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Modeling of spatial structure and development of plants: a review

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Abstract

Developmental models of plant structure capture the spatial arrangement of plant components and their development over time. Simulation results can be presented as schematic or realistic images of plants, and computer animations of developmental processes. The methods of model construction combine a variety of mathematical notions and techniques, from regression analysis and function fitting to Markov processes and Lindenmayer systems (L-systems). This paper presents an overview of the wide range of spatial model categories, including both empirical and causal (mechanistic) models. An emphasis is put on L-systems and their extensions, viewed as a unifying framework for spatial model construction. © 1998 Elsevier Science B.V.

Keywords: Plant; Lindenmayer system; Markov process; Simulation

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1. Introduction

Mathematical models in botany correspond to various levels of plant organization. In this paper, we focus on *spatial organization* of individual plants. A plant is viewed as a configuration of discrete constructional units or *modules*, which develop over time. Modules represent repeating components of plant structure, such as flowers, leaves, and internodes, or groupings of these components, such as metamers (single internodes with an associated leaf and lateral bud) and branches (Harper and Bell, 1979; Waller and Steingraeber, 1985; Porter, 1989; Bell, 1991). [1] The modeling task is focused on the description of plant structure and development as the integration of the development and functioning of individual modules.

As with other models of nature, computer models of plant structure and development can be divided into *empirical* (descriptive) or *causal* (mechanistic, physiologically based). The distinction between these two classes is described authoritatively by Thornley and Johnson (1990). Summarizing their point, empirical models represent the acquired data in a more convenient form, and are useful in making practical predictions based on the interpolation of these data. In contrast, mechanistic models follow the traditional reductionist method of the natural sciences, provide explanations and responses that integrate the underlying mechanisms, and contribute to our *understanding* of the processes under study.

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[1] A different meaning of the term ‘module’ is also found in the literature (Hallé, 1986; Barlow, 1989; Room et al., 1994).

The distinction between empirical and causal models parallels the relation between the *top–down (analytic)* and *bottom–up (synthetic)* approaches to modeling. In the top–down case, the construction of the model is based on the analysis of empirical data. In the bottom–up case, the model synthesizes known or postulated mechanisms of development. The emphasis is on the properties of the whole model that *emerge* from the interactions between individual components. In the most abstract form, construction of models with emergent properties crosses the line dividing biology and artificial life (Langton, 1988; Taylor, 1992).

The spatial modeling of plants is a highly interdisciplinary area. Botany and applied plant sciences are at the root of many approaches to model construction, and are an important domain for model applications. Nevertheless, many convincing plant models were created within computer graphics, with visual effect in mind (Bloomenthal, 1985; Reeves and Blau, 1985; Weber and Penn, 1995; Deussen and Lintermann, 1997). The underlying modeling and visualization techniques are important from a biological perspective, because realistic presentation adds credibility to the models and facilitates their validation based on comparisons with nature (Prusinkiewicz, 1997a). Computer graphics has also contributed methods for calculating light reflectance and distribution in simulated environments (Foley et al., 1990). These methods are important in the modeling of plants taking into account their local light conditions (Section 5.4.) and in the application of spatial models to remote sensing (Borel et al., 1991; Goel et al., 1991; Lewis and Muller, 1992; Govaerts, 1995).

Lindenmayer systems (*L-systems*) are another interdisciplinary component of architectural plant modeling. They originated within theoretical biology (Lindenmayer, 1968) and were extensively studied by mathematicians and computer scientists (Herman and Rozenberg, 1975) before they became an effective modeling tool (Prusinkiewicz and Lindenmayer, 1990). A historical perspective of L-system applications was presented by Prusinkiewicz (1997b). L-systems belong to the class of mathematical formalisms known as rewriting systems or formal grammars (Salomaa, 1973). To a biologist they offer a conceptual framework for constructing developmental plant models and expressing them in special-purpose *modeling languages* (Prusinkiewicz and Lindenmayer, 1990; Hanan, 1992; Kurth, 1994). The use of a modeling language makes it possible to simulate the development of a variety of organisms, from algae to herbaceous plants to trees, using the same simulation program with different input files. This approach has the following benefits.

- The programming effort needed to develop L-system models of specific plants is significantly reduced in comparison to the effort needed to implement the same models in a general-purpose programming language, such as Fortran or C. [2]
- The models can be easily modified during experimentation. These modifications are not limited to the values of numerical parameters, but may also involve fundamental changes in model definition and operation.

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[2] The programming effort needed to develop specific models may also be reduced using appropriate software libraries, shared between various models. Such libraries have been created within the framework of L-systems (Guzy, 1995; Hammel, 1996) and outside of it (Perttunen et al., 1996).

- The L-system language makes it possible to document models in a compact and precise manner (for example, in publications).
- The expression of models in the same language facilitates their comparisons.

Reflecting these advantages, all models illustrating this paper have been created or reproduced from the original publications using the L-system-based simulation program cpfg, included in the Virtual Plant Laboratory (Prusinkiewicz, 1996).

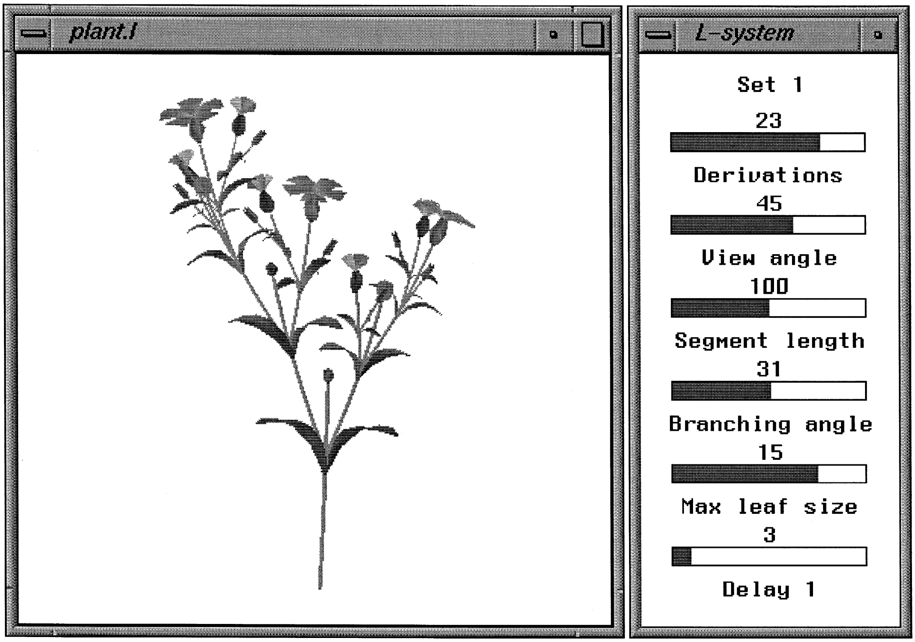
2. Data acquisition

2.1. Qualitative description of plant architecture

Data acquisition is the starting point for constructing all plant models, yet the type of data used may vary greatly. On the most qualitative end of the spectrum, one finds the *architectural unit*, introduced by Edelin (1977) to characterize plants within the conceptual framework of *architectural models* proposed by Hallé et al. (1978). The morphological characteristics incorporated into an architectural unit can be directly observed or estimated without an extensive use of measuring instruments. They include, among others: the orientation of branches (e.g. orthotropic or plagiotropic), type of branching (monopodial or sympodial), persistence of branches (indefinite, long or short), degree of lateral shoot development as a function of their position on the mother branch (acrotony, mesotony or basitony), type of meristematic activity (rhythmic or continuous), number of internodes per growth unit, leaf arrangement (phyllotaxis), and position of reproductive organs on the branches (terminal or lateral). An authoritative description of these and other notions used to specify plant architecture is presented by Bell (1991) and Caraglio and Barthélémy (1997). The architectural unit is a set of these characteristics, given for all branch orders. Examples of architectural description of specific trees in terms of architectural units are presented by Atger and Edelin (1995) and Prosperi et al. (1995).

Plant architecture is a dynamic concept, in the sense that the observed structural features reflect plant development over time. As stated by Hallé et al. (1978), ‘‘The idea of a form implicitly contains also the history of such a form.’’ Correspondingly, the architectural unit may be viewed as a sequence of branch types created over time, rather than merely a set of branch types. ‘‘In this sequence, leading from axis 1 to the ultimate axes following the specific branching pattern, each branch is the expression of a particular state of meristematic activity and the branch series as a whole can be considered to be tracking the overall activity’’ (Barthélémy et al., 1991).

By itself, qualitative characterization is insufficient to construct a spatial model of a plant. Nevertheless, interactive computer graphics makes it possible to incorporate the lengths of internodes, the magnitudes of branching angles, and other quantitative aspects into a model, even if these characteristics were not explicitly measured. The observed architectural features form the basis of a model, in which the quantitative aspects are parametrized. The parameter values are manipulated interactively to achieve proper appearance of the plant. This technique can be traced to the first computer tree models



Set 1
23
Derivations
45
View angle
100
Segment length
31
Branching angle
15
Max leaf size
3
Delay 1

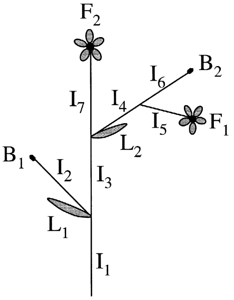
Fig. 1. Example of a plant model (*Lychnis coronaria*) based on a qualitative description of the architecture (Robinson, 1986). Parameter values have been set interactively using the control panel on the right to achieve proper appearance of the visual model.

devised by Honda (1971). It was also applied by Prusinkiewicz and Lindenmayer (1990) to model various types of inflorescence (Fig. 1). An extended graphical interface, which makes it possible to manipulate parameters of the model as well as its underlying topological structure using graphical operations on the screen, has been recently proposed by Deussen and Lintermann (1997).

2.2. Description of plant topology

A description of a plant in terms of its architectural unit assumes a generalization performed before the observed features are recorded. These features do not characterize specific branches of a specific plant, but represent general characteristics of branches of a given order in any specimen of a given species.

Plant maps (McClelland, 1916; Constable, 1991) can be considered the first step towards characterizing the structure of particular plants. This description captures the branching *topology*, that is the aspects of the arrangement of branches, organs, and other features that do not depend on the structure's geometry (the lengths of internodes and the magnitudes of the branching angles). Plant maps can be recorded using various notations. For example, Hanan and Room (1996) adapted for this purpose the bracketed string notation introduced by Lindenmayer (1968). The essence of this notation is illustrated in Fig. 2. A different notation was described by Rey et al. (1997).



$I_1[L_1][I_2B_1]I_3[L_2][I_4[I_5F_1]I_6B_2]I_7F_2$

Fig. 2. A hypothetical branching structure and the description of its topology using the bracketed string notation. I: internode, L: leaf, B: bud, F: flower.

A refinement of the topological description of plants has been proposed by Godin and Caraglio (1996). Their formalism, called *multiscale tree graphs,* makes it possible to specify plant topology at different scales and levels of detail, and incorporate temporal aspects into the descriptions. Multiscale tree graphs form the basis of a coding language implemented in AMAPmod, an interactive program for analyzing the topological structure of plants (Godin et al., 1997a,b). The need for multiscale representation of plant architecture is also discussed by Remphrey and Prusinkiewicz (1997).

2.3. Measurement of plant geometry

The processes of plant measurement and modeling influence each other. The initial, hypothetical architectural model guides the first phase of data acquisition. Shortcomings of the model that results from the incorporation of these data reveal the areas in which more data are needed. The cyclic process of model refinement continues until the desired characteristics of the model have been reached. The choice of features to be measured depends on the nature of the model (empirical or causal), its desired accuracy, spatial scale, level of detail, time scope, and resolution (Remphrey and Prusinkiewicz, 1997).

Geometric features of small plants or plant parts can be measured using calipers and a protractor. Unfortunately, this process is slow and costly. A faster method is to use a three-dimensional digitizer, which records positions of selected features (for example, the nodes of the branching structure) pointed to by the operator using a hand-held probe. Digitizers used in the practice of plant measurement operate on a variety of principles (Moulia and Sinoquet, 1993), including the measurement of the angles between the joints of an articulated arm (Lang, 1990), propagation time of (ultra)sound between the probe and a set of microphones (Sinoquet et al., 1991; Room et al., 1996), and the distribution of a magnetic field around the probe (Sinoquet and Rivet, 1997; Smith and Curtis, 1996). Proper software makes it possible to enter measured data directly into a database, complement them with additional information identifying the feature being measured (e.g. position of a node, leaf, flower, or fruit), and schematically represent the measured plant on the computer screen for visual feedback and error checking (Hanan and Room, 1996, 1997). The application of three-dimensional digitizers is limited by the volume within which the measuring devices operate (currently not exceeding several cubic meters), and the participation of a human operator. Circumventing the volume limitation, Ivanov et al. (1994, 1995) used images obtained by a pair of cameras (stereovision) to collect structural data of maize plants in a field. This technique is limited to the top elements of the canopy (visible from both cameras) and, at present, requires manual identification and digitization of matching leaves in both images by an operator. The elimination of the operator's involvement using computer vision techniques is an open research problem.

Models of plant development are based on the observation and measurement of plants over time. The frequency of these actions may vary greatly. For example, an interval of 1 min may be appropriate for time-lapse photography of opening flowers. On the other hand, developmental models of trees and shrubs may be based on measurements made at yearly intervals (Remphrey et al., 1983).

At a conceptual level, methods for expressing plant geometry at different levels of spatial detail are needed as a natural extension of the multiscale tree graphs for representing plant topology. The general problem of representing geometric objects at different levels of spatial detail (multiresolution representations) was addressed in computer graphics by Hoppe (1997), among others, but the proposed solutions have not yet been adapted to highly branching plant structures. A related issue is the reconciliation of numerical data at different levels of resolution (for example, the measured length of an entire branch with the sum of the length of the internodes), which may exhibit inconsistencies due to numerical errors. This issue has not yet been considered in the literature.

3. Empirical models of plant structure

3.1. Reconstruction models

Reconstruction of three-dimensional plant structure based directly on the raw data obtained by plant measurement can be considered the extreme case of empirical plant modeling. The resulting *reconstruction models* can be created dynamically, during the measurement process (Hanan and Room, 1997), or after all the measurements have been completed (Smith et al., 1992; Sinoquet and Rivet, 1997; Smith and Curtis, 1996; Godin et al., 1997a,b). Smith et al. (1992, 1994) indicate the value of reconstruction models in the analysis of spatial distribution of plant organs in the plant canopy (fruit in kiwifruit vines). Reconstruction models may also be useful in such applications as computer-assisted landscape and garden design, inclusion in plant registries, and advertising of plant varieties to customers (C. Davidson, personal communication). Recent effort towards standardization of the Virtual Reality Modeling Language (VRML) for representing and transferring three-dimensional models over the Internet (Hartman and Wernecke, 1996) may popularize this type of models. Nevertheless, reconstruction models have several drawbacks:

- they incorporate a large amount of raw data, and consequently are represented by relatively large data files;
- they represent features of a single plant specimen and cannot be manipulated to obtain other representatives of the same species;
- they have no predictive value (although they may assist in data analysis leading to predictions).

3.2. *Curve fitting*

Statistical methods of data analysis (regression analysis in particular) make it possible to overcome the drawbacks of reconstruction models by fitting empirical curves to the measured data. For instance, this approach was used by Remphrey and Powell (1984, 1985, 1987) to create *statistical reconstruction models* of *Larix laricina* samplings. Further examples of statistical plant analysis at the structural level are presented by Davidson and Remphrey (1990, 1994) and Remphrey and Davidson (1994). As categorized by Remphrey and Prusinkiewicz (1997), a spatial model constructed by curve fitting may be *deterministic* (representing the best fit, and ignoring the variance of parameters) or *stochastic* (allowing for the variation of the parameters values consistent with their distribution obtained through statistical analysis). For early examples of the construction of stochastic models, see Nishida (1980) and de Reffye (1981a,b, 1983).

3.3. *Paracladial relationships*

An interesting aspect of empirical model construction is the unraveling of similarities between an entire branch and its parts. To capture these similarities at the topological level, Frijters and Lindenmayer (1976) used the notion of a *paracladium*. This notion was originally introduced by Troll (1964), who described an inflorescence as ‘‘a system consisting of the main florescence and of paracladia. Paracladia are branches which repeat the florescence of the main axis and which on their turn can give rise to paracladia on their own’’ (Frijters and Lindenmayer, 1976). For example, the arrangement of the second-order branches along the axis of a first-order branch of a lilac inflorescence (*Syringa vulgaris*) approximately repeats the arrangement of the first-order branches on the main axis of the same inflorescence. Thus, each branch can be considered a small version—a paracladium—of the entire structure. The presence of paracladia is closely related to the process of plant development. ‘‘The ‘program’ which is responsible for the development of the main axis (the mother branch) is followed repeatedly in each of the paracladia. Furthermore, since the main axis can produce paracladia, we must assume that paracladia of first order can in turn give rise to paracladia of second order and so forth’’ (Lindenmayer, 1977).

Studying compound structures corresponding to this description, Frijters and Lindenmayer (1976) observed that the number of internodes in the daughter branch (y in Fig. 3a) and in the overhanging part of the mother branch (x) are often related by a linear function, which they called a *uniform paracladial relationship*. For example, in Fig. 3b,

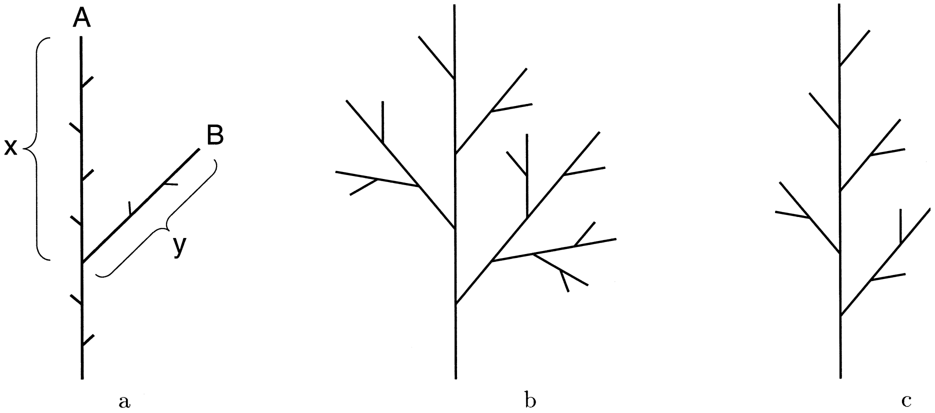


Fig. 3. Definition of the overhanging part x of mother branch A with respect to the daughter branch B (a), and schematic branching structures with paracladial formulas $y = x$ (b) and $y = 0.5x$ (c). Based on the works of Frijters and Lindenmayer (1976) and Lindenmayer (1977).

the number of internodes in each lateral branch is equal to the number of internodes in the entire overhanging part of the main axis ($y = x$). On the other hand, in Fig. 3c, each (even-numbered) branch has one half the number of internodes found in the overhanging part of the main axis ($y = 0.5x$). A structure that exhibits a linear paracladial relationship can be modeled in a particularly concise manner, because the topology of each branch is determined by its position on the mother branch. Nonlinear paracladial relationships are also possible, but have not yet been investigated.

3.4. *Self-similarity*

The repetitive hierarchical organization may be reflected not only in the topology of a branching structure, but also in its geometry. Specifically, we say that a geometric object (such as a branching structure) is *self-similar* if its parts are geometrically similar to the whole. Self-similarity is the distinctive feature of *fractals* (Mandelbrot, 1982; Falconer, 1990). A key theorem characterizing self-similar objects has been obtained by Hutchinson (1981). It states that if an object can be decomposed into a finite number of reduced copies of itself, it is completely described by the set of transformations that map the whole object onto its parts. This set of transformations is called an *Iterated Function System* or *IFS* (Barnsley and Demko, 1985) and can be used to reconstruct the original object using a number of computational methods; for example, see Hart and DeFanti (1991) and Hepting et al. (1991). Barnsley and Demko (1985) extended Hutchinson's result to objects that are only approximately self-similar, and gave it the name of *collage theorem*. The collage theorem was applied to construct extremely compact IFS models of highly self-similar structures, in particular fern fronds (Barnsley and Demko, 1985; Barnsley, 1988). Subsequent *recurrent* extension of Iterated Function Systems (Barnsley et al., 1989) made it possible to characterize structures satisfying a relaxed condition of self-similarity (parts of the structure may result from the transformations of other parts, rather than the transformations of the entire structure). Examples of branching structures modeled using recurrent IFS and their relation to L-systems were presented by Prusinkiewicz and Hammel (1991, 1994). To date, applications of iterated function systems to the modeling of plants have been investigated mainly from the computer graphics perspective. Their relevance to biology is yet to be determined.

4. Simulation of plant development: empirical models

Developmental models introduce two new elements, compared to models of static structures: the emergence of new modules during development, and the growth of individual modules over time. These processes can be conveniently characterized within the framework of L-systems (Lindenmayer, 1968, 1971). L-systems can be used to express both empirical and mechanistic models. In this section, we focus on empirical models, leaving the discussion of mechanistic models to Section 5.

L-systems are typically described using the terminology of formal language theory (Salomaa, 1973; Herman and Rozenberg, 1975). We give instead their intuitive description, which emphasizes the biological interpretation of all terms.

4.1. L-systems

The essence of development at the modular level can be regarded as a sequence of events, in which *predecessor* or *parent* modules are replaced by configurations of *successor* or *child* modules. The rules of replacement are called *productions*. It is assumed that the number of different module types is finite, and all modules of the same type behave in the same manner. Consequently, the development of a large structure (configuration of modules) can be characterized by a finite set of rules. An L-system is simply a specification of the set of all module types that can be found in a given organism, the set of productions that apply to these modules, and the initial configuration of modules (the *axiom*), from which the development begins.

For example, Fig. 4 shows the development of a stylized compound leaf including two types of modules, the *apices* and the *internodes*. An apex yields a structure that consists of two internodes, two lateral apices, and a replica of the main apex. An internode elongates by a constant scaling factor. The developmental sequence begins with a single apex, and yields an intricate branching structure in spite of the simplicity of the underlying L-system.

This description leaves open the questions of what notation to use to specify the productions, and what data structures to choose to represent a growing plant in a simulation program based on L-systems. Lindenmayer (1968) addressed these questions by introducing the *bracketed string notation*, which was outlined in Section 2.2., in the context of plant mapping (Fig. 2). A branching structure is represented by a string of symbols corresponding to plant modules, with the branches enclosed in square brackets. Originally, the bracketed strings were intended to capture only the topology of the described structures. Nevertheless, a subsequent extension called the *turtle interpreta-*

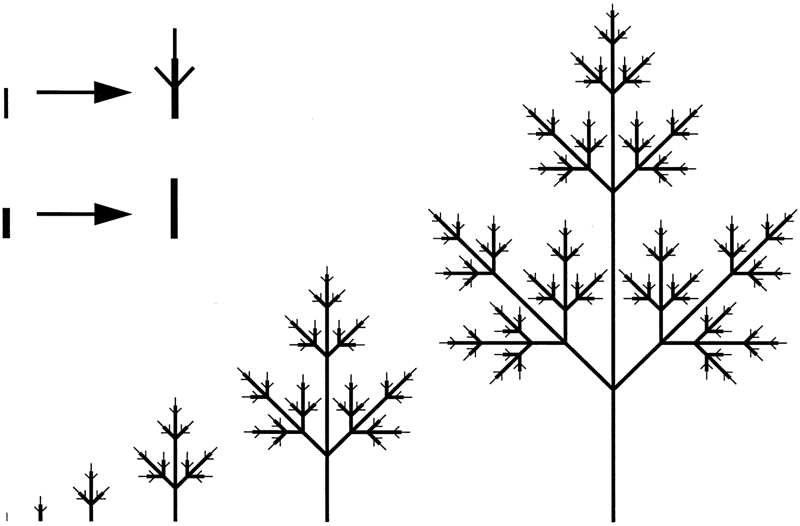


Fig. 4. Developmental model of a compound leaf, modeled as a configuration of apices (thin lines) and internodes (thick lines). The inset represents production rules that govern this development. From Prusinkiewicz et al. (1997b).

tion made it possible to describe plant geometry as well (Prusinkiewicz, 1986, 1987). In addition, *parametric L-systems* made it possible to quantify measurable characteristics associated with individual modules, such as the length and width of internodes, and the magnitude of the branching angles (Prusinkiewicz and Hanan, 1990; Prusinkiewicz and Lindenmayer, 1990; Hanan, 1992). Productions are specified using the standard notation of formal language theory, with a reserved symbol (an arrow) separating the predecessor from the successor (Lindenmayer, 1971). For example, an L-system model of the compound leaf in Fig. 4 is written as follows:

$$\begin{aligned} &\omega: A(1) \\ &p_1: A(s) \to I(s)[-(45)A(s)][+(45)A(s)]I(s)A(s) \\ &p_2: I(s) \to I(2*s) \end{aligned} \tag{1}$$

The growing structure consists of two module types, apices A and internodes I. The parameter s determines the size (length) of any of the modules. The initial structure ω is an apex A of unit length. Production p_1 specifies that an apex yields a structure consisting of two internodes I, two lateral apices A, and a replica of the main apex A. The symbols $+$ and $-$ do not represent components of the growing structure, but indicate that the lateral apices are positioned at an angle of $+45°$ and $-45°$ with respect to their supporting mother branch. Production p_2 states that an internode elongates by a factor of two in each simulation step. A list of commonly used L-system symbols with a predefined geometric interpretation is given by Prusinkiewicz and Lindenmayer (1990).

A central observation underlying L-system simulations is that the application of productions, that is the replacement of predecessor modules by their successors, can be carried out at the level of their bracketed string representation. For example, the first steps of a simulation using L-system (1) yield the following sequence of structures:

$$\begin{aligned} \text{Initial structure:}\quad & A(1) \\ \text{Step 1:}\quad & I(1)[-(45)A(1)][+(45)A(1)]I(1)A(1) \\ \text{Step 2:}\quad & I(2)[-(45)I(1)[-(45)A(1)][+(45)A(1)]I(1)A(1)] \\ & [+(45)I(1)[-(45)A(1)][+(45)A(1)]I(1)A(1)]I(2) \\ & I(1)[-(45)A(1)][+(45)A(1)]I(1)A(1) \end{aligned} \tag{2}$$

The bracketed strings are easily manipulated by a computer program, and form the key data structure of most simulation programs based on L-systems. For instance, Prusinkiewicz and Hanan (1989) (Appendix A) present the listing of a simple program that uses nonparametric bracketed strings, and Hanan (1992) describes details concerning the use of parametric strings. The conversion of strings to three-dimensional graphical objects has been extensively documented by Prusinkiewicz and Lindenmayer (1990) and Prusinkiewicz et al. (1997b); recent extensions were introduced by Kurth (1994) and Měch (1997). Other data structures may also be used in conjunction with L-systems. For example, Hammel (1996) describes an implementation in which structures are represented as linked lists with tree topology.

The inherent capability of L-systems to describe the *development* of plants, rather than just their static structure, is illustrated by a number of developmental plant models. Models with mainly empirical characteristics have been proposed for various racemose and cymose inflorescences (Frijters, 1978; Prusinkiewicz et al., 1988; Prusinkiewicz and Lindenmayer, 1990), green ash shoots (Prusinkiewicz et al., 1994b), young green ash trees (Remphrey and Prusinkiewicz, 1997), Norway spruce trees (Kurth and Lanwert, 1995), cotton plants (Room and Hanan, 1995), bean plants (Hanan, 1995), maize shoots (Fournier, 1995), maize root systems (Shibusawa, 1994), and seaweed (Corbit and Garbary, 1993; Schneider et al., 1994). A novel use of L-systems has been proposed by Battjes and Bachmann (1996), who related L-system parameter values to genetic variation between modeled plants (four species of *Microseris*, a herbaceous plant in the aster family).

The L-systems outlined above belong to the simplest, *context-free* class. This term means that a production can be applied to a module irrespective of its adjacent modules (neighbors in the tree structure). In causal models, it is often convenient to use *context-sensitive* L-systems, in which the applicability or outcome of a production depends not only on the module being replaced, but also on its neighbors. Such L-systems are discussed in Section 5.

4.2. The process view of development

We can emphasize the dynamic aspect of plant modeling using the concept of a *process*, defined as a sequence of events ordered in time (Kreutzer, 1986). At any moment, a process is characterized by a number of parameters, called its *state*. Over time, the process may change its state, create new processes, become inactive, be reactivated, or cease to exist. These notions, with a very practical meaning in computer science (Tanenbaum, 1987), can also be applied to characterize plant modules, in particular the apices (de Reffye, 1981a,b, 1982, 1983; de Reffye et al., 1988; Barczi et al., 1997). For instance, an active apex may grow and create internodes, leaves, and buds. Production of a bud may initiate a new sequence of events, and therefore be regarded as a creation of a new active process. On the other hand, a bud may be dormant and remain inactive until it is activated by another process. Finally, an apex may die and cease to exist. Examples of paths of development involving elaborate state changes have been presented by Bell (1994).

As an example of the process point of view, let us consider the changes in apical activity taking place during the development of a closed racemose inflorescence. Fig. 5a indicates that the apex first produces a sequence of internodes with leaves, then switches to the production of lateral flowers, and eventually creates a terminal flower. We can describe this progression of activities using a *state transition graph* (a *finite automaton* or *finite state machine* in the automata theory) in which nodes represent states, the short arrow distinguishes the initial state, and arcs (directed edges) represent state transitions and the activities associated with them (Fig. 5b). For instance, the two arcs originating at node *A* indicate that an apex in state *A* may produce an internode and a leaf and remain in state *A*, or produce an internode and a lateral flower and switch to state *B*. As there is no edge from node *B* to node *A*, the apex cannot revert to the production of leaves once the production of flowers has begun.

In causal models, the switch from the vegetative to the flowering condition may be triggered by some external event, such as an environmental influence or the arrival of a signal propagating through the plant body (Prusinkiewicz and Lindenmayer, 1990). In contrast, empirical models often assume a stochastic mechanism, in which transitions are

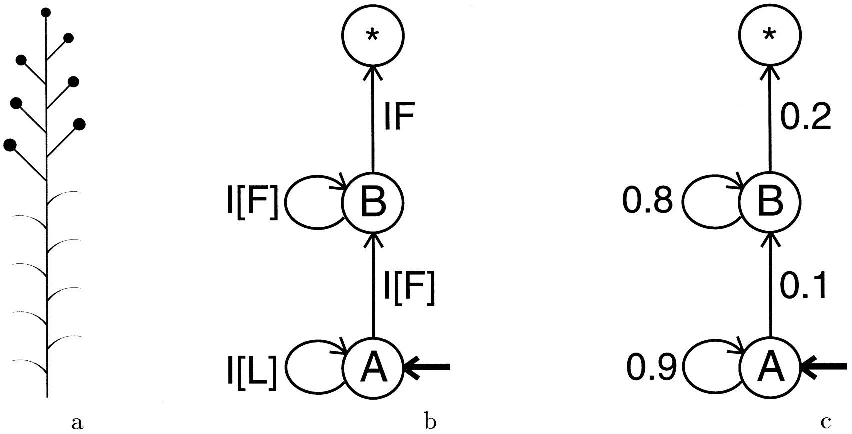


Fig. 5. A racemose inflorescence (a), the state transition diagram illustrating the progression of apical states (b), and a sample Markov chain corresponding to this progression (c).

selected according to some probabilities. A state diagram with associated probabilities is called a *discrete Markov process*, a *Markov chain*, or a *probabilistic automaton* (Luenberger, 1979). For example, the Markov chain shown in Fig. 5c indicates that, after producing a leaf, the apex will remain in state A with probability 0.9, or switch to state B with probability 0.1.

A key issue in the use of Markov chains for modeling is the inference of the set of states, transitions, and probabilities from empirical data. Godin et al. (1997a,b) describe a software package which makes it possible to define and manipulate Markov chains (and their variations) interactively, until their behavior matches the observed probability distributions. For further discussion and examples of the application of Markov processes to plant modeling, see Maillette (1990), Yoda and Suzuki (1993), Costes and Guédon (1996, 1997), Guédon (1997), and Barczi et al. (1997).

A model based on a Markov chain can be expressed using a *stochastic L-system* (Eichhorst and Savitch, 1980; Nishida, 1980; Yokomori, 1980). A stochastic L-system includes several productions with the same predecessor. A particular successor is selected according to the probabilities associated with the productions. For example, the following stochastic L-system generated the sample racemose structure shown in Fig. 5a according to the Markov chain in Fig. 5c.

$$\begin{array}{lrl} \omega: & A & \\ p_1: & A \overset{0.9}{\rightarrow} & I[L]A \\ p_2: & A \overset{0.1}{\rightarrow} & I[F(1)]B \\ p_3: & B \overset{0.8}{\rightarrow} & I[F(1)]B \\ p_4: & B \overset{0.2}{\rightarrow} & IF(1) \\ p_5: & F(s) \rightarrow & F(s*1.1) \end{array} \tag{3}$$

This example shows that the formalisms of Markov processes and L-systems can be used jointly, with a Markov process providing a stochastic description of the fate of the individual apices, and the L-system integrating the development of these apices and other plant components into a comprehensive model of the entire developing plant.

4.3. Discrete-time simulation of development

According to the original definition of L-systems, productions are applied *in parallel*, with all modules being replaced simultaneously in every simulation step (Lindenmayer, 1968; Lindenmayer and Jürgensen, 1992). The parallel operation of L-systems reflects the fact that all parts of a plant develop at the same time, and that the time separating consecutive simulation steps can often be conveniently interpreted as a *plastochron*, or time separating production of consecutive nodes (Erickson and Michelini, 1957). Nevertheless, Hogeweg (1978, 1980) pointed out that the assumption of *synchronous* replacement of all modules by their successors at precisely the same time is too strong, and does not have a biological justification. Consequently, she proposed to simulate development within the framework of *discrete-event simulation*, in which individual events may occur at arbitrary points in time (Kreutzer, 1986). An ordered sequence of events to be simulated is then organized into a data structure called the *event queue*, managed by a simulator component called the *scheduler*. The scheduler advances time to the next event and initiates actions associated with it; these actions may, in particular, insert new events into the queue. An application of this principle to the simulation of plant development was described in detail by Blaise (1991).

4.4. Continuous-time simulation of development

Neither synchronous nor discrete-event simulation capture the continuous developmental processes that take place between the events. To overcome this limitation, Prusinkiewicz et al. (1993) and Hammel (1996) introduced a continuous-time extension of L-systems called *differential L-systems*, which is based on the paradigm of *combined discrete–continuous simulation* (Fahrland, 1970; Kreutzer, 1986). A module is created and ceases to exist in discrete events, as in the case of discrete-event simulation. Between the events, parameters of a module change in a continuous manner. An event is triggered if a function of these parameters reaches a threshold value.

The combined discrete–continuous view of development is illustrated in Fig. 6. Module M_2 is created at time t_α as one of two descendants of the initial module M_1. It develops in the interval $[t_\alpha, t_\beta)$, and ceases to exist at time t_β, giving rise to two new modules M_4 and M_5. These modules will develop over some time, create new modules at the end of their existence, and so on.

Parameters involved in module development may represent features inherent in a module, such as the length of an internode, the size of a bud, or the magnitude of a branching angle, or external factors, such as time, temperature, temperature sum, day length, or light sum. Examples of the application of differential L-systems to the animation of plant development are presented by Prusinkiewicz et al. (1993) and Hammel (1996).

4.5. Growth functions

Gradual changes of parameter values may be specified using differential or algebraic functions of time called *growth functions* (Huxley, 1932; Reeve and Huxely, 1945;

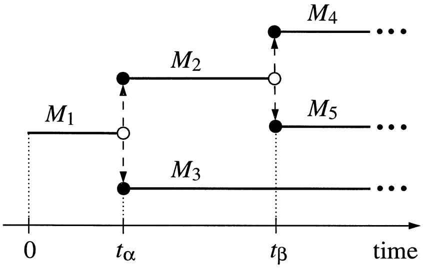


Fig. 6. Fragment of the lineage tree of a hypothetical modular structure. From Prusinkiewicz et al. (1993).

Richards and Kavanagh, 1945). In empirical models, growth functions are found by fitting mathematical functions to data using statistical methods, as discussed in general terms by Hunt (1979). A wide range of functions with different degrees of biological justification have been proposed in the literature reviewed by Richards (1969), Żelawski and Sztencel (1981), and Sztencel and Żelawski (1984). Specifically, parameters representing geometric features of a module, such as internode length, leaf size, and branching angles, often increase according to *sigmoidal* functions, which means that they initially increase in value slowly, then accelerate, and eventually level off near or at the maximum value (Thompson, 1952).

A popular example of a sigmoidal function is Velhurst's *logistic* function (Edelstein-Keshet, 1988; p. 212) defined by the equation:

$$\frac{\mathrm{d}x}{\mathrm{d}t} = r\left(1 - \frac{x}{x_{\max}}\right)x \tag{4}$$

with a properly chosen initial value x_0 (Fig. 7a). Another example is the cubic function:

$$x(t) = -2\frac{\Delta x}{T^3}t^3 + 3\frac{\Delta x}{T^2}t^2 + x_{\min} \tag{5}$$

which increases sigmoidally from $x_{\min}$ to $x_{\max} = x_{\min} + \Delta x$ when t changes from 0 to T (Fig. 7b). Both functions were employed in a developmental model of *Fraxinus pennsylvanica* shoots and leaves described by Prusinkiewicz et al. (1994b) and shown in Fig. 8. The logistic function, presumed to have a more sound biological justification, was chosen to approximate growth on the basis of measured data (the expansion of rachis segments and leaflets). The coefficients were estimated using regression analysis. In contrast, the cubic function was applied where detailed data were not available (specifically, to simulate the gradual increase of branching angles over time). In this case, function parameters were manipulated interactively to match the developmental patterns observed in the field and recorded on photographs of developing shoots. The straightforward interpretation of function parameters and their link with interactive computer graphics techniques for curve specification (Foley et al., 1990; Chap. 11.2) facilitated this manipulation.

The logistic function does not have enough parameters to allow for flexible fitting to empirical data. Several other growth curves, such as the monomolecular function and the

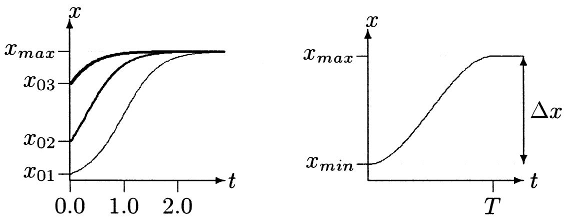


Fig. 7. Examples of sigmoidal growth functions. (a) A family of logistic functions plotted using $r = 3.0$ for different initial values x_0. (b) A cubic function $x(t)$ extended by constant function $x = x_{\max}$ for $t > T$. From Prusinkiewicz et al. (1993).

Fig. 8. Simulation of the expansion of a *F. pennsylvanica* shoot over the course of 35 days. Adapted from Prusinkiewicz et al. (1994b).

Gompertz function, are limited in the same way (Richards, 1959). To overcome this limitation, Richards (1959) proposed a family of growth functions

$$x(t) = \left(A^{1-m} - \beta e^{-kt}\right)^{\frac{1}{1-m}} \tag{6}$$

with four parameters A, m, β, and k. Although polynomial functions of the third or higher degree may provide comparable or better approximations (Venus and Causton, 1979), the Richards function has been widely used in modeling practice. For example, Berghage and Heins (1991) applied it to model the elongation of internodes in poinsettia, Lieth and Carpenter (1990) to model stem elongation and leaf unfolding in Easter lily, and Larsen and Lieth (1992) to model shoot elongation in chrysanthemum.

5. Simulation of plant development: causal models

5.1. Information flow in growing plants

Communication between modules plays a crucial role in the control of developmental processes in plants. Lindenmayer (1968, 1982) distinguished two forms of communication: *lineage* (also called *cellular descent*), which represents information transfer from a parent module to its children, and *interaction*, which represents information transfer between coexisting modules. In the latter case, the information exchange may be *endogenous* (between adjacent modules of the structure, as defined by its topology), or *exogenous* (through the space embedding the structure) (Bell, 1986; Prusinkiewicz, 1994). The flow of water, hormones, or nutrients through the vascular system of a plant are examples of endogenous information transfer, whereas the shading of lower branches by upper ones is a form of exogenous transfer. This classification is used to organize the discussion of causal models below.

5.2. Development controlled by lineage

By definition, development is controlled by lineage if the fate of each module is determined by its own history (Lindenmayer, 1975). Within the formalism of L-systems, development controlled by lineage is expressed using the formalism of *context-free* L-systems (also known as OL-systems; Lindenmayer, 1971) and their parametric and differential extensions outlined in Section 4. It is difficult to formulate a clear dividing line between empirical models and causal models controlled by lineage; the key criterion appears to be the degree to which the model can be justified in terms of fundamental mechanisms of development. For example, we may regard the leaf model given in Eq. (1) as a causal model controlled by lineage, if we view production p_1 as a manifestation of the cyclic nature of the activities of the apex.

Progress of time is the force that drives models controlled by lineage; consequently, time-related variables, such as delays and rates of growth, play an important role. For example, in the model of *L. coronaria* shown in Fig. 1 one lateral branch always develops ahead of the other branch supported at the same branching point (Prusinkiewicz et al., 1988; Prusinkiewicz and Lindenmayer, 1990), which explains the asymmetry observed in the plant structure (Robinson, 1986).

A key question that has to be asked when constructing a causal model is whether the postulated control mechanism is powerful enough to simulate an observed developmental sequence. The theory of L-systems offers many results that characterize different classes of control mechanisms (Herman and Rozenberg, 1975; Lindenmayer, 1987). Although most results are rather abstract, some do apply to practical model construction. For example, Frijters and Lindenmayer (1976) observed that acrotonic structures are difficult to obtain in models controlled by lineage; this observation was formalized by Prusinkiewicz and Kari (1996). A similar difficulty occurs when modeling basipetal flowering sequences (Lindenmayer, 1984; Janssen and Lindenmayer, 1987). Simple models of these phenomena can be obtained, however, assuming endogenous control mechanisms.

5.3. Development controlled by endogenous mechanisms

Endogenous control relies on the flow of information *through the structure* of the growing plant. The information exchanged between the modules may represent discrete *signals* (for example, the presence of a hormone triggering the transformation of a bud to a flower), or quantifiable *values* (for example, the concentration of photosynthates

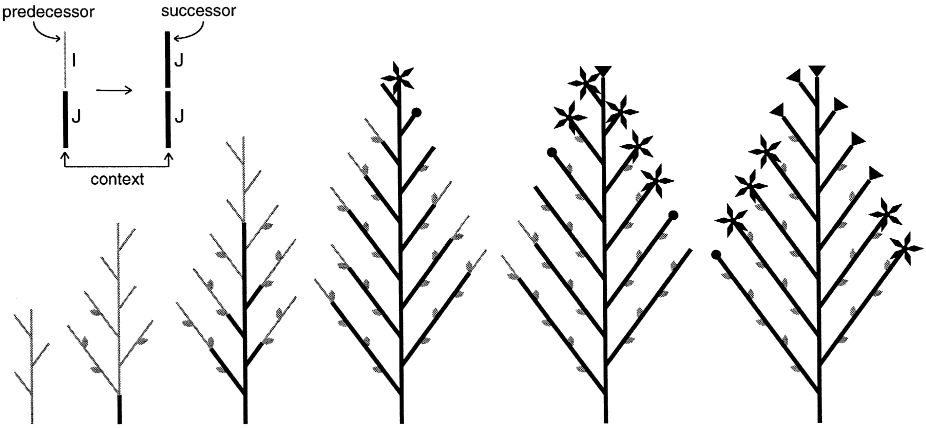


Fig. 9. Development of an inflorescence controlled by a signal. The inset shows the context-sensitive production that propagates the signal acropetally. Adapted from Prusinkiewicz and Hanan (1989).

produced by leaves). Endogenous information flow can be conveniently captured using the formalism of *context-sensitive* L-systems. In this case, a production can be applied to a particular module only if this module has some specific neighbors. For example, Fig. 9 shows a hypothetical model of a growing inflorescence, in which flowering is induced by an upward-moving (acropetal) signal. The context-sensitive production describing signal propagation states that if a module I is not yet reached by a signal, and it is situated immediately above a module J already reached by a signal, then I will be transformed into J in the next simulation step. Another context-sensitive production transforms an apex reached by a signal into a flowering bud, leading to a flower. As shown by Lindenmayer (1984) and Janssen and Lindenmayer (1987), and further illustrated by Prusinkiewicz and Hanan (1989) and Prusinkiewicz and Lindenmayer (1990), the flowering sequence in this model depends on the relationship between the plastochron of the main axis, plastochron of the lateral branches, and the respective propagation rates of the flower-inducing signal. In particular, the model is capable of generating basipetal flowering sequences.

In the above example, discrete information was transferred between the modules of a developing structure. In nature, however, developmental processes are often controlled in a more modulated way, by the quantity of substances (*resources*) exchanged between the modules. An early developmental model of branching structures making use of quantitative information flow was proposed by Borchert and Honda (1984). Below we outline an extension of this model, which captures the partitioning of resources between the shoot and the root (Prusinkiewicz et al., 1997a,b).

Borchert and Honda postulated that the development of a branching structure is controlled by a flow or *flux* of substances, which propagate from the base of the structure towards the apices and supply them with materials needed for growth. When the flux reaching an apex exceeds a predefined threshold value, the apex bifurcates and initiates a lateral branch; otherwise it remains inactive. At branching points the flux is

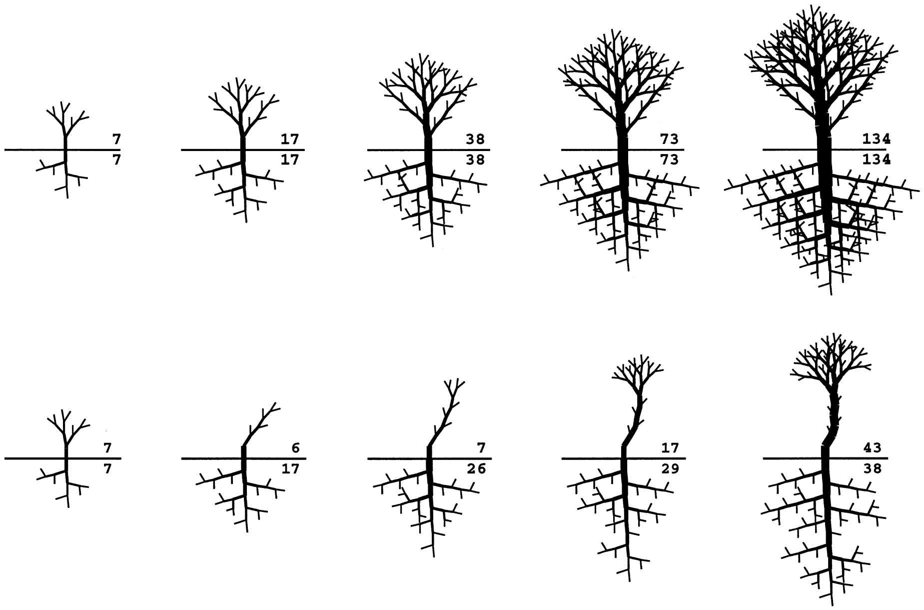


Fig. 10. Application of Borchert and Honda's model to the simulation of a complete plant. The development of an undamaged plant (top row) is compared with the development of a plant with a damaged shoot (bottom row). The numbers of live apices in the shoot and root are indicated above and below the ground level. Adapted from Prusinkiewicz et al. (1997b).

distributed according to the types of the supported internodes (straight or lateral) and the numbers of apices in the corresponding branches.

In the case shown in Fig. 10, two structures representing the shoot and the root of a plant are generated simultaneously. The flux penetrating the root at the beginning of a developmental cycle is assumed to be proportional to the number of apices in the shoot; reciprocally, the flux penetrating the shoot is proportional to the number of apices in the root. These assumptions form a crude approximation of plant physiology, whereby the photosynthates produced by the shoot fuel the development of the root, and water and mineral compounds gathered by the root are required for the development of the shoot. The model also captures an increase of internode width over time, and a gradual assumption of the position of a straight segment by its sister lateral segment, after the straight segment has been lost. The developmental sequence shown in the top row of Fig. 10 represents the development of an undamaged plant. The shoot and the root develop in concert. The bottom row illustrates development affected by damage to the shoot. The removal of a shoot branch slows down the development of the root; on the other hand, the large size of the root, compared to the remaining shoot, fuels a fast re-growth of the shoot. Eventually, the plant is able to redress the balance between the size of the shoot and the root.

Applications of context-sensitive L-systems are not limited to the simulation of endogenous information flow in plants. For example, the same formalism has been used to simulate movements of an insect foraging on a plant (Prusinkiewicz et al., 1997a,b).

5.4. Development of plants interacting with their environment

The incorporation of interactions between a plant and its environment is one of the most important issues in the domain of plant modeling (Fisher, 1992; Room et al., 1994; Sachs and Novoplansky, 1995). Its solution is needed to construct predictive models suitable for applications ranging from computer-assisted landscape and garden design to the determination of crop and lumber yields in agriculture and forestry.

Using characteristics of the information flow between a plant and its environment as the classification key, we can distinguish three forms of interaction and the associated models of plant–environment systems.

1. The plant is affected by global properties of the environment, such as day length controlling the initiation of flowering (Frijters and Lindenmayer, 1974) or daily minimum and maximum temperatures modulating the growth rate (Hanan, 1995).

2. The plant is affected by local properties of the environment, such as the presence of obstacles controlling the spread of grass (Arvo and Kirk, 1988) and directing the growth of tree roots (Greene, 1991), geometry of support for climbing plants (Arvo and Kirk, 1988; Greene, 1989; Prusinkiewicz et al., 1997b), soil resistance and temperature in various soil layers (Diggle, 1988), and predefined geometry of surfaces to which plant branches are pruned (Prusinkiewicz et al., 1994a).

3. The plant interacts with the environment in an information feedback loop, where the environment affects the plant and the plant reciprocally affects the environment. Specific models capture: (i) competition for *space* (including collision detection and access to light) between segments of essentially two-dimensional schematic branching structures (Cohen, 1967; Honda et al., 1981; Bell, 1986; Ford, 1987; Ford et al., 1990; Kaandorp, 1994; Kurth, 1994); (ii) competition between root tips for *nutrients* and *water* transported in soil (Liddell and Hansen, 1993; Clausnitzer and Hopmans, 1994); this mechanism is related to competition between growing branches of corals and sponges for nutrients diffusing in water (Kaandorp, 1994); (iii) competition for *light* between shoots of herbaceous plants (Greene, 1989) and branches of trees (Honda et al., 1981; Kanamaru et al., 1992; Chen et al., 1993; Chiba et al., 1994a,b; Takenaka, 1994; de Reffye et al., 1995). Although some phenomena belong quite naturally to one of these groups, the classification of others may depend on the level of abstraction. For example, an approximate model may consider temperature as a global property of the environment, a more detailed one may express temperature locally as a function of distance from the ground, and a yet more detailed model may take into account the changes of temperature determined by the distribution of radiative energy between plant parts. Thus, the above classification is useful primarily from the modeling perspective, since different techniques are required to capture phenomena in each class.

The first comprehensive approach, introducing a methodology for modeling plants interacting with the environment, was developed by Blaise (1991). Another approach, based on the notion of L-systems, has been proposed by Měch and Prusinkiewicz (1996), and expanded upon by Měch (1997). This second approach is summarized below.

As described by Hart (1990), every environmentally controlled phenomenon can be considered as a chain of causally linked events. After a stimulus is perceived by the plant, information in some form is transported through the plant body (unless the site of stimulus perception coincides with the site of response), and the plant reacts. This reaction reciprocally affects the environment, causing its modification that in turn affects the plant. For example, roots growing in the soil can absorb or extract water (depending on the water concentration in their vicinity). This initiates a flow of water in the soil towards the depleted areas, which in turn affects further growth of the roots (Gardner, 1960; Clausnitzer and Hopmans, 1994).

According to this description, the interaction of a plant with the environment can be conceptualized as two concurrent processes that communicate with each other, thus forming a feedback loop of information flow. The plant process performs the following functions: reception of information about the environment in the form of scalar or vector values representing the stimuli perceived by specific organs; transport and processing of information inside the plant; and generation of response in the form of growth changes (e.g. development of new branches) and direct output of information to the environment (e.g. uptake and excretion of substances by a root tip). Similarly, the environmental process includes mechanisms for the: perception of the plant's actions; simulation of internal processes in the environment (e.g. the diffusion of substances or propagation of light); and presentation of the modified environment in a form perceivable by the plant.

For the purposes of simulation, the environment is represented as a scalar or vector field. Modules of a growing plant can test values of this field at points of interest, and send values that affect the field at specific locations. Sample models constructed according to this scheme are outlined below.

Fig. 11 shows a two-dimensional model of a root seeking water in the soil during its development. The initial water distribution formed an S-shaped zone of high water

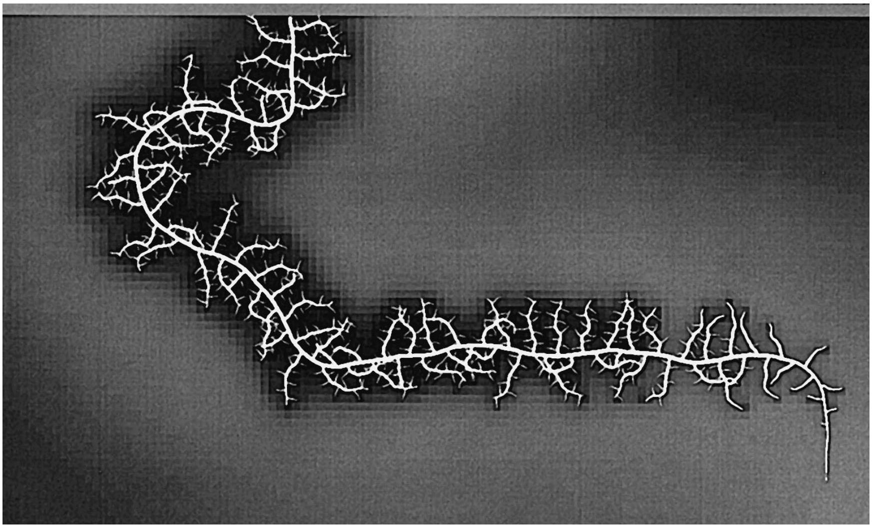


Fig. 11. A two-dimensional model of a root interacting with water in soil. Background colors represent concentrations of water diffusing in soil. From Měch and Prusinkiewicz (1996).

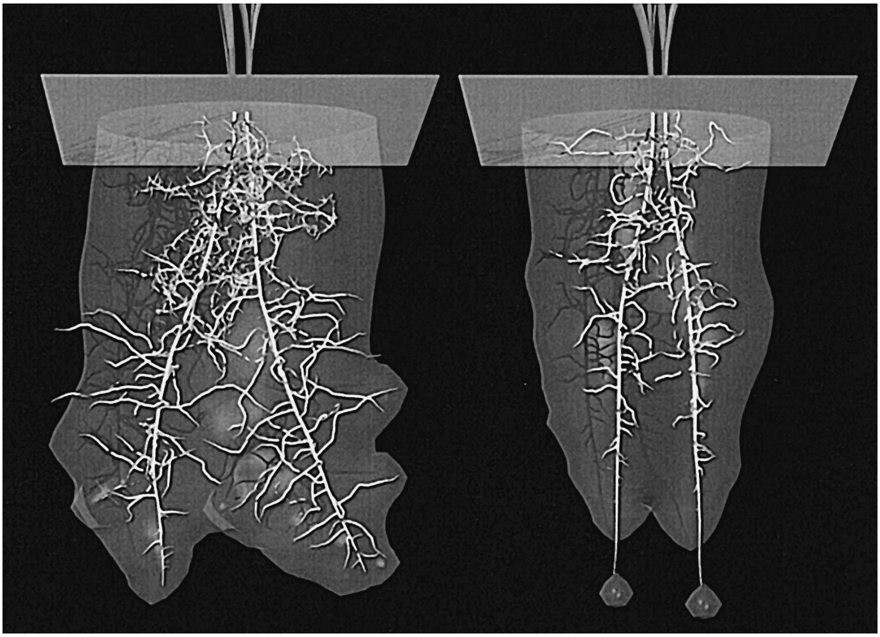


Fig. 12. A three-dimensional root model. Water concentration is visualized by semi-transparent iso-surfaces (Wyvill et al., 1986) surrounding the roots. As a result of competition for water, the roots grow away from each other. The divergence between their main axes depends on the spread of the rootlets, which grow faster on the left then on the right. From Měch and Prusinkiewicz (1996).

concentration. The growing tips of the main root and rootlets absorb water that diffuses in the soil. The decreased water concentration is indicated by dark areas surrounding the root system. In the areas with insufficient water concentration, the rootlets cease to grow before they have reached their potential length.

Fig. 12 shows a three-dimensional extension of this model based on the work of Clausnitzer and Hopmans (1994). Water concentration is visualized by a semi-transparent iso-surface surrounding the roots. As a result of competition for water, the main roots grow away from each other. This behavior is an emergent property of the model.

Fig. 13 shows a model of a horse chestnut tree inspired primarily by the work of Takenaka (1994). The branches compete for light from the sky hemisphere. Clusters of leaves cast shadows on branches further down. An apex in shade does not produce new branches. Products of photosynthesis are transported from the leaves towards the base of the tree. If the amount of photosynthates reaching the base of a branch is below a threshold value, the branch is considered a liability and is shed from the tree. Thus, the distribution of branches in the crown is controlled by their competition for light.

Fig. 14 further illustrates the impact of competition for light on tree growth. The simulation reveals essential differences between the shape of the crown in the middle of a stand, at the edge, and at the corner. In particular, the tree in the middle retains only the upper part of its crown. Simulations of this type may assist in choosing an optimum distance for planting trees, where self-pruning is maximized (reducing knots in the wood

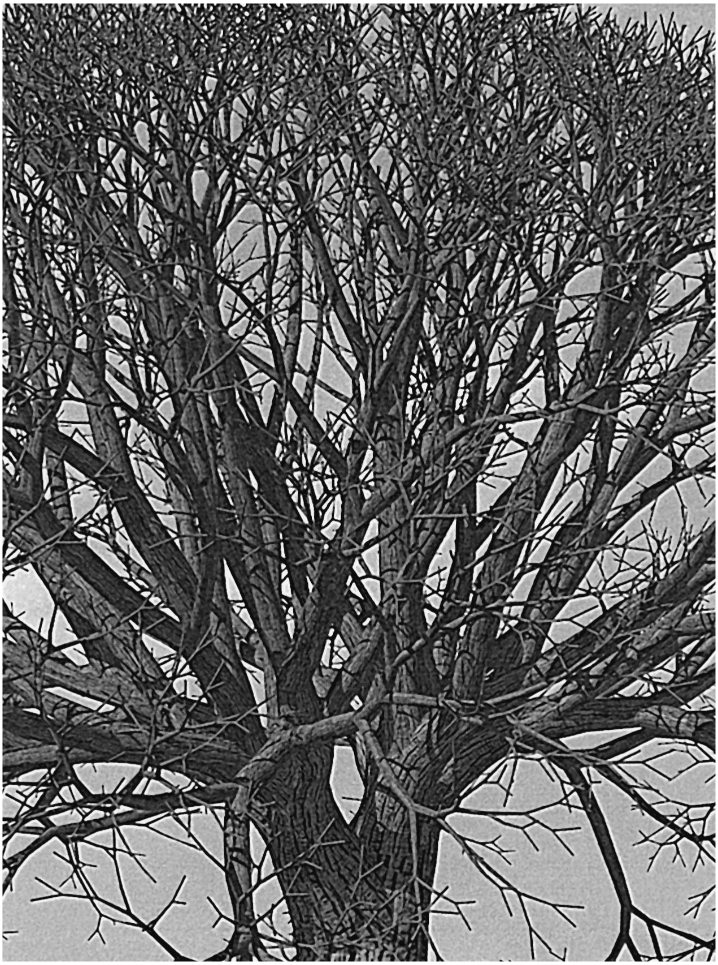


Fig. 13. A tree model with branches competing for access to light, shown without the leaves. From Měch and Prusinkiewicz (1996).

and the amount of cleaning that trees require before transport), yet space between the trees is sufficient to allow for unimpeded growth of trunks in height and diameter.

The response of trees to pruning is another important phenomenon in which the development of a plant is affected by external factors (Prusinkiewicz et al., 1994a). As described, for example, by Hallé et al. (1978) (Chap. 4) and Bell (1991) (p. 298), during the normal development of a tree many buds remain dormant and do not produce new branches. These buds may be subsequently activated by the removal of leading buds from the branch system, which results in an environmentally-adjusted tree architecture. The model depicted schematically in Fig. 15 represents the extreme case of this process, where buds are activated only as a result of pruning. The developing structure is confined to a square, and the apices test whether they are within or outside this area.

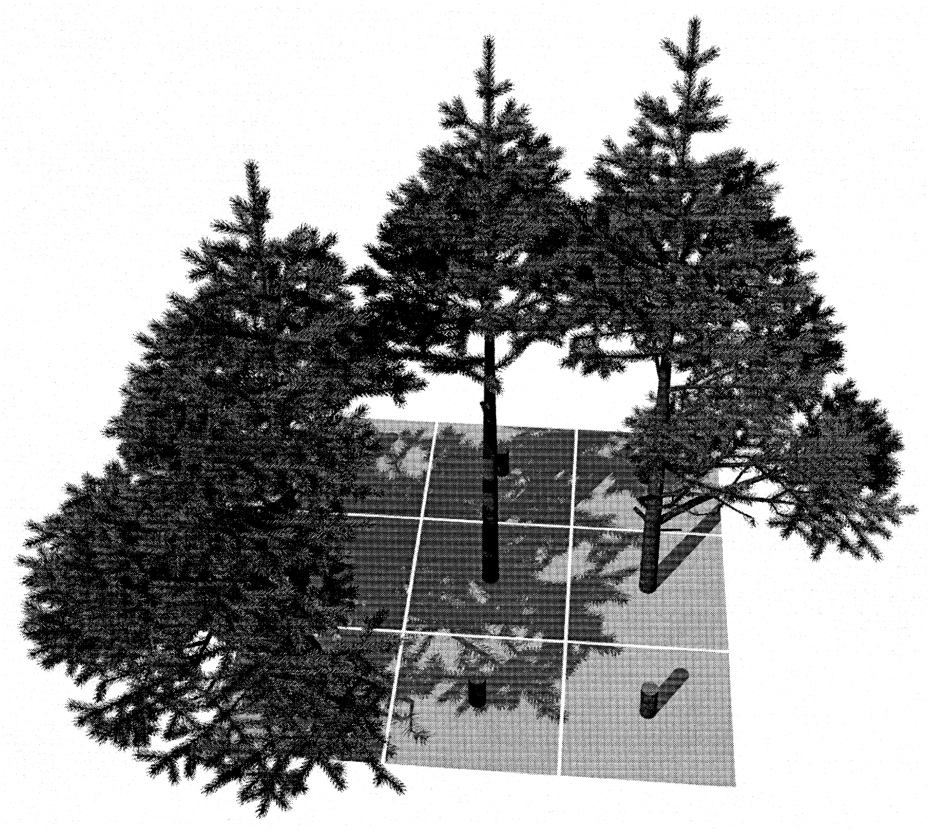


Fig. 14. Relationship between tree form and its position in a stand. From Měch and Prusinkiewicz (1996).

During the initial phase of development the apex of the main axis creates a sequence of internodes and dormant buds. After crossing the bounding square the apex is pruned and a basipetal signal is sent to activate the nearest dormant bud. The activated bud initiates a lateral branch, which grows in the same manner as the initial structure (traumatic reiteration). After crossing the bounding square, the apex of the reiterated branch is also pruned, and the bud-activating signal is generated again. The final structure results from the repetition of this process.

A three-dimensional extension of the above model is shown in Fig. 16. In this case, some of the newly created buds initiate new branches spontaneously, yielding a tree structure. Pruning constrains the outline of the growing tree to a bounding box and activates dormant buds, which increases the density of branches and leaves near the box boundaries.

The model of plant response to pruning can be used to model topiary forms. For example, Fig. 17 presents a synthetic view of a part of the Levens Hall garden in England, laid out at the beginning of the 18th century and considered the most famous

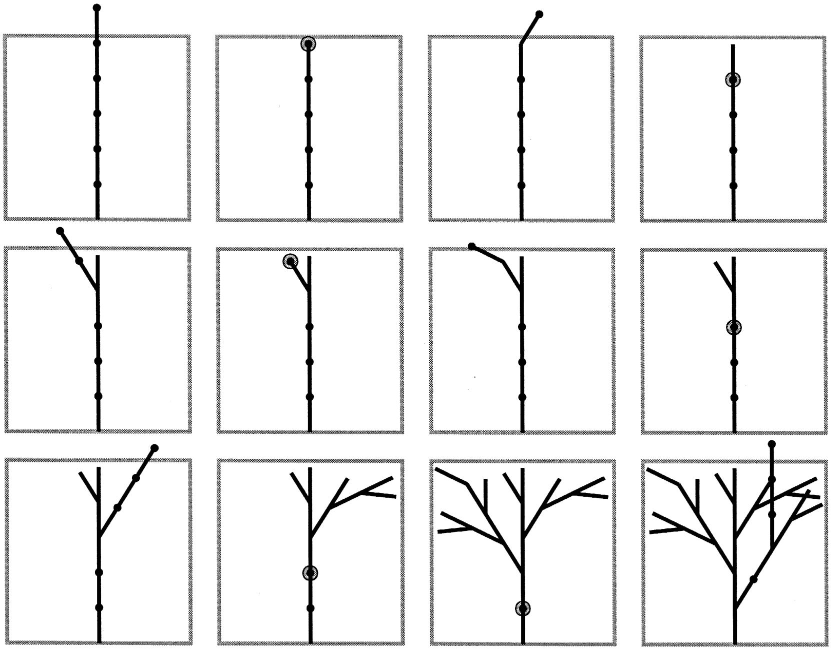


Fig. 15. A simple model of a tree's response to pruning. Top row: simulation steps 6, 7, 8, and 10; middle row: steps 12, 13, 14, and 17; bottom row: steps 20, 40, 75, and 94. Small black dots indicate dormant buds, the circles indicate the position of a signal. From Prusinkiewicz et al. (1994a).

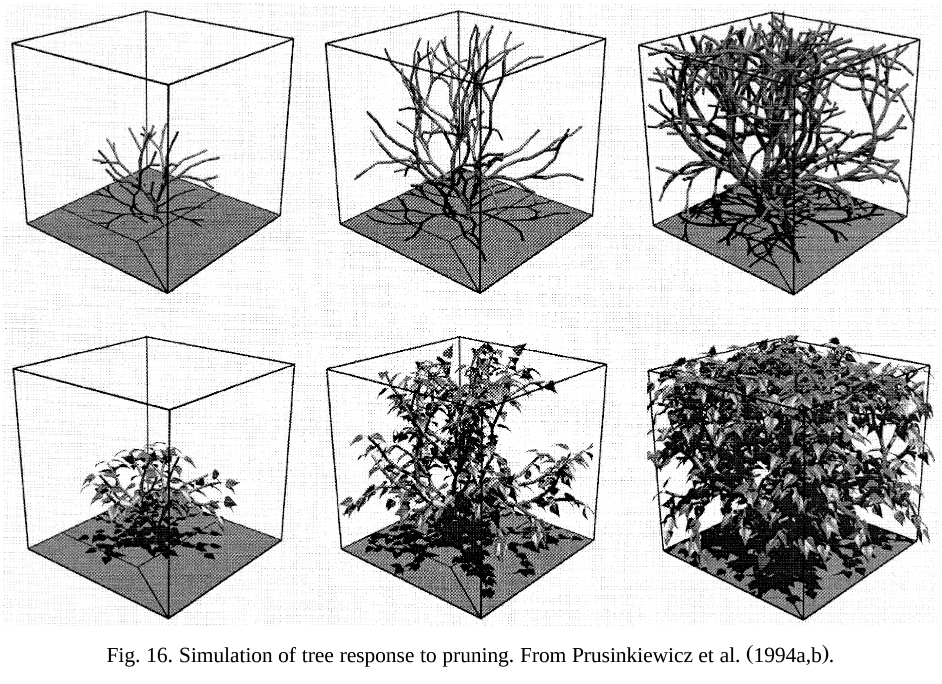


Fig. 16. Simulation of tree response to pruning. From Prusinkiewicz et al. (1994a,b).

Fig. 17. A model of the topiary garden at Levens Hall, England. From Prusinkiewicz et al. (1997b).

topiary garden in the world (Coats, 1963; pp. 52–57). For other models of topiary trees, see Prusinkiewicz et al. (1994a).

The scope of this survey does not allow for a detailed description of individual models, and a complete account of phenomena that have been captured, at various levels of accuracy, by causal models developed to date. It is important to realize, however, that the technology for creating complex mechanistic models already exists and can be applied to capture phenomena of relevance to botany, agriculture, horticulture, and forestry.

6. Applications of architectural plant models

The modeling of plant architecture is an active research area, with some empirical models already achieving the predictive value needed in practical applications. Examples include the following.

- A model of flowering rose shoot development as a function of air temperature (Pasian and Lieth, 1994), intended to predict the timing of harvest in commercial greenhouse rose production.
- Models of stem elongation, leaf unfolding (Lieth and Carpenter, 1990) and flower bud elongation (Fisher et al., 1996b) in Easter lily; these models are intended to precisely control the flowering date by manipulating greenhouse air temperature.
- Models of stem elongation in poinsettia as a function of temperature (Berghage and Heins, 1991) and photoperiod treatments (manipulation of the short-day date) (Fisher et al., 1996a); these models are intended to use various treatments as a means for controlling plant height.
- Models of shoot elongation retardation in chrysanthemum caused by the application of daminozide (Larsen and Lieth, 1992; Lieth and Larsen, 1993); these models are intended to predict the final shoot length reduction resulting from single or multiple daminozide application at various dates.

The above models capture selected topological and geometrical features of the modeled plants. They have not been accompanied by realistic visualizations, which would require collection of more comprehensive data.

The architectural modeling of entire plants is at the point where the methodology of model construction is relatively well understood, well calibrated empirical models of selected plants are being developed, and mechanistic models are subject of active research. In this context, Room et al. (1996) presented a list of prospective applications of the architectural plant models; those pertinent to horticulture are listed below.

- Identification of horticultural treatments (pruning and pinching, temperature and day length manipulation, application of chemicals, etc.) aimed at the optimization of plant size, shape, quality, and timing of flower production.
- Identification of optimal strategies for pruning and spacing trees.
- Computer-assisted garden design; simulation of interplanting for continuous flower displays.
- Improved understanding of disease dynamics through simulation of pathogen deposition and growth in the microclimates produced by developing plants.
- Improved definition of action thresholds for pest management through simulation of interactions between plant architecture, pesticide deposition, and insect movement and feeding.
- Specification of target ‘designer plants’ by identification of architectures optimal for interception of light, harvestability, damage compensation, aesthetic appeal, etc.

- Exploration of hypotheses relating physiology of plant development and information in genes to integrated 3D structures.
- Presentation of three-dimensional plant models for inclusion in plant registries and advertising of plant varieties to customers.

While the computer science techniques involved in the specification and visualization of the models seem to be relatively mature, the development of well calibrated empirical models of specific plants remains a labor-intensive task, and construction of faithful mechanistic models is a current research problem. Fortunately, the value of architectural models is not limited to support of decision making processes, and extends to the process of model construction itself. This point of view was clearly stated by Bell (1986):

> The very process of constructing computer simulations to reproduce a particular branching structure can be a useful experience in its own right, even without proceeding to the use of such a simulation to test an hypothesis. Either the morphology of the organism must be recorded in considerable detail or the underlying features of its developmental architecture fully appreciated... Shortcomings of the model will soon become apparent as ‘mistakes’ which are readily identifiable qualitatively but are not always easy to quantify.

7. Conclusions

In contrast to crop models, which describe plants in global terms such as biomass, yield, and number of flowers and fruits, architectural plant models attempt to capture spatial arrangement of plant components and their development over time. Recent progress in the methodology of model construction forms the base on which well calibrated models of specific plants have begun to be built. Their availability will allow for the realization of the anticipated practical applications of architectural models.

This survey has been focused on the modeling of branching architecture of plants. Quantitative characteristics of plant organs can be described using growth functions in a manner similar to plant architecture (Section 4.5). Examples include leaf area (Mutsaers, 1983a,b) and fruit size (Gandar et al., 1996). These characteristics, however, do not suffice to reproduce details of organ shape and development. Consequently, visual representations of plant organs have been created using interactive modeling techniques devised in computer graphics (Prusinkiewicz and Lindenmayer, 1990; Hanan, 1992; Deussen and Lintermann, 1997; Měch, 1997). A biologically better motivated approach, based on the distribution of growth rates in the growing surface or volume is a topic of current research (Dimian, 1997).

An interesting and largely open problem is the integration of architectural plant models with crop models. On one hand, such integration could benefit crop models, for example, by providing a sound basis for calculating light distribution in canopy (Govaerts, 1995; Chelle, 1997; Měch, 1997). On the other hand, crop models can provide information driving models of individual plants, for example, the distribution of temperature as a function of distance from the ground. It can be expected that the spatial scale, accuracy, and computational complexity of simulations will be easier to control in the integrated models than in either the crop models or the architectural models alone.

On the conceptual plane, the relationship between L-systems and process-based models deserves a more detailed study than has been possible within the limits of this survey (Section 4.2). In particular, the incorporation of complex state transitions described by Bell (1994) into developmental plant models may offer a framework that will facilitate construction of causal models.

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