Study on Plant Growth Behaviors Simulated by the Functional-Structural Plant Model — GreenLab

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Abstract

As known, there are many intrinsic and extrinsic factors influencing plant growth and plant architecture. Considering some of the main factors related with plant structures, photosynthesis, organogenesis, and their interactions, recently a new plant growth model, named as GreenLab, is developed. In this paper, GreenLab model is first simply explained, and then used to analyze different plant behaviors.

Keywords: analysis, behavior, plant model, simulation

1 Introduction

Plants' growth reveals very different behaviors during their growing process, which aroused scientists' interests in studying their botanical patterns since many years ago. As reported by botanists, there are many intrinsic and extrinsic factors, for example the factors related with plant structures, photosynthesis, and organogenesis, influencing plant behaviors, i.e. plant growth. Therefore, plant growth model based on botanical knowledge in fact is to simulate the actions of these factors on plant growth. The first models that have simulated plant production, use general concepts available at the field level, such as Leaf Area Index (LAI), average height of plant, biomass production by compartments (leaves, fruits, …). Softwares such as EPIC[1] and TOMGRO[2] compute the crop biomass of a plant in a physical environment. The lacks of feedback between plant growing process, plant architecture and phenology have been identified as a more or less limitation for plant crops prediction.

Recently new structural-functional plant growth models and the corresponding softwares were presented to simulate the full plant morphogenesis (L-system[3], Visual Plant[4], Lignum[5], AMAPhydro[6], GROGRA[7], COTTON[8]). Although they employed different approaches in time description and plant organization, they share common points of view: plant growth must be computed step by step and the biomass is distributed inside the plant architecture; organs are characterized by their plasticity depending on allometric rules during their expansion. Such models are not really mathematical models but empirical simulation process based on discret events. This causes three main inconveniences: (1) the computational time is very long for big plants such as trees, which is not good for the optimization and calibration of plant parameters based on experimental data; (2) the behavior of the simulation process is unknown from a mathematical point of view; (3) bugs proof is difficult to set, and it is quite possible to fit pretty well the parameters of the bugged model with such techniques as Genetic Algorithms.

The models and their derivative softwares (AMAPsim[9] and AMAPhydro[6]) developed in CIRAD have the features as follows: (1) Automaton used in AMAPsim[9] for simulating organogenesis can construct complex plant architectures without functioning with a preset geometry; (2) AMAPhydro[9] can simulate plant functioning only for simple plant structure; (3) Both softwares have been impeded by the computational time.

In order to avoid the above problems, we try to build a mathematical model based on the similar assumptions with that in AMAPsim[9] and AMAPhydro[6] by extracting the hidden equations during the simulation process of both softwares. This leads to a new structural-functional plant growth model named as GreenLab which can run faster with interesting mathematical properties. By introducing some mathematical functions dependent on the parameters representing the main factors deduced from botanical nature of plant, GreenLab model can simulate the flow of energy and nutrients within single plant under stable environmental conditions, and the interaction between plant extrinsic structure and plant intrinsic functions (photosynthesis and organogenesis).

The organization of the rest of this paper is as follows: in Section 2, GreenLab model is briefly introduced; In Section 3, GreenLab model is used to analyze plant behaviors; The interactions between some designated plant architectural models and their biomass production are shown in Section 4; Finally the related discussions of GreenLab model are given in Section 5.

2 GreenLab Model

GreenLab model is a structural-functional plant growth model that combines plant Organogenesis and plant Photosynthesis by using Halle defined plant architectural models [10], duel-scale automaton theory [11], substructure-based algorithm [12] and the formula related with photosynthesis discussed later. It can simulate plant growing behaviours in a recurrent way.

As we know, plant budding from a germinating seed starts as a tiny shoot and root system with enough stored material, called as biomass in GreenLab, for its very first growth, and then plant grows step by step into the final structure built by different organs, represented by O (O is respectively B for leaves, I for internodes, and F for flowers or fruits) in an iterative pattern, which is the principle of substructure-based algorithm [12]. Generally, leaves and internodes appear in the beginning of every plant growing stage (measured in Growth Cycle in GreenLab), and fruits and rings (for secondary growth) appear at the end of every plant growing stage or just specific ones. After the leaves form, they become the most active and prominent plant organs. During plant growing process, the non-senescent leaves in one plant structure are the productive engines and the main "open window" of plants. They make photosynthesis by utilizing carbon dioxide from the air, light energy and temperature from the sun, and some water provided by the root system to produce the materials, called as biomass, for plant development --- new organs' generation and former organs' expansion in the next growing stage. So, at certain growing stage i, the number of leaves in a k ($k \geq i$) stages aged plant structure, which is calculated by the substructure-based algorithm[12], is $N_{i,k}^{B}$. It depends on plant architectural model and the leaf's life span t_B. The exposing area of each leaf and the ability of each leaf to make photosynthesis are the important factors for plant growth. We suppose implicitly in the following text that the named organs are non-senescent. It is reasonable to suppose that the biomass produced by each leaf appearing at growing stage i in plant structure at growing age k depends on its current exposing surface $A_{i,k}^{B}$ according to an empirical non-linear function $f\,(E_k, A_{i,k}^{B}, r_1, r_2)$, whereby, E_k represents the water use efficiency of each leaf at growing age k, r_1 and r_2 are hidden parameters to be computed from observation data by using optimization methods[13]. In GreenLab, E_k is set to constant E, and Equation 1 is used to approximate the observations of leaf functioning during plant growing process:

$$f(A_{i,k}^{B}, r_1, r_2) = \frac{E}{\dfrac{r_1}{A_{i,k}^{B}} + r_2}. \tag{1}$$

Suppose the leaves begin to appear at the very first growing stage, and the total biomass of the whole plant at growing age k, represented as Q_k, is most partly from photosynthesis made by all the leaves. Therefore, we consider Q_k as the sum of all the leaves' contributions plus the reserves dQ mobilized from the seed. For simplification, we suppose there is no biomass contribution from the seed to plant growth after the very first growing stage, i.e. $dQ = 0$ $(k > 1)$. Therefore, Q_k can be expressed as Equation 2:

$$Q_k = \begin{cases} \sum_{i=1}^{k} f(A_{i,k}^{B}, r_1, r_2) \cdot N_{i,k}^{B} & 1 \le k \le t \,\&\, k \le t_B \\ \sum_{i=k-t_B+1}^{k} f(A_{i,k}^{B}, r_1, r_2) \cdot N_{i,k}^{B} & 1 \le k \le t \,\&\, k > t_B \end{cases}. \tag{2}$$

The biomass produced by leaves is redistributed to the rest of plant where it can be used for the growth of organs like leaves themselves, internodes, buds, flowers or fruits (if exist) and rings (secondary growth), etc., therefore different plant behaviors result from the number of all the organs O , which is calculated by the substructure-based algorithm[12], and the abilities of these organs O to obtain biomass. These abilities depend on the sink strength that is modeled by a constant p_O and a function ϕ_j^{O} that represents the sink variation related to the organ's expansion during the life span of organ O, expressed as t_O. Assume $\sum_{O} p_O = 1$, $\sum_{j=1}^{t_O} \phi_j^{O} = 1$, and $\phi_k^{O} = 0$ when $k > t_O$, so the actual sink strength of j aged organ O is $p_O \phi_j^{O} (1 \le j \le t_O)$. For the organ O appearing at growing age i in the plant structure at growing age k, the biomass obtained by this organ is computed by formula 3:

$$q_{i,k}^{O} = \begin{cases} 0; & 1 \le i < T_O; 1 \le k < T_O \\ \sum_{j=i}^{k} \dfrac{p_O \cdot \phi_{j-i+1}^{O} \cdot Q_{j-1}}{D_j}; & 1 \le T_O \le i \le k \le i + t_O - 1 \\ \sum_{j=i}^{i+t_O-1} \dfrac{p_O \cdot \phi_{j-i+1}^{O} \cdot Q_{j-1}}{D_j}; & k > i + t_O - 1 \ge 1 \,\&\, i \ge T_O \ge 1 \end{cases}. \tag{3}$$

where T_O is the very first appearing time of organ O in the plant structure; D_j is the bulk demand of all the non-senescent organs during their life spans t_O, described by Equation 4:

$$D_j = \sum_{O} \sum_{i=1}^{t_O} p_O \cdot N^{O}_{i,j-i+1} \cdot \phi^{O}_{i} \quad . \tag{4}$$

In GreenLab model, plants are regarded as fresh (wet) biomass transportation system, which allows the volumes of plant organs roughly equal to their biomass storage without losing the botanical natures of plants. Therefore, leaf surface $A^{B}_{i,k}$ can be calculated from the result of its volume divided by its thickness e (suppose all the leaves have the same thickness), i.e.

$$A^{B}_{i,k} = \frac{q^{B}_{i,k}}{e}.$$

Up to now, we have presented the main factors that influence plant behaviors in mathematical way. Note that GreenLab model just considers the effect of predictable factors on plant growth entirely controlled by the above equations, which will be analysed in Section 3 where we suppose there are always non-senescent leaves during plant growth.

3 Mathematical Analysis of Plant Behaviors

Section 2 gives us the formula related with photosynthesis. By combining Equation 2 and 3, we can have formula 5 with a more clear representation of the general relationship among the biomass production through photosynthesis, the number of non-senescent organs through organogenesis and the biomass distribution among these organs, which completely determines plant growth behaviours:

$$Q_k = E \cdot \sum_{i=1}^{t_B} \frac{N^{B}_{k-i+1,k} \cdot \sum_{j=1}^{i} \frac{\phi^{B}_{j} \cdot Q_{k-(i-j)-1}}{D_{k-(i-j)}}}{\alpha + \beta \cdot \sum_{j=1}^{i} \frac{\phi^{B}_{j} \cdot Q_{k-(i-j)-1}}{D_{k-(i-j)}}} \quad . \tag{5}$$

where $\alpha = \frac{r_1 . e}{p_B}$; $\beta = r_2$; $k \geq t_B$.

For the convenience of analysing plant behaviours, we rewrite formula 5 in the following way:

$$\frac{Q_k}{D_{k+1}} = E \cdot \sum_{i=1}^{t_B} \frac{\frac{N^{B}_{k-i+1,k}}{D_{k+1}} \cdot \sum_{j=1}^{i} \frac{\phi^{B}_{j} \cdot Q_{k-(i-j)-1}}{D_{k-(i-j)}}}{\alpha + \beta \cdot \sum_{j=1}^{i} \frac{\phi^{B}_{j} \cdot Q_{k-(i-j)-1}}{D_{k-(i-j)}}} \quad . \tag{6}$$

From Equation 4, we can see that the ratio $\frac{N^{B}_{k-i+1,k}}{D_{k+1}}$ is a constant, say γ, when ϕ^{O}_{i} is given. Equation 6 thus shows us the evolution of $\frac{Q_k}{D_{k+1}}$, replaced with χ_k, when plant growing age k increases. Note that χ_k may reach a limit χ, which is the solution of the following equation:

$$1 = E \cdot \sum_{i=1}^{t_B} \frac{\gamma \cdot \sum_{j=1}^{i} \phi_j^B}{\alpha + \chi \cdot \beta \cdot \sum_{j=1}^{i} \phi_j^B} \quad . \tag{7}$$

There are different plant behaviours controlled by the above equations. Generally, plant will die if the total plant biomass production decreases step by step until zero with the organs becoming smaller and smaller; or else the plant may grow indefinitely only if the following condition is satisfied:

$$\frac{\alpha}{E} \le \sum_{i=1}^{t_B} (t_B - i + 1) \cdot \phi_i^B \cdot \tag{8}$$

The followings are several special cases deduced from the above equations.

- When $\beta=0$, i.e. $r_2 = 0$, from Equation (1), we can see that the biomass production of each leaf is then proportional to its surface, while the total Biomass production doesn't depend on the number of leaves or on the architectural model, and the volumes of the organs are in inverse proportion to their numbers. Taking Leeuwenberg model as an example, the number of leaves produced at plant growing age k is M^k (M is the number of lateral buds per article), and the sizes of leaves and internodes can increase or decrease indefinitely while the biomass product can increase indefinitely.
- When $\beta > 0$, the biomass production of each leaf has no linear relationship with its surface, the plant behaviour depends on Equation 7 and the biomass production depends on the number of leaves.
- In the case that χ_k reaches a limit value χ, the total biomass production, the bulk demand and the number of organs indefinitely increase with plant age, while the size of each organ will reach a limit. This happens when plant has an infinite growth without branch pruning. When the bulk demand D_k also reaches a limit value D_l, the number of organs, the size of each organ and the total biomass production will keep constant. This happens when plant has a constant crown with branch self-pruning. D_l can be computed from Equation 4, and the limit total biomass production Q_l can be obtained from χ, the solution of Equation 7.

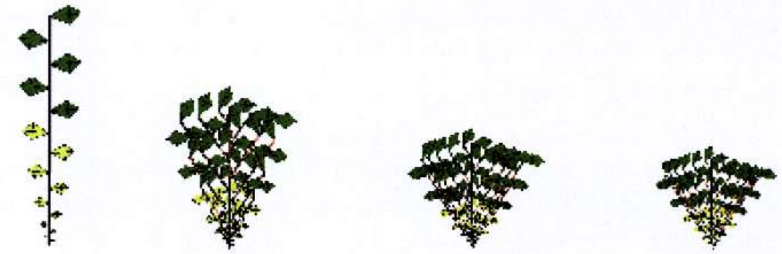
4 Interactions between Biomass Productions and Plant Structure

From the equations given in Section 2 and 3, we can see that there exist interactions between plant biomass production and plant structure. In GreenLab, the number of organs computed by the substructure-based algorithm is supposed to be the result of a pure genetic process that is not influenced by biomass production, while the sizes of organs depend on biomass production. On the other hand, plant structure has also influence on Photosynthesis: the less the number and the size of the leaves are, the less the plant biomass production is, and vice versa. Here, we will give some results (Fig.1~Fig.4) in the general cases of $\alpha > 0$and $\beta > 0$ by taking three kinds of simple plant architectural models: Corner model, Roux Model and Leeuwenberg model, as the examples to explain the interactions between plant biomass production and plant structure defined in Halle theory [10].

The plant of Corner model has a single stem with continuous growth (for example, Palm Tree. See Fig.1 (a)). The plant of Roux model has a continuous growth with a monopodial branching pattern and a single stem bearing secondary branches at each node. Its branches are supposed to grow during t_2 stages ($t_2 \geq 0$). Coffee tree is a fair specimen of Roux model. For the plant of Roux model, when plant age is bigger than branch duration time t_2, the plant crown will keep a constant size, which means that the number of organs, the size for each organ and the total plant biomass production will tend to be stable (See Fig.1(b), Fig.2). The limit value of the total plant biomass production, Q_l, can be computed by $Q_l = \left(\frac{E \cdot t_B - \alpha}{\beta}\right) \cdot (t_2 + 1)$, from which, we can see that the bigger t_2 is, the more the total plant biomass production is, while the smaller the size of the plant structure is (Fig.2). If t_2 = 0, the single stem plant corresponds to a pruned Roux model. For the pruned Roux model, the sizes of its organs are much bigger than that of the organs of the branched plant while its total biomass production is less. This can be well observed on plant such as Cotton [14]. The plant of Leeuwenberg model has a growth with a sympodial branching pattern (See Fig.1 (c), Fig.3), for example Casava tree. For the plant of Leeuwenberg model, the total biomass production increases with plant age; meanwhile the organs' sizes decrease or remain stable. It can be demonstrated that when plant age is old enough, the total plant biomass production will roughly follow the equation: $Q_k \approx M \cdot Q_{k-1}$ and the size of each leaf will reach a maximum value q_l^B . $q_l^B = p_B \cdot \xi$ if $\xi > 0$ and $\xi = \frac{E}{\beta} \cdot \frac{1 - M^{t_B}}{(1-M)M^{t_B}} - \frac{\alpha}{\beta}$. Otherwise, if $\xi \leq 0$, the size of each leaf will decrease, while the biomass production will indefinitely increase if Equation 8 is tenable. Fig.1 shows us the 3D plants respectively of Corner model, Roux model and Leeuwenberg model designated with the same functioning parameters (without fruits) in GreenLab. They have the same total biomass production, while differ in the sizes of the organs (leaves) depending on the non-senescent organs in different plant structures. We can see that the organs' sizes of the plant of Corner model are the biggest among the three designated plant in Fig.1. Fig.4 shows the biomass distribution curves for different organs of Roux model with fruits and the corresponding 3D plant. The organs' sizes increase with the plant age until the limit values that can be computed from Equation 7.

(a) Corner model (b) Roux model (c) Leeuwenberg model

Fig.1 Three different architectural models with same functioning parameters (without fruits)

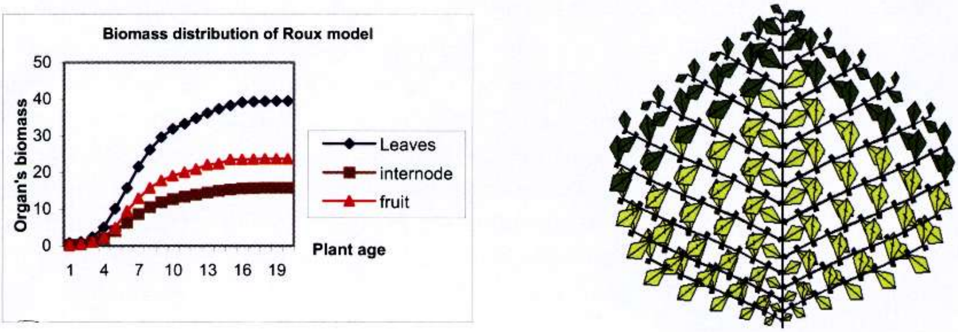


(a) $t_2 = 0$ (b) $t_2 = 5$ (c) $t_2 = 10$ (d) $t_2 = 15$

Fig.2 Influence of branch duration t_2 on Roux plant development

(a) (b)

Fig.3 Sympodial growth with limit organs' sizes. (a) the organs' sizes decrease. (b) the organs' sizes increase until a limit. In both cases, the total plant biomass increases exponentially



(a) (b)

Fig.4 Biomass distribution and 3D plant of Roux model with fruits appearing

5 Discussions

GreenLab model is a dynamic structural-functional plant growth model where plant biomass production and plant structure interact during the whole plant growing process. In GreenLab model, the plant shape has a high plasticity thanks to the organ's allometry, and the parameters related with organogenesis (metamer organization …) are derived from the real plant architecture and then used in the automaton that monitors the organ's production. Meanwhile the parameters that control the biomass production and allocation are hidden parameters that are computed from observation data of real plants by using heuristic methods. The organs in plant structure play their roles of sinks and/or sources during plant growing process according to certain plant functions. Modifying their functioning parameters is of direct consequence to plant behaviour, and thus plant growth can be controlled by GreenLab model. Equation 7 controls the sizes of the organs that depend on the bulk sources and the bulk demand of all the sinks in the plant. The ratio of Source to Demand at each growing stage is obviously the most important factor in GreenLab model. Equation 8 involved in GreenLab model is a very general and necessary condition for indefinite plant growth. The experiments on cultivated plants[13] such as maize, sunflower demonstrate that GreenLab model can simulate different plant behaviours which match with the observations on the real plant and it will be a useful tool to control plant growth and to optimize the crops, which is of great meaning for agronomy.

References

1 J. R. Williams, C.A. Jones, J.R. Kiniry, D.A. *Spanel: The EPIC crop growth model*, Trans. Am. Soc. Agric. Eng. 32 (1989) pp. 497-511.

2 C. Gary , J.F. Barczi.,N. Bertin, M. Tchamitchian: *Simulation interactive de la croissance d'une plante de tomate en fonction de son environnement et de sa conduite (modèle TOMGRO),* in: Bouchon J., Les Colloques. I.N.R.A. Edition, Architecture des arbres fruitiers et forestiers. 1995, pp. 333-343.

3 P. Prusinkievicz, M. Hammel, J. Hanan, R. Mech, L-systems: from the theory to visual models of plants, in : Michalewicz M.T. (Ed), Plants to Ecosystems:Advances in *Computational Life Sciences I*, *CSIRO* Publishing, Melbourne, *1997*, pp. *1-27*.

4 N. Chiba, K. Ohshida, K. Muraoka, M. Mura, and N. Saito: A growth model having the abilities of growth- regulations for simulating visual mature of botanical trees. *Computer & Graphics*, Vol. 18, No. 4, pp. 469~479, 1994.

5 J. Perttunen, R. Sievänen, E. Nikinmaa, LIGNUM: A model combining the structure and functioning of trees, *Ecol. Model*. 108 (1998) 189-198.

6 Ph. De Reffye, T. Fourcaud, F. Blaise, D. Barthélémy, F. Houllier: A functional model of tree growth and tree architecture, *Silva Fenn*. 31 (1997) 297-311.

7 W. Kurth, B. Sloboda, Growth grammars simulating trees – an extension of L-systems incorporating local variables and sensitivity, *Silva Fenn*. 31 (1997) 285-295.

8 E. Jallas. Improved model-based decision support by modeling cotton variability and using evolutionary algorithms. *Ph.D. dissertation Missipi State University*. May 1998.

9 J. F. Barczi, Ph. De Reffye, Y. Caraglio: Essai sur l'identification et la mise en oeuvre des paramètres nécessaires à la simulation d'une architecture végétale : le logiciel AMAPsim. *In: Modélisation et simulation de l'architecture des végétaux*. J. Bouchon, P. de Reffye and D. Barthélémy (Eds). *Science Update*, 1997. INRA Editions, Paris, France, pp. 205-254.

10 F. Halle, R. Oldeman, and P. Tomlinson: *Tropical Trees and Forest: an architectural analysis. Springer-Verlag, Berlin,* 1978.

11 X. Zhao, Ph. De Reffye, F.L.Xiong, B.G.Hu, Z.G.Zhan: Dual-scale Automaton Model for Virtual Plant Development. *The Chinese Journal of Computers*, 2001, 24(6), 608-617.

12 H.-P. Yan, J. F. Barczi, Ph. De Reffye, B.-G. Hu, M. Jaeger and J. Le Roux: *Fast Algorithms of Plant Computation Based on Substructure Instances*. In proceedings of WSCG'2002 - the 10-th International Conference in Central Europe on Computer Graphics, Visualization and Computer Vision'2002 in co-operation with EUROGRAPHICS, Vol.10, No.3, pp. 145-153, 2002.

13 Zh.G. Zhan, Y.M. Wang, P. De Reffye: A Structure-Function Model for Single Stemmed Plant Growth. *International Conference on Agricultural Science and Technology*, Beijing, 8th Nov. 2001.

14 Ph. de Reffye, F. Blaise, S. Chemouny, S. Jaffuel, T. Fourcaud, F. Houllier: Calibration of hydraulic growth model on the architecture of cotton plants, Agronomie 19 (1999)265-280.