

# Characterization of architectural tree models using L–systems and Petri nets

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## Abstract

We propose a symbolic notation inspired by L–systems and a graphical representation based on Petri nets to formally describe architectural tree models introduced by Hallé and Oldeman (HO models). The two formalisms are related, but lead to visually different model presentations and are preferable in different applications. Specifically, L–systems are useful as an input for simulation programs, whereas Petri net graphs lend themselves to more intuitive comprehension of some aspects of the models. We focus on the developmental fate of the apices, configuration of the branching points, and plagiotropy and orthotropy of tree axes as the key characteristics of HO models. Contrary to the original HO classification, we do not consider the distinction between continuous and rhythmic growth. With this limitation, in this paper we are able to characterize most HO models using L–systems and Petri nets.

## Reference

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**Key words:** architectural tree model, branching, L-system, Petri net.

## Résumé

Nous proposons une notation symbolique inspirée par les systèmes de Lindenmayer, ainsi qu'une représentation graphique fondée sur les réseaux de Petri, pour caractériser formellement les modèles architecturaux qui avait été introduit par Hallé et Oldeman (dits modèles HO). Les deux formalismes ont des représentations visuelles distinctes et sont préférables dans des domaines d'application différents, malgré leur liaison sur le plan conceptuel. Spécifiquement, les L-systèmes se voient utiles pour entrer des modèles d'arbres aux programmes de simulation, pendant que les réseaux de Petri se prêtent mieux à la compréhension intuitive des modèles. Nous utilisons les deux formalismes pour caractériser les modèles HO aux termes du développement des méristèmes apicaux, les configurations des points de ramification, et la distinction entre la plagiotropie et l'orthotropie des axes. Par contre, nous ignorons la distinction entre la croissance continue et rythmique, un des facteurs majeurs considérés par Hallé et Oldeman. Etant donné cette limitation, nous présentons les L-systèmes et les réseaux de Petri qui décrivent la majorité des modèles HO.

**Mots-clés:** modèle architectural d'un arbre, ramification, L-système, réseau de Petri.

## 1. Introduction

The term *tree architecture* refers to the essential qualitative features of the structure and development of a tree crown. Hallé and Oldeman (1970) proposed to group tree architectures into 23 classes, called *architectural models*. This *HO classification* was subsequently expanded and popularized by Hallé, Oldeman and Tomlinson (1978), and concisely presented by Bell (1991). Although other schemes for classifying tree architectures also exist (a short survey is presented by Robinson, 1996), the HO classification is the most widely used one.

The HO classification was formulated in terms of a verbal description of the individual architectural models, accompanied by schematic drawings of representative trees. Although the classification criteria have been succinctly stated (Barthelemy, Edelin and Hallé, 1991), the HO classification remains descriptive in character, making it difficult to discern the essential features of each class and analyze logical relationships between them. To address these limitations, we propose a formal characterization of the architectural tree models based on the following criteria:

- The sequencing of developmental events including, in particular, the developmental fate of the apices,
- The configuration of branching points, taking into account:
  - distinction between terminal and lateral apices,
  - dominance relationships between the apices,
  - position of vegetative and flowering apices;
- plagiotropy and orthotropy of axes.

We express the individual models using a symbolic notation inspired by Lindenmayer systems (Prusinkiewicz and Lindenmayer, 1990) and a graphical representation based on Petri nets (Peterson, 1981). L-systems already have many applications in botany, including a classification of inflorescences (*op. cit.*, Chapter 3). Botanical applications of Petri nets have also been reported (*e.g.*, Lück and Lück, 1991; Barlow, 1994). In the descriptions of tree architectures, these formalisms lead to visually different presentation of the models and may be preferable in different applications. Specifically, the symbolic notation of L-systems makes them particularly useful as an input for simulation programs, whereas the graphical representation of Petri nets lends itself to more intuitive analysis and comprehension of the models. Nevertheless, both formalisms are related to each other, as both of them emphasize developmental aspects of the architectural models. This is the key difference from a previous approach to formalize the HO classification (Robinson, 1996), which was focused on the static aspects of crown structure.

Our proposed formalisms provide only a partial characterization of the sequence of developmental events (mathematically, a partial ordering relation in the set of events). Consequently, we do not capture the distinction between rhythmic and continuous growth, which was one of the classification criteria used by Hallé and Oldeman. With this limitation, we are able to use the proposed formalisms to characterize the HO models and apply them to simulate individual tree species.

## 2. Specification of developmental patterns

In order to describe architectural tree models we need to address two problems: the description of individual trees and the description of classes of trees – the architectural models. Difficulties stem from the unbound number of components that may constitute an individual tree and the unbound number of related yet varied architectures that may belong to a single model. A formal description of architectural tree models must thus provide a finite, compact, precise and intuitively understandable description of the unbound tree structures and their classes.

The HO classification is based on the postulate that a plant can be viewed as a population of iterated (repeating) discrete units. We will consider relatively small units, such as primary meristems, branch segments (internodes), leaves and flowers, which we will call *modules* according to one of the accepted uses of this term (Bell 1991, p. 284). Although a tree may consist of a large

number of individual modules, we assume that they exhibit only a finite number of different behaviors. This assumption reduces the description of the unbound number of individual modules to the description of a finite number of behaviors that define module *types* or *states*. A tree structure emerges from a (real or simulated) process of development, during which each module may grow, change type, produce new modules or die according to the rules proper to its type.

In order to fully relate the behavior of modules in a growing tree to the resulting tree structure, we must also define how these modules are connected to each other and organized in space. Specification of connections between plant modules (*i.e.*, the *topology* of a plant) is a relatively straightforward task, because the neighborhood relations between the individual cells, and by extension the modules, are determined upon their creation (plant cells and modules do not move with respect to each other). Consequently, topology of the whole structure can be inferred from the rules that characterize the creation of the modules. Similar rules can be used to specify changes in spatial relations between the modules due to their growth and reorientation.

The rules describing the behavior of modules need not be deterministic and may allow for developmental choices. This provides a means for characterizing not only an individual tree, but also an entire class of related tree architectures, using a finite set of rules. This set thus becomes a formal specification of an architectural model.

The concept of describing a plant as a growing assembly of modules governed by a small number of rules is formalized in the notion of *L-systems*. They were originally introduced to describe relatively simple multicellular organisms (Lindenmayer, 1968), but subsequently have been extended to higher plants (Prusinkiewicz and Lindenmayer, 1990; Prusinkiewicz *et al.*, 1997; for a historical perspective see Prusinkiewicz, 1999). The essence of an L-system is a set of one or more developmental rules, called *productions* in the standard L-system terminology. Intuitively, a production specifies that a component of the structure, identified with the production's *predecessor*, will be replaced by a structure consisting of zero, one, or more components, called the *successor*. The execution of a production corresponds to the progress of time by some interval (often a plastochron). For example, Figure 1 shows the production that captures the development of a monopodial branching structure.

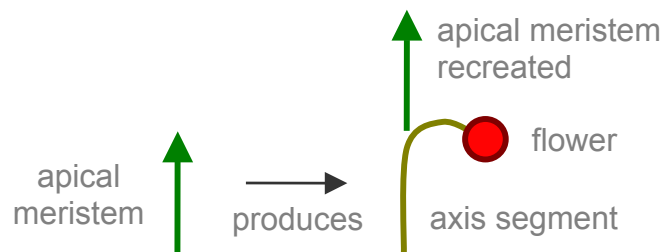


Figure 1. Example of an L-system production

The apical meristem – the predecessor – is replaced by an axis segment that supports a lateral flower and is followed by the apical meristem that continues the development of the axis. Repetitive application of this production yields a sequence of consecutive stages of the development of the plant (a *developmental sequence*), as shown in Figure 2. The development begins with an initial structure (a single apex in this case), called the *axiom* in the L-system

terminology. Each production application extends this structure by one segment with the associated flower. A monopodial structure results.

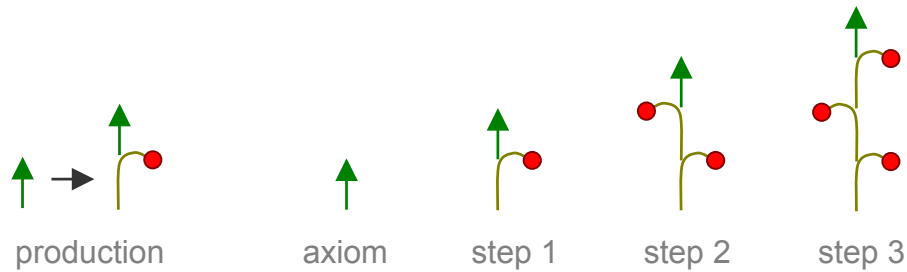


Figure 2. Developmental sequence generated using the L-system production from Figure 1

A crucial feature of the L-system theory is a symbolic notation, based on the representation of plant modules by letters. Sequences of letters denote modules arranged consecutively along an axis. Square brackets enclose branches. An example of L-system specification using the symbolic notation is shown in Figure 3. The symbolic notation makes it possible to specify L-systems textually as an input to simulation programs, and characterize various patterns of development in a concise, non-ambiguous form. This latter capability made it possible to classify inflorescence types using the L-system notation (Prusinkiewicz and Lindenmayer, 1990) and is further employed to characterize architectural tree models in the present paper.



Figure 3. An L-system and its symbolic representation

Biologists often think and describe plant development in terms of cyclic activities of meristems. L-systems do not specify these activities explicitly; one needs to analyze one or more developmental sequences generated by an L-system to fully comprehend the developmental choices and fates of different module types. In order to visualize these fates more directly, Lindenmayer (1975) proposed to represent state transitions generated by an L-system model using cyclic “dependence graphs”. Related techniques for specifying the fates of apices include flowcharts (*e.g.*, Bell, 1994; Kellogg, 2000), finite-state automata, and Markov chains (see Prusinkiewicz 1998 for a review). Unfortunately, all these notions are limited to the description of sequential processes. In biological terms this means that they capture the activities and state transitions of a single module, but they do

not properly describe concurrent aspects of development, such as the simultaneous activities of the main apex and the lateral apices that it has produced.

*Petri nets* and their graphical representation, *Petri net graphs*, are a well-established formalism for describing concurrent processes in computer science (Peterson, 1981). They were first applied to describe plant development by Lück, Raoul and Lück (1983), and further investigated in this context by Lück and Lück (1991) and Barlow (1989, 1994). In this paper we introduce Petri nets as a graphical means of specifying architectural tree models. They can be used in this capacity on their own or treated as a visualization for the operation of the corresponding L-systems. In the latter case, they extend Lindenmayer’s intuitive notion of dependence graphs to parallel processes.

Let us consider a sample event in the life of a plant, for example “A bud becomes a flower.” If the bud is denoted by symbol A and the flower is denoted by symbol K, this event can be captured by the L-system production  $A \rightarrow K$ . This same event can also be described by a Petri net graph shown in Figure 4. This graph consists of four types of objects: circles called *places*, a bar called a *transition*, and two types of directed arcs: from a place to a transition and from a transition to a place. The arcs are oriented to indicate that the leftmost place is the *input* of the transition, and the rightmost place is the *output* of the transition. The input represents the precondition of the event represented by the transition: a bud must exist in order to become a flower. The output represents the postcondition: once the event takes place (a transition fires, in the Petri net terminology), a flower will exist.

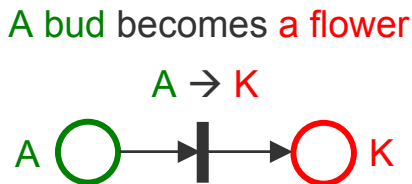


Figure 4. A sentence and its representations as an L-system production and as a Petri net graph

The fact that the pre- and/or post-conditions are satisfied can be indicated by placing dots, called *tokens*, in the appropriate places. The marking, or the assignment of tokens to places, changes as a result of firing transitions during the execution of the Petri net. The execution of the Petri net associated with the sentence “A bud becomes a flower” is shown in Figure 5. The middle stage, with the token placed at the transition, is not a part of the standard Petri net representation, but helps conceptualizing the idea that the execution of a Petri net proceeds by moving tokens between places along arcs.

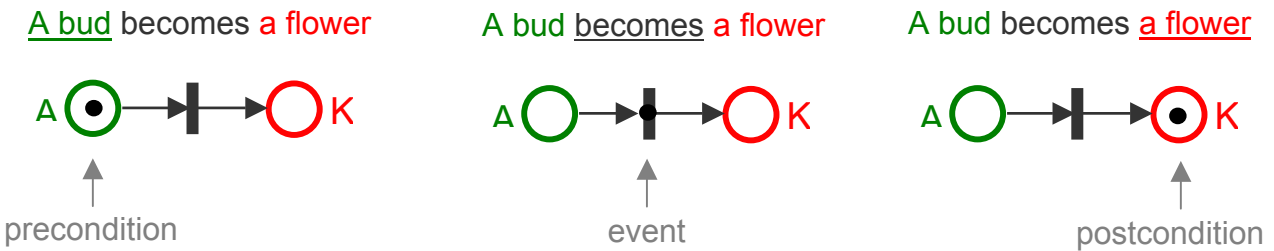


Figure 5. Execution of a marked Petri net

As described by Peterson (1981), a Petri net graph may in general have any number of arcs, provided that they only connect places to transitions and transitions to places. Furthermore, a place in a marked Petri net may contain an arbitrary number of tokens. A transition is enabled if each of

its input places has at least as many tokens as it has arcs to this transition (multiple tokens are needed for multiple input arcs). An enabled transition may fire by removing tokens from all its input places, one per input arc, and creating new tokens that are distributed to the output places, again one per arc. Since a transition may have different numbers of input and output arcs, the firing of a transition may change the total number of tokens present in a marked Petri net.

In the architectural modeling applications:

- places represent types and states of modules,
- transitions represent events in which modules change state, produce new modules, or disappear,
- tokens represent the numbers of modules of each type currently present in the structure.

For example, Figure 6 compares the L-system and developmental sequence discussed earlier (*c.f.* Figures 1 to 3) with the corresponding Petri net graph. The comparison reveals that Petri net graphs visualize the cyclical character of the activities of the apical meristem A more explicitly than L-systems do. On the other hand, Petri net markings provide only a summary account of the number of modules present in the structure, whereas L-system and the resulting developmental sequence also indicates how these modules are connected into a structure. The monopodial developmental pattern captured by both formalisms is characteristic of Corner’s architectural model (Hallé, Oldeman, Tomlinson, 1978).

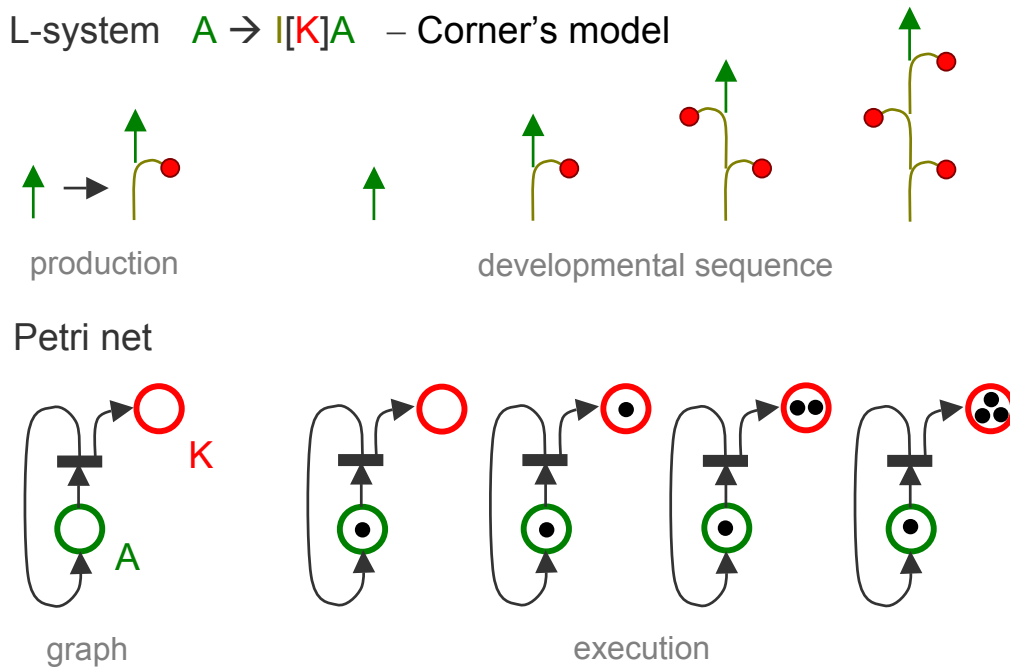


Figure 6. L-system production, developmental sequence, and the corresponding Petri net description of Corner’s architectural model. For the sake of simplicity, internodes are not explicitly represented in this and subsequent Petri net graphs.

To increase the descriptive power of Petri net graphs, we introduce an additional drawing convention. An output arc placed in the middle of a transition indicates the production of a module

in the straight or terminal position with respect to its predecessor. In contrast, an output arc placed off-center indicates the production of a lateral module. For example, this convention makes it possible to distinguish Petri nets that represent Corner's model (Figure 6) and Chamberlain's model (Figure 7). Whereas the axis in Corner's model is formed as a sequence of modules in straight position with respect to each other, the axis in the Chamberlain's model is formed as a sequence of modules in a lateral position.

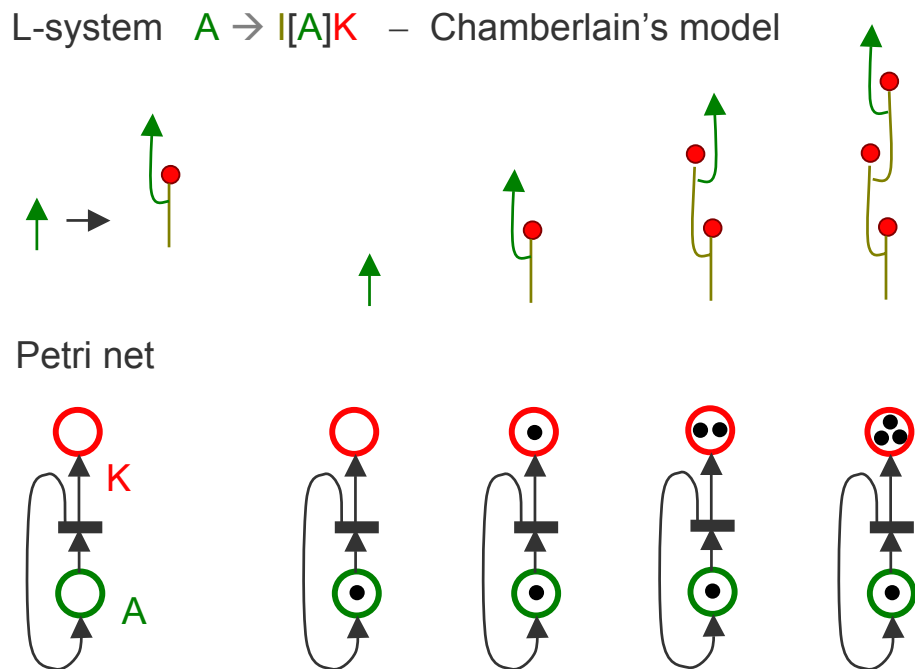


Figure 7. L-system production, developmental sequence, and the corresponding Petri net description of Chamberlain's architectural model

Additional aspects of L-system models and Petri nets appear in the characterization of HO models presented in the next section. The capability of both L-systems and Petri nets to capture parallel aspects of development occurs in the simplest form in Shoute's and Leeuwenberg's models (Figures 15 and 16, respectively). For instance, in Leeuwenberg's model, an apex A produces a branch segment I followed by two lateral apices A that will carry further development, as well as a terminal flower or inflorescence K that will disappear after some time. All apices present in the structure may act simultaneously. This simultaneity is captured by the parallel application of productions in the developmental sequence generated by the L-system, and by the concurrent firing of transitions in the Petri net. (We ignore here the important differences between synchronous application of productions postulated by the formal definition of L-systems and asynchronous firing of transitions postulated by the definition of Petri nets).

As illustrated by Leeuwenberg's model, multiple output arcs from a transition indicate parallel production of modules: new tokens are created to mark all output places. In contrast, multiple arcs that leave a particular place indicate a choice of developmental paths: a token can be used to fire one or another transition, but cannot be used to fire both of them simultaneously. A developmental



choice occurs, for example, in Rauh’s model, in which an apex may produce either a lateral branch or a lateral inflorescence at any developmental step. Rauh’s model is illustrated in Figure 13.

### 3. L-system and Petri net characterizations of HO models

#### 3.1. Preliminaries

The following descriptions present our characterization of the HO architectural models using L-systems and Petri nets. We have focused on the fate of apices and branching patterns, including the position of flowering when sufficient information was available. The L-system models also capture the spatial orientation of branches. On the other hand, the distinction between rhythmic and continuous growth was not taken into account, and models that are similar except for this trait have been grouped together. In addition, we have omitted two HO models (McClure’s and Tomlinson’s). Their original description (Hallé, Oldeman, Tomlinson, 1978) refers to characteristics that are not present in other models (*e.g.*, multiple trunks and stolons), making comparisons difficult.

Our terminology pertinent to the description of branch axes and branching point configurations is summarized in Figure 8. The term axis denotes any linear stem structure from its origin to its extremity (Millet, Bouchard and Edelin, 1999). An axis may include *monopodial* or *sympodial* branching points. A monopodial axis is a sequence of branch segments, each of which extends its predecessor in the terminal position. Sympodial branching indicates that the child axis or axes appear in the lateral position.

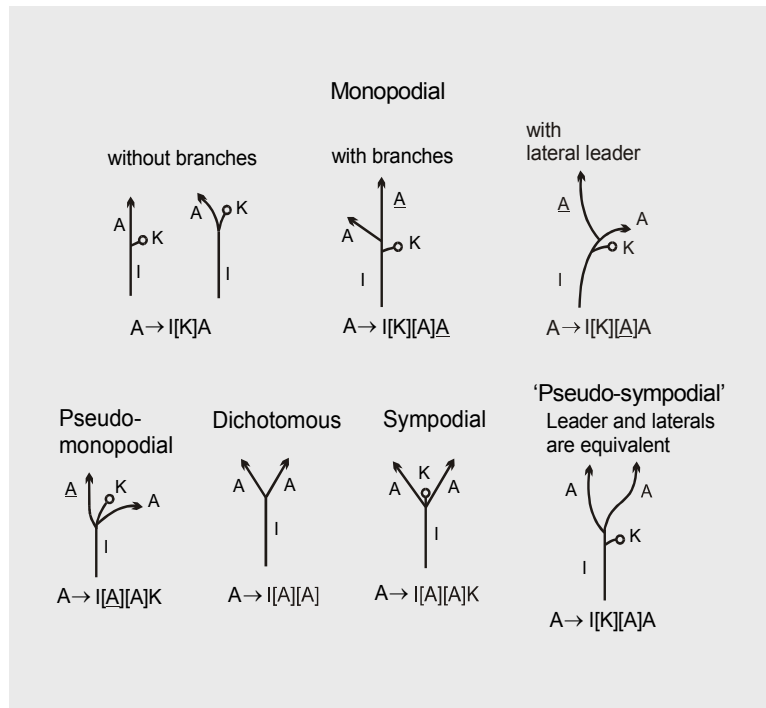


Figure 8. Branching point configurations

If a dominant lateral apex takes over the role of the terminal apex that has aborted, produced a terminal inflorescence, or has become dominated, the sympodial branching produces a *pseudo-monopodial* axis. It is also possible that the development is monopodial but the leading shoot of the axis arises laterally. Another potential variation occurs when the terminal and lateral shoots have similar vigor, forming a *pseudo-sympodium*. The resulting

structure is fundamentally monopodial, but the vigorous branches often form forks. Finally, *dichotomous* branching occurs when the meristem splits forming two new meristems, neither of which is produced in the axil of a leaf.

### 3.2. The models

We have organized our characterization of HO models by beginning with the relatively simple unbranched and monopodial types, discussing sympodial and dichotomous types next, moving on to the models that combine monopodial, pseudo-monopodial and/or sympodial branching in the same tree, and concluding with models in which the formation of axes is related to the gradual reorientation of branch segments.

**Holttum's model.** A tree conforming to this model has only one meristem and therefore it is not branched. The meristem eventually differentiates into an inflorescence. After fruit maturity, the tree dies. Typically, this model is represented by palm-like trees with large leaves.

In the L-system production, the apex  $A$  produces an orthotropic segment  $O$  and a terminal inflorescence  $K$  (Figure 9). The Petri net graph shows an apex  $A$  eventually differentiating into an inflorescence  $K$ . Since the plant is not branched, the apex  $A$  does not recreate itself.

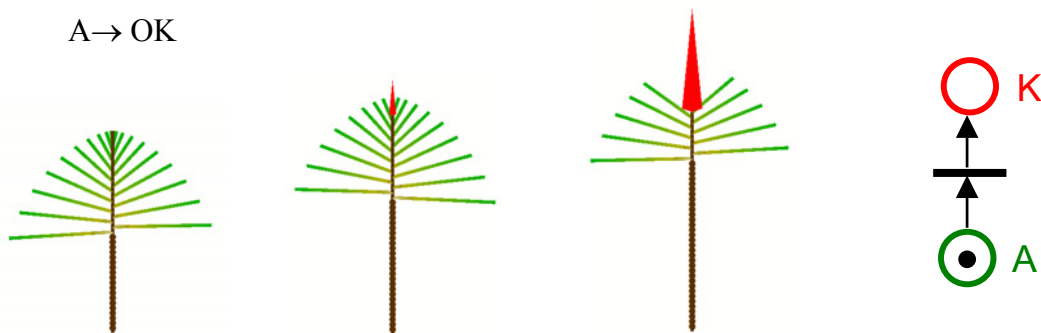


Figure 9. L-system production, three stages of simulated plant development, and Petri net for Holttum's model. The modeled plant approximates *Corypha elata*.

**Corner's model.** A tree conforming to this model has a single, monopodial, orthotropic and non-branching trunk constructed by one vegetative meristem. Inflorescences are axillary and growth is therefore indeterminate. Examples include some palms, tree ferns and female cycads.

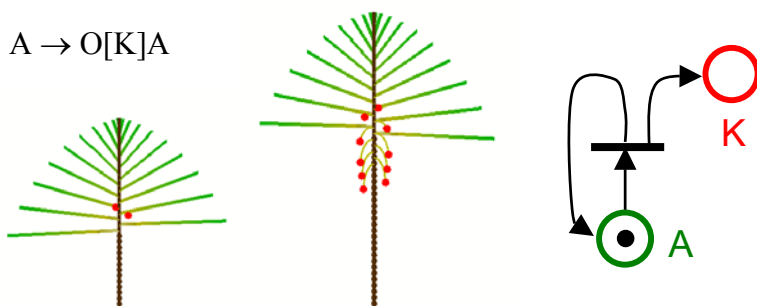


Fig. 10. L-system production, two stages of simulated plant development, and Petri net for Corner's model

L-system and Petri net for Corner's model were used as examples in Section 2 and are also presented in Figure 10. The disappearance (abscission) of old fruits is not explicitly expressed in these and subsequent models.

**Roux and Cook's models.** The trunk is monopodial, and indeterminate. The branches are plagiotropic, usually monopodial and indeterminate with lateral flowers. Growth is continuous in both models and the main difference is that in Cook's model the branches are phyllomorphic (that is, axes are morphologically recognizable as branches but are equivalent to compound leaves). Coffee is a familiar example exemplifying Roux's model. The rubber tree, *Castilla elastica* is an example of Cook's model.

The L-system and Petri net specifications (Figure 11) reflect the single-compound character of this architectural model. The main-axis apex A produces a sequence of orthotropic trunk segments O with lateral apices B. Apices B produce plagiotropic segments P with lateral flowers K.

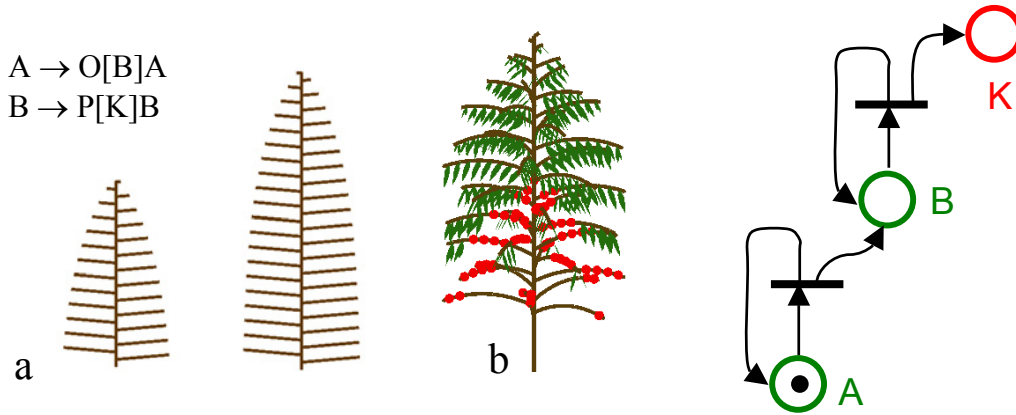


Figure 11. L-system productions, Petri net, and simulations of models of Roux (a) and Cook (b)

**Massart's model.** The growth of the trunk is monopodial, rhythmic, and indeterminate. Main branches are plagiotropic and are produced in whorls. Familiar examples include Norfolk Island pine (*Araucaria heterophylla*) and species of fir.

The L-system and Petri net specifications (Figure 12) reflect the double-compound character of this architectural model. The main-axis apex A produces the trunk as a sequence of orthotropic segments O and the associated whorls of lateral apices B. These apices create plagiotropic first-order branches. Each branch segment P is associated with a lateral flower of inflorescence K or with apex C that will create a second-order branch. The second-order branches consist of plagiotropic segments P with lateral flowers K.

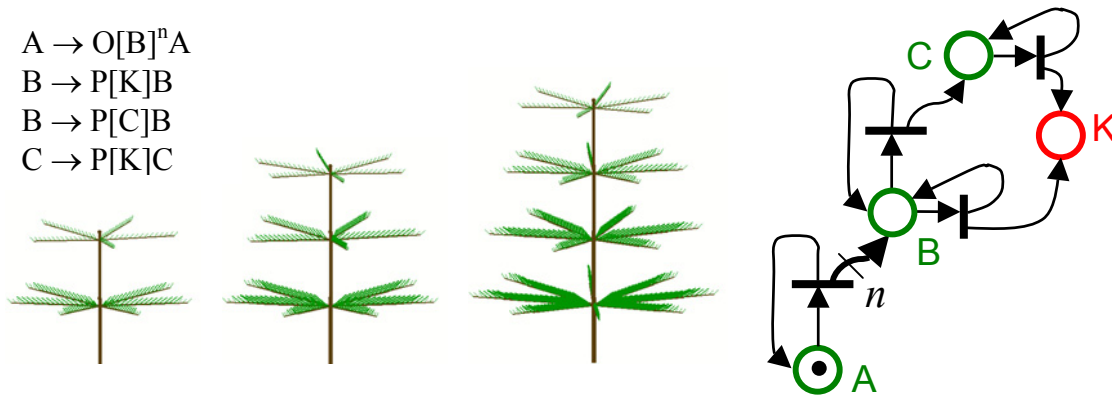


Figure 12. L-system productions, three stages of simulated plant development and Petri net for Massart's model

**Rauh and Attim's models.** The trunk is monopodial. Branches are orthotropic and morphogenetically equivalent to the trunk. Flowering is always lateral. Growth is rhythmic in Rauh's model and more or less continuous in Attim's model. Temperate examples of Rauh's model include ash, oak, pine, maple, and larch. Attim's model is represented by mangrove.

In the L-system, apex A produces an orthotropic segment with the associated flower K, or recreates itself in both the terminal or lateral positions (Figure 13). These developmental choices are also represented in the Petri net.

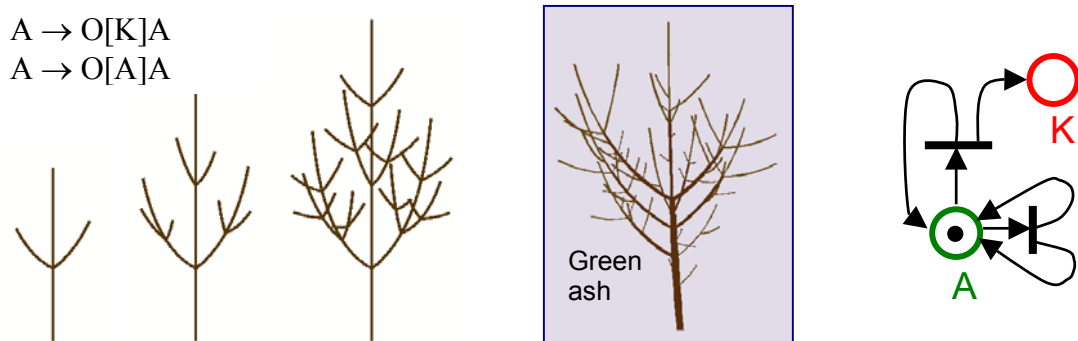


Figure 13. L-system productions, three stages of simulated development, and Petri net for Rauh and Attim's models. Inset shows a simulated green ash tree, which is a representative of Rauh's model.

**Chamberlain's model.** The main axis is an orthotropic pseudo-monopodium. The development of each sympodial unit is terminated by the formation of an inflorescence. Examples include some cycads and the common indoor plant *Philodendron selloum*.

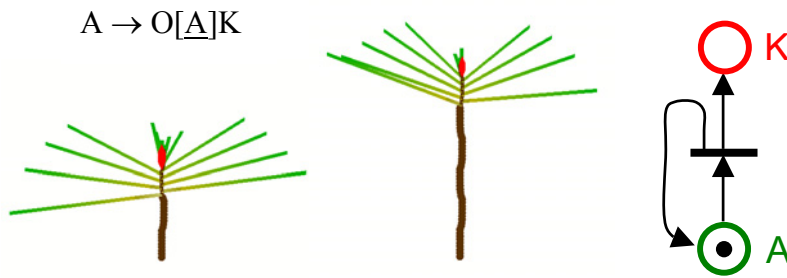
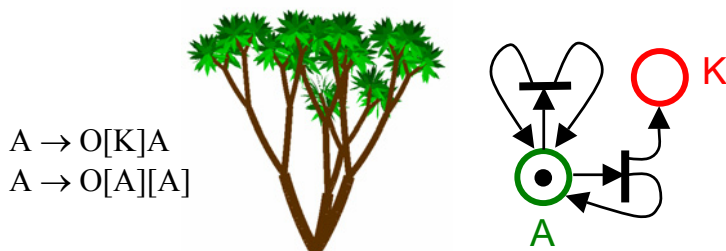


Figure 14. L-system production, two stages of simulated development, and Petri net for Chamberlain's model

The L-system and Petri net for Chamberlain's model were used as examples in Section 2 and are also presented in Figure 14.

**Shoute's model.** The tree has one or more orthotropic or obliquely oriented trunks. After the formation of a branch segment, a meristem splits by equal dichotomy to form two new branches.

Flowers are always lateral. The model is exhibited by Doum palm and the extinct *Lepidodendron*.



The L-system and Petri net specifications of this model reflect the developmental choices of an apex, which may produce an orthotropic segment with a lateral flower or divide and recreate itself in two lateral positions (Figure 15).

**Leeuwenberg's model.** The tree consists of orthotropic modules forming a branched sympodium with no distinct main stem. Each module bears a terminal inflorescence. Examples include sumac, many lilacs, and dogwoods.

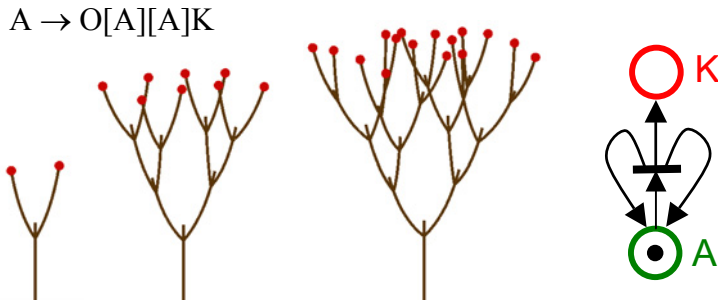


Figure 16. L-system production, three stages of simulated development, and Petri net for Leeuwenberg's model

In the L-system, apex A produces an orthotropic segment O with a terminal inflorescence K, and recreates itself in two lateral positions (Figure 16). The activities of the apex are also clearly visualized by the Petri net.

**Scarrone and Stone's models.** The trunk is monopodial, indeterminate and bears orthotropic branches. The branches ramify sympodially by substitution of the terminal inflorescence. The main difference between the models is that growth is rhythmic in Scarrone's model and continuous in Stone's model. Examples include horsechestnut (Scarrone) and species of *Pandamus* (Stone).

The L-system and Petri net graph indicate that Scarrone and Stone's models can be viewed formally as compositions of Corner and Leeuwenberg's models (Figure 17). Corner's model specifies the trunk as a monopodial structure bearing lateral organs, which in this case are entire branches rather than inflorescences. Leeuwenberg's model specifies the structure of the branches.

**Petit's model.** The monopodial, orthotropic trunk grows continuously and produces sympodial

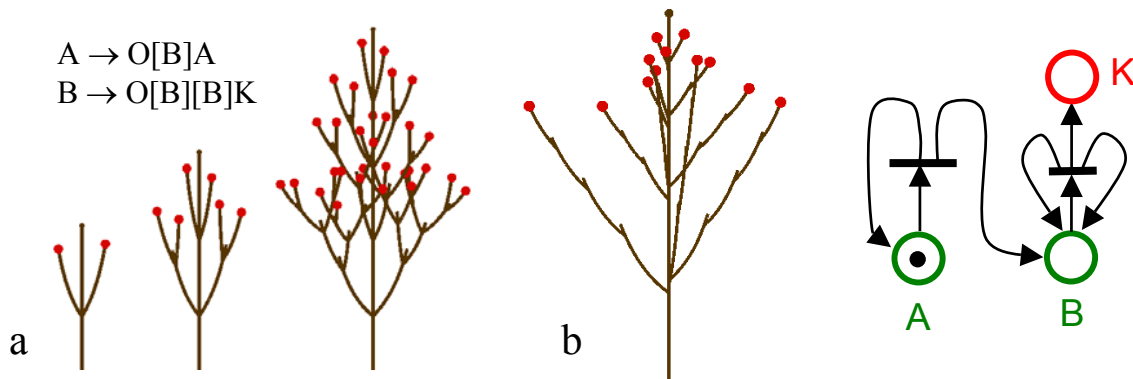
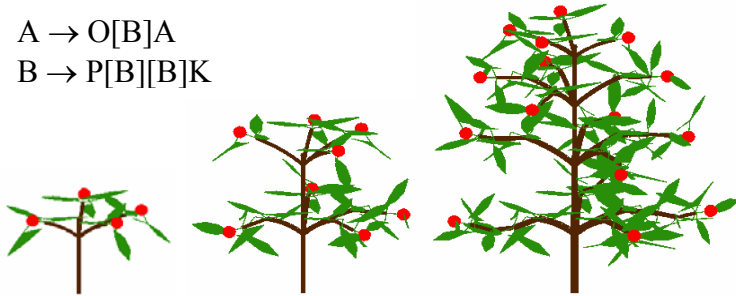


Figure 17. L-system for Scarrone and Stone's models, three stages of simulated development according to Scarrone's model (a, *Biddens* sp.), a structure generated using Stone's model (b, *Pandamus tectorius*), and Petri net for both models

plagiotropic branches. Inflorescences are terminal. Examples include *Morinda citrifolia* and cotton.

$A \rightarrow O[B]A$   
 $B \rightarrow P[B][B]K$



The L-system for Petit's model differs from that of Scarrone and Stone's models only by the plagiotropic, as opposed to orthotropic, orientation of the lateral branches (Figure 18). As branch orientation is not reflected in our Petri net graphs, the Petri net is the same for all three models.

Figure 18. L-system productions and three stages simulated development for Petit's model. Petri net is the same as for Scarrone and Stone's models

**Fagerlind's model.** The monopodial trunk has whorled tiers of plagiotropic branches that are sympodial by apposition. Renewal shoots arise where the plagiotropic segment turns up and eventually forms a terminal inflorescence. An example is *Magnolia grandiflora*.

In the L-system, the main-axis apex A produces a sequence of orthotropic segments O with the associated whorls of terminal buds B. Each B produces a plagiotropic branch segment B and recreates itself in two lateral positions, whereas the apex in the terminal position changes its state to C, to produce a relatively short orthotropic segment with a terminal inflorescence (Figure 19). The activities and changes of state of apices are clearly visualized by the Petri net.

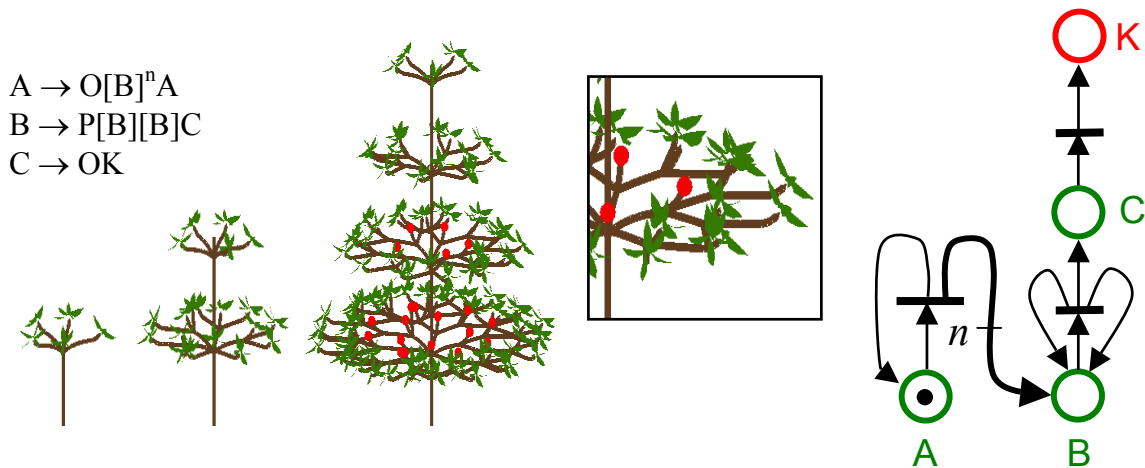


Figure 19. L-system productions, three stages of simulated development, and Petri net for Fagerlind's model. The inset shows a close-up of the branching pattern.

**Aubréville's model.** The trunk is monopodial, producing whorls of plagiotropic branches that are sympodial by apposition. Each renewal shoot has a long plagiotropic basal segment followed by an indeterminate orthotropic segment. The terminal meristem of each segment remains active to produce successive clusters of leaves with lateral flowers. Well-studied examples include species of *Terminalia*.

The L-system and Petri net for Aubréville's model reveal that it formally differs from Fagerlind's model only in the fate of the apex C (Figure 20). In Aubréville's model the orthotropic segment

that terminates a plagiotropic branch is indeterminate and bears lateral flowers, whereas in Fagerlind's model it is determinate and bears a terminal inflorescence.

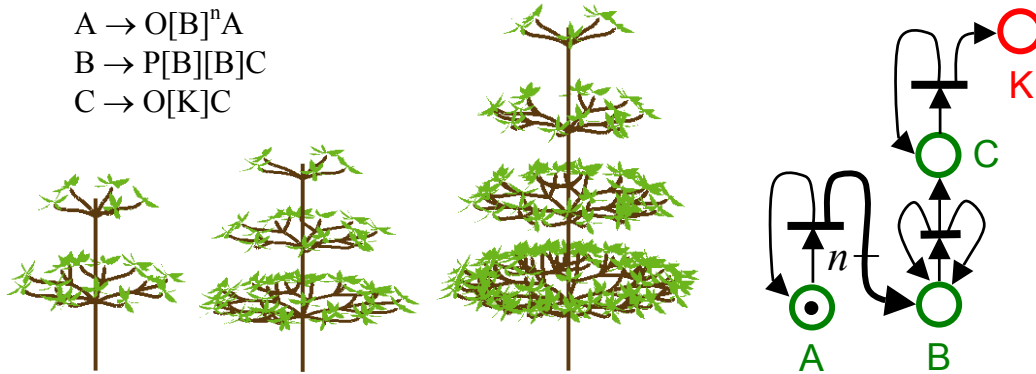


Figure 20. L-system productions, three stages of simulated development, and Petri net for Aubréville's model

**Koriba's model.** A pseudo-monopodial trunk is formed by a sequence of branches that are sympodial by substitution of the terminal inflorescence. Although all branches are initially equivalent, one branch becomes more erect and dominant and forms the relay axis. Examples include sandbox tree and species of *Catalpa*.

The L-system specifies that an apex  $A$  produces an orthotropic segment  $O$  terminated by an

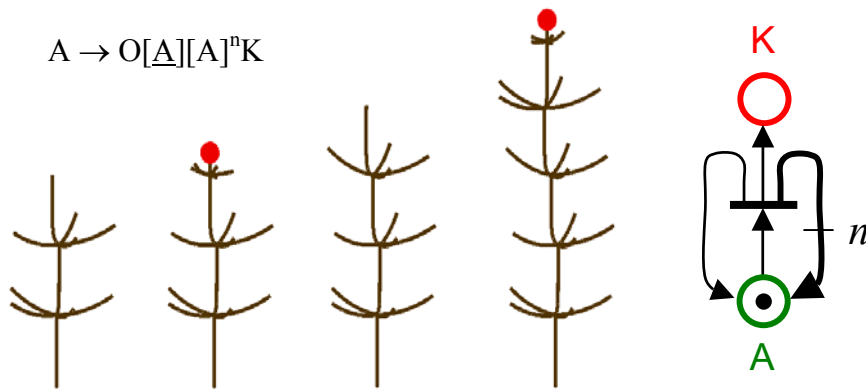


Figure 21. L-system production, four stages of simulated development, and Petri net for Koriba's model.

inflorescence  $K$  and recreates itself in a whorl of  $n+1$  lateral apices (Figure 21). One of these apices is dominant (indicated by  $\underline{A}$ ). The creation of terminal inflorescence and creation of  $n+1$  non-equivalent lateral apices are also captured by the Petri net. The bold arc with the associated label  $n$  is a shorthand notation for a set of  $n$  arcs.

**Prévost's model.** A pseudo-monopodial trunk is formed by a sequence of proleptic, subdistal branches. The branches arise distally, are sylleptic and plagiotropic by substitution of the terminal inflorescence. This model is common in the genus *Cordia*.

In the L-system, the trunk apex  $A$  produces an orthotropic segment  $O$  and recreates itself as a dominant subdistal lateral apex  $\underline{A}$  (Figure 22). The development of segment  $O$  further continues by addition of a distal segment  $O'$  that support terminal inflorescence  $K$  and a whorl of lateral apices  $B$ . Each apex  $B$  produces a plagiotropic sympodial branch, with flowers  $K$  terminating the

individual branch segments. Formally, the structure of branches is the same as in Petit's model. The Petri net captures the fate of apices, but does not provide details regarding their dominance relations and relative position and orientation of branches.

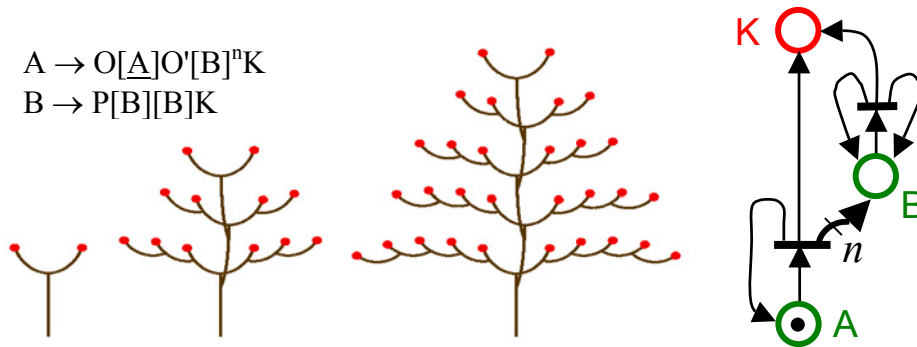


Figure 22. L-system productions, three stages of simulated development, and Petri net for Prévost's model

**Nozeran's model.** The trunk is pseudo-monopodial. The apex of the trunk aborts and a tier of sylleptic, plagiotropic branches forms distally. A proleptic, subdistal orthotropic shoot forms the next relay axis. Flowering is often lateral but may be terminal. An example is cocoa (*Theobroma cacao*).

The L-system and Petri net specify the development of the trunk and branches in a manner similar to Prévost's model, except that apices A and B abort (as indicated by X) instead of producing terminal flowers or inflorescences (Figure 23). In Nozeran's model, flowers K are produced in a lateral position by apices B, as a developmental alternative to branching.

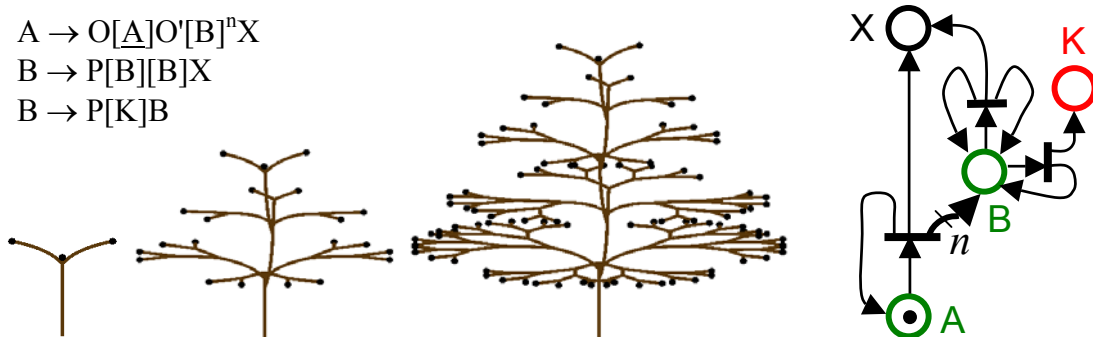


Figure 23. L-system productions, three stages of simulated development, and Petri net for Nozeran's model

**Mangenot's model.** A pseudo-monopodial main axis is built by the superposition of lateral shoots formed on the curve of parent shoots with mixed orientation. The distal plagiotropic segment of each shoot becomes a branch. One of the best-known temperate examples is highbush blueberry, *Vaccinium corymbosum*.



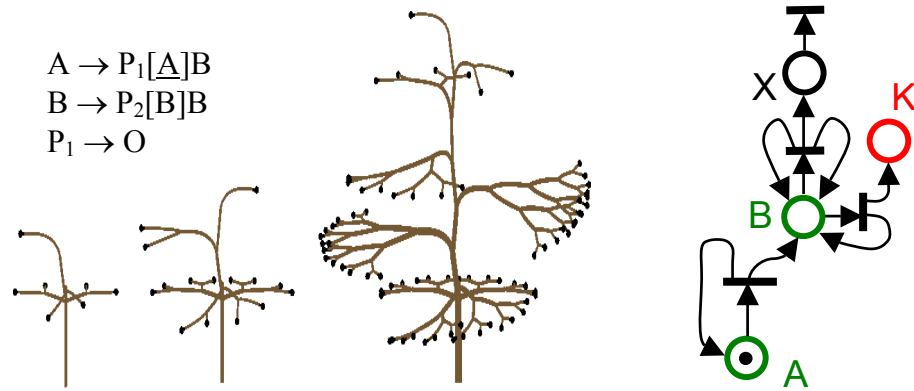


Figure 24. L-system productions, three stages of simulated development, and Petri net for Mangenot's model

In the L-system, the apex  $A$  produces an orthotropic segment and recreates itself in a dominant lateral position ( $\underline{A}$ ). Meanwhile, the terminal apex changes its state to  $B$ , and formally follows the same path of development as the lateral apices in Nozeran's model (Figure 24). The similarity between Nozeran's and Mangenot's models is further reflected in the similarity of their respective Petri nets.

**Champagnat's model.** As in Mangenot's model, pseudo-monopodial axes in Champagnat's model are built by the superposition of lateral shoots formed on the curve of parent shoots with mixed orientation. The distal portion is initially orthotropic, but becomes pendulous under its own weight, which creates a plagiotropic appearance. A single main stem is rarely evident. Temperate examples include species of *Rosa*, *Sambucus*, and *Rubus*.



Figure 25. L-system productions, four stages of simulated development, and Petri net for Champagnat's model. The arrows in the first drawing indicate the direction of shoot reorientation.

The L-system captures the essence of Champagnat's model by distinguishing two types of orthotropic branch segments, denoted  $O_1$  and  $O_2$  (Figure 25). The apex  $A$  produces an orthotropic axis segment  $O_1$  before changing state to  $B$ . An apex  $B$  produces a branching structure made of segments  $O_2$ . These segments are initially orthotropic, but gradually change their orientation to

plagiotropic. Meanwhile, the apex  $A$  recreates itself in the dominant lateral position ( $A$ ) at the boundary between segments  $O_1$  and  $O_2$ . This leads to the production of a pseudo-monopodial axis formed by a sequence of segments  $O_1$ . The Petri net shown in Figure 25 is a comparatively less useful representation of Champagnat’s model, as it does not capture the reorientation of branch segments. On the other hand, it clearly depicts the fate of the apices.

**Troll’s model.** Branch segments initially are plagiotropic; the tree grows in height because the basal portions become secondarily erect. Axis development is sympodial and renewal shoots arise at the bend of parent shoots. The distal part becomes a branch that may or may not be determinate.

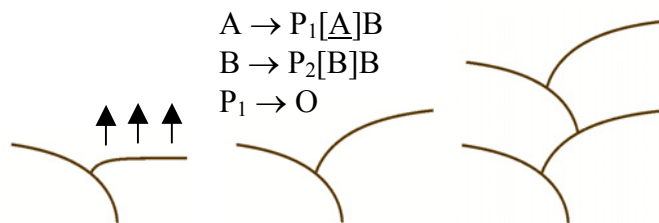


Figure 26. L-system and simulated development illustrating Troll’s model. The arrows in the first drawing indicate the direction of shoot reorientation.

Temperate examples include species of *Ulmus*, *Celtis* and *Prunus*.

This L-system (Figure 26) reverses the axis formation in Champagnat’s model: initially all branch segments are now plagiotropic, and proximal parts become secondarily orthotropic. Since our Petri net specifications do not capture branch (re)orientation, the Petri net for Troll’s model is the same as for Champagnat’s model.

#### 4. Discussion

In this paper, we have proposed L-systems and Petri nets as a formal method for characterizing HO architectural tree models. Both formalisms help understand the essence of these models by providing clear, concise, and unambiguous descriptions. L-systems and Petri nets also facilitate comparisons between models (for example, Prévost’s vs. Nozeran’s model and Champagnat vs. Troll’s model), and make it possible to describe more complex models as a composition of simpler ones (*c.f.* our description of Scarrone and Stone’s models in terms of Corner and Leeuwenberg’s models). In addition, the L-systems that characterize the architectural models may serve as a foundation for constructing simulation models of specific trees.

We have introduced simple extensions of both formalisms to increase their expressive power. In the case of L-systems, we indicate dominant apices by underscoring symbols that represent them. In the case of Petri nets, we use a simple drawing convention to distinguish between the terminal and lateral apices. A comparison of both formalisms indicates that L-systems provide a more complete characterization of the architectural models, since they capture the configuration of the branching points and the dominance relation between the apices. On the other hand, Petri nets provide a more intuitive representation of the fate of apices.

Although both L-systems and Petri nets capture the simultaneous development of different parts of a growing organism, in theory they treat simultaneity in a very different manner. According to the formal definition (Lindenmayer, 1968; Prusinkiewicz and Lindenmayer, 1990), L-systems operate in discrete time intervals, with all modules being transformed in synchronous steps. In contrast, Petri nets operate asynchronously, in concurrent events that may take place at any instant of continuous time. A careful analysis of these differences is an interesting problem open for further research. Its solution may lead to a better understanding of the relation between L-systems and

Petri nets in the context of biological applications, and serve as the basis for formally characterizing the differences between continuous and rhythmic growth.

Since the seminal work by Hallé and Oldeman (1970), new concepts such as the architectural unit, intercalation, and tree metamorphosis have been introduced to architectural tree analysis. They provide the conceptual framework and vocabulary for increasingly complete and accurate characterization of tree architectures (see review by Edelin, Moulia and Tabourel, 1995). A formal characterization of these new concepts is also an interesting problem open for further study.

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