

Self-similar analysis of plant architecture reveals hierarchical classes of meristem states

Christophe Godin¹ and Pascal Ferraro²

¹ INRIA, Equipe Virtual Plants, UMR DAP, Montpellier, France

² LABRI, Université de Bordeaux I, France
(on leave of absence at the University of Calgary)

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Introduction

Apical meristems are small embryogenic regions, located at the tip of plant axes, that build up plant organs by cellular division. The production of the meristems depends on their internal physical, physiological and genetic state and is controlled by contextual factors (like micro-environment, availability of nutrients, *etc.*). In principle, the number of variables that may be used to define the state of a meristem, taking account the nature and the concentrations of molecules in each cell, their position, the physical stresses at each point, the geometry of cells, their genetic contents, *etc.*, is infinitely large. Due to this intrinsic complexity, and to the current lack of hindsight on processes at such small scales, the connection between a meristem state, its micro-environment and what it produces at varying time scales seems until now largely out of reach.

However, the remarkable organization of plants at macroscopic scales makes the situation not so hopeless. The fact that plants are made up of the repetition of many similar components, at different scales e.g. (Arber, 1950; Hallé et al., 1978; Gatsuk et al., 1980; Harper et al., 1986; Barthélémy et al., 1997; Godin and Caraglio, 1998), provides macroscopic evidence for regularities and similarities in processes that drive meristem activity at microscopic scales.

In this paper, we propose to formalize this connection between macroscopic observations and microscopic, mostly invisible, processes. To achieve this connection, we formulate the following simplifying, though fundamental, scaling hypothesis during growth :

Scaling hypothesis: *If two branching structures in a plant are similar, they were (probably) produced by meristems with similar states and contexts.*

In other terms, if we consider the function that associates each branching structure of a plant with the state of the meristem that produced it, this scaling hypothesis states that this function is continuous. Note that this implicitly requires that metrics are defined on both the branching system space and the meristem state space. In this presentation, we shall show that it is possible to use this idealized - but useful - hypothesis to organize the multitude of meristem states and contexts by classes of equivalence with respect to the similarity of what they produce.

In this first approach, the similarity between branching systems is considered to be purely structural (no geometry is taken into account for instance). Due to the nested nature of these structures, we show that the study of similarities between all parts of a plant boils down to studying the self-similar nature of the plant structure. Based on previous attempts to quantify self-similarity in plants (Prusinkiewicz, 2004; Ferraro et al., 2005), we introduce a new method that enables us to define the degree of self-similarity of any plant as a departure coefficient from pure self-similarity. As a by-product, the method enables us to identify hierarchies of classes of meristem states.

From biology to mathematical formalization: modelling plant architecture self-similarity

Different strategies can be used to define an equivalence relationship between branching systems. They can be equivalent because they have the same root diameter, because they have the same size or because they bear the same number of flowers. Here we consider structural equivalence. Formally, this comes down to defining a notion of isomorphism between branching systems. In (Ferraro et al., 2005), we defined isomorphism between axial branching systems (i.e. branching systems for which a trunk is defined). Here we consider a less restrictive class of isomorphism between branching systems which holds for any type of tree structure. In the following, any graph G is represented by a pair (V, E) where V is the set of vertices of G and E its set of edges (i.e. a set of oriented pairs of vertices). A tree-graph is a graph for which a particular vertex, called the root, is identified and such that any vertex different from the root is linked to the root by a unique oriented path in the graph (see (Godin and Caraglio, 1998) for detailed definitions).

Definition 1 (tree isomorphism). Let $T_1 = (V_1, E_1)$ and $T_2 = (V_2, E_2)$ be two rooted trees. A bijection ϕ from V_1 to V_2 is a tree isomorphism if for each edge $(x, y) \in E_1$, $(\phi(x), \phi(y)) \in E_2$. We note $T_1 \equiv T_2$.

To compute whether two branching structures T_1 and T_2 are isomorphic, we use a notion of edit-distance between trees (Zhang, 1996; Ferraro and Godin, 2000). The distance between T_1 and T_2 , $D(T_1, T_2)$, is defined as the minimal number of elementary edit operations (insert, delete or match vertices) that is necessary to transform T_1 into T_2 . This distance has the following property: $D(T_1, T_2) = 0 \Leftrightarrow T_1 \equiv T_2$.

Definition 2 (Reduction of a tree). Let T be a tree, we denote by $\mathcal{R}(T)$ the graph obtained by quotienting T by the equivalence relation \equiv . We call this graph the reduction of T .

This definition relies on the construction of a graph corresponding to the reduction of the initial tree, when all the structural redundancy has been removed. It can be shown that this graph is a directed acyclic graph (DAG) and that there exists an algorithm that can compute this DAG in time $O(|T|^2 \ln |T|)$ (Godin and Ferraro, 2007). Let us call *linear* a DAG for which there exists a path going through all its vertices. Then, by definition, we say that a tree T is *self-similar* if $\mathcal{R}(T)$ is linear.

Under the scaling hypothesis, the nodes of $\mathcal{R}(T)$ can be interpreted as meristem states, and the edge between two states would denote the occurrence of a meristem differentiation (from the initial to the final state). Paths in $\mathcal{R}(T)$ therefore denote all possible meristem differentiation sequences. In self-similar plants, there is thus a unique differentiation sequence for all the meristems of the plant.

Among all the self-similar trees, let us denote $\mathcal{S}(T)$ the subset of self-similar trees that contain T . Then, we consider trees T^* in this set that minimize the distance to T .

Definition 3 (Smallest Self-similar Tree, SST). Let T be a tree and $\mathcal{S}(T)$ be the set of all the self-similar trees that contain T . Then, we define the set of smallest self-similar trees containing T by: $SST(T) = \{T^* | T^* = \underset{T' \in \mathcal{S}(T)}{\operatorname{argmin}} D(T, T')\}$

We show that, for any tree T , it is possible to find an element $T^* \in \text{SST}(T)$ in polynomial time³ $O(h \times w \times \ln(w))$, and give the corresponding algorithm (Godin and Ferraro, 2007). In addition, the algorithm returns the mapping from T^* to T that corresponds to the minimal distance $D(T, T^*)$. Under the scaling hypothesis, this makes it possible to associate with each tree T a single sequence of states. This sequence may be interpreted as the template differentiation sequence of the plant meristems. Thanks to the mapping from T^* to T , each branching system of the original plant may then be associated with one of these computed, hypothetical, meristem states, representing the state of the meristem that produced this branching system.

Hierarchical organization of meristem states in Rice

The above approach was tested on different plant architectures. We present here results corresponding to the analysis of a rice panicle (Fig. 1.a), already described in (Ferraro et al., 2005). The topological structure of the panicle T is depicted in Fig. 1.b.

We first computed the reduction tree $\mathcal{R}(T)$, (Fig. 1.c). This graph, from which the original tree can be reconstructed (Godin and Ferraro, 2007), is not linear and shows a number of different meristem differentiation sequences. By computing an element T^* of $\text{SST}(T)$ (Fig. 1.d), it is possible to find a single sequence of meristem state differentiation that best corresponds to the original plant. The states of this sequence can be subsequently projected onto the original topological structure using the resulting mapping from T^* to T , thus providing an interpretation of the entire structure in terms of meristem differentiation (Fig. 1.e).

Perspectives: from mathematical formalism back to biology

The above approach makes it possible to formally retrieve the sequences of meristem state differentiation corresponding to each axis of a given plant. Based on the scaling hypothesis and its variants, this opens up the perspective to use such an analysis on various plant species as a guiding principle to further investigate the notion of meristem state and differentiation at a bio-molecular and genetic levels, in the spirit of the pioneering work described in (Prusinkiewicz et al., 2007).

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³ h and w represents respectively the height (*i.e.* the length of the minimum path between the initial node and any leaf) and the width of $\mathcal{R}(T)$ (*i.e.* the maximum number of nodes at a given height in $\mathcal{R}(T)$)

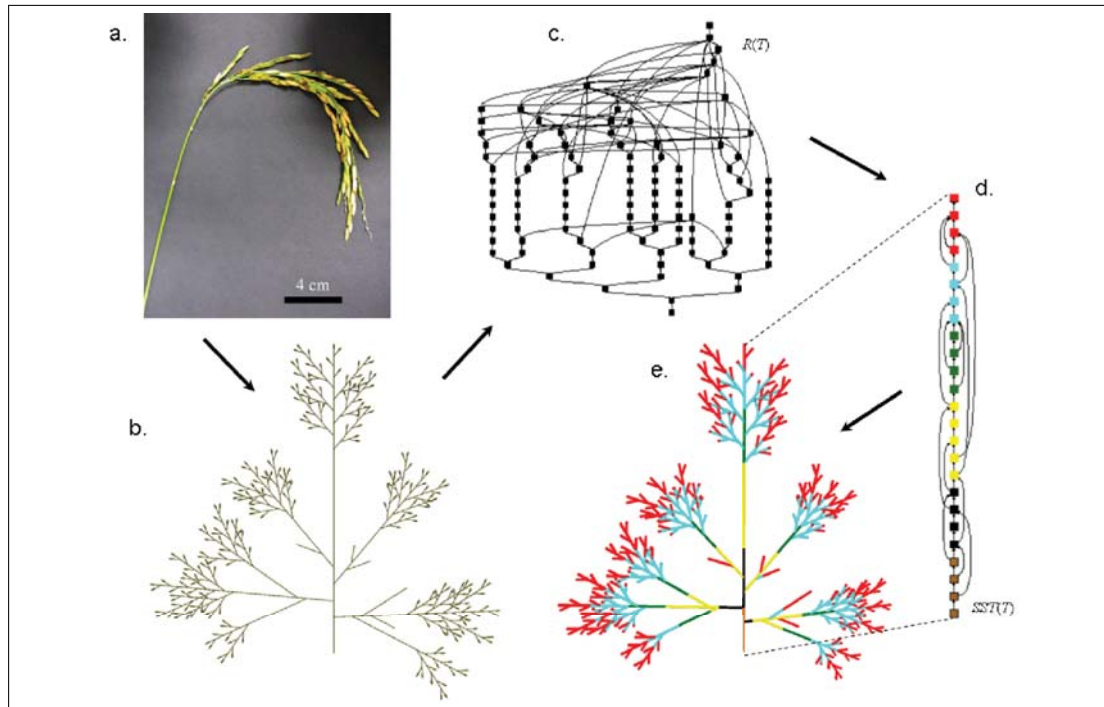


Figure 1. a. A rice panicle photograph and b. its topological structure (courtesy of C. Paul-Victor, Y. Caraglio). c. Its reduction as a DAG, d. the corresponding DAG of its smallest self-similar tree and e. the projection of meristem states onto its topological structure.

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