

A mathematical model of plant structure dynamics

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Abstract

In this article we present a mathematical model of plant structure dynamics by introducing Dynamic Botanic Graph (DBG) for linear and branch growth patterns. DBG is designed for better integration of topological growth patterns and physiological laws into plant architecture models, such that a complete functional-structural description of plant growth could be readily achieved. Substructure is an efficient simulation algorithm in tree theory. We interpret substructure formulae in the context of DBG, and its efficiency is proven to be linearly proportional to the number of physiological ages and the number of chronological ages.

Key words: dynamic botanic graph, substructure, plant structure dynamics

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 (FSPM [1]) provides matter productions and shapes of plant elementary constituents (i.e. individual organs). FSPMs play an important role in diverse applications in agronomy [25], computer graphics [16], [4], and plant physiology [3]. There are recent studies on FSPM in different spatio-temporal organizations [22], [15], [7], however, a general description

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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 (or topological) model, deals with mainly topological structure, which was initialized by Hallé et al [12] and has been investigated featured by Multiscale Tree Graph [9], L-systems [17], and automaton [2]. MTG provides a rigorous mathematical description of multiscale 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. Much effort has been paid to the generation of plant image, and interface to physiological knowledge has been proposed [14]. In the L-systems approach, 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) [30], there is a lack of incremental description of plant structure dynamics.

In this article, we present a mathematical model of plant structure dynamics, which intends to balance the merits of different architectural models. The model 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 or chronological age. The graph definition of multiscale structure is kept. The model is designed 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 the model dynamic botanic graph.

The paper is organized as follows. Section 2 is devoted to botanic background knowledge, in which the model spatio-temporal characteristics is introduced. Section 4 describes the DBG formulation. Simulation efficiency of substructure for complex tree structure is illustrated in section 5. The comparison with other architecture models is discussed in section 6, followed by the conclusion and perspective of section 7.

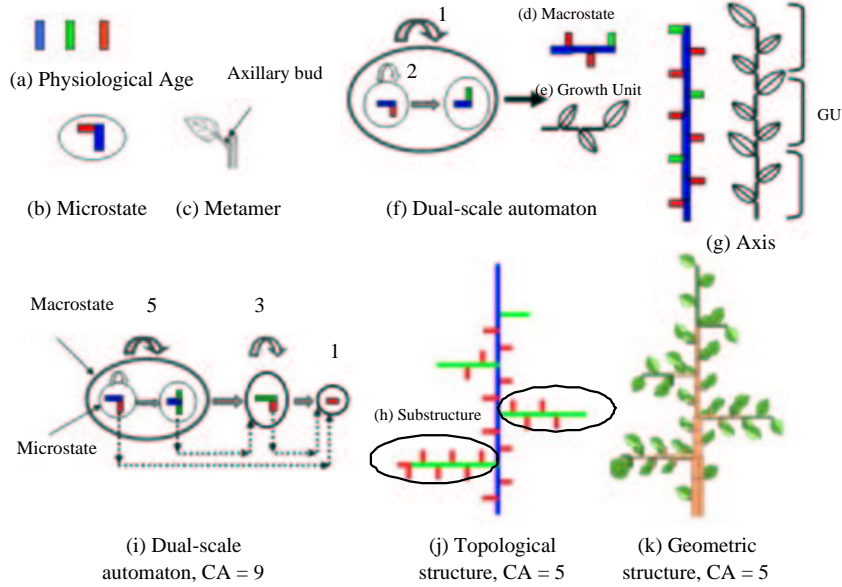


Fig. 1. Botanic notions and dual-scale automaton.

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 [21]. 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.

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 $m_{pq}(k, n)$:

- The CA n of the plant.
- The CA k of the metamer, that is, the organs of this metamer have appeared

for k GCs.

- The PA $p \in \mathcal{P} = \{1, \dots, P\}$ of the bearing axis that the metamer belongs.
- The PA $q \in \mathcal{P}'_p = \{0\} \cup \{p, \dots, P\}$ of the branches that result from the axillary buds of the metamer.

Here $q = 0$ indicates no axillary buds, P is the maximal PA, there are totally $f(P)$ types of metamers:

$$f(P) = \sum_{i=1}^P (i+1) = \frac{P(P+3)}{2} \quad (1)$$

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 , $q \in \mathcal{P}'_p = \{p, \dots, P\}$. 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 [30]

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).

example 1

The parameters for the plant is as

$$\begin{aligned}
 P = 3, N = 9; \quad b_{pq} = 1, \forall q \in Q_p; \quad r_{13} = 2, r_{12} = 1, r_{23} = 2; \\
 \tau_1 = 5, \tau_2 = 3, \tau_3 = 1; \quad \mu_1 = 2, \mu_2 = 3, \mu_3 = \bullet
 \end{aligned}
 \tag{2}$$

where \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. \square

4 Dynamic Botanic Graph

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 [30].

We emphasize that DSA is already equipped with concept of Chronological Age, however, it lacks the description of a CA-based dynamics. We enforce the DSA formularization by introducing Dynamic Botanic Graph (DBG). 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; and by “graph”, we refer to the resulting graph of automata state transition. In order to compare DBG with L-systems, we adopt some notations from [17], [18]. The frontier between DSA and L-systems is somehow blurred in the presentation of DBG.

4.1 Formulation

Definition 1 We summarize the configuration matrices as follows

$$\left\{ \begin{array}{ll} \vec{\mu} \equiv [\mu_p]_{1 \times P}, & \text{Mutation vector of PAs for apical buds} \\ \vec{\tau} \equiv [\tau_p]_{1 \times P}, & \text{Repetition vector for macrostates } U_p, p \in \mathcal{P} \\ \vec{\varphi}^o \equiv [\varphi_i^o]_{1 \times N}, & \text{Functioning vector for } o\text{-type organ} \\ \mathbf{R} \equiv [r_{pq}]_{P \times (P+1)}, & \text{Repetition matrix for microstate } m_{pq} \text{ in } U_p \\ \mathbf{B} \equiv [b_{pq}^B]_{P \times P}, & \text{Count matrix for axillary bud in metamer } m_{pq} \\ \mathbf{M}_o \equiv [m_{pq}^o]_{P \times (P+1)}, & \text{Count matrix for organs in metamer } m_{pq}, o \in \{b, f\} \end{array} \right. \quad (3)$$

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,

$$q_1 \prec q_2, \quad (4)$$

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

$$U_p = \prod_{q \in \mathcal{Q}_p} m_{pq}^{r_{pq}} \quad (5)$$

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 $\prod_{q \in \mathcal{Q}_p}$ follows an implicit ascending order of q .

For the next GC, the axillary buds m_{pq}^L and the apical bud of TM $m_{p\bar{q}}^T$ 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

$$\begin{aligned} p_1 : m_{pq}^L &\mapsto U_q \quad q \in \mathcal{Q}_p \\ p_2 : m_{p\bar{q}}^T &\mapsto U_p \quad r < \tau_p \\ p_3 : m_{p\bar{q}}^T &\mapsto U_{\mu_p} \quad r = \tau_p \end{aligned} \quad (6)$$

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

Definition 5 *DBG 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 (or graph, defined in section 5) generated at GC n . Plants always start to grow from seeds, thus we neglect the initial string (or graph).*

4.2 Examples

example 2 : Holttum model

Holttum model is a very simple unbranched structure terminated by an inflorescence ([17], 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

$$\mathbf{R} = (1 \ 0), \mathbf{M}_o = (1 \ 0), \mathbf{B} = \emptyset, \vec{\mu} = (\bullet), \vec{\tau} = (n+1), \vec{\varphi}^d = \mathbf{I}, \vec{\varphi}^j = (\underbrace{0 \dots 0}_n \ 1) \quad (1)$$

The *growth grammar* \mathbb{P} is

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

The CA-based *organogenesis dynamics*

$$G(i) = m_{10}^i, \quad i = 1, \dots, n+1 \quad (7)$$

□

example 3: DBG formularization of DSA example 1

From example 1, we have

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

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

$$\mathbf{R} = \begin{pmatrix} 0 & 0 & 1 & 2 \\ 0 & 0 & 0 & 2 \\ 1 & 0 & 0 & 0 \end{pmatrix}, \mathbf{B} = \begin{pmatrix} 0 & 1 & 1 \\ 0 & 0 & 1 \\ 0 & 0 & 0 \end{pmatrix}, \mathbf{M}_a = \begin{pmatrix} 0 & 0 & 1 & 1 \\ 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 \end{pmatrix}, \quad (8)$$

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

The growth grammar is as (6) abstracts. Macrostates are marked with the accolades $\{ \}$. The U_p is interpreted as

$$\begin{aligned} U_1 : m_{13}^2 \cdot m_{12} \\ U_2 : m_{23}^2 \\ U_3 : m_{30} \end{aligned} \quad (9)$$

□

4.3 Botanical explanations

Definition 6 *Definition of auxiliary alphabet for DBG strings.*

For convenience the parentheses () is used to mark certain part of the strings, but does not mean any additional operation. When a metamer m_{pq} has dormant buds, it is marked as \underline{m}_{pq} , and after its buds grow into new metamers, it is marked as \overline{m}_{pq} . Similar to the notions in [18], one can add auxiliary letters to analysis the strings in DBG. For instance, let V be extended by $V_E = V \cup \{ [,]\}$ and $V_{\#} = V \cup \{\#\}$. The words that are bracketed by $[,]$ are lateral branches. The branches can be covered up by $\#$ to show the marked axis.

We list the organogenesis for example 3 at each CA as (10).

$$CA 1 : \underline{m}_{13}^2 \cdot \underline{m}_{12}$$

$$CA 2 : (\overline{m}_{13}[\underline{m}_{30}])^2 \cdot \overline{m}_{12}[\{\underline{m}_{23}^2\}] \cdot \{\underline{m}_{13}^2 \cdot \underline{m}_{12}\}$$

$$CA 3 : (\overline{m}_{13}[\overline{m}_{30}])^2 \cdot \overline{m}_{12}[(\overline{m}_{23}[\underline{m}_{30}])^2\{\underline{m}_{23}^2\}] \\ \cdot (\overline{m}_{13}[\underline{m}_{30}])^2 \cdot \overline{m}_{12}[\{\underline{m}_{23}^2\}] \cdot \{\underline{m}_{13}^2 \cdot \underline{m}_{12}\}$$

$$CA 4 : (\overline{m}_{13}[\overline{m}_{30}])^2 \cdot \overline{m}_{12}[(\overline{m}_{23}[\overline{m}_{30}])^2 \cdot (\overline{m}_{23}[\underline{m}_{30}])^2 \cdot \underline{m}_{23}^2] \\ \cdot (\overline{m}_{13}[\overline{m}_{30}])^2 \cdot \overline{m}_{12}[(\overline{m}_{23}[\underline{m}_{30}])^2\{\underline{m}_{23}^2\}] \\ \cdot (\overline{m}_{13}[\underline{m}_{30}])^2 \cdot \overline{m}_{12}[\{\underline{m}_{23}^2\}] \cdot \{\underline{m}_{13}^2 \cdot \underline{m}_{12}\}$$

$$CA 5 : (\overline{m}_{13}[\overline{m}_{30}])^2 \cdot \overline{m}_{12}[(\overline{m}_{23}[\overline{m}_{30}])^2 \cdot (\overline{m}_{23}[\overline{m}_{30}])^2 \cdot (\overline{m}_{23}[\underline{m}_{30}])^2 \cdot \{\underline{m}_{30}\}] \\ \cdot (\overline{m}_{13}[\overline{m}_{30}])^2 \cdot \overline{m}_{12}[(\overline{m}_{23}[\overline{m}_{30}])^2 \cdot (\overline{m}_{23}[\underline{m}_{30}])^2 \cdot \underline{m}_{23}^2] \\ \cdot (\overline{m}_{13}[\overline{m}_{30}])^2 \cdot \overline{m}_{12}[(\overline{m}_{23}[\underline{m}_{30}])^2\{\underline{m}_{23}^2\}] \\ \cdot (\overline{m}_{13}[\underline{m}_{30}])^2 \cdot \overline{m}_{12}[\{\underline{m}_{23}^2\}] \cdot \{\underline{m}_{13}^2 \cdot \underline{m}_{12}\}$$

$$CA 6 : (\overline{m}_{13}[\overline{m}_{30}])^2 \cdot \overline{m}_{12}[(\overline{m}_{23}[\overline{m}_{30}])^2 \cdot (\overline{m}_{23}[\overline{m}_{30}])^2 \cdot (\overline{m}_{23}[\overline{m}_{30}])^2 \cdot \{\overline{m}_{30}\}] \\ \cdot (\overline{m}_{13}[\overline{m}_{30}])^2 \cdot \overline{m}_{12}[(\overline{m}_{23}[\overline{m}_{30}])^2 \cdot (\overline{m}_{23}[\overline{m}_{30}])^2 \cdot (\overline{m}_{23}[\underline{m}_{30}])^2 \cdot \underline{m}_{30}] \\ \cdot (\overline{m}_{13}[\overline{m}_{30}])^2 \cdot \overline{m}_{12}[(\overline{m}_{23}[\overline{m}_{30}])^2\{(\overline{m}_{23}[\underline{m}_{30}])^2\} \cdot \{\underline{m}_{23}^2\}] \\ \cdot (\overline{m}_{13}[\overline{m}_{30}])^2 \cdot \overline{m}_{12}[(\overline{m}_{23}[\underline{m}_{30}])^2 \cdot \{\underline{m}_{23}^2\}] \\ \cdot \{(\overline{m}_{13}[\underline{m}_{30}])^2 \cdot \overline{m}_{12}[\underline{m}_{23}^2]\} \cdot \underline{m}_{23}^2$$

$$[\mathbf{s}_{13}] = [\mathbf{s}_{23}] = [\overline{m}_{30}]; [\mathbf{s}_{12}] = [(\overline{m}_{23}[\underline{m}_{30}])^2 \underline{m}_{23}^2]$$

Definition 7 *Length function:*

The expected number of new buds in some $GU U_l$ that result from for bud m_{pq}^B is named length function of metamer m_{pq} , denoted \lg , and equals to (rule 6)

$$\lg(m_{pq}^B) = b_{i,\overline{m}}^A + \sum_{m \in \mathcal{Q}_l} r_{lm} b_{lm} \quad (11)$$

The length function of growth unit U_l is defined as $\lg(U_l) = \lg(m_{pq}^B)$

Some botanical notions can be illustrated by DBG. For instance, sympodial development of a metamer m_{pq} can be simulated by defining a physiological mutation of death ($\mu_p = \bullet$) for its apical bud m_{pq}^A , and a reiteration of axillary bud, that is, $q = p$. Implementation of rhythmic growth (not considered yet in [20]) is straight-forward by the macrostate/microstate definition. Acrotonic growth of macrostate U_p can be described as

$$\lg(\mathbf{s}_{pq_1}) < \lg(\mathbf{s}_{pq_2}), \quad q_1 \prec q_2, \quad q_1, q_2 \in \mathcal{Q}_p \quad (12)$$

where let length function \lg of branch \mathbf{s}_{pq} , $q \in \mathcal{Q}_p$ signifies the number of letters other than [and] in word \mathbf{s}_{pq} .

5 Substructure concept

The substructure concept is interpreted in the context of DBG, as leads to the proof of substructure dynamics formulae and the linear substructure complexity.

5.1 Formulation

Definition 8 *Substructure is a tree graph [9] $\mathbf{h} = (\mathcal{V}, \mathcal{E}, < \cdot >)$, where \mathcal{V} is the set of vertices, \mathcal{E} is the set of edges between two adjacent vertices, $< \cdot >$ is a mapping from \mathcal{E} to $\mathcal{V} \times \mathcal{V}$ called incidence function. For instance, when edge e is incident with vertices x and y , we have $< e > = (x, y)$, with its initial extremities denoted by $< e | = x$ and with its its final extremities $| e > = y$. Two complementary link relationships are defined on the edges, that is, the succession relationship “<” and the branching relationship “+”, denoted by the map,*

$$\theta : \mathcal{E} \mapsto \{'+', '<'\} \quad (13)$$

In our case, we have $\mathcal{V} \subseteq M$, where M is defined in definition 5. The root vertex of substructure of PA p is the first metamer m_{pq} of U_p .

Definition 9 The substructure $\mathbf{b}_p = (\mathcal{V}, \mathcal{E}, < . >)$ is called Bearing Axis (BA) of PA p , if

$$\begin{aligned} \mathcal{V} &= \{m_{lq} | l \in \{p, \mu_p, \dots, \mu_P\}, q \in \mathcal{Q}_l\} \\ \mathcal{E} &= \{e | < e > = (m_{lq_i}, m_{lq_j}), l \in \{p, \mu_p, \dots, \mu_P\}, q_i \prec q_j, \quad q_i, q_j \in \mathcal{Q}_l\} \\ \theta : \mathcal{E} &\mapsto \{ '<' \} \end{aligned} \quad (14)$$

Definition 10 Branching substructure of PA p is defined as the bearing axis \mathbf{b}_p together with all the lateral substructures associated with \mathbf{b}_p , denoted as S_p . Note that the root vertices of these lateral substructures are m_{lq} , $l \in \{p, \mu_p, \dots, \mu_P\}, \underline{q} \in \mathcal{Q}_l$.

From the definition of branching structure, we can observe a recursive mechanism, that is, the lateral branching structures are composed of branching structures with same or higher PA.

Definition 11 Macrostate substructure R_p of PA p is defined as the macrostate U_p together with all the lateral substructures associated with U_p , denoted as R_p , that is, R_p is part (subgraph) of S_p .

Both S_p and R_p can bear new metamers during the GC, as consequently change their topological structures. We therefore denote $S_p(k)$ and $R_p(k)$ as the substructures that appeared k GC before, that is, the substructures has a CA k . When considering CA n of the whole plant individual, the geometric properties of substructures $S_p(k)$ and $R_p(k)$ evolve accordingly, hence substructures are denoted as $S_p(k, n)$ and $R_p(k, n)$ in this case. Therefore the complete plant is $S_1(n, n)$. The bud that is destined to bear S_p is denoted as s_p .

Definition 12 Two substructures $\mathbf{h}_1 = (\mathcal{V}_1, \mathcal{E}_1, < . >)$ and $\mathbf{h}_2 = (\mathcal{V}_2, \mathcal{E}_2, < . >)$ are called identical (denoted by $\mathbf{h}_1 = \mathbf{h}_2$), if $\mathcal{V}_1 = \mathcal{V}_2$ and $\mathcal{E}_1 = \mathcal{E}_2$.

Proposition 1 All the branching substructure $S_p(k)$ of PA p and CA k , are identical.

Definition 13 The substructure difference h between $S_1 = (\mathcal{V}_1, \mathcal{E}_1, < . >)$ and

$S_2 = (\mathcal{V}_2, \mathcal{E}_2, \langle \cdot \rangle)$ is defined as a directed graph, such that

$$\begin{aligned} h &= S_1 \setminus S_2 = (\mathcal{V}, \mathcal{E}, \langle \cdot \rangle) \\ \{\nu \in \mathcal{V} : \nu \in \mathcal{V}_1 \text{ and } \nu \notin \mathcal{V}_2\} \\ \{\epsilon \in \mathcal{E} : \epsilon \in \mathcal{E}_1 \text{ and } \epsilon \notin \mathcal{E}_2\} \end{aligned} \quad (15)$$

Theorem 1 *Substructure dynamics is governed by the following formulae [6]*

$$S_p(0) = s_p, \quad (16)$$

$$S_p(k) = R_p(k) \cdot S_p(k-1), \quad 0 < k \leq \tau_p, \quad (17)$$

$$S_p(k) = T_p(k) \cdot S_{\mu_p}(k - \tau_p), \quad k > \tau_p, \quad (18)$$

with

$$R_p(k) = \prod_{q \in \mathcal{Q}_p} \left\{ m_{pq}(k) [S_q(k-1)]^{b_{pq}} \right\}^{r_{pq}} \quad (19)$$

$$T_p(k) = \prod_{l=k}^{k-\tau_p+1} R_p(l) \quad (20)$$

proof

- (i) Let us start from $S_p(0) = s_p$
- (ii) The first macrostate U_p of S_p is born of s_p according to *growth grammar* (6) p_2 : $s_p \mapsto U_p$. We have $R_p(1) = U_p$, and $S_p(1) = R_p(1) \cdot S_p(0) = U_p$.
- (iii) Considering $S_p(k-1)$ and $S_p(k)$ with $0 < k \leq \tau_p$, branching substructure $S_p(k-1)$ is formed by $(k-1)$ times of application of *growth grammar* (6) p_2 on bearing axis of PA p . Substructure $S_p(k) \setminus R_p(k)$ at CA k is also formed by $(k-1)$ times of applications of *growth grammar* (6) p_2 on bearing axis of PA p , hence $S_p(k-1)$ and $S_p(k) \setminus R_p(k)$ are identical (proposition 1). Therefore

$$S_p(k) = R_p(k) \cdot S_p(k) \setminus R_p(k) = R_p(k) \cdot S_p(k-1)$$

and by applying the definition 3 of GU formulation and *growth grammar* (6) p_1 on metamers m_{pq} , we have

$$R_p(k) = \prod_{q \in \mathcal{Q}_p} \left\{ m_{pq}(k) [S_q(k-1)]^{b_{pq}} \right\}^{r_{pq}}$$

- (iv) Considering $S_p(k)$ with $k = \tau_p + 1$, the apical bud of TGU U_p mutes according to *growth grammar* (6) p_3 : $m_{p\bar{q}}^T \mapsto U_{\mu_p}$ to form an GU of a terminal branching substructure S_{μ_p} , after τ_p times of occupation of U_p in the bearing axis \mathbf{b}_p . The substructure $S_p(k)$ is then composed of terminal substructure S_{μ_p} and a series of τ_p

macrostate substructure R_p with ascending CA from the top (CA 2) to the bottom (CA k) in \mathbf{b}_p . That is

$$S_p(k = \tau_p + 1) = R_p(\tau_p + 1) \cdot R_p(\tau_p) \dots R_p(2) \cdot S_{\mu_p}(1)$$

or in form of

$$S_p(k = \tau_p + 1) = T_p(k) \cdot S_{\mu_p}(k - \tau_p)$$

$$T_p(k = \tau_p + 1) = \prod_{l=k}^{k-\tau_p+1} R_p(l)$$

(v) For $k > \tau_p + 1$, there will be aging process of substructure S_{μ_p} and τ_p macrostate substructure R_p , thus the formulae (18) and (20) are straightforward. \blacksquare

Definition 14 *Complexity definition*

The complexity of DBG dynamics is defined as the application times of DBG growth grammar. The complexity of branching substructure is defined as times of branching substructure sticking.

Theorem 2 For sufficiently complex plant, the Complexity of DBG dynamics is at least exponentially related to plant chronological age; the complexity of branching substructure dynamics is at most linearly related to the number of physiological ages and the number of chronological ages.

proof

Plant can undergo indefinite (infinite) growth, however, for fixed plant growth CA k , $k < \infty$, the increment times of substructure sticking at CA k is denoted ω_k

(i)

For DBA dynamics, when $k = 1$, there is one application of growth grammar 6 $p_2 : s_1 \mapsto U_1$, thus $\omega_1 = 1$, the number of buds associated with U_1 (definition 7) is

$$\alpha_1 = \lg(s_1) = \lg(U_1) = b_{1\bar{q}}^A + \sum_{q \in \mathcal{Q}_1} r_{1q} b_{1q}$$

when $k = 2$, there are α_1 applications of growth grammar 6, $\omega_2 = \alpha_1$. The length function of U_{2i} , which appears in GC 2, is $\alpha_{2i} = \lg(U_{2i})$, $i = 1, \dots, \omega_2$. Denote

$\alpha_2 = \min_i \alpha_{2i}$, we have $\omega_3 = \sum_{i=1}^{\omega_2} \alpha_{2i} \geq \omega_2 \cdot \alpha_2$. For CA k , we have similar results

$\omega_k \geq \omega_{k-1} \cdot \alpha_{k-1}$. Let $\alpha = \min_i \alpha_i$, we have recursive relation, $\omega_k \geq \alpha \cdot \omega_{k-1}$, that is,

(ii)

For branching substructure dynamics, let $m_{pq}(k)$ be one application of a branching substructure. The term $[S_q(k-1)]^{b_{pq}}$ signifies b_{pq} attachments of $S_q(k-1)$. The increment of sticking times for branching substructure of PA p at its CA k is denoted $\omega_{p,k}$. Consider theorem 1, we have $\forall p \in \mathcal{P}$,

$$\omega_{p,k} = r_{pq}(1 + b_{pq}) + 1, \quad 0 < k \leq \tau_p \tag{21}$$

$$\omega_{p,k} = \tau_p \cdot r_{pq}(1 + b_{pq}) + 1, \quad k > \tau_p \tag{22}$$

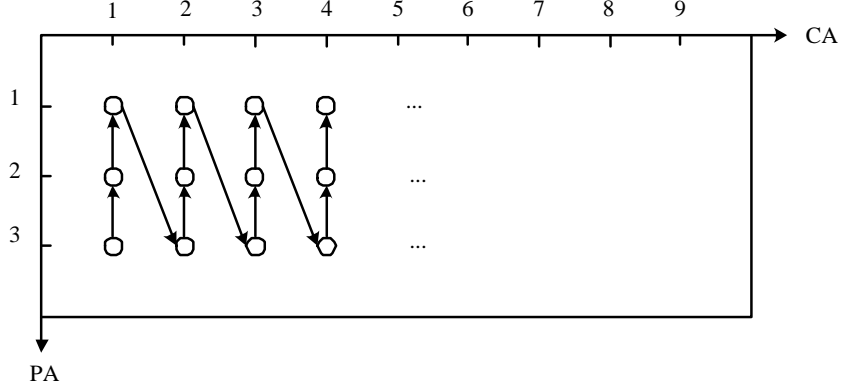


Fig. 2. Computational sequence of substructure, where ‘o’ signifies substructure at corresponding grid of PA and CA, and ‘→’ indicates the calculation sequence.

(a) Suppose that all substructure $S_p(k)$ can be retrieved from substructure library $\mathcal{S} = \{S_p(k), 1 \leq p \leq P, 1 \leq k \leq N\}$. For whole individual plant, $p = 1$. Let $\beta_1 = \max_i \omega_{1,i}$, we have $\omega_k = \omega_{1,k} \leq \beta_1$.

(b) When there is no substructure library, one has to firstly set up the substructure library, the calculation sequence is thus from physiological-old and chronological-young substructure to physiological-young and chronological-old substructure (figure 2). Let $\beta^k = \max_p \omega_{p,k}$, then $\omega_k = \sum_{p=1}^P \omega_{p,k} \leq P \cdot \beta^k$. Let $\beta = \max_k \beta^k, 1 \leq k \leq N$, we have $\omega_k \leq P \cdot \beta$, that is to say, the substructure complexity is linearly proportional to number of physiological ages and number of chronological ages. Figure 3 shows the substructure computational graph for example 3.

Note that (1) substructure $S_P(k)$ of maximal PA P is the concatenation of metamer m_{P0} ; (2) once $S_P(N)$ is calculated, the substructure library is constructed simultaneously. We can then perform more efficient simulation of case (a); (3) usually $\beta \gg \alpha$; and (4) substructure management is not considered (i.e. queries of substructures).

■

5.2 Remarks

The applications of DBG rules and branching substructure attachments are comparable. The plant computation usually concerns with counting processes or drawing procedures of organs. For the former, a number is associated with each macrostate for DBG rules and each substructure in theorem 1; for a organ drawing procedure, it corresponds to a copy of computer memory for macrostate or substructure.

The substructure concept is sketched as a highly efficient computational algo-

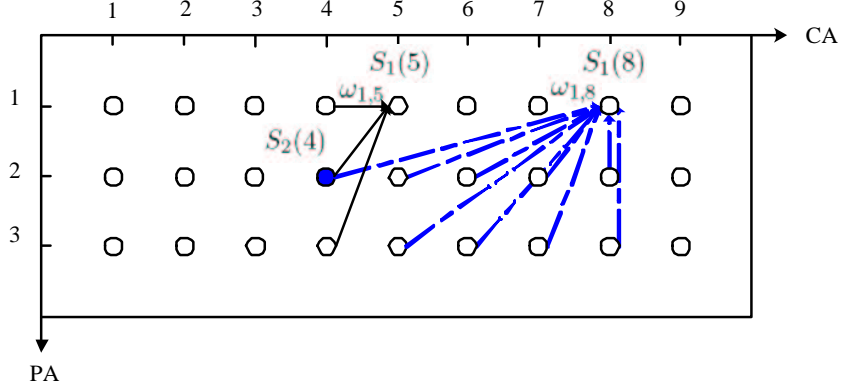


Fig. 3. Computational graph of substructure $S_1(5)$ and $S_1(8)$ in example 3 with $\omega_{1,5}$ and $\omega_{1,8}$ as their incremental sticking times of substructures, where ‘o’ signifies substructure at corresponding grid of PA and CA. Arrows ‘ \rightarrow ’ and ‘ $- \rightarrow$ ’ indicate sticking of physiological-old and chronological-young substructures. Note that we just plot the computational graph for one GC, in fact the graph can be processed recursively, say physiological-old and chronological-young substructures can be linked to substructure $S_2(4)$ (marked as \bullet).

rithm ([27], [13]) that features mainly in that (i) *once and for all* calculations of substructure instances form a substructure library for both topological and geometric information; (ii) the strategy, to be *temporally economic at the cost of spatial storage*, is carried out *in a reverse manner* for drawing and counting process.

The disadvantage of substructure approach is the lost of flexibility. For example when considering varying and heterogeneous environmental conditions within canopy, the two $S_2(4)$ (marked as ‘ \bullet ’ in figure 3) called by $S_1(5)$ and $S_1(8)$ respectively are topologically identical but geometrically different, since two $S_2(4)$ undergo different environmental conditions. We thus have to consider environment differences for each substructure of PA p and of CA k for the construction of substructure library \mathcal{S} , consequently the size of the substructure library will be enormously increased. For efficient simulation, approximation methods for environment conditions have to be subtly designed, otherwise one can perform simulation metamer by metamer governed by DBG rules.

6 Comparison between DBG/substructure and other morphogenesis models

6.1 Comparison between L-systems and DBG/substructure

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* [17]. Let V^* denote the set of all words over V , and V^+ the set of all nonempty words over V , then $\omega \in V^+$, $\mathbb{P} \subset V \times V^*$. A production rule $p = (a, \chi) \in \mathbb{P}$ is written as $a \rightarrow \chi$, signifying that the letter $a \in V$ be substituted by word χ . L-systems representation for Holttum model in example 2 is as follows ([17], page 65)

$$\begin{aligned}
 \omega &: a_0 \\
 p_i &: a_i \rightarrow I[L]a_{i+1} \quad 0 \leq i \leq n-1 \\
 p_n &: a_n \rightarrow I[L]A \\
 p_{n+1} &: A \rightarrow K
 \end{aligned} \tag{23}$$

where the brackets $[]$ delimit branching structures. The $n + 2$ productions indicates that after n steps of repetition of rewriting *vegetative apex* $a_i, 0 \leq i \leq n - 1$ by a module that consists of an internode I , a branching leaf L , and a new apex a_{i+1} , the plant differentiates in the module that consists of an internode, a branching leaf and a flowering apex A , then A transforms into an inflorescence (flower) K .

The differences between DBG dynamics (7) and L-systems (23) 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) DBG 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 $\vec{\varphi}^f$ without a consideration of flowering apex.

Both L-systems and DBG/substructure aim at the description of the complex-enough plant structure based on a relatively small set of rules (*database amplification* in [23]). The rules for L-systems are strictly local, and the specification of L-systems is not a trivial task [20]. Indeed, even for simple plants like in

example 3, the L-systems implementation will be much more complex. In addition, Prusinkiewicz and Kari prove that with only local productions, the subapical bracket deterministic L-systems can not simulate acrotonic growth [19]. In other words, we need global information.

By contrast, DBG/substructure focus on the response of the following question: How global patterns, like the Hallé's 23 architectural model, are implemented by relative local growth rules of hierarchical botanic entities?

The local growth rules of microstate/macrostate are complemented by the configuration Λ of global patterns. Thus in addition to a CA-based dynamics, DBG/substructure also takes advantage of the self-similarity thanks to its botanic clarity, efficiency can thus be achieved (theorem 2).

L-systems, as a general tool, are more powerful. For instance the letters can have other interpretation, i.e. cell; the local rules or *productions* are more flexible; and the rewriting system possibly serves as the analysis of self-replication [24]. Whereas DBG/substructure is more efficient (since it narrows itself in plant botanic structures), as is important in realistic applications, such as optimal control, calibration, etc [26].

6.2 On Multiscale Tree Graph (MTG) and DBG/substructure

Godin and Caraglio investigate plant topological structures, and introduce multiscale tree graph ([9]) as the backbone of AMAPmod software, which is developed for the purpose of a formal and computational analysis of plant architecture patterns based on a platform of a measurement database [10], benefiting from Hidden Markovian statistics [11].

Both DBG/substructure and MTG originate from AMAP research group, therefore they share the same botanic notions, such as internode, GU, bearing axis, etc. DBG even adopts from MTG the graph definition of substructure. The aim of MTG is to extract structural patterns from database of measurement, whereas DBG/substructure in reverse profits from the given plant patterns and provides a mathematical description of plant structure dynamics. In figure 4 we show an intermediate interpretation of DBG for *example 3* at chronological age 5 and its corresponding MTG.

7 Conclusion and perspective

A mathematical model of plant structure dynamics has been introduced by balancing the merits of different architecture models in the formulation of dy-

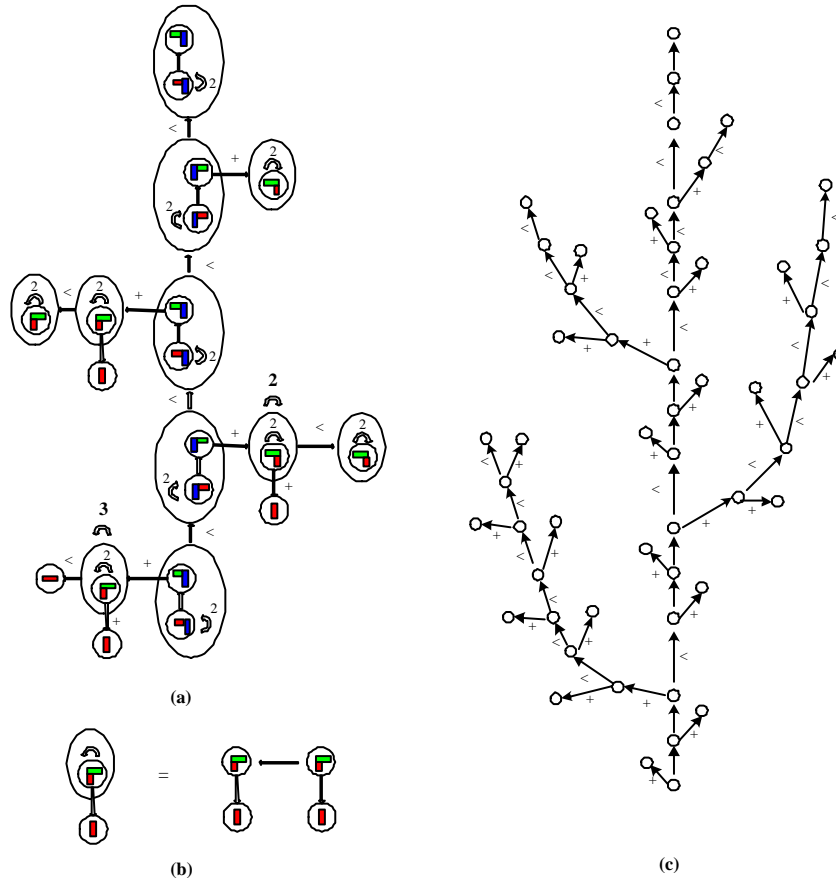


Fig. 4. (a) DBG Interpretation of *example 3* at CA 5; (b) Abbreviation notion; (c) The corresponding MTG graph

dynamic botanic graph. Substructure has been proven to be efficient simulation algorithms in the context of DBG.

Dynamic botanic graph is ready to be expanded into a complete functional-structural plant model by fulfilling physiological laws. The introduction of a soil water moisture model exemplifies such integration, as leads to possible agronomic applications on optimal irrigations [25]. Attempts in this direction can also be found in GreenLab model [28]. For calibration and validation of the model, please refer to [5], [29]. Further collaborations with botanists are needed to enrich the growth grammar, such that broader growth patterns can be represented.

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