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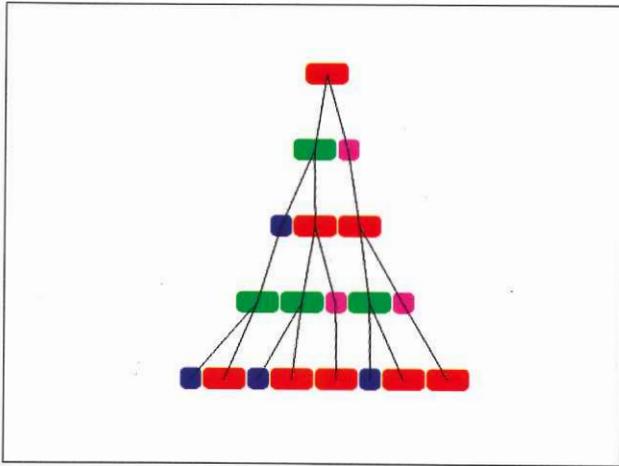
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figure 1. development of a filament (*Anabaena catenula*)

garden of L

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An attempt to re-create the structures and processes of life is immensely appealing to the imagination, balancing on the frontier between science and fiction. Known results [Langton 1988] range from the design of self-reproducing genetic messages to the replication of social behavior of animals. Between these extremes lie models of self-assembling viruses and simulations of multicellular organism development. As in physically-based modeling, where an astonishing degree of realism has been obtained by adhering to the fundamental laws of physics, realistic models of living structures can be produced by referring to biological mechanisms of development. The challenge of biologically-based modeling is reinforced by the fact that biological laws are often expressed qualitatively, without providing enough detail to construct a definitive model. Consequently, an attempt to simulate reality brings an insight into the nature of the underlying biological processes and structures.

In this article we outline our recent results related to the modeling of plants and simulation of their development. Many of these results were obtained in cooperation with Professor Lindenmayer and his students from the Theoretical Biology Group at the University of Utrecht. Technical details are presented in a paper by Prusinkiewicz, Lindenmayer and Hanan [1988].

As the primary tool for the modeling of plants, we employ the formalism of L-systems, originated by Lindenmayer [1968] as a mathematical description of plant development on the cellular level, and introduced to computer graphics by Smith [1984]. This formalism represents a plant structure using a sequence of symbols, each cor-

responding to a plant component or "module". In the modeling of lower plants, such as bacteria, algae, or fungi, symbols usually represent individual cells. In the case of higher plants, such as herbaceous plants and trees, cells are too low-level to serve as the basic modules. Consequently, the model is usually expressed in terms of structural components such as internodes (tree segments between two consecutive branching points), apices, and organs (leaves, flowers and fruits).

The process of producing new modules from existing ones is essential to biological development. On the microscopic scale, cells subdivide and produce new cells. On the larger scale, apices initiate new branches terminated with their own apices. The formalism of L-systems represents such processes using rewriting rules or productions. These terms, borrowed from formal language theory, denote rules for the substitution of string symbols. In contrast to the wider known Chomsky grammars which operate in a sequential manner, L-systems are inherently parallel. In other words, all symbols in a string are rewritten in a single step. This corresponds with the developmental processes in plants, where subdivision may occur simultaneously in many plant parts.

For example, let us consider the developmental simulation of a multicellular filament such as is found in the bacteria *Anabaena catenula* and various algae [Mitchison and Wilcox 1972, Lindenmayer 1982]. The symbols a and b represent cytological states of the cells (these states correspond with their sizes and readiness to divide). The subscripts l and r indicate cell polarity, specifying the positions in which the daughter cells of type a and b will be produced. The development is governed by an L-system comprised of four rules:

$$a_r \longrightarrow a_l b_r, \ a_l \longrightarrow b_l a_r, \ b_r \longrightarrow a_r \ \text{and} \ b_l \longrightarrow a_l$$

Starting from a single cell a_r, this L-system generates the following sequence of strings:

a_r
$a_l b_r$
$b_l a_r a_r$
$a_l a_l b_r a_l b_r$
$b_l a_r b_l a_r a_r b_l a_r a_r$

...

Under a microscope, the cells appear as cylinders of various lengths. The a-type cells are longer than the b-type cells. The corresponding schematic image of filament development is shown in Figure 1.

In spite of its simplicity, the above example illustrates two important features of L-systems. First, the formalism is capable of amplifying the data base [Smith 1984], i.e. producing large, complex structures from very concise descriptions. Secondly, this amplification occurs by simulating the developmental processes which yield particular structures in nature. Thus, a model constructed with biological processes in mind can be directly applied to show entire developmental sequences. This point is illustrated by Figures 2-4.

Figure 2 represents four developmental stages of a leaf of the moss *Phascum cuspidatum*. *Phascum* leaves consist of single layers of cells, which makes them particularly suitable for detailed analysis under a microscope. An extension of L-systems from strings to graphs with cycles was introduced by Lindenmayer and Rozenberg [1979] under the name of map L-systems, and first applied to automatically plot cellular structures by de Does and Lindenmayer [1983]. The model shown in Figure 2 was generated using a map L-system devised by Martin de Boer.
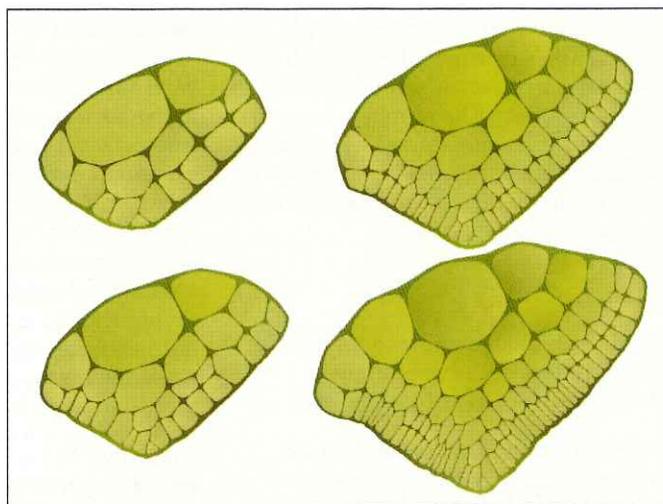
Figure 3 shows the development of a flowering plant, *Lychnis coronaria*. Its growth pattern was analyzed and expressed mathematically using a formalism similar to L-systems by Robinson [1986]. Figure 4 shows the development of *Mycelis muralis*, analyzed and formalized by Janssen and Lindenmayer [1987]. The flowering sequence of *Mycelis* is quite complicated from the viewpoint of control mechanisms employed by the plant. This is exhibited by the basipetal flowering sequence, i.e. progression of the blooming zone from the topmost parts of the plant towards its base. Since the oldest branches are near the plant base and the youngest ones are near the top, the basipetal sequence is counter-intuitive: the younger a branch is, the sooner it will produce flowers! In living plants such effects are controlled by hormones which flow across the branches and time subordinate processes. Accordingly, simulated flow of three hormones is the key to the *Mycelis* model.
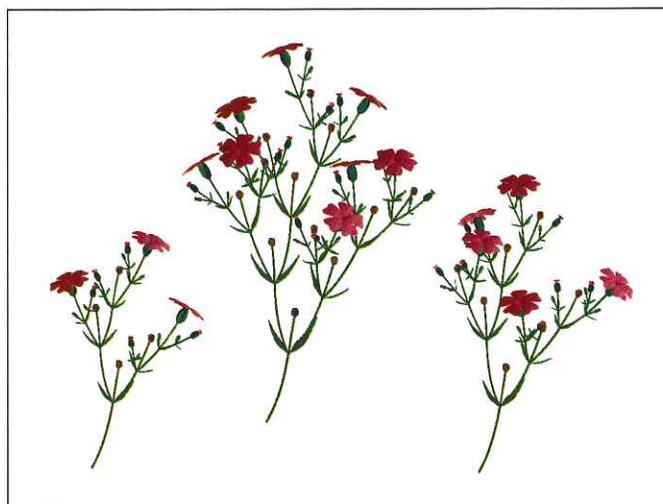
To present the link between biological reality and model construction in more detail, let us consider the example of a synthetic image "The Garden of L" (see cover). The central object of the scene is a lilac inflorescence. Its model incorporates the following rules, based on the analysis of real inflorescences:

1. topology

a) The inflorescence has a recursive structure, with lower branches approximately replicating the higher portion of the inflorescence.

b) The first 2-8 lateral branches, counting from the

figures 2-4: *Phascum cuspidatum, Lychnis coronaria, Mycelis muralis*

apex of the mother branch, consist of an internode terminated by a single flower. The subsequent lateral (child) branches carry second-order (grandchild) branches. The number of second-order branches carried by a lateral branch increases linearly while traveling along a mother branch axis from the apex towards the base.

2. branching angles

a) Lateral branches occur in pairs. The axes of the consecutive pairs lie in planes perpendicular to each other.

b) The branching angle between the axes of the mother and the child branch is equal to 60 degrees.

c) If A is a mother branch, B is its child branch, and C and D are two grandchildren closest to the base of B, then the plane containing the axes of branches C and D is perpendicular to the plane defined by the axes of branches A and B.

3. proportions

a) All flowers within an inflorescence are approximately in the same developmental phase and have the same size.

b) The lengths of consecutive internodes along any axis form an arithmetic series, with the longest internode at the axis base.

c) The mother axis internode and the lateral internodes originating at a given branching point all have approximately the same length.

The information about proportions is the most difficult to infer, not only in the case of lilac, but generally in all plants. In contrast to the branching angles, which are fairly constant within a given plant species, the internode lengths are strongly influenced by the environment in which the plant develops. Consequently, the general rules governing proportions between plant components are masked by individual

variations. A statistical analysis of a large number of inflorescences could reveal the underlying rules, but would be very time-consuming (and deadly to the flora around the graphics lab). In practice, it is simpler to assume the existence of a functional relationship between the lengths of the consecutive segments and their ordering numbers, and experimentally choose a function yielding correct proportions of the entire structure. In the case of the lilac inflorescence, the correct proportions were obtained assuming a linear function.

According to the developmental approach to modeling, the target plant structure results from a simulated growth process. In the case of lilac inflorescences, the consecutive segments of each axis as well as the lateral branches are produced exclusively by the apex (this type of development is known as subapical growth). As the internodes elongate in time, their lengths gradually increase while progressing from young internodes near the apex towards the older ones situated near the base. Thus, the spatial structure of an inflorescence results from the timing of the underlying developmental processes.

The branching structure of internodes forms the inflorescence skeleton, bearing the individual flowers. A single flower is small compared to the size of the entire inflorescence and can be adequately modeled by a collection of five bicubic surfaces which represent the four petals and the calyx. In contrast, the foreground lilac leaves in the Garden of L result from developmental processes. The midrib and the lateral "veins" form branching structures on which the blades are built. The overall leaf shape results from the sequence of angles under which the veins meet the midrib, and the relationship between their respective growth rates.

An interesting problem is related to the positioning of leaves on twigs. In

principle, the leaves follow a pattern similar to that of lateral branches in inflorescences. They occur in pairs, with the stems of the consecutive pairs lying in planes perpendicular to each other and branch from the twig at an angle of 60 degrees. However, external factors, namely gravity and sun light, play an essential role in positioning the leaves so that they hang down and have blades facing the sun. The combined effect of gravity (negative geotropism) and sunlight is also responsible for curving the twigs up. These effects can be observed in the background lilac twigs. The specimen-to-specimen variation between the twigs was simulated by incorporating stochastic mechanisms into L-systems.

Compared to the lilac inflorescences, the apple twigs appearing in the upper left corner of the Garden of L and detailed in Figure 5 have a relatively simple structure. The short lateral branches leave the main axis at equal intervals. Each branch carries six leaves and six flowers. Essential to the model is the spiral arrangement of lateral branches along the main axis, and leaves encircling each branch. In both cases, the angle between consecutively placed elements (branches of leaves) is close to 137.5 degrees. Stevens [1974] provides the following intuitive explanation:

"Why that special angle? Because it has something to do with plant tissues? No. The angle only sets the points in proper relation to one another, so that each point makes a small angle with the older point in the previous whorl and a large angle with the younger point. That relation comes about quite naturally in the meristem of the plant as a direct result of each stalk's fitting the gaps of other stalks. ... The plant uses no mathematics, it simply grows the stalks where they have the most room."

The angle of 137.5 degrees also occurs in the daisies which grow in the lower right corner of the Garden of L; a magnified view of the flower capitulum is shown in Figure 6. The spiral arrangement of the florets results from the following formula, attributed to Erickson:

$$\partial = n*137.5° \qquad r = C \ \sqrt{n})$$

where:

- ∂ is the angle between a reference direction and the position vector of the n-th floret in the polar coordinate system originating at the capitulum center, and

- r is the distance between the capitulum center and the center of the n-th floret, given a constant scaling parameter.

The square-root relationship between the distance r and the floret ordering number n has a geometric explanation. Assuming that all florets have the same size and are densely packed, the total number of florets which fit inside a disk of radius r is proportional to the disk area. Thus, the ordering number n of the most extremely positioned floret in the capitula is proportional to r^2, or $r = C \sqrt{(n)}$.

Let us abstract from the details of the Garden of L to look at plant modeling from a larger perspective. What are the implications of the biologically-based approach? In the practical domain, plant models are useful in at least two areas. On one hand, simulated plants can be incorporated into computer-generated images of architectural projects, thus increasing their degree of realism. The developmental nature of the model makes it possible to anticipate landscape changes over time. On the other hand, computer simulations offer an unprecedented tool for the quantitative analysis of developmental mechanisms in plants. Real-life processes which occur in the time scale of months or years can be speeded up to seconds or minutes during computer simulations. Critical parameters, such as hormone propagation rates, can be easily modified. Hypothetical control mechanisms can be implemented and their implications visualized.

The realistic rendering of developmental models creates an illusion of life. It is easy to forget the underlying mathematical formalism and simply see plants growing, self-replicating, responding to external factors, even mutating. Although they are mere computer processes, we are fascinated by their life-like appearance and behavior.

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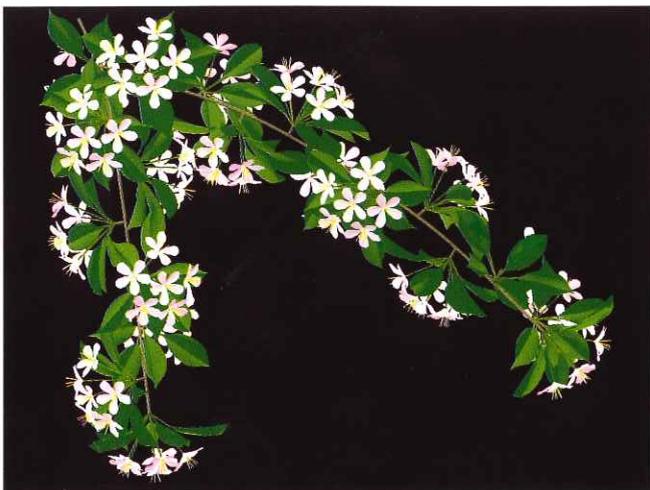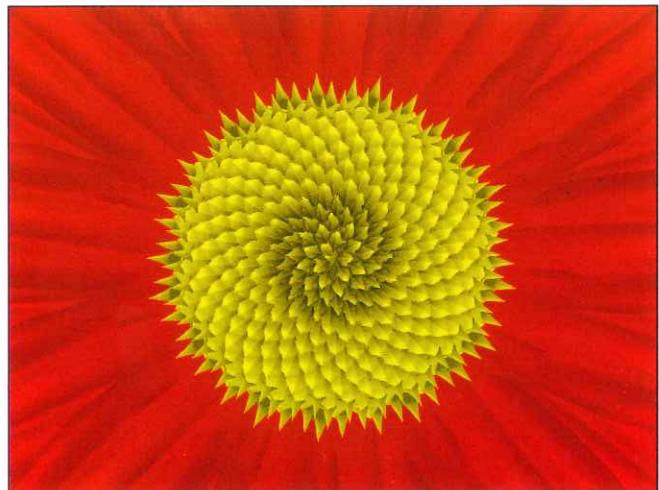Stevens, P. S. [1974]: *Patterns in Nature*. Little, Brown and Co., Boston.

figure 5: an apple twig

figure 6: capitulum of the painted daisy