furthermore, the main study takes account of the volume of the fresh organs in order to build the plant architecture.

2.2 On the scale effect

The botanical knowledge and the physiological functioning have to be adapted to the macroscopic level of the plant architecture. Each level of observation gets its sets of laws and it is not obvious to deduce the laws applicable to an upper scale from the lower scale. On the other hand these upper laws can be directly assessed at the level of observation that is used. For instance Boltzman from his sophisticated Gaz kinetic has found again by integration, the crude Mariot law ($PV=C^{te}$) that was successfully used already from 200

years ago. It is risky to think that what we observe will be explained by exploring a lower scale, because this process has no ending! Moreover, when going down, the measurements are more complicate to conduct by adding precisions and increasing number of parameters to estimate. Eventually the fuzzy accuracy on the parameters of the lower scale increases dramatically the imprecision in the upper scale functioning. It is necessarily that we endeavour to find the relevant laws in botany and physiology at the level of the plant architecture, that enable a model to control the plant development.

2.3 On the plant architecture

The existing GMs and FSMs use botanical modulus (metamer, growth unit) that are propagated numerous times in the structure to build the final plant architecture. For herbaceous and shrubs the cost is low, but for big trees, the cost is heavy. L-systems or other algorithms rely on the details of the plant constitution represented by the organs. Their parallel algorithms of construction with discrete events are blind and with numerous repeated operations one by one from an organ, to a metamer, to a growth unit, to a twig, and so on. Therefore, as far as these algorithms are not multilevel and do not integrate the botanical knowledge at the size of a plant architecture, a branch with same physiological age and same chronological age will be reconstructed from beginning as many times whenever it is found in the tree structure. Clearly this way will become a bottleneck particularly for construction of trees and forests stands.

2.4 On the plant functioning

The physiological rules that are used currently in PBMs and FSMs to compute biomass acquisition and biomass partitioning are not given at the scale of the plant growth and the plant architecture. Researchers try to control the single leaf functioning in its local environment upon light, temperature and water stress with a short time period. The transpiration is under control of the stomata opening, and the rate of photosynthesis is computed at a micro-scale level. In that case all the leaves have a different environment and thus a different behaviour. The temptation is then to describe thinly the plant architecture and its local environment in order to obtain the global plant photosynthesis by integration of the light interception leaf by leaf. For herbaceous this can be performed on simple plants such as sunflower, but for trees it can lead to be intractable even if good optimisations are carried on [13].

The short time period that is needed to perform the biomass diffusion equation inside the plant structure between neighbouring metamers also increases the computing time [14,15]. Not only the topological structure has to be built, but also the carbohydrates diffusion process to be explored step by step. Sievanen [4] stated that the computing time for biomass acquisition and biomass partitioning is at least 3 times longer than the time necessary for building the topological structure and it is proportional to the total number of organs. Thus, adding the plant functioning to the plant architecture model leads to unbearable times for achieving reliable simulation results.

3 Relevant Assumptions to Build an Efficient Dynamical Model for Plants Growth and Architecture

3.1 Method

We propose here on what is necessary and sufficient to build at a relevant level for an FSM

that provides the whole plant architecture both from organogenesis and biomass production and partitioning. At first, we assume that plants do not suffer any kind of stress. Stressed plants can be assessed later by comparison with the normal plants. With the normal plants, the organs play their true roles with a simplified functioning to reflect the real dynamic process. Then, we need to select a proper scale that can represent efficient average effects and sufficient to fit architecture for a real plant. Using the scale of the plant architecture, the functioning is not measured instantaneously, but as the final result of the cumulated plant construction process. We propose an inverse method to trace back the average source and sink processes that give birth to the 3D plant. Since some hidden parameters are estimated from observation data, the proposed method will build a process-based model rather than a regression model to establish the dynamical relationships of sources and sinks for plants.

3.2 For plant architecture

The plant description is suggested to be hierarchically organized using botanical notion of physiological age (PA), and represented in a recurrent form. The PA presents the organs differentiation based on a genetic program. The PAs concern not only the organs (leaves, flowers, internodes, roots), but also the axis types of a plant and the branches organisations [16]. For instance on a coffee tree, there are two types: orthotropic trunk and the plagiotropic branches. Usually, it needs less than 6 PAs in a tree. The oldest PA is the ultimate state of differentiation for an axis, that is usually short and without branching. Organs, such as leaves, flowers, internodes, are sub PA differentiations, linking to the main PA of the metamer.

- The metamer is a set that is compounded of organs (internode (pith + rings), buds, leaves). All the necessary information for a given PA is stored at this level. It concerns the number of organs, their geometries and their functioning.
- The growth unit (GU) is a set of metamers built by a bud during a growth cycle (GC). These metamers can be of different kinds and ordered by botanical rules as acrotony.
- The bearing axis (BA) is a set of GU of the same kind that gives birth to the main axis of branch.
- The substructure is a set of a bearing axis with branched substructures on it, whose PAs are older than the BA one.

A substructure $S(n,p)$ is entirely designed by its chronological age (CA) n and its PA p. If PA =1 , the substructure is the whole plant or a reiteration. Otherwise they are branches or twigs. The model must work at a substructure level, because the whole set is known in details. So constructing a tree is only to stack substructures ordered in CA and PA together in a proper manner.

The combinatory between PA and CA is not heavy. In the case of a tree, for PA =1, the main structure can grows over 60 years. But for PA =2 (main branch) we have CA <15, PA= 3 (normal branch) CA <8, and PA = 5 (twigs) CA ≤3. So there are less than 30 kinds of branches (with no stochastic considerations).

3.3 For plant functioning

A unit time period for plant development

The time unit for organogenesis and photosynthesis must be consistent, insuring a good synchronization on both bud-by-bud processes. In the plant architecture, the leafy axes

undergo a primary growth by adding new metamers rhythmically at their tops. The time needed between two organs creations, ranges from several days (herbaceous, shrubs) to one year (temperate trees) and it is variable, up to the environmental conditions. It becomes quite stable if we choose a thermal time. The sum of daily temperatures received for a given plant during this period for primary growth is quite constant and so called "the Law of Sum of Temperatures"(LST) in agronomy. We define the growth cycle (GC) as the thermal time unit necessary to increase the plant organogenesis of one step. During the GC all the working buds may produce new metamers according to their PA and CA.

On the other hand, on long periods the plant biomass acquisition is quite proportional to the plant transpiration. This phenomenon is known as Water Use Efficiency (WUE). Since WUE is generally considered constant over a long period, say, a season [17], at the level of GC, the fluctuations of WUE is reasonable to be denoted by its average value WUE(n) at GC(n). Thus we will rely on the laws of LST and WUE to monitor simultaneously both organs and biomass plant production. These laws are quite reliable and exactly at the scale of the plant architecture.

The biomass acquisition and partitioning

The biomass computed from the water transpiration is fresh biomass to fill the plant organs. Each leaf will have a transpiration depending on its surface area. The biomass produced by each leaf is added and stored into a pool that is contributed by all organs according to their sink strengths. The initial seed and the leaves are sources. Leaves, internodes, fruits and rings are sinks. The sink duration in GC is equal to the organ expansion time and its values are not necessarily constant. The root system is not described but is considered as a big sink that runs from the first cycle of growth to the current plant age.

What goes to an organ is proportional to its sink value, to the pool amount of biomass reserves divided by the total organs sinks (that is named the plant demand). The demand of the plant at GC(n), is obtained by a scalar product between the number of organs N^O_{n-k+1} of PA O that appeared at GC(n-k+1) multiplied by their sink P^O_k corresponding to their expansion status at GC(k) . The biomass partitioning in the plant structure is the final result of the step by step diffusion process between neighbouring GUs of the photosynthesis produced by the leaves. As the time period of a GC is long enough, no costly diffusion process has to be performed, but immediate biomass allocation in the plant architecture according to the sinks values. So the organs sizes are the result of several steps of biomass allocation during their expansion time. All the organs of the same CA and PA, have same sizes for a given plant age.

4 The Particular Case of GreenLab Model: A Dynamical Formalism

4.1 Presentation

We present here the generic dynamical model of plant growth and plant architecture GreenLab, built by a Sino-French team of researchers. This model is the direct new generation of AMAPsimI [18] and AMAPhydro [12] (that are respectively GMs and FSMs models built in CIRAD), for the assumptions about organogenesis, biomass acquisition and partitioning. AMAPsimI has a high level of details in botany but no functioning and the architecture is built upon pure geometrical rules. AMAPhydro has a

functioning that computes the sizes of the organs up to sources and sinks relationships and organs allometry with a crude accuracy in the plant architecture description.

GreenLab model merges the advantages of the both parent models and suppress totally their drawbacks, by its mathematical formalism. It permits to model from a single plant to a population of plants with a high efficiency. A forest stand of the same tree construct by GreenLab can be no much cost than a single tree of the same kind by AMAPsimI or AMAPhydro!

4.2 Qualitative assumptions

GreenLab model endeavours to select simple relevant biological assumptions in order to run a pure mathematical model and to take advantage of it, i.e. a very fast computing that leads to optimisation and control.

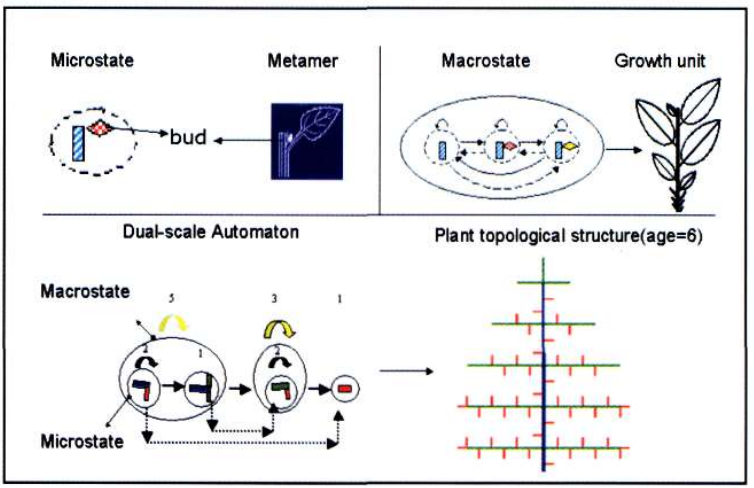

Fig.1 GreenLab dual-scale automaton for organogenesis [19]

Firstly, we use the same growth cycle for plant organs production and biomass fabrication in order to link the two processes and to generate feedback. For an herbaceous a GC will correspond to the period necessary to build up a new metamer upon the reliable thermal time law. The GC will be one year for a temperate tree. The organ creation is done immediately at the beginning of the GCs. The organogenesis for most of the plants architectures can be modelised by a Dual Scale Automaton (DSA), that monitors the occupancy and transition laws within and between the different states of the buds differentiations and designed by the PAs [19]. The metamer at the lower level is considered as a microstate and the GU at the upper one as a macrostate (Fig.1). The series of macrostates and microstates correspond to Semi-Markov chains that can give birth to determined or stochastic plants (see [20]) and that can be assessed from the empirical data [21]. The DSA model can build with a great efficiency all the inflorescences and the tree architectural models [22].

This period of GC will be also used to compute the cumulated biomass fabrication upon the environmental parameters due to the reliable WUE notion (Fig.2). We suppose here that all the leaves have the same environmental conditions. We consider that the biomass is stored in a pool of reserves. The memory of the system is set to one, and all the reserves are distributed among the organs at each growth cycle by direct allocation according to the sinks

values.The sum of the sinks is named the plant demand [23,24].

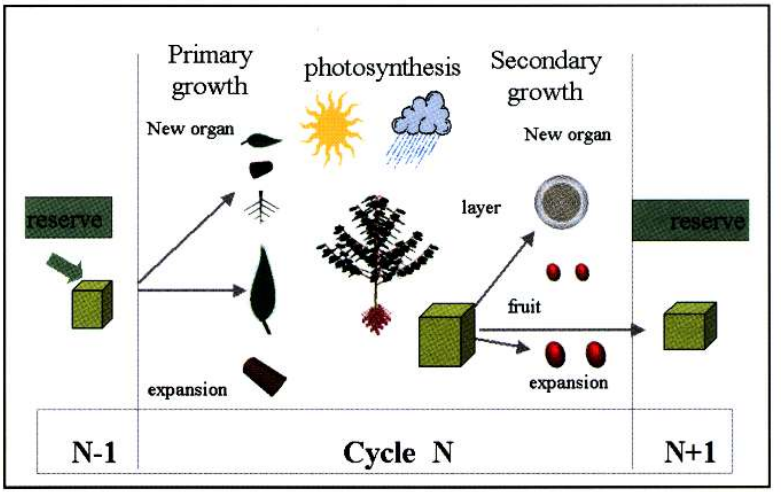

Fig.2 Discrete events for biomass acquisition and partitioning

4.3 Quantitative equations

The GreenLab model is built with a set of equations depending on the previous assumptions. Here we summarize the model description. More details are presented in other papers of this symposium. The formalism of the mathematical model is presented here in a simple way resulting of a direct modelling. A tentative to give a more achieved shape related to automatic control theory is presented in [24].

4.4 Organogenesis: the plant substructure decomposition

This is a typical bottleneck in the computation. Because the parallelism and the discrete events mode, the computing time of simulation can be tremendous for big trees and forests. To overcome this difficulty, GreenLab takes advantages of the plant architecture organized by the PA notion. The buds differentiations create a patchwork of similar patterns of substructures that can be repeated in the main architecture numerous times according to each CA and PA [25].

Suppose a tree with mth PA and finite growth for the axes that have a limited repetition number of GU at each kth PA: N_K. Beyond this limit the terminal bud can then undergo a mutation and change of PA (say k+1), and the last mth PA can only die. So there are m kinds of substructures here that are represented by arrays whose fields contained the cumulated number of metamers according to their PAs. A structure S_k^t is defined by its chronological age CA= t and its physiological age PA = k. It contains all the cumulated numbers of metamers produced from its birth until the tth GC.

$$\left[S_1^t\right]=\left[s_{1,1} \quad s_{1,2} \quad \cdots \quad s_{1,m}\right]^t,\ \left[S_2^t\right]=\left[0 \quad s_{2,2} \quad \cdots \quad s_{2,m}\right]^t,\ \cdots\ \left[S_m^t\right]=\left[0 \quad 0 \cdots \quad s_{m,m}\right]^t$$

All the items with $i > j$ are null according to the rules of the PA production. The structure 1 sum up all the produced items of different PA at the current tth CA, for the whole plant.

Let u_k be the number of metamers by GU for a given kth P; $n_{i,j}$ be the number of

substructures of the *j*th PA sticking on a GU of the *i*th PA.We have to stick the lateral and the terminal substructures directly on the bearing axis of the *k*th PA, according to their position as follows (Fig.3):

$$\left[S_k^t\right] = t \cdot \left[u_k\right] + \sum_{i=1}^{t-1} \sum_{j=k+1}^{m} \left(n_{k,j} \cdot \left[S_j^i\right]\right) \qquad (t \le N_k) \tag{1}$$

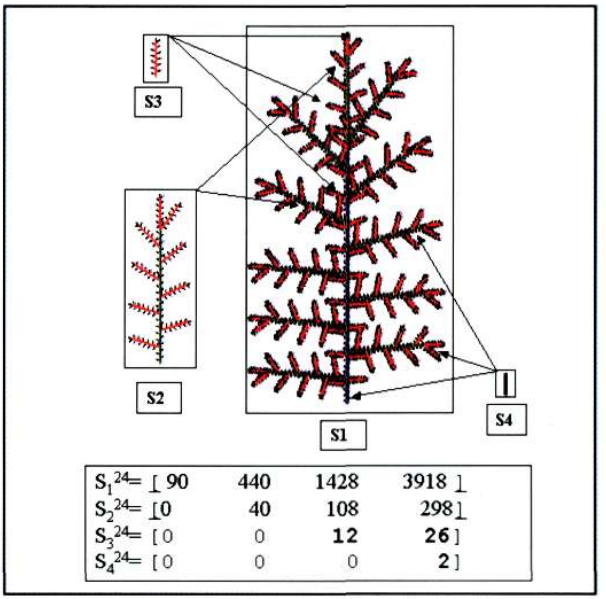

Fig.3 The substructure decomposition of a tree. Example of an achieved complex tree with PA=4 and with finite growth at CA=24

If $t > N_k$, and along the trunk, an apical terminal substructure of physiological age n is born, so we have:

$$\left[S_k^t\right] = N_k \cdot \left[u_k\right] + \sum_{i=t-N_k}^{t-1} \sum_{j=k+1}^{m} \left(n_{k,j} \cdot \left[S_j^i\right]\right) + \left[S_{k+1}^{t-N_k}\right] \qquad (t > N_k \;\&\; k < m) \tag{2}$$

This plant construction algorithm is very fast. Obviously the computing cost on time depends only of $t*m$ and not of the number of organs produced. The substructures are constructed from a double loop, i.e. from the oldest PA=m to PA=1, from the youngest CA=1 to the final CA=t. A library of substructures is created at each PA=k for each CA, that will be used to dress the bearing axes of PA k-1.

As the number of organs by metamers is botanically known, eventually GreenLab provides a mathematical tool that enables to compute the organs production of a virtual plant very quickly and thus suppresses the drawback of counting the organs production one by one from a simulation.

4.5 Biomass acquisition

Each leaf produces biomass that will fill the pool of reserves according to an empirical nonlinear function depending of its surface A, of hidden parameters to assess r_1, r_2, and of water use efficiency at GC k: $E(k)$. We suppose that the size of the leaves depends of its age of apparition when the plant architecture was the kth GC aged. The number of leaves of this

kind produced is N_k^L, so the plant production is

$$Q_n = \sum_{k=1}^{N} N_k^L \cdot f(A_k, r_1, r_2, E(k)) \tag{3}$$

The empirical shape chosen for the leaf functioning in GreenLab is:

$$f(A_k, r_1, r_2, E) = \frac{E}{r_1 / A_k + r_2} \tag{4}$$

that is a nonlinear function. The shape of the leaf production function is not a feature of the model that supports any kind. It is up to the researcher choice.

The biomass production is ready to compute, because the N_k^L are provided from a fast algorithm derivated from Equation (1).

4.6 Biomass partition

Each organ has a biomass potential attraction value that we name the sink or the organ demand. This sink $p_k(i)$ depends on the organ PA k and on its expansion GC i. To normalize the sink function p we set

$$\sum_{i=1}^{t_L} p_{L_\cdot} = (i) = 1$$

for the leaves. All the other sink functions will have their sum depending on this normalization according to their sink strengths. The shape chosen for p is up to the user but this function should be able to fit properly any kind of numerical variations of the sinks according to the organ CA, it must be flexible enough, giving bell shapes, i or j shapes, etc. [26].

We define the plant demand at CA n as the total biomass attraction for the organs of any kinds (leaves, internodes, fruits , layers., roots) by the function:

$$D_n = \sum_{o=L,I,F} \sum_{i=1}^{n} N_{n-i+1}^o \cdot p_o(i) \tag{5}$$

The demand is immediate to compute, because the N_k^L are provided again from the fast algorithm (1).

This gives instantaneously the biomass $\Delta q^o_{i,n}$ that comes into an organ of type O created at the GC n-i+1 inside the plant architecture and the total cumulated biomass $q^o_{i,n}$.

$$\Delta q^o_{i,n} = \frac{p_o(i)}{D_n} Q_{n-1}; \quad q^o_{i,n} = \sum_{i=1}^{n} \Delta q^o_{i,j} \tag{6}$$

Eventually the organ geometry will depend on its apparent density for its volume and of its allometric rules for its sizes in the three dimensions. All this features can be directly measured from the organ shapes.

4.7 General recurrent formula in GreenLab

We suppose here that the leaf thickness e be constant. Then the leaf surface is deduced simply from (6) by dividing the leaf volume by the thickness. Then Equation (3) can be rewritten as

$$Q_n = E \cdot \sum_{i=1}^{t_B} \frac{N_{n-i+1}^{L} \cdot \sum_{j=1}^{i} \frac{p_L(j) \cdot Q_{n-(i-j)-1}}{D_{n-(i-j)}}}{\alpha + \beta \cdot \sum_{j=1}^{i} \frac{p_L(j) \cdot Q_{n-(i-j)-1}}{D_{n-(i-j)}}}, \tag{7}$$

where $\alpha = r_1 \cdot e$; $\beta = r_2$; and t_B is the period for leaf functioning in GC.

Equation (7) is a generic recurrent relation that monitors all the plant development corresponding to any given architecture coming from the dual-scale automaton [19,20]. It gives the total biomass produced by the plant architecture at each CA. The computing time of this equation depends only on the number of PA and CA of the plant, so it is very fast. The asymptotic behaviour of (7) is studied in [27].

5 Applications of Substructures Algorithms in GreenLab

Substructures can have many potential features. Not only they are an array of metamers production, but they can also be a set of polygons representing the geometry of a branch, of finite elements for mechanics, of clusters for radiosity, or a simplified representation of the real branch and even a "big leaf" with global source and sink that give the same result as the complex branch. Here we present some advantages of the method.

5.1 Building a 3D architecture

The way to compute the number of organs by Equation (1) and the way to construct the tree is similar [25,28]. We suppose here that all the organ sizes are known from Equation (6) and the allometric rules. We can extend the role of substructures to be a set of polygons that stores the geometric shapes of the substructures into a library. They become a "meta-organ". To build a 3D plant, we have only to add crude geometrical operations as translation and rotation according to the internodes sizes, branching angles and phyllotaxy. Positioning a substructure in the plant architecture needs the same operation that for a simple 3D organ. It has 3D initial coordinates and first and secondary directions.

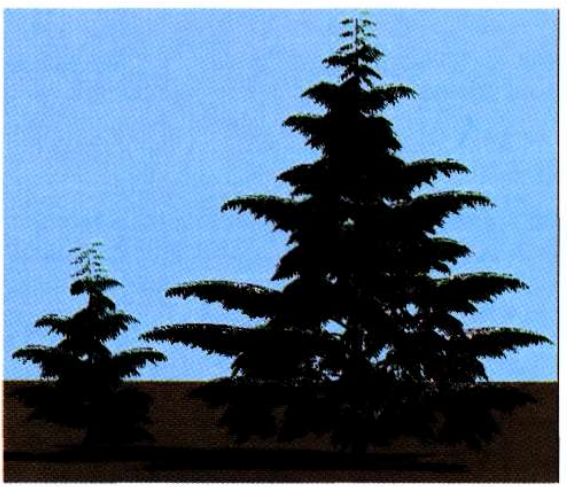

Fig.4 Rendering of simulated trees used for performance comparisons in Table 1

Table 1 Data in computing time (seconds) comparison between substructures and bud-by-bud simulation [25]

Plant age	Substructures	Bud-by-bud simulation
5 years	0.1	3.3
10 years	0.3	437.2
15 years	0.7	4743.0

The way to build the plant architecture is not natural as GMs models do, faking the natural bud-by-bud growth process with a high cost of time. Firstly we construct the unbranched axes of maximum PA m, with their internodes and organs at all their CA. This constitutes the first part of the library. Then we construct all the bearing axes of PA m-1 at every CA, and we stick on them all the organs and the previous substructures m PA aged at the right CA and positioning. We obtain the second part of the library. After m iterations on PA and t iterations on CA, the whole plant (structure 1) is constructed at CA t. Fig. 4 shows a tree with about several hundred thousand items, built with both algorithms. The final results are identical but the substructure method runs about 5000 faster [25](see Table 1). Eventually this method decreases dramatically the computing time and affords the architecture models to be used in agronomy. The span of simulation is thus proportional to $m*t$ instead of the number of organs to creat.

5.2 Generating stochastic trees

The substructure method enables to compute and simulate stochastic trees with a high degree of efficiency [28]. The organogenesis model [19] can be randomised with a stochastic organs production if we define at each GC, probabilities for branching, growing or dying. At this stage it is supposed that the organogenesis, although stochastic, is independent from the photosynthesis. These probabilities can be computed from direct observations on plant architecture [29]. As a consequence, for a given CA the organs and the biomass productions will be distributed according to a statistical distribution.

5.3 Computing stochastic plants

There are two problems to solve: to compute the stochastic metamers distribution and the stochastic biomass distribution induced by the former one. As the metamers distribution comes from a parallel stochastic process, it is very close to a discrete normal distribution. So the mean and the variance are quite sufficient to design the distribution shape with accuracy.

The statistical distribution of metamers

A substructure in the stochastic case can be designed by a set of means and variances for the metamers produced inside, for all PAs. As means and variances are additive, the algorithm (1) for stacking substructures to build the plant, once adapted to random plants, works perfectly well, although covariances have to be assessed properly [30].

Starting from the highest unbranched PA m, we can compute the moments of the distribution by mathematical formulas, according to the given probabilities. Descending the PAs, the recurrent algorithm assembles together the moments of the bearing axis with the ones of the branched substructures until we reach the main substructure 1 at the final CA.

This algorithm computes theoretical means and variances of all the substructures for every CA and PA very quickly. Comparing with the classical parallel Monte Carlo

simulation with discrete events the advantage is obvious. The last approach cannot compute the mean and the variance, but only count the organs one by one, up to the simulation process. So it needs to simulate with a big sample size of stochastic plants to assess the empirical distribution, which is quite unbearable in the case of big trees that have heavy computational times. These mathematical algorithms are useful for the stochastic parameters computation of the model. An example is also shown on roots system in [31].

The statistical distribution of biomass

As the number of leaves is changing from a plant to another one, for the same PA and CA, the biomass production will follow also a statistical distribution. Equation (7) can be written simply when the organs functioning time is one GC as:

$$Q_n = G(X_n, Q_{n-1}) = \frac{EX_n Q_{n-1}}{AX_n + BQ_{n-1}}$$

It is possible to assess the mean and the variance of the biomass produced using differential statistic. So a good approximation of the biomass distribution is given by the mean and the variance at CA = n as follow:

$$E(Q_n) \approx G(X_n, Q_{n-1}) + \frac{1}{2}\left(G''_X.Var(X_n) + G''_Q.Var(Q_{n-1}) + 2G''_{XQ}.Cov(X_n, Q_{n-1})\right)$$

$$Var(Q_n) \approx \left(G'_X\right)^2.Var(X_n) + \left(G'_Q\right)^2.Var(Q_{n-1}) + 2 * f'_X.f'_Q.Cov(X_n, Q_{n-1})$$

The system needs to compute the covariances between the productions of the different CA [30]. We can see on Fig.5 that the theoretical algorithm fits pretty well both stochastic organs and biomass productions, for a plant with buds probabilities for branching, growing and dying.

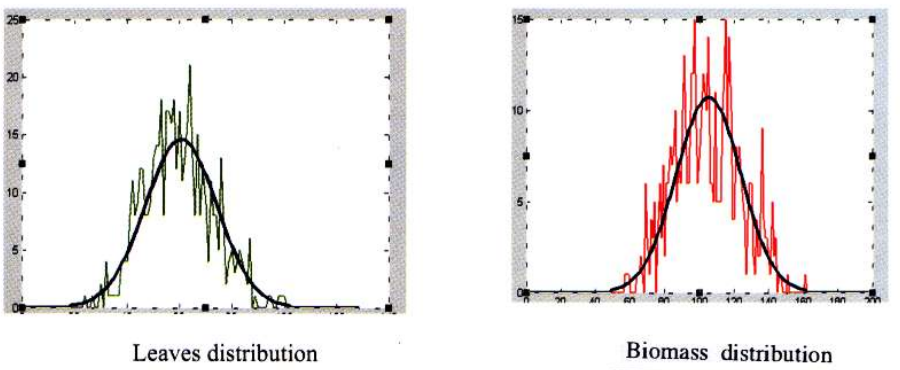

Fig.5 Comparison between the theoretical distributions and the simulations of the yields of a full stochastic plant at CA=20 (250 samples of trees for stochastic simulations)

This plant has PA = 3, and the probabilities for branching, growing and surviving are set to 0.5, 0.8, 0.9 for all PAs. The GU is made of one metamer that bears 2 branches of the upper PA. The correlations between the productions of layers of metamers from two successive GC are quite high ($r > 0.9$). The correlation between biomass and leaves number ($r > 0.7$) is less because it is filtered by formula (7). These results are synthetic and do not need a plant reconstruction although they rely on the details of the architecture functioning. They can be used for optimisation. For many experiments they can be quite sufficient to

assess the means and the variances of the yield.

5.4 Simulating stochastic plants and forests

Substructures give a new way to construct stochastic plants. We can create for each CA and PA a collection of stochastic substructures that will be stored in the library [28]. The number of repetitions by sets is deliberately limited for efficiency. So the same stochastic substructure of given PA and CA can be chosen several times at random during the growth process to build the tree architecture. Comparing with a classical Monte Carlo method, the random quality of the substructure obtained is poor, although it is possible to refine it by increasing the size of the repetitions in the library set. For computer graphics needs, the repetition number can be quite few (less than 6). Suppose that the repetition number of substructures by set is n, the number of PA is m and the plant age is t, the span of the simulation will be proportional to: $n*m*t$. Once the simulation is completed we will construct n different stochastic trees, whose means and variances are estimations of the theoretical ones.

So comparing with a determined plant we keep the same advantage. The first tree builds a substructure library that will be used by the other trees. Then the construction span from the second tree is to compare to the one of a determined tree.

5.5 Computing discrete geometry

Once a substructure is computed geometrically and stored in the library, it is a stiff object, that cannot bend. Nevertheless bending is an important feature for branches and organs to get realistic tree shapes. A suitable solution is to simulate geometrically the same substructures with different orientations from verticality [30]. For instance 6 repetitions could be 30°, 60°, 90°, 120°, 150°, 180° and 3 repetitions: 45°, 90°, 135°. When a substructure has to be placed into the tree architecture, the angle of its bearing axis with verticality is known (primary direction). Then the closest corresponding substructure for orientation will be chosen in the library and set in place. According to the architectural model the geometric repetitions will be different. Two are sufficient for a fir tree with a good approximation (0° for the trunk orientation and 90° for the branches). But for a weeping willow at least 6 repetitions are necessary (Fig.6). This discrete geometry method has a great advantage. It speeds up the geometric computing, and its difference with the continuous geometry is not obvious if the number of repetitions of orientations from verticality is judicious. The excess charge for the first tree is few, and not significant for a forest making. If g is the number of substructures repetitions for geometry, the time to build the forest will be proportional to $g*n*m*t$. So the library of substructures will have eventually 4 entry points for CA, PA, stochastic repetitions and geometry.

5.6 Secondary growth

The secondary growth is the fact of the Cambium activity that adds a new ring at each internode for each GC. The biomass coming from each leaf is put down in each internode along the path that leads to the roots. This can be done by a step by step diffusion process [14,32], but it is quite time consuming. The substructure method provides a quick algorithm to do this [33]. The ring surface of an internode according to Shinozaki observations [32], is proportional to the leaf surface that it is seen above. (or: the number of leaves seen). It is possible to compute the number of leaves seen from every GU of a bearing axis belonging

to a given substructure by a simple operation. This number can be seen as a weight to capture biomass. Each GU has also a sink *pc* for the ring. It needs two steps to compute the ring thickness:

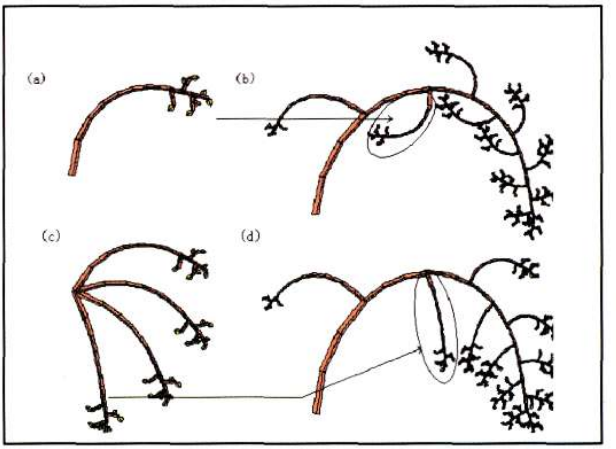

Fig.6 Plant (b) has only one kind of bending, the shape is wrong. Plant (d) can chose among 4 repetitions the more suitable one, the shape is good

- To compute the total biomass available for rings:

$$Qc(n) = \frac{pc \cdot N_{\mathrm{GU}}^{n-1}}{D(n)} Q(n-1) \tag{8}$$

where *pc* is the sink for the ring of a GU, *D(n)* is the plant demand, *Q(n-1)* the biomass reserve and N_{GU}^{n-1} the number of GU that is concerned for rings at GC=*n*.

- To compute the ring volume at a given position in a bearing axis.

$$qv_{p,t}^{\mathrm{GU}}(k) = \frac{N_{p,t}^{L}(k)}{\sum_{pa,ca,k} N_{p,t}^{L}(k)} Qc(n) \tag{9}$$

where $N_{p,t}^{L}(k)$ is the number of leaves seen by a bearing axis from the GU=*k* from beginning and belonging to a substructure PA = *p*, CA = *t* aged.

$\sum_{pa,ca,k} N_{p,t}^{L}(k)$ is the total of all these numbers that are propagated in the tree structure.

If a substructure is dead, the number of leaves is null, so the corresponding rings are also null. The diameter of the GU is then obtained easily by stacking all the rings along a GU length. A complex case is shown in Fig.7. Some substructures are completed, others are still growing. The diameters are computed by the direct biomass allocation to the rings, according to formula (8) and (9) that are computed quickly.

6 Behaviour, Optimization and Control of GreenLab Model

The advantage of a mathematical model is that one can study its behaviour. For an FSM its means what will be the organs numbers and their sizes during the growth process [27]. Equation (7) allows studying the plant growth behaviour and predicting the yield according

to the architectural model and the environmental conditions. The model has a high degree of flexibility, because the sizes of the organs depend of their expansions and of the sources-sinks relationships. For instance the model predicts well the qualitative answer to various pruning conditions: on a cotton plant (Fig.8), pruning the branches at their initiation makes the remaining metamers of the trunk much bigger [34].

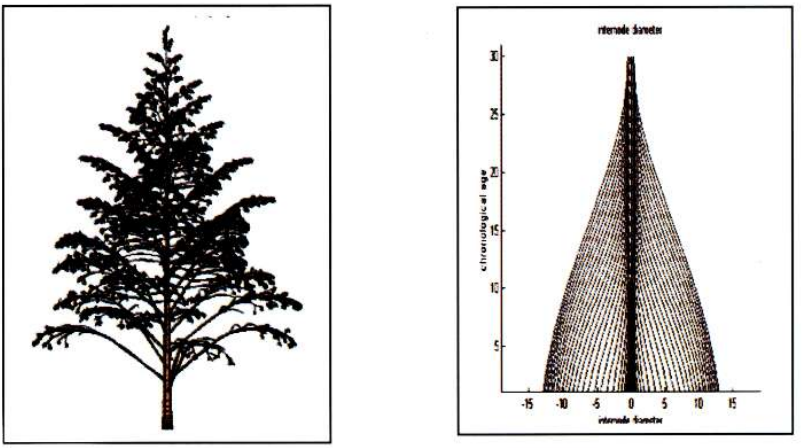

Fig.7 Visualization of a tree of (GC =30) with the rings (layers of biomass) in its trunk

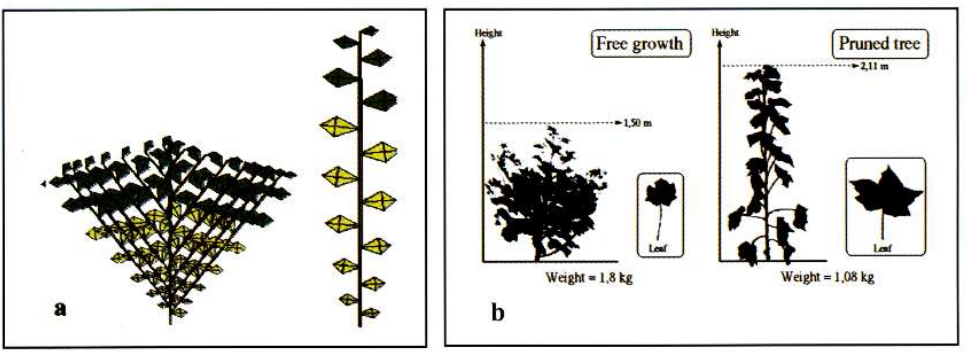

Fig.8 Effect of branch pruning on a plant during the growth. (a) Simulation of pruning, (b) real observations on cotton plant

Another important feature is the ability to compute the hidden parameters of the GreenLab model. The leaf functioning, and the organs sinks cannot be directly measured on the plant architecture, but has to be assessed by optimisation. The way is to minimize the differences simultaneously between all the metamers resulting of the computation and the data from the measured architecture. The calibration study is a bottleneck of many models because the optimisation can last a long time. For the program Cotton [10] that uses genetic algorithms it can run several days. For AMAPhydro model that uses Simulated Annealing [34], it last several hours and the accuracy on the parameters is low.

Here we use the Generalized Least Square Method (GLSM). It is derivative based and a strong convergence is insured by Newtown algorithm. Within 6 iterations the solution is founded in no more than few seconds. The model GreenLab has been successfully fitted to

cultivated plant, such as maize, sunflower [26,35,36].

But the size of a given plant architecture depends at the same time of the climate factor and of the sources-sinks relationship and their effects are mixed. While the first one tends to be out of control in an open field, the second one is more stable due to it has a genetic origin.

The GreenLab model is widely opened to optimisation as many dynamical models [37, 38]. It is possible theoretically to optimise the parameters of the model to get a better yield under limited conditions. If the parameters are continuous (as sink values) mathem atical algorithms can be used, meanwhile, when they are integers values (as organs numbers) only computer algorithms are available (as genetic algorithms). A cost function is usually associated to the optimisation process.

Dynamical models allow controllin g the plant development under cost functions. It is then theoretically possible to optimise the environment of the virtual plant in order to have the best yield. Here we consider a simple case for irrigation. If the water supply is limited, then how to optimise the daily water supply during the plant development? To summarize, the soil and the plant have transpirations. The water content in the soil at each GC depends of the water inputs and outputs and it is contained between a wilt and a field capacity th reshold. We assume that the climate efficiency (parameter E(n)) is proportional to the rate of water in the soil. Then the plant grows with a feedback with the water supply at each GC. According the GreenLab and the water budget models, optimal control can provide the best shape for a given family of curves that gives the daily irrigation. No one can give better results [39]. Optimal control could be used also to the date of treatments for pesticide, fertilizers. It is the most efficient mathematical tool for monitoring the plant growth in interaction with external factors.

7 Discussion

The goal of this paper is to construct a well-balanced functional-structural model between organogenesis and biomass acquisition and partitioning at the plant architecture level. It needs relevant choices and simplifications between the differ ent domains involved. First of all we have shown that the growth period must be the same for both architecture and functioning in order to build a dynamical system synchronized with interactions. Otherwise the FSM could be only kinetic and simply forced. The Growth Cycle is chosen which links to the thermal time so that the bud functioning and the leaf transpiration can be monitored at the same time. Eventually we are interested by the cumulative photosynthesis during the GC, what is provided by the reliable W.U.E. As this time period is not too short as it is in a PBM, it will not impede the growth simulation with too many iterations. Nevertheless, it remains the bottleneck due to the huge organs number to set in place in trees and plantations and the cumbersome method of bud-by-bud simulations with discrete events. As in all the quoted FMS in this paper, the computing time for organogenesis is proportional to the organs number to set in place and the computing time for biomass acquisition and partitioning i s at least 3 times over the first one, one cannot see practically how to use FSM for forest stand functioning. Fortunately, botany gives us the way to skip the problem by providing the Physiological Age notion, which enables us to do relevant botanical instantiations in the plant structure and reduce the computing time dramatically.

A bud becomes an automaton with different states and transitions that generate automatically a substructure at a given chronological age whose composition can be

computed from automaton theory. It is possible to create a library that contains all sets of substructures, starting from the oldest PA until 1 for all the CAs. Eventually building a tree is very fast by stacking substructures.

We propose the GreenLab model that deserves all these previous features [24]. It is no more a bud-by-bud simulation that imitates the plant growth, but a fast algorithm that gives exactly in the same conditions, the same results. The computing time then, becomes proportional to the number of PA and to the plant CA. Thus the drawbacks of the previous FSM are totally suppressed. GreenLab model emphasizes the interactions between architecture and functioning. As it is a mathematical model, the reliability of it is much higher than in the simulated models. The behaviour can be studied, and parameters optimization and growth control up to external conditions can be contemplate. Moreover the substructure method provides elegant algorithms for computing secondary growth, as well as stochastic behaviours. This powerful tool makes possible to build forest stands faster than a single tree according to the previous simulation methods.

Results of GreenLab are encouraging. Environmental effects and genetic processes are quite separated. If the absolute sizes of the organs depend of the physical environment, the relative sizes depends mainly of the sources and sinks relationships that run the feedbacks between plant functioning and plant architecture. It is possible to fit pretty well the model to the cultivated plants.

However GreenLab model is not completed yet. Two major issues are still in progress:

(1) The feedback between the photosynthesis and the organogenesis. This will allow fruit shedding, buds rests and deaths, and variable GU for trees. That means that the plant plasticity is limited to the organs geometry and the organogenesis for now is runing independently.

(2) The passage from a single plant to a plantation for the functioning. It needs to design properly the light interception and the water transpiration at the level of the field taking advantage of the GreenLab model features.

We are optimistic for these tasks, and the substructures method makes them possible.

List of some terms and abbreviations

Bearing axis:	The set of the GU of the same PA, produced by a bud and that constitutes a leafy axis that bears substructures.
DSA:	Dual—Scale Automaton.
Macrostate:	The state of the PA of the GU.
Metamer:	The elementary set of organs internode, leaves, axillary buds, fruits, produced by a bud.
Microstate:	The state of the PA of a metamer.
CA:	Chronological Age. The age of an organ, a substructure or a plant in GC.
DM:	Dry Matter. The biomass result of the CO2 assimilation in the plant from photosynthesis.
FSM:	Functional-Structural Model. A complex combination of PBM and GM to simulate the whole plant development.
FM:	Fresh Matter. The total biomass assimilation in the plant water + DM. (Water is about 80%).
GC:	Cumulated temperature necessary to put in place a new GU. It is the thermal time unit.
GM:	Geometrical Model. For building 3D plants architecture.

GU: The metamers set in place by a bud in the same period of growth. (one or several metamers).

LST: Law of Sum of Temperatures. The cumulated temperature monitors the speed of organogenesis.

PA: Physiological Age. The states of differentiation of the organs, axes and substructures in a plant architecture.

PBM: Process Base Model. Functioning model for Biomass acquisition and partitioning.

WUE: Water Use Efficiency. The Biomass acquisition (BM and DM) is proportional to the water transpiration during the whole plant development.

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