Visual Models of Morphogenesis

Abstract Rapid progress in the modeling of biological structures and simulation of their development has occurred over the last few years. It has been coupled with the visualization of simulation results, which has led to a better understanding of morphogenesis and given rise to new procedural techniques for realistic image synthesis. This paper reviews selected models of morphogenesis with a significant visual component.

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If a natural object or organism demonstrates consistency of form ..., such symmetry is the consequence of Something rather than Nothing.

Adrian D. Bell [3]

Introduction

In the 1984 paper, "Plants, Fractals, and Formal Languages" [60], addressed to the computer graphics audience, Smith coined the term *database amplification* to denote the synthesis of complex images from small data sets. A generalization of this notion, called *emergence*, became a central concept of *Artificial Life*. According to Taylor [62, p. 31], emergence is a process in which a collection of interacting units acquires qualitatively new properties that cannot be reduced to a simple superposition of individual contributions. A well-known example of emergence is given by the *game of life* [19, 20], where complex patterns develop in an array of square cells governed by strikingly simple local rules. The development of patterns and forms in the domain of living organisms has been termed *morphogenesis*.

The relationship between the rules expressing the behavior of individual components and the resulting developmental processes, patterns, and forms is often nonintuitive and difficult to grasp. Consequently, computer simulations play an essential role in the study of morphogenesis. The objectives of such simulations were analyzed and illustrated using many examples by Bell [4], who grouped them as follows:

- analysis of the nature and complexity of the mechanisms that control the developmental processes,
- a better understanding of the form and development of specific organisms, acquired in the process of constructing models faithful to the biological reality,
- analysis of the impact of individual parameters on the overall form or pattern; this leads to a better appreciation of their relationship, and gives an insight into the direction of evolutionary changes,

- computer-assisted teaching,
- graphic design, computer art, and landscape architecture.

Visualization techniques offered by computer graphics facilitate the interpretation and evaluation of simulation results. In the absence of a formal measure of what makes two patterns or forms look alike, it is often necessary to rely on visual inspection while comparing the models with the reality. For example, Plate 1 shows a photograph and a model of the shell *Natica enzona*, juxtaposed to facilitate the comparison. The natural and synthetic pigmentation patterns differ in details, yet we perceive them as similar. Photorealistic presentation adds credibility to this observation by removing artifacts that might affect the comparison. We conclude that the underlying mathematical model of shell pigmentation pattern is plausible, although visual inspection obviously does not constitute a definitive validation.

This paper reviews mathematical models of morphogenesis capable of producing realistic images of biological patterns and forms. It begins with a list of notions useful in characterizing these models, then presents selected case studies. An extension of this work may lead to a taxonomy of the models of morphogenesis, systematically contrasting their underlying assumptions and exposing approaches that require further exploration.

2 Features of Models of Morphogenesis

Historically, the study of morphogenesis has been approached from two directions. The first one consists of viewing form as a derivative of growth, and was formulated by d'Arcy Thompson [63, p. 79]: "It is obvious that the *form* of an organism is determined by its rate of *growth* in various directions; hence rate of growth deserves to be studied as a necessary preliminary to the theoretical study of form."

The second direction focuses on the flow of substances through a medium and was initiated by Turing [65, p. 38]: "The systems considered consist of masses of tissues which are *not growing*, but within which certain substances are reacting chemically, and through which they are diffusing. These substances are called *morphogens*, the word being intended to convey the idea of a form producer."

The distinction between these two directions is captured as the first characteristic of the models, presented in the following list. Other characteristics also determine the essential properties of the models and influence the design of the simulation software.

- 1. Models may occupy constant space or may expand (and contract) over time. In the latter case, the expansion may be limited to the boundary of the structure or may take place in the interior as well.
- 2. Models may be structure-oriented, focusing on the components (modules) of the developing structure, or space-oriented, capturing the whole space that embeds this structure. A model in the first category typically describes where each component of the structure is located. A model in the second category describes what is located at (or what is the state of) each point of space.
- 3. The developing structure and the space that embeds it may be continuous or discrete. The state characterizing each module or point in space may be chosen from a continuous or discrete domain. The model may operate in continuous or discrete time.
- 4. Models may have different topologies, such as a nonbranching filament (a linear

arrangement of components), a branching structure, a network (graph with cycles), a two-dimensional surface, or a three-dimensional solid object.

- 5. The neighborhood relations between modules may be fixed at the time of their creation (determined by the division pattern of modules), or the modules may be mobile. By analogy, in the case of continuous structures, the developmental processes may be viewed as taking place in an elastic medium or in a fluid.
- 6. Communication between the modules may have the form of lineage (information transfer from the parent module to its offspring) or interaction (information transfer between coexisting modules). In the latter case, the information flow may be endogenous (between adjacent components of the model) or exogenous (through the space embedding the model). Similar notions can be applied to continuous structures.

The last categorization captures the crucial aspects of the flow of control information during morphogenesis, first emphasized by Lindenmayer [34, 35]. Refering to branching structures, Bell [4] proposed to call patterns created using these modes of communication blind, self-regulatory, or sighted, and offered the following intuitive descriptions:

- In blind patterns, branch initiation is controlled by the parent module, independently of the remainder of the structure and the environment in which this structure develops.
- In self-regulatory patterns, branch initiation is controlled potentially by the whole developing structure, using communication via the existing components of this structure.
- In sighted patterns, the initiation of a new branch is influenced by factors detected by its parent in the immediate neighborhood, such as proximity of other organisms or parts of the same organism.

In the following survey of selected models of morphogenesis, the distinction between space- and structure-oriented models serves as the main key, while the communication modes further characterize the structure-oriented models.

3 Space-Oriented Models

3.1 Reaction-Diffusion Pattern Models

Reaction-diffusion models were developed by Turing [65] to explain the "breakdown of symmetry and homogeneity," leading to the emergence of patterns in initially homogeneous, continuous media. The patterns result from the interaction between two or more morphogens that diffuse in the medium and enter into chemical reactions with each other. Mathematically, this process is captured by a system of partial differential equations. For properly chosen equations and parameter values, the uniform distribution of morphogens is unstable. Random fluctuations are amplified and produce a stable pattern of high and low concentrations.

Reaction-diffusion models have been extensively studied in theoretical biology, where they provide plausible explanations of many observed phenomena [28, 42, 47]. Ouyang and Swinney [49] recently validated the basic assumptions of these models by realizing reaction-diffusion processes in chemical experiments. In computer graphics, Turk [66] applied the original Turing equations to generate spot patterns, and a five-morphogen system proposed by Meinhardt [42, chap. 12] to generate stripe patterns



Figure 1. A venation pattern generated using Meinhardt's model of netlike structures on a hexagonal grid.

covering three-dimensional models of animals. Meinhardt and Klinger [43–45] applied the reaction-diffusion model to capture pigmentation patterns in shells. In this case, an observable pattern does not reflect a steady-state distribution of morphogens on the surface of the shell, but depicts the evolution of morphogen concentrations on the growing edge over time. Meinhardt's model has been applied by Fowler, Meinhardt, and Prusinkiewicz [15] to synthesize realistic images of shells (Plate 2). Pigmentation patterns have also been synthesized by Ermentrout, Campbell, and Oster [10], assuming that the concentration of the pigment is controlled by neural activities of the mollusc's mantle. As noted by Murray [47, p. 518], the reaction-diffusion and the neural activity models postulate similar types of information exchange along the shell edge (shortrange activation and long-range inhibition).

Reaction-diffusion models may also be suitable for explaining and synthesizing the visually attractive arrangements of fish and reptile scales, patterns on butterfly wings, and coloring of flower petals. The generation of these patterns remains, to a large extent, an open problem.

3.2 A Reaction-Diffusion Model of Differentiation

Meinhardt [41] (see also [42, chap. 15]) extended reaction-diffusion models to capture differentiation of netlike structures from an undifferentiated medium. Figure 1 shows a venation pattern produced using his model. The reaction-diffusion equations are solved on a hexagonal grid (in this case). The state of each cell is characterized by concentrations of four morphogens, one of which determines whether a cell is in a differentiated state and belongs to the structure or in a nondifferentiated state and belongs to the structure or in a nondifferentiated state and belongs succession of differentiated cells, extending at the growing tip of the filament. During the development, the tip may split, creating dichotomous branches. At a sufficient distance from the tip (monitored by decreasing concentration of another morphogen,



Plate I. A photograph and a model of Natica enzona (Fowler, Meinhardt, & Prusinkiewicz, 1992).



Plate 2. Three shell models with pigmentation patterns generated using the reaction-diffusion models: *Volutoconus bednalli*, *Oliva porphyria*, and *Conus marmoreus* (Fowler, Meinhardt, & Prusinkiewicz, 1992).





Plate 3. The Eden model of accretive growth. Colors indicate the times in which cells are adjoined to the cluster (James & Prusinkiewicz, 1993).



Plate 4. Diffusion-limited growth. Colors indicate concentrations of nutrients in the medium (James & Prusinkiewicz, 1993).





Plate 5. A model of a sponge-like structure (Kaandorp, 1992).



Plate 6. A model of a tree trunk with roots (Greene, 1991).





Plate 7. Developmental model of Mycelis muralis (Prusinkiewicz & Hanan, 1987).



Plate 8. Development of a hawkweed flower *Hieracium umbellatum* simulated using a differential L-system (Hammel & Prusinkiewicz, 1993).

Plate E



Plate 9. Spruce trees synthesized using a particle system model expressed as a stochastic L-system (Orth, 1993).



Plate 10. A garden with trimmed trees (MacKenzie, 1993).





Plate II. A photograph of thalli of Microsorium linguaeforme (de Boer, 1988).



Plate 12. Development of a thallus of *Microsorium linguaeforme* simulated using a map L-system (Fracchia, Prusinkiewicz, & de Boer, 1990).



Plate 13. Simulation of mobile cells interacting in a continuous medium (Fleischer & Barr, 1993).

the inhibitor, produced by the tip), the filament initiates lateral branches. Next-order branches are formed in a similar way if no growing tips are nearby.

This model combines continuous and discrete components. On the one hand, the diffusion of morphogens is described using a set of differential equations, if one assumes a conceptually continuous medium. On the other hand, differentiation is described at the level of discrete cells.

3.3 Diffusion-Limited Accretive Growth

In many developmental processes, there is an obvious distinction between the structure and the surrounding medium. The focus of the model is then on the structure and its gradual expansion along the border, termed *accretive growth* [31].

Eden [9] simulated the accretive growth of a cell cluster in a square lattice by sequentially adjoining randomly selected cells to the structure formed during previous steps (Plate 3). Meakin [40] (see also [68]) improved this model by assuming that the growth rate (the probability of adjoining a new cell) depends on the local concentration of nutrients that diffuse from a surrounding exterior source and are consumed by the growing structure. The structure generated by this diffusion-limited growth model depends on the choice of parameters and may display a branching fractal character common with the diffusion-limited aggregation models (Plate 4), discussed later. Fujikawa and Matsushita [18, 39] showed that these models faithfully capture the growth of colonies of a bacterial species *Bacillus subtilis* on agar plates. Kaandorp [31, 32] applied a three-dimensional variant of the diffusion-limited growth to simulate and visualize the development of corals and sponges that expand in the direction of the largest concentration of nutrients (Plate 5). A branching topology is an emerging property of these structures, resulting from the higher gradient of nutrient concentration near the tips of the branches than near the origin of the structure.

3.4 Diffusion-Limited Aggregation

Witten and Sander [70] proposed a discrete counterpart of diffusion-limited growth, called *diffusion-limited aggregation* (DLA) (see also [68]), which captures diffusion of nutrients by simulating random movement of particles in a grid. The growing structure originates with a single fixed cell. Free particles move in the grid, with the displacement direction chosen at random on each simulation step. Once a moving particle touches the structure, it sticks to it rigidly.

Diffusion-limited aggregation has attracted considerable research interest, due in part to the fractal character of the emerging branching structures. It is a faithful model of many physical phenomena, such as the deposition of metallic ions on an electrode. It neglects, however, the active role of the organism using nutrients to build its body.

3.5 Cellular Automata

Cellular automata [64] can be considered a discrete-space counterpart of reactiondiffusion models. The space is represented by a uniform grid, with each site or cell characterized by a state chosen from a finite set. Time advances in discrete steps, and all cells change their states according to the same rule, which describes the next state as a function of the previous state of a cell and its close neighbors.

Young [71] proposed a cellular-automaton model of animal coat patterns using only two cell states: pigmented or not (Figure 2). Camazine [5] applied a cellular automaton to convincingly reproduce the pattern of a rabbit fish. The resulting patterns are similar to those obtained using continuous reaction-diffusion equations.

In general, the next-state function need not be related to the diffusion of morphogens. Ulam [67] pioneered the application of cellular automata to the simulation of the development of branching structures, where the discrete space provides a medium



Figure 2. Patterns generated using a discrete counterpart of the reaction-diffusion model, proposed by Young.



Figure 3. A branching structure generated by Ulam's cellular automaton operating on a square grid.

for detecting collisions between branches. Figure 3 shows a pattern he termed *Maltese crosses*. The structure begins with a single seed cell and spreads within the (conceptually infinite) square grid of automata. In each iteration, the pattern expands to the adjacent cells, unless the resulting branches would collide. Figure 4 illustrates the same principle on a triangular grid. A slice of this pattern contained in a 60° wedge is reminiscent of a tree; as noticed by Stevens [61, pp. 127–131], this appearance can be reinforced by modifying branching angles while preserving the topology of the model.

3.6 Voxel Automata

Three-dimensional extensions of cellular automata, called *voxel automata* [24], have been used in computer graphics to model aspects of plant development strongly affected by the environment. Arvo and Kirk [2] and Greene [23] applied them to simulate the growth of climbing plants, attaching themselves to predefined objects in space.



Figure 4. Branching structures generated by Ulam's cellular automaton operating on a triangular grid. Lines connect the centers of cells occupied by the growing structure.

Subsequently, Greene [24] extended this technique to capture variations in the diameter of branches and roots of a tree, and applied it to simulate the growth of roots searching their path through rocks in the ground, as shown in Plate 6. In this case, the voxels do not represent elements of the structure on the "all or nothing" basis but hold information about the run of the individual strands that compose branches and roots of the tree. This information is used to keep groups of strands together and guide their development between obstacles in the environment.

3.7 Development in Expanding Space

The models discussed so far can grow only on their boundary. Gottlieb [22] overcame this limitation by proposing a geometric model of development, in which the space expands uniformly. A predefined starting structure is placed in a small square grid (e.g., consisting of 2×2 cells). New branches are created by connecting the centers of grid cells to the structure, provided that the Euclidean distance between a particular center point and the structure is greater than a given threshold. The structure and the cellular space are then scaled twofold, the cells are subdivided, and connections to the centers of the new cells are made as in the previous step. This process is equivalent to the subdivision of the grid combined with the reduction of the threshold distance. The construction is repeated until the desired level of detail is reached, as presented on the left side of Figure 5. The right side of this figure shows the result of applying Gottlieb's method to model leaf venation. This application has a clear biological justification: As a leaf grows, its vascular system is developing in order to maintain the capacity for translocating water, nutrients, and products of photosynthesis to and from all parts of the blade. The model exhibits the hierarchical organization of the veins, but there is still a discrepancy between their layout and patterns observed in nature. Faithful modeling of leaf venation remains an open problem.

4 Structure-Oriented Models

In contrast to space-oriented models, which describe the entire space including the modeled structure, structure-oriented models focus only on the development of components that constitute the structure.



Figure 5. Principle of Gottlieb's method for pattern generation, and a venation pattern obtained using this method.

4.1 L-Systems

L-systems simulate the development of linear and branching structures built from discrete modules [34]. The development can be controlled by lineage (in context-free, or 0L-systems) and by endogenous interaction (in context-sensitive, or IL-systems). The modules represent individual cells of simple multicellular organisms, or larger modules of higher plants (e.g., internodes, apices, leaves, and branches). L-systems were originally limited to the specification of the topology of branching structures, but subsequent geometric interpretations have made it possible to visualize simulation results [52, 53]. For example, Plate 7 shows a simulated development of the herbaceous plant *Mycelis muralis*.

Although L-systems were introduced as a purely discrete model [36], practical applications revealed the need for shifting their various aspects to the continuous domain. Parametric L-systems [27, 52] have made it possible to assign continuous attributes to modules, such as the concentrations of substances propagating in a structure. Differential L-systems [51] extended this formalism to the continuous time domain, facilitating computer animation of developmental processes. For example, Plate 8 shows selected phases of the development of the hawkweed flower *Hieracium umbellatum*, simulated using differential L-systems.

L-systems are related to several other plant models. As shown by Prusinkiewicz and Lindenmayer [52, chap. 2], parametric L-systems can reproduce the tree models developed by Aono and Kunii [1], which in turn were based on models by Honda [29]. Françon [17] observed that L-systems can also capture the models of tree architecture classified by Hallé, Oldeman, and Tomlinson [26], and the AMAP models originated by de Reffye and his collaborators (for example, see [8]). Orth [48] constructed stochastic L-systems that approximately emulate the particle-system models of trees and grass proposed by Reeves and Blau [56] (Plate 9). Further analysis is needed to establish detailed relationships between all these models.

4.2 Branching Structures with Exogenous Control

While L-systems do not capture, in principle, the exogenous control mechanisms (the models are not "sighted"), such mechanisms were included in a number of other models of branching structures. Historically, the first model was proposed in 1967 by Cohen [6], who considered the development of a two-dimensional branching structure guided by a continuous "density field." The gradient of the density function indicated the least crowded regions available for the apical growth of each branch. Cohen suggested that his model may approximate the venation patterns in leaves, and the growth and branching of neural axons. A related model of the axon growth was proposed by Gierer [21]. Bell [3] and Ford [14] investigated idealized models of branching structures that included a mechanism for aborting the development of modules surrounded by an excess of neighbors. Honda, Tomlinson, and Fisher [30] used a similar technique to capture branch interactions in the trees Terminalia catappa and Cornus alternifolia. An interesting aspect of their study was a comparison of the exogenous limitation of branching (by proximity to other branches) with an endogenous mechanism (accumulation of regulatory substances propagating through the growing structure). The inhibition of branch production due to local overcrowding was also included in a model of *Pinaceae* by Ford, Avery, and Ford [13]. A model of treelike structures that developed according to the amount and direction of incoming light was proposed by Kanamaru and Takahashi [33]. This model generated fairly realistic crown shapes, thus illustrating the crucial impact of light on tree morphogenesis. Bell [4] outlined a model of clover, which integrated exogenous and endogenous control factors. Growth of buds was controlled by photosynthate exported from leaflets, but leaflets failed to produce photosynthate if they were shaded by other leaflets. Bell noted that the outcome of the simulation was difficult to predict, and simulation played an important role in understanding the resulting form. Combinations of exogenous and endogenous factors were subsequently incorporated in a comprehensive model of poplar trees [55]. Prusinkiewicz and McFadzean [54] and MacKenzie [38] reported preliminary results on incorporating exogenous control mechanisms into L-systems. The captured phenomena included collisions between pairs of branches, the branches and the environment, the removal of leaves shaded by other leaves and branches, and the response of plants to trimming. This work may lead to practical applications in the modeling of gardens for landscape design purposes (Plate 10). Recent surveys of models of plants have been given by Fisher [11] and Room, Maillette, and Hanan [58].

4.3 Map L-Systems

Map L-systems [37] extend the expressive power of L-systems beyond branching structures to graphs with cycles, called *maps*, representing cellular layers. Their geometrical interpretation is more difficult than that of branching structures, because the presence of cycles makes it impossible to assign metric properties to the model using local rules. For example, the angles between the edges of a quadrilateral cycle must sum to 360° and, therefore, cannot be specified independently from each other. Fracchia, Prusinkiewicz, and de Boer [16] (see also [52, chap. 7]) proposed a physically based solution to this problem. The cells are assumed to have physical properties, osmotic pressure and wall tension, and they form a final configuration by mechanically pushing each other until an equilibrium is reached.

Map L-systems have been successfully applied to model fern gametophytes [7, 52]. For example, Plates 11 and 12 compare a microphotograph and computer-generated images of the fern thallus *Microsorium linguaeforme*. The natural and the simulated shapes look alike, which supports the hypothesis that the timing and orientation of cell divisions are the dominant factors determining the global thallus shape.

Map L-systems with geometric interpretation operate by first establishing the neighborhood relations between the cells, then assigning geometric parameters to the resulting graph. This approach is biologically justified in multicellular plant structures, because plant cells are tightly cemented together, but is inappropriate in models of animal tissues, because animal cells can move with respect to each other. A model of morphogenesis addressing this problem is described next.

4.4 Mobile Cells in a Continuous Medium

Fleischer and Barr [12] proposed an extensible simulation framework for studying morphogenesis that focused on the generation of connectivity patterns during neural development. Their model consists of discrete cells embedded in a continuous substrate. The actions of the cells are divided into continuous processes (grow, move) and discrete events (divide, create a dendrite, die). The cells move in response to physical forces and interact with other cells and the substrate through mechanical, chemical, and electrical means. Internally, the activity of each cell is governed by a set of differential equations that depend on the cell's state and the local environment. These equations represent the "genetic information" of the cell and describe the changes to an array of variables controlling the cell's behavior (movements, growth, divisions). The substrate acts as a medium in which chemical substances diffuse, dissipate, and enter into reactions. A sample frame from a simulation carried out in this environment is shown in Plate 13. The yellow cells appear first, then some of them differentiate into blue cells. The blue cells grow and gradually form a connected skeleton.

Map L-systems and the Fleischer-Barr model present opposite approaches to the definition of multicellular structures. In map L-systems, grammar-based rules specify a model's topology, which subsequently determines its geometry. The cells cannot move with respect to each other. On the other hand, in the Fleischer-Barr model, cell movements determine their relative positions; the resulting clusters of adjacent cells indirectly specify topological properties of the emerging structure. The work of Mjolsness, Sharp, and Reinitz [46] presents a step toward a synthesis of both approaches: a model in which spatial relationships between the cells *and* grammar-based productions can be combined to specify dynamic changes in system configuration.

Although the Fleischer-Barr model is directed at the study of morphogenesis, it may also provide a unifying framework for considering other phenomena in which autonomous agents move in space and interact. In the computer graphics context, these include behavioral animation, exemplified by Reynolds' [57] model of flocks, herds, and schools, and by Wejchert and Haumann's [69] model of leaves flying in the air.

5 Conclusions

This paper presented a survey of selected models of morphogenesis that use computer graphics techniques to visualize the results of simulations. The models were divided into two main classes, space- and structure-oriented, and were further characterized from the viewpoint of information flow between the components of the developing structures. The space-oriented models capture the flow of information in the medium but usually have only limited capability to describe expansion of the medium and of the structure embedded in it: Growth is limited to the boundary. The structure-oriented models, on the other hand, can simulate the expansion of the whole structure, but they do not inherently capture the information flow through the medium. The selection of the best approach is an important part of modeling a given phenomenon, as described by Segel [59, p. xi]: "A good mathematical model—though distorted and hence "wrong," like any simplified representation of reality—will reveal some essential components of

complex phenomenon. The process of modeling makes one concentrate on separating the essential from the inessential."

In some cases, similar patterns or developmental sequences can be generated by fundamentally different models. For example, the Maltese crosses shown in Figure 3 were generated using a cellular automaton that explicitly detected and eliminated collisions between branches, but exactly the same pattern can be generated using a context-free L-system. The pigmentation pattern of an *Oliva* shell shown in Plate 2 was generated using a reaction-diffusion model, but similar patterns can be obtained using cellular automata and context-sensitive L-systems. Lindenmayer [34] proposed to address such equivalences in a formal way:

In view of the large number of possible models which give rise to similar morphogenetic patterns, the most important problem is that of narrowing down the set of possibilities. This can be ultimately done on the basis of experimental evidence only. But a better theoretical understanding of equivalence relationships among models of different types would help considerably to sharpen the questions asked in the experiments.

A formal theory of pattern complexity would be an important step in this direction. Traditional measures of complexity, such as the time and space needed by a Turing machine to execute an algorithm, fail to quantify the flow of information between components of a developing pattern or structure. Therefore, a more specialized theory is needed to evaluate formally the alternatives and provide measurable criteria for selecting the most plausible model of an observed phenomenon. An interesting feature of this methodology is that computer science is being applied to study processes taking place in nature. Gruska and Jürgensen [25] comment, "Computer science' should be considered as a science with aims similar to those of physics. The information processing world is as rich and as important as the physical world for mankind."

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