

A New Mathematical Formulation for Plant Structure Dynamics

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ABSTRACT. In this paper a new mathematical formulation for plant structure dynamics is presented. We enhance the formulation of dual scale automaton by introducing botanic growth rules for an explicit description of chronological-age based structure dynamics. The merits of different plant architectural models are combined. The botanic concepts are introduced for not only the efficient simulations, but also the better integration of topological growth patterns and physiological laws, such that a complete functional-structural description of plant growth could be readily achieved.

RÉSUMÉ. Dans cet article nous présentons une nouvelle formulation mathématique pour la dynamique de la structure de plante. Nous renforçons la formulation de l'automate des échelles duales en présentant des règles de croissance botaniques pour une description explicite de la dynamique de la structure basée sur la notion âge chronologique. Les mérites des modèles architecturaux sont combinés. Les concepts botaniques sont présentés pour non seulement des simulations efficaces, mais aussi pour améliorer les intégrations des modèles topologiques de croissance et des lois physiologiques. Des modélisations complètes de l'architecture et du fonctionnement des plantes peuvent être approché grâce à cette formulation.

KEYWORDS : plant growth model, structure dynamics, mathematical formulation

MOTS-CLÉS : modèle de croissance de plantes, dynamique de la structure, formulation mathématique

1. Introduction

By plant functional-structural dynamics, we mean that plant grows along time driven by morphogenesis rules and by physiological laws. When environmental conditions and geometrical descriptions are available, the simulation of functional-structural plant model provides matter productions and shapes of plant elementary constituents (i.e. individual organs). FSPMs play an important role in diverse applications in agronomy, computer graphics, and plant physiology. There are recent studies on FSPM in different spatio-temporal organizations [4], however, a general description of plant functional-structural features remains to be an open problem due to experimental and physiological reasons.

Plant structure refers to topological architecture and geometrical information. The latter involves the location, orientation and the form of plant constituents in its three-dimensional canopy; the former describes the topological connections of these constituents. Architectural model, dealing with mainly topological structure, has been investigated featured by Multiscale Tree Graph [2], L-systems [3], and automaton [6]. MTG provides a rigorous mathematical description of mutliscale topological structures, however, these description are rather static snapshot of the the growth of plant structure (termed by plant structure dynamics), but not growth driven by morphogenesis rules. L-systems are general tools for modelling growing structure by rewriting grammars, however, botanic concepts, such as that of multiscale structure, are not closely integrated, as somehow impedes their simulation efficiency and their applications in agronomy. For the approach of automaton, i.e. Dual-Scale Automaton (DSA) [6], there is a lack of incremental description of plant structure dynamics.

In this paper, we present a mathematical formulation of plant structure dynamics, which intents to balance the merits of different architectural models. This formulation is naturally a descendant of the dual-scale automaton. The botanic knowledge is respected by adopting the notions from AMAP research group. Growth grammars are introduced to model the morphogenesis governed by a botanic clock named growth cycle. The formulation is for the integration of not only topological growth patterns discovered by botanists, but also physiological laws when considering varying environment conditions. The attempt is supposed to leap one step further in plant structure dynamics towards a general description of complete functional-structural plant characteristics. We name this approach dynamic botanic formulation.

The paper is organized as follows. Section 2 is devoted to botanic background knowledge, in which the plant spatio-temporal characteristics is introduced. DSA is briefly discussed in section 3, and we describe the formulation details in section 4. The comparison with L-systems is also discussed, followed by the conclusions of section 5.

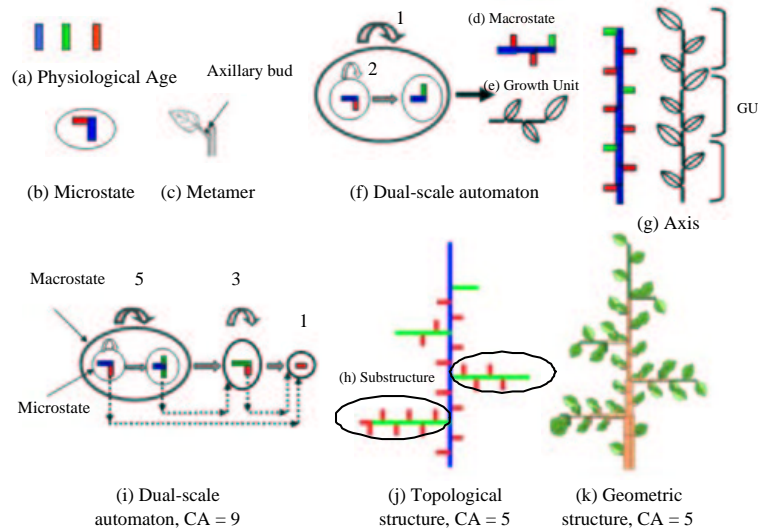


Figure 1. Botanic notions and dual-scale automaton.

2. Notations

Plant structure dynamics is featured by its temporal-spatio characteristics. Plant topological structure is organized as series of a hierarchically ascending scales: metamer, Growth Unit (GU for short), Bearing Axis (BA), substructure, and the whole plant individual (see figure 1). The architectural elementary entity, *metamer*, is composed of a node, the internode from beneath, the apical bud, the associated organs, i.e. leaves or fruits, and the axillary buds that can develop into a branch afterwards. The metamorphic variations of metamers are characterized by a notion of Physiological Age (PA) that refers to metamorphic phases from vegetative development to floral stage. The temporal organization is based on the assumption that plant undergo Growth Cycles (GC) of a biological clock. During each GC the plant metabolism results in the emergence of a cohort of new organs. The organ growth time is counted by the number of GCs, termed Chronological Age (CA).

At each GC for one metamer of Physiological Age p , (i) an apical buds (initially set as seed) forms one GU of a set of new metamers that construct the axis, (ii) each axillary bud gives birth to one GU that construct the secondary branches. The two kinds of growth process consequently produce apical and/or lateral *substructures* that represent the self-similarity within the plant whole structure. The new metamers born of both apical and axillary buds may have the same PA p or a higher PA q . Thus the metamer is identified

by 4 indices and denoted as $m_{pq}(k, n)$: (i) The CA n of the plant; (ii) The CA k of the metamer, that is, the organs of this metamer have appeared for k GCs; (iii) The PA $p \in \mathcal{P} = \{1, \dots, P\}$ of the bearing axis that the metamer belongs; (iv) The PA $q \in \mathcal{P}' = \{0\} \cup \{p, \dots, P\}$ of the branches that result from the axillary buds of the metamer.

Here $q = 0$ indicates no axillary buds, P is the maximal PA. A metamer may bear several organs of o -type, whose number is denoted by $m_{pq}^o(k, n)$ ($o \in \mathcal{O} = \{e, a, f, c, r\}$, where e stands for internodes, a for leaves, f for fruits, c for layers or rings, r for root), as well as apical bud $m_{pq}^A(k, n)$ of number b_{pq}^A and several axillary buds $m_{pq}^L(k, n)$ of number b_{pq}^L , $q \in \mathcal{P}' = \{p, \dots, P\}$. Usually b_{pq}^A equals one or zero (death of apical bud).

Metamers of same CA k at different plant CA, say n and $n + 1$, have different sizes, due to the environment oscillations and the change of sink abilities of that type of organ to attract biomass. However when considering topological structures, the geometry of organs is not of our interest, therefore metamer $m_{pq}(k, n)$ is reduced to m_{pq} with two indices p and q , for buds similarly we have m_{pq}^B for $m_{pq}^B(k, n)$, $B \in \mathcal{B} = \{A, L\}$.

3. Dual-Scale Automaton [6]

Now we consider the topological occupation of organogenesis. The Growth Unit of PA p , denoted as U_p , is a succession of metamers m_{pq} repeated r_{pq} times, here q for U_p is chosen from a PA index set $\mathcal{Q}_p \subseteq \mathcal{P}'_p$ according to biological rules or observations. The bearing axis is a concatenation of GU of different PAs together with the final apical bud. The apical bud of U_p can die or mute to older PA μ_p after τ_p -times repetitions of U_p . The axillary buds of metamer m_{pq} produce U_q that starts the growth of the secondary branches.

The process above can be described by *dual-scale automaton* thanks to the notions of macrostate and microstate. Microstate is defined to be the metamer that is characterized by the PA of its bearing axis and the PA of its axillary buds, and macrostate corresponds to the growth unit. Therefore a macrostate consists of succession of microstates. The concatenation of macrostates reflects the rhythmic growth, and forms the topological structure of the whole plant (figure 1). The parameters for the plant in figure 1 is as follows: $P = 3, N = 9$; $b_{pq} = 1, \forall q \in \mathcal{Q}_p$; $r_{13} = 2, r_{12} = 1, r_{23} = 2$; $\tau_1 = 5, \tau_2 = 3, \tau_3 = 1$; $\mu_1 = 2, \mu_2 = 3, \mu_3 = \bullet$.

Here \bullet denote death. N is the maximal plant CA. The status transition graph of dual-scale automaton for this example is shown in figure 1.

4. Dynamic Botanic Formulation

Diagrams in figure 1 are rather directed graphs resulting from the state transitions of automata. The transition functions for both macrostate and microstate automata are given descriptively in [6]. In this paper we introduce Dynamic Botanic formulation. By “dynamic”, we mean that the CA-based organogenesis dynamics can be better elucidated by the notion of *growth grammar*; by “botanic” we highlight the botanic organization of macrostate/microstate. We adopt some notations from [3].

4.1. Formulation

Definition 1 We summarize the configuration matrices as follows

$$\left\{ \begin{array}{ll} \vec{\mu} & \equiv [\mu_p]_{1 \times P}, & \text{Mutation vector of PAs for apical buds} \\ \vec{\tau} & \equiv [\tau_p]_{1 \times P}, & \text{Repetition vector for macrostates } U_p, p \in \mathcal{P} \\ \vec{\varphi}^o & \equiv [\varphi_i^o]_{1 \times N}, & \text{Functioning vector for o-type organ} \\ \mathbf{R} & \equiv [r_{pq}]_{P \times (P+1)}, & \text{Repetition matrix for microstate } m_{pq} \text{ in } U_p \\ \mathbf{B} & \equiv [b_{pq}^B]_{P \times P}, & \text{Count matrix for axillary bud in metamer } m_{pq} \\ \mathbf{M}_o & \equiv [m_{pq}^o]_{P \times (P+1)}, & \text{Count matrix for organs in metamer } m_{pq}, o \in \{b, f\} \end{array} \right. \quad (1)$$

Functioning status φ_i^o indicate the appearance of o-type organ, precisely 0 for inexistence, 1 for appearance, herein N is the maximal Chronological Age. The p -row of microstate repetition matrix \mathbf{R} signifies the repetition time r_{pq} of metamer m_{pq} in macrostate U_p . When $q \notin \mathcal{Q}_p$, we have $r_{pq} = 0$. Usually the occurrences of different types of metamers comply with a ascending order of q . The first column of \mathbf{R} corresponds the repetition time of metamers that have no axillary buds. The $p + 1$ column of p -row indicates r_{pp} times of repetition of metamer m_{pp} and so on. In the case of all metamers have axillary buds, we denote $\bar{\mathbf{R}}$ for residue matrix after the erasion of the first column of \mathbf{R} (0-valued), similarly $\bar{\mathbf{M}}_o$ for \mathbf{M}_o .

The configuration Λ is defined as set of configuration matrices $\Lambda = \{\vec{\mu}, \vec{\tau}, \mathbf{R}, \mathbf{B}, \mathbf{M}_o\}$.

Definition 2 We define the succession order of metamer occupation in macrostate U_p , that is, for $q_1, q_2 \in \mathcal{Q}_p$, succession order;

$$q_1 \prec q_2, \quad (2)$$

means that the apical bud $m_{pq_1}^A$ gives birth to metamer m_{pq_2} . The metamer m_{pq_1} is called the ascendant of metamer m_{pq_2} , and in reverse m_{pq_2} is the descendant of m_{pq_1} . The last metamer in U_p is called Terminal Metamer (TM) of U_p . The first index in the ordered sequence \mathcal{Q}_p is denoted by \underline{q} , and the last \bar{q} , thus TM of PA p is denoted by $m_{p\bar{q}}$.

Definition 3 *Growth Unit formulation*

The Growth Unit U_p of PA p is a succession of metamers, each metamer except TM gives birth to its descendant during certain period, the so-called **plastonchron**, we denote the formulation of Growth Unit U_p for one Growth Cycle as

$$U_p = \prod_{q \in \mathcal{Q}_p} m_{pq}^{r_{pq}} \quad (3)$$

The relation $a \cdot b$ means adjacent occupation of metamer a and b on the axis (note that the relation \cdot bears no commutativity, that is, $a \cdot b \cdot c \neq a \cdot c \cdot b$). There are totally $\sum_{q \in \mathcal{Q}_p} r_{pq}$ plastonchrons in one GC. The sequence $\prod_{q \in \mathcal{Q}_q}$ follows an implicit ascending order of q .

For the next GC, the axillary buds m_{pq}^L and the apical bud of TM m_{pq}^T will give birth to new Growth Units according to the following definition of growth grammar.

Definition 4 *Growth grammar:*

For growth unit U_p that repeats r times in its corresponding bearing axis, the growth grammar or rule for its associated buds m_{pq}^B , $B = \{L, T\}$ can be abstracted as

$$\begin{aligned} p_1 : m_{pq}^L &\mapsto U_q & q \in \mathcal{Q}_p \\ p_2 : m_{pq}^T &\mapsto U_p & r < \tau_p \\ p_3 : m_{pq}^T &\mapsto U_{\mu_p} & r = \tau_p \end{aligned} \quad (4)$$

The corresponding $U_p, r = \tau_p$ is called *Terminal Growth Unit (TGU)*.

Definition 5 *Dynamic Botanic formulation is a triplet $G(n) = \langle M, \mathbb{P}, \Lambda \rangle$, where $M = \{m_{pq}\}_{p \in \mathcal{P}, q \in \mathcal{Q}_p}$ is an alphabet of metamers with maximum number $P(P+3)/2$, \mathbb{P} is the growth grammar, and Λ is the configuration, $G(n)$ is the string generated at GC n . Plants always start to grow from seeds, thus we neglect the initial string.*

4.2. Formulation examples

Example 1 : Holttum model

Holttum model is a very simple unbranched structure terminated by an inflorescence ([3], page 65). In this case, we have the maximal PA $P = 1$, the maximal CA $N = n + 1$. There is only one metamer ($M = \{m_{10}\}$) for macrostate U_1 , that is $U_1 = m_{10}$. The configuration Λ is as

$$\mathbf{R} = (1 \ 0), \mathbf{M}_\bullet = (1 \ 0), \mathbf{B} = \emptyset, \vec{\mu} = (\bullet), \vec{\tau} = (n+1), \vec{\varphi}^a = \mathbf{I}, \vec{\varphi}^f = (\underbrace{0 \dots 0}_n \ 1)$$

The *growth grammar* \mathbb{P} is

$$\begin{aligned} p_2 : m_{10}^T &\mapsto m_{10} & r < n+1 \\ p_3 : m_{10}^T &\mapsto \bullet & r = n+1 \end{aligned}$$

The CA-based *organogenesis dynamics*

$$G(i) = m_{10}^i, \quad i = 1, \dots, n+1 \quad (5)$$

Example 2: Dynamic Botanic formularization of the plant in figure 1

Let

$$N = 9, P = 3, M = \{m_{13}, m_{12}, m_{23}, m_{30}\}$$

The *configuration* Λ is as follows (\bullet denotes the death)

$$\mathbf{R} = \begin{pmatrix} 0 & 0 & 1 & 2 \\ 0 & 0 & 0 & 2 \\ 1 & 0 & 0 & 0 \end{pmatrix}, \mathbf{B} = \begin{pmatrix} 0 & 1 & 1 \\ 0 & 0 & 1 \\ 0 & 0 & 0 \end{pmatrix}, \mathbf{M}_a = \begin{pmatrix} 0 & 0 & 1 & 1 \\ 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 \end{pmatrix}, \quad (6)$$

$$\vec{\tau} = (5 \ 3 \ 1), \vec{\mu} = (2 \ 3 \ \bullet), \vec{\varphi}^a = \mathbf{I} = (1 \ 1 \ 1 \ 1 \ 1 \ 1 \ 1 \ 1 \ 1)$$

The growth grammar is as (4) abstracts. Macrostates are marked with the accolades $\{ \}$. The U_p is interpreted as

$$\begin{aligned} U_1 &: m_{13}^2 \cdot m_{12} \\ U_2 &: m_{23}^2 \\ U_3 &: m_{30} \end{aligned} \quad (7)$$

Comparison with L-systems

In brief, a simplest L-systems is a triplet $G = \langle V, \omega, \mathbb{P} \rangle$, where V is the *alphabet* that includes all the letters of the system, *axiom* ω is the initial nonempty word for rewriting according to a finite set of rewriting rules \mathbb{P} , called *productions* [3]. L-systems representation for Holttum model in example 1 can be found in [3] (page 65).

The differences between dynamic botanic formulation and L-systems for Holttum model lie mainly in (i) for the former organs are organized into botanic notions of metamer

and growth unit etc., whereas for the latter there is no such botanic organizations; (ii) botanic grammars are fixed according to botanic knowledge, by contrast, productions of L-systems are flexible and have to be designed skillfully; (iii) the flower comes into being after a so-called count process for the latter, whereas for the former, the appearance of flower is governed by functioning vector $\vec{\varphi}^j$ without a consideration of flowering apex.

L-systems are more general tools, however, the specification of the production rules is not a trivial task due to the lack of botanic clarity. Indeed even for simple plants as in *example 2*, the L-systems implementation will be much more complex.

5. Conclusion and perspective

A new mathematical formulation of plant structure dynamics has been introduced by balancing the merits of different architecture models. Thanks to the integration of botanic knowledge, simulation efficiency of structure dynamics can be achieved (substructure concept in [5]). The extension to stochastic botanic growth grammars is natural. This formulation is also ready to be integrated into a complete functional-structural plant model by fulfilling physiological laws (see attempts in [5]). Further collaborations with botanists are needed to enrich the growth grammar, such that broader growth patterns can be represented.

6. References

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