

Simulation Modeling of Plants and Plant Ecosystems

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Reference

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The result is increasingly accurate and realistic-looking 3D simulations of plant biology, ecology, and the physiological processes governing plant growth, including the effects of light.

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PRZEMYSŁAW PRUSINKIEWICZ

THE MODELING OF PLANTS AND PLANT ecosystems has the captivating appeal of reproducing the visual beauty of nature while providing insights into the way nature works. This interplay between art and science is rooted in history and can be traced at least as far back as Leonardo da Vinci, whose notes about plant architecture 500 years ago remain valid today. The interdisciplinary character of plant modeling research is echoed by the diversity of existing and prospective applications of the models.

The complex architecture of plants consisting of many individual units, including branches, leaves, and flowers, is difficult to reproduce using traditional modeling techniques, which are better suited for artificial rather than natural objects; the difficulty increases when trying to model entire plant ecosystems. Simulation of plant development, based on botanical knowledge, offers a solution.

Simulation of natural phenomena is one of the most powerful methods for creating realistic models, animations, and rendered images in computer

graphics. These simulations are often based in physics, possibly involving the mechanics of objects subject to forces in physically based modeling and animations or the optics of light propagation and distribution in radiative energy in rendering. Over the last 15 years, steady progress has also been made in the simulation of the biological processes governing plant development. This progress has led to biologically justified and visually realistic models of plants and plant ecosystems.

Applications are divided into two broad categories: image synthesis and scientific visualization. In image-synthesis applications, the visual presentation of the models is the main objective; consequently, the modeling methods for image synthesis emphasize the ease of specifying and interactively manipulating the models [6, 12]. In contrast, models developed for scientific and scientific-visualization purposes emphasize the biological accuracy of the simulated processes and structures [1, 8]. These models integrate our knowledge of plants and make it possible to examine hypotheses when the



CLOSE-UP OF A DAISY CAPITULUM (CREATED BY DEBORAH R. FOWLER)



exact processes of plant growth and evolution are not known by botanists. Here, I describe the state of the biologically motivated modeling methodology, focusing on a dominant technique, called L-systems, a mathematical theory of plant development directly applicable to computer simulations.

Modular Architecture of Plants

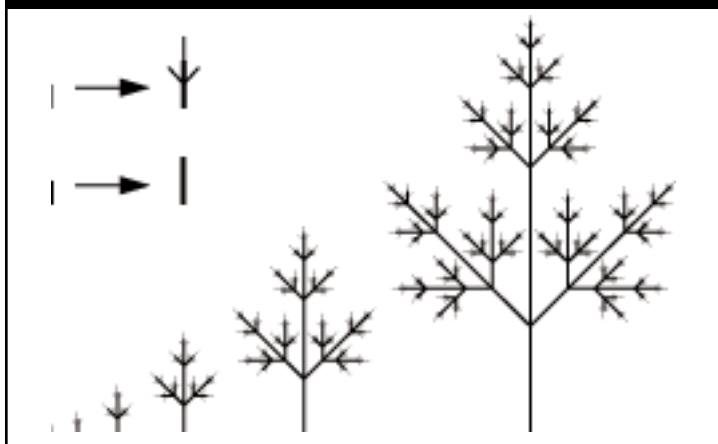
The diversity of plant forms in nature, amplified by plants' adaptation to their environments, might leave the impression that it is impossible to capture this variety in a unified and universally applicable way. Fortunately, botanists and ecologists have developed general concepts allowing us to consider not only individual plants but entire plant ecosystems from a common perspective. It is therefore possible for computer scientists to develop multipurpose plant-modeling software that can be used to simulate different plant species and operate at different levels of abstraction. The resulting models include "descriptive" models, which are limited to a geometric characterization of plant structure and development, and "functional-structural" models, or virtual plants, which also capture the physiological processes governing plant growth [8].

The interwoven postulates of "modular plant architecture" and "a plant as a population of modules" are the key unifying concepts in all this software. Accordingly, a plant can be viewed as a modular structure consisting of relatively independent, repetitive units, such as leaves, flowers, buds, and branch segments. This view makes it possible to perform a number of fundamental virtual modeling functions:

- Describe the development of a plant using a small set of rules characterizing entire classes of modules, rather than individual modules;
- Characterize the physiological mechanisms controlling plant development in terms of information flow among the individual modules; and
- Apply similar modeling methodologies to individual plants (populations of modules) and entire plant ecosystems (populations of plants).

The concept of describing the development of a potentially unbound, or arbitrarily large, plant structure using a finite set of rules applying to all objects of the same type was introduced in 1968 by the biologist Aristid Lindenmayer [5] and is formally expressed in the definition of L-systems, as Lindenmayer defined it. An L-system model [10] is specified by listing the following three components:

Figure 1. L-system productions and the resulting developmental sequence of a compound leaf model. The apices are shown as thin lines, the internodes as thick lines [9].



- The set of module types, or "alphabet," of the L-system;
- The set of rewriting rules, or "productions," that capture the behavior of individual modules over predetermined time intervals; and
- The initial structure, or "axiom."

The terminology and structure of the L-system definition are evocative of formal language theory. Indeed, L-systems can be viewed as a type of formal grammar, distinguished from the better known Chomsky grammars, which are widely used to formally characterize both natural and programming languages, by their parallel application of productions. This parallelism reflects the simultaneous progress of time in all parts of the modeled plant.

Figure 1 illustrates the concept of L-systems through a simple model of a compound carrot-like leaf. This L-system operates on two classes of modules: terminal branch segments, called "apices," and the remaining segments, called "internodes." According to the first production of this L-system, an apex yields a branching structure consisting of an apex continuing the main axis, two lateral apices, and two internodes. The second production states that, over the same time interval, an internode doubles its length. The figure shows a developmental sequence generated from a single apex. In each step, all apices and internodes are transformed in parallel by their respective productions. The result is the intricate branching structure of a compound leaf.

This developing leaf has a fractal structure; that is, individual branches of different orders are similar to each other and to the whole leaf. This is an example

of the often-observed self-similarity of plants and results from the repetitive production of branches by the apices, followed by the gradual elongation of the internodes. The relationship between L-systems and fractals extends beyond plant models; L-systems can also be used to generate classic space-filling curves and other linear fractals discovered and popularized by Benoit Mandelbrot [10]. On the other hand, L-systems also capture structures and developmental processes in plants that do not have a fractal character.

Information Flow in a Developing Plant

The relative independence of plant modules raises the question of how these modules communicate and interact with one another. It is convenient to distinguish three forms of communication [9] among plant modules:

Lineage. The transfer of information from a parent module to its children. For instance, both productions in the compound leaf model in Figure 1 represent this form of information transfer, since the type and parameters of the predecessor modules define the successor structures completely.

Endogenous interaction.

The interaction resulting from information transfer between adjacent elements of the branching plant structure. The information could represent water, minerals, hormones, or the products of photosynthesis transported by plant tissues.

Exogenous interaction. The interaction resulting from information transfer through the physical space in which plants grow. Examples are the competition for space and light by branches of a tree and the competition for water by roots.

This classification of communication forces among plant modules is convenient in modeling practice, because different programming constructs are needed to express different communication forms. They can be most clearly differentiated using symbolic representation of productions, called “bracketed string notation” [5, 10]. The axes of a branching structure are represented by sequences of letters indicating the types of the constituent modules. Branches are enclosed in square brackets.

Bracketed string notation plays an important role in practice, because it provides the foundation in programming languages for specifying plant models.

Lineage, conceptually the simplest form of information transfer, is expressed using context-free productions, in which the predecessor is a single module. For example, the productions governing development of the compound leaf in Figure 1 have the form:

$$A \mapsto I(1)[+A][-A]I(1)A$$

$$I(x) \mapsto I(2x)$$

where A denotes the apex, $I(x)$ denotes an internode of length x , and the auxiliary symbols $+$ and $-$ indicate branching directions. In contrast, endogenous

interactions require the use of context-sensitive productions. In the case of such productions, the successor of a module being replaced by a production depends not only on this module itself but also on its neighbors. For example, production $S < I \mapsto S$, where $<$ separates the left context S from the strict predecessor I , will replace an I with an S only if there already is an S to the left of the I . Successive applications of this production to the initial string $SIIII$ will produce the

sequence of strings $SSIII$, $SSSII$, $SSSSII$, $SSSSSI$, $SSSSSS$. Thus, if S denotes an internode that has been reached by a signal (such as one representing a hormone) and I is an internode that has not yet been reached, the sequence can be interpreted as the propagation of a signal from the left to the right end of a sequence of internodes. Similarly, the right-context-sensitive production $I > S \mapsto S$ applied to the string $IIIIIS$ captures the flow of information from right to left.

Using parameters, a model can capture not only qualitative aspects of information flow—the absence or presence of a signal—but also quantitative measures, such as concentrations of water, minerals, and the products of photosynthesis transported by the plant [7]. Moreover, productions with a two-sided context make it possible to express communication mechanisms lacking a predefined direction, such as the diffusion of substances from modules with higher concentrations of a particular substance to modules with lower concentrations [10].

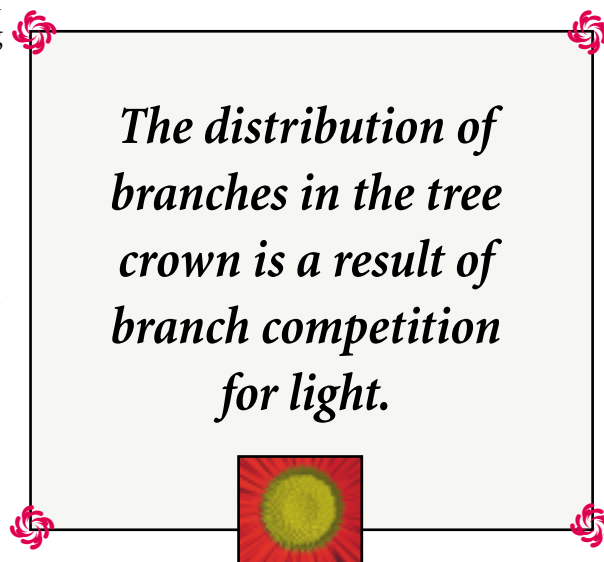


Figure 2. Models of green coneflower (left) and cacti (right) obtained using the collision-based algorithm [3].



Plant models governed by lineage and endogenous interaction can be viewed as closed cybernetic systems, because control information comes from the plant models themselves. In contrast, models involving exogenous interactions are “open” in the cybernetic sense. The information exchange between a plant and its environment can be conceptualized as a feedback loop in which the environment affects the plant and the plant reciprocally affects the environment. For example, a branch’s development may depend on its local light environment, which in turn depends on the shadows cast by other branches. Similarly, the development of roots may depend on the distribution of water in the soil, which is in turn affected by the absorption of the water by the roots.

To communicate with the environment, plant models need input and output constructs. Within the framework of L-systems, these constructs are called “communication modules” [7]. Syntactically, a communication module is treated the same way as any other symbol with associated parameters that might appear in an L-system production. However, parameter values of a communications module are not manipulated by L-system productions; instead, they

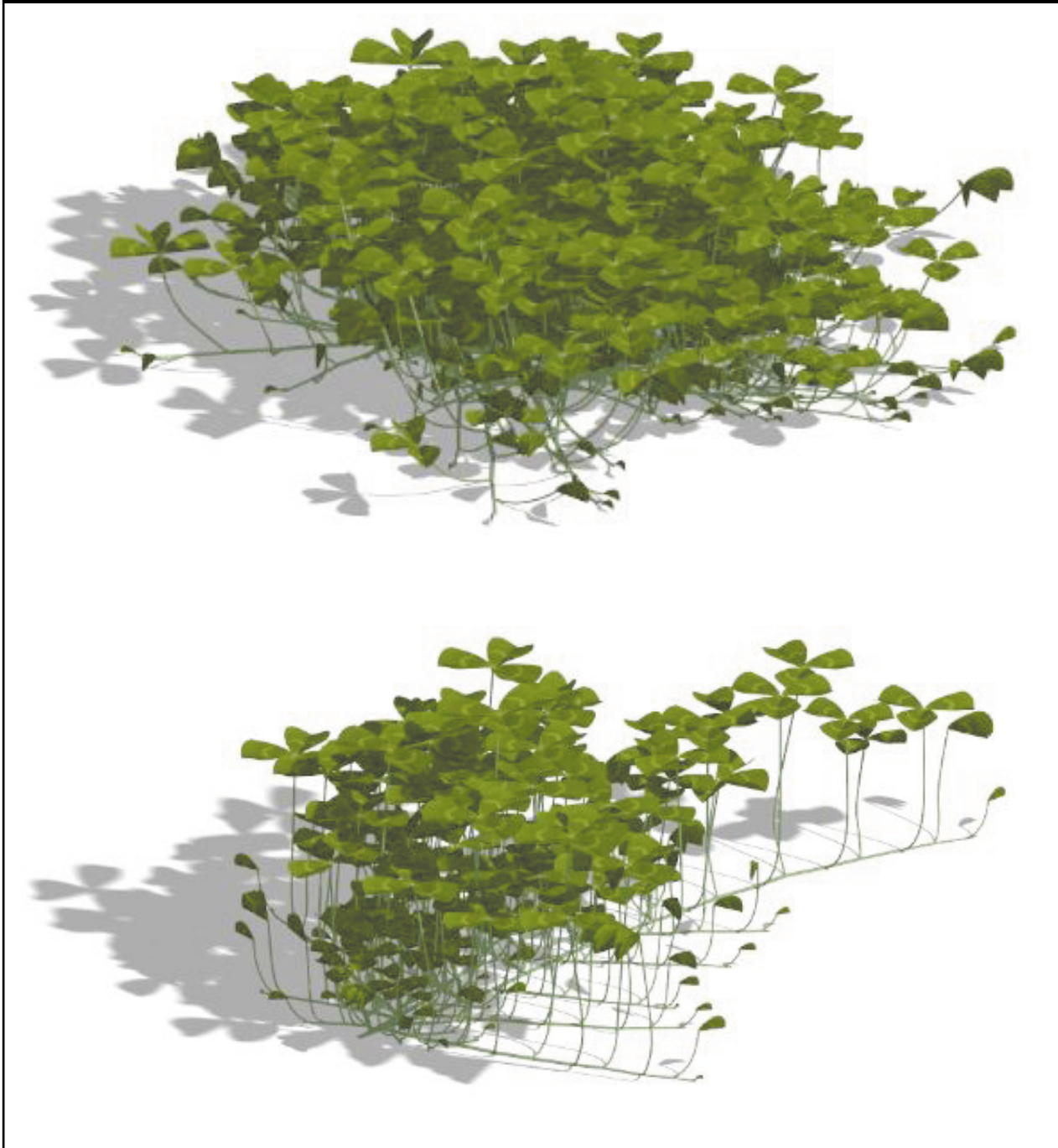
are sent to the environment (along with information indicating the position of the communication module in space), processed by the environment, and eventually set to new values representing the environment’s response.

Plant Development As Competition for Space

The three classes of control mechanisms—lineage, endogenous interaction, and exogenous interaction—make it possible to simulate an astounding variety of physiological processes and their resulting plant forms. They also reveal analogies between processes and structures taking place at different spatial scales and levels of plant organization. To illustrate this point, I focus on competition for space—one of the most critical biological aspects of plant development.

At a relatively small scale, competition for space is manifested by the arrangement of individual organs, such as leaves and flowers. This arrangement often takes the form of spiral patterns in which initials of the individual organs, or “primordia,” are tightly packed on their supporting surface, or the “recepta-

Figure 3. Models of clover plants, with branches and leaves competing for space mediated by light. The plant grown in full light (top) has a different shape from the one grown in shade (bottom) [4].

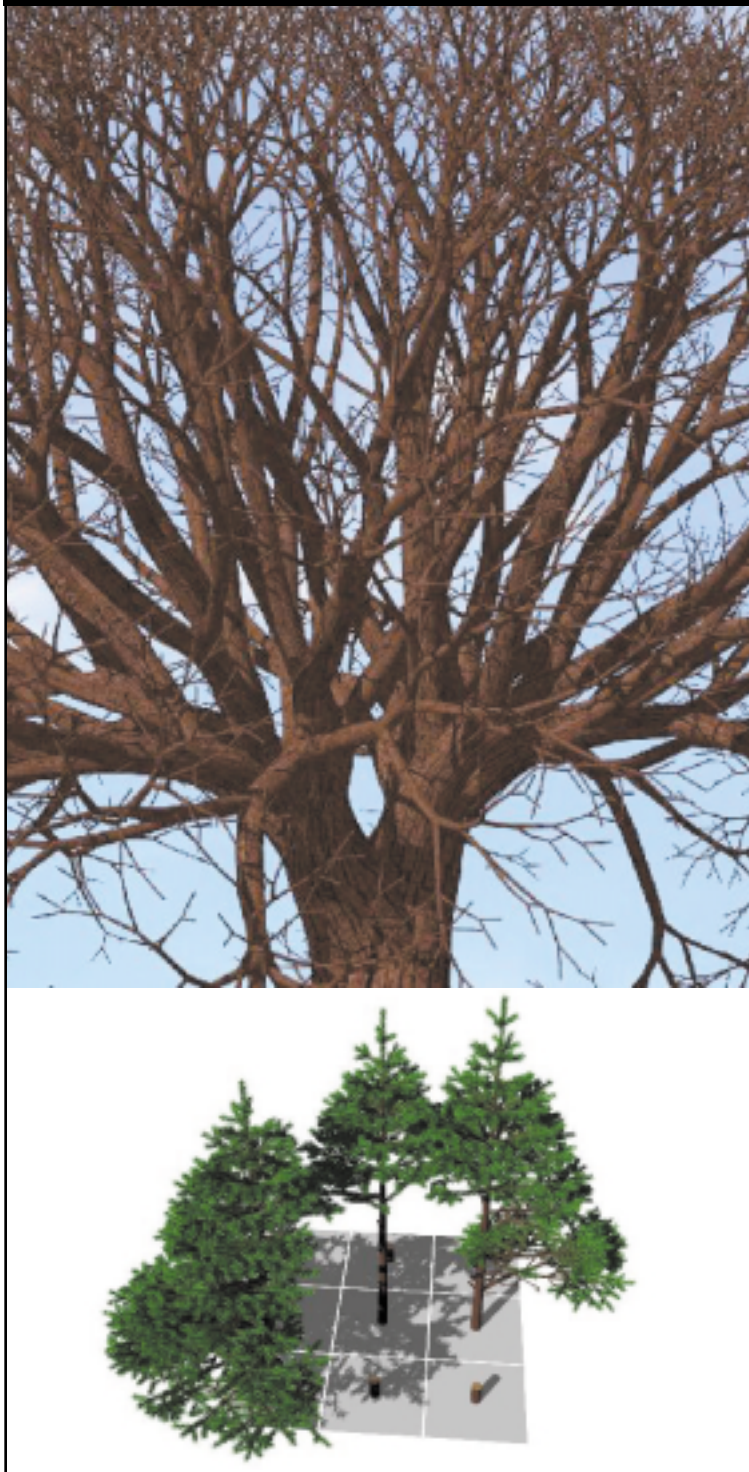


cle.” These patterns are commonly referred to as “spiral phyllotaxis,” which means literally the arrangement of leaves on the stem and in relation to each other; it is also commonly used to denote the arrangement of organs other than leaves as well. It is often observed in nature that the angle between consecutively issued primordia seen from the center of the receptacle approximates the golden angle $\phi \approx 137.5^\circ$ [10], which results from the partition of the

full angle of 360° by the “golden mean” number, one of the most important and extensively studied numbers in mathematics. For a long time, mathematicians and botanists have been fascinated by the frequent appearance of the golden angle and the regularity of the emerging spiral patterns in many plants and plant organs, including pine cones and sunflower heads.

Fully causal models have not yet led to realistic

Figure 4. Functional-structural models of a horse chestnut tree (a) and a stand of coniferous trees (b) simulating the effects of photosynthesis. Light reaching leaves causes production of photosynthates, which are used for maintaining leaves and branch segments and producing new branches. The surplus is transported toward the base of the tree. The tree sheds branches using more photosynthates than they produce [7].

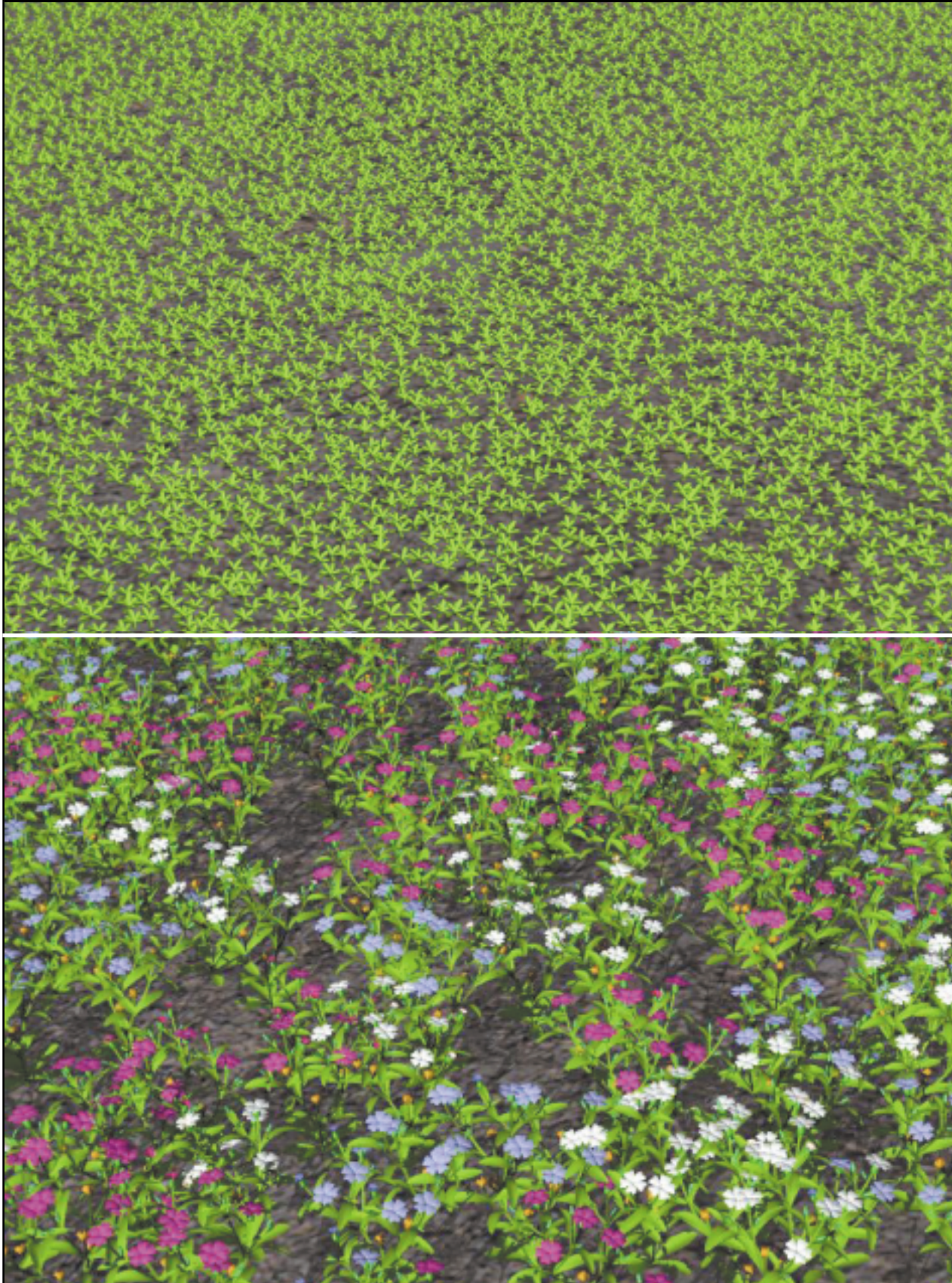


visualizations, but phyllotactic arrangements of plant organs have been reproduced by models including descriptive terms. For example, in the so-called collision-based model of spiral phyllotaxis [3], the golden angle is assumed as given, but the model uses an exogenous control mechanism—collisions between consecutively issued primordia—to space primordia with respect to each other in the radial direction. Figure 2 shows a flower head and an arrangement of cacti modeled using this principle.

In the case of phyllotaxis, competition for space leads to the positioning of the individual plant organs. In other cases, competition may determine whether or not organs, such as branches, will be formed or maintained by the plant. In nature, the proximity of other organs and competition for space are often mediated by light. For example, Figure 3 shows a model of clover in two contrasting light conditions. From biological studies, it is known that clover (as well as other plants) is sensitive not only to the intensity of light, which directly affects photosynthesis, but also by the ratio of the red and far-red components of the light spectrum [4]. This ratio is decreased in the light reflected by leaves and contributes to the perception of shade by the plant's light-sensitive organs.

In the model in Figure 3 (described in detail in [4]), light determines the length of internodes, the size and elevation of leaves, and the delay between the emergence of lateral buds and their further development into branches. The relationships between the local light environment and plant growth have been modeled according to experimental data. Light distribution was simulated using the Monte-Carlo method and stochastic sampling techniques. The model reveals the effect of self-shading and red/far-red ratio decrease on plant architecture; in the absence of these phenomena, patches of clover would become unrealistically dense. Moreover, external light conditions affect the shapes of the patches, which are approximately circular in high-intensity light and become elongated in low-intensity light. These changes correspond to observations of clover in nature.

Figure 5. Two stages of a simulation of self-thinning. Initially, the field consists of a large number of small plants (top); this number decreases as the plants grow and compete for space (bottom) [2].



In these models, the sites at which plant organs perceive environmental information—collision with other organs in phyllotaxis and local light intensity in clover organs—were assumed to be the same as the sites of the plant's responses. But in nature, this collocation of the sites of perception and response often is not the case. For example, the model of a deciduous tree in Figure 4a combines open L-system constructs for capturing interactions with the environment and context-sensitive productions for expressing transportation and allocation of resources within the plant [7]. (The physiological basis for this model was proposed by A. Takenaka [11].) Leaves (not shown so as to not block the tree's architecture) produce carbohydrates according to the amount of light they receive. These carbohydrates are used for maintaining the leaves themselves, for the branches supporting them, and possibly for the production of new branches. The surplus is transported by the branch toward the base of the tree. If the amount of resources needed to maintain the branch exceeds the amount it produces, and this state persists for some time, the tree sheds the branch. Thus, the distribution of branches in the tree crown is a result of branch competition for light.

Figure 4b shows a stand of coniferous trees, modeled according to the same principle. Six trees were removed from the stand to reveal the relationship between the shape of the crown and the position of the remaining trees. The trees at the corner and on the edge have asymmetric crowns; they retain their branches all the way down to the tree base when exposed to light. The tree in the center of the stand retains only its upper branches; lower branches were shed due to insufficient light. This result conforms to biological observations and could be used to estimate the optimal distance for planting real trees.

The group of trees in Figure 4b was modeled using the same technique as if a single tree were being modeled. Extensions of this approach to ecosystems with hundreds or thousands of plants are conceptually possible but present computationally challenging tasks. However, the time and space complexity of simulations can be reduced if they perform at two levels—

whole ecosystem and individual plant [2]. The distribution of plants and their general characteristics, such as size and age, are determined first. Detailed plant models, conforming to these characteristics, are then substituted for the coarse models. Figure 5 shows an example of an application of this technique. The model captures the essence of “self-thinning,” a fundamental ecological process in which the number of plants in a field decreases gradually as the individual plants grow in size and therefore compete for space.

The concept that a plant can be viewed as a population of its components bridges the modeling of individual plants with the modeling of entire ecosystems; therefore, processes and structures occurring at a wide variety of levels can be captured in a unified manner.

Conclusions and Further Research

Simulation-based plant modeling makes it possible to capture the mechanisms of plant development in a biologically sound and visually realistic manner. The interdisciplinary character

of plant modeling research is reflected in the diversity of existing and prospective applications of the models. Some models seek to increase our knowledge of plant development and apply this knowledge to plant management in horticulture, agriculture, and forestry. Virtual plants are being introduced to study the effects of pruning, pinching, and spacing on plant development, analyze the effects of grazing on pasture plants, and investigate the effects of pesticides on insects foraging on plants [8]. Simulation models are also being used to analyze optimal plant design from an evolutionary perspective.

Other models focus on image-synthesis applications. Such models have been included in computer animations and games, manipulated in virtual reality installations, incorporated into animations and multimedia presentations for educational purposes, used to visualize the development of extinct plants, incorporated into computer-assisted landscape and garden designs, and applied to the visual-impact analysis of forest harvesting. Realistic plant models have also been proposed for use in plant registries (holding descriptions of different plant varieties developed by breeders) and for advertising orna-

Conceptually, the most exciting open problem is how to incorporate genetic mechanisms into the simulation models of plants.



mental plant varieties to potential customers.

Experience with simulation-based plant modeling also reveals problems requiring further research. Construction of well-calibrated models of individual plant species is a tedious process, because it requires extensive experimental data and may involve examination of alternative models when the exact nature of the processes in plants is not well understood. Development of a methodology that would accelerate construction of well-calibrated models is therefore important to biologists and applied plant scientists.

Conceptually, the most exciting open problem is how to incorporate genetic mechanisms into the simulation models of plants. This research question could lead to new insights into the fundamental mechanisms of development—from genes all the way to the final forms of the plants around us—and further advance our understanding of nature through the synergy of biology, computer science, and art. **□**

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