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PHYSICALLY-BASED GRAPHICAL INTERPRETATION OF MARKER CELLWORK L-SYSTEMS

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ABSTRACT: Map L-systems with dynamic interpretation have been successfully applied to the modeling of the development of two-dimensional cell layers [3, 4]. We extend this technique to three-dimensional cellular structures. The seminal notion of three-dimensional *cyclic edge-label-controlled OL-systems*, termed *cellworks*, was introduced by A. Lindenmayer [8]. We provide an alternative definition of cellworks using *markers*, and use it as a formal basis for a simulation program. Cell geometry is viewed as the result of mechanical cell interactions due to osmotic pressure and wall tension. Developmental sequences can be animated by considering periods of continuous expansion delimited by instantaneous cell divisions. As an example, the method is applied to visualize the development of a three-dimensional epidermal cell layer.

Keywords: computer graphics, mathematical modeling in biology, simulation, visualization of development, map L-system, cellwork L-system, dynamic model.

CONTENTS

0. INTRODUCTION

An important issue in plant morphology is the study of cell division patterns, that is, the spatial and temporal organization of cell divisions in tissues. In the past, the modeling of cellular structures focused mainly on the development of branching and nonbranching filaments, represented by string and bracketed L-systems [7], and two-dimensional planar and spherical cell layers whose topology was described by map L-systems [10]. Such methods are described in [1, 15]. This paper presents a method for simulating and visualizing the development of three-dimensional multicellular structures.

The practical motivation for this work is related to two applications. As a *research tool*, graphical simulations make it possible to study the impact of cell divisions on cell arrangement and global shape formation. As a *visualization tool*, simulations provide a method for presenting features that cannot be captured using time-lapse photography. For example, pseudocolor may be introduced to distinguish groups of cells descending from a specific ancestor or to indicate cell age. Inconspicuous structural elements, such as new division walls, can be emphasized.

The modeling method consists of two stages. First, the *topology* of the cell division patterns is expressed using the formalism of *cellwork L-systems*. At this stage, the neighborhood relations between cells are established, but the cell shapes remain unspecified. Next, cell *geometry* is modeled using a dynamic method that takes into account the osmotic pressure inside the cells and the tension of cell walls. The development can be animated by considering periods of continuous cell expansion, delimited by instantaneous cell divisions.

This paper is organized as follows. Section 1. focuses on the simulation of cellular development at the topological level. After a brief survey of previous three-dimensional models, the formalism of marker-based cellwork L-systems is proposed to describe cell neighborhood. Section 2. presents a dynamic model for the specification of cell geometry, given the topology. In section 3., the method is applied to model the development of epidermal cells. Section 4. discusses open problems.

1. THREE-DIMENSIONAL MODELS AND CELLWORK L-SYSTEMS

Various models have been proposed for the modeling of three-dimensional cellular structures. Rules whose main control elements were cell walls have been informally presented by Korn [6] and the Lücks [11]. Double wall stereomap

generating systems were introduced by the Lücks [12] to model walls in three-dimensional space, but were somewhat difficult to interpret geometrically. Recently, the Lücks [13] presented the formalism of double-wall cellwork L-systems for modeling plant meristems.

We propose a method which extends the notion of two-dimensional single-wall marker map L-systems to three-dimensions, based on the structures operated on by the cyclic cellwork L-systems introduced by Lindenmayer [8]. An initial, more restricted version of our method was considered in [4].

1.1. Cellworks

In order to capture the structure of three-dimensional cellular tissues, Lindenmayer [8] proposed an extension of map L-systems called *cellwork* L-systems. The notion of a cellwork is characterized as follows.

- A cellwork is a finite set of *cells*. Each cell is surrounded by one or more *walls* (faces).
- Each wall is surrounded by a boundary consisting of a finite, circular sequence of *edges* which meet at *vertices*.
- Walls cannot intersect without forming an edge, although there can be walls without edges (in the case of cells shaped as spheres or tori).
- Every wall is part of the boundary of a cell, and the set of walls is connected.
- Each edge has one or two vertices associated with it. Edges cannot cross without forming a vertex and there are no vertices without an associated edge.
- Every edge is a part of the boundary of a wall, and the set of edges is connected.

1.2. mBPCOL-systems

The process of cell division can be expressed as cellwork rewriting. This notion is an extension of map rewriting. Several map-rewriting systems have been described in the past [9]. To capture the development of three-dimensional structures we extend two-dimensional mBPMOL-systems, proposed by Nakamura, Lindenmayer, and Aizawa [14] as a refinement of the basic concept of map L-systems

introduced by Lindenmayer and Rozenberg [10], to the formalism of *marker Binary Propagating Cellwork OL-systems.* The name is derived as follows. A *cellwork OL-system* is a parallel rewriting system which operates on cellworks and modifies cells irrespective of the states of other neighboring cells (a *context-free* mechanism). The system is *binary* in that a cell can split into at most two daughter cells. It is *propagating* in the sense that edges cannot be erased, thus cells cannot fuse or die. The *markers* represent a technique for specifying the positions of inserted edges used to split the walls and divide cells.

An mBPCOL-system $\mathcal{G}$ is defined by a finite alphabet of *edge labels* Σ, a finite alphabet of *wall labels* Γ, a *starting cellwork* ω, and a finite set of *edge productions* P. The initial cellwork ω is specified as a list of walls and their bounding edges. Edges may be directed or neutral, indicated by the presence or absence of arrows above edge labels. Each production is of the form $A : \beta \rightarrow \alpha$, where the edge $A \in \Sigma$ is the *predecessor*; the string $\beta \in \{\Gamma^+, *\}$ is a list of *applicable walls* ($*$ denotes all walls); and the string α, composed of edge labels from Σ, wall labels from Γ, and symbols [and], is the *successor.* The sequence of symbols outside the square brackets describes the subdivision pattern of the successor. Pairs of matching brackets [and] delimit *markers* which specify possible attachment sites for new edges and walls. Arrows indicate the directions of the successor edges and markers with respect to the predecessor edge. For successor edges, the right arrow indicates a direction consistent with the predecessor edge, the left arrow indicates the opposite direction, and no arrow is neutral. In the case of markers, the right arrow indicates an outward orientation from the predecessor edge, the left arrow indicates an inward orientation, and no arrow is neutral. The list β contains all walls into which a marker should be inserted. In addition to the labels for edges and markers, a successor specifies the labels of walls which may be created as a result of production application.

For example, production $\vec{A}$: $1\dot{4} \rightarrow \vec{D}\ \overleftarrow{C}_2[\vec{E}_5]_3\vec{B}\ F$ applies to the edge A if it belongs to one or more walls labeled 1 or 4 (Figure 1a). The predecessor edge is subdivided into four edges D, C, B and F. During a derivation step, marker E is introduced into all walls of type 1 or 4 which share edge A (Figure 1b), and can be connected with a matching marker inserted into the same wall by another production. As a result, the wall will split into two. The daughter wall created before the matched marker in the direction of the predecessor edge A will be labeled 2, and the wall formed after the marker will be labeled 3 (Figure 1c). Markers E can be connected only if both productions assign labels to the daughter walls in a consistent way. Otherwise, the markers are considered non-matching

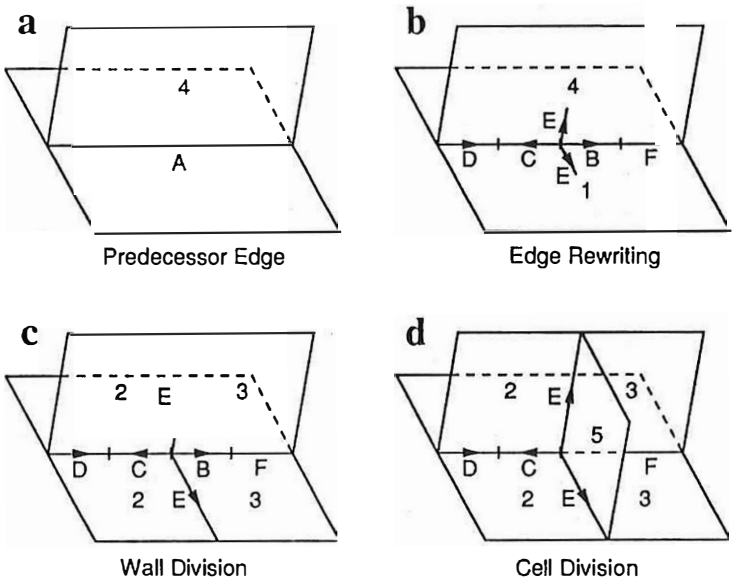


Figure 1: The phases of a derivation step.

and are discarded. If several walls bounding a cell split in such a way that the sequence of new edges forms a closed contour, a new wall bound by these edges may be created. In order for this to occur, all markers involved must specify the same label for the new wall, 5 in this example (Figure 1d).

The limitation of the scope of a production to specific walls may create a consistency problem while rewriting edges. For instance, assume that walls 1 and 2 share edge A, and the following productions are in P:

$$p_1 : \vec{A}{:}\, 1 \rightarrow \vec{C}\overleftarrow{E}$$
$$p_2 : \vec{A}{:}\, 2 \rightarrow A\vec{B}$$

Productions p_1 and p_2 are inconsistent since they specify two different partitions of the same edge. We assume the mBPCOL-systems under consideration are free of such inconsistencies. This does not preclude the possibility of applying several productions simultaneously to the same edge. For example, a production pair,

$$p_1 : \vec{A}{:}\, 1 \rightarrow \vec{C}_2[\vec{F}_3]_4\overleftarrow{E}$$
$$p_2 : \vec{A}{:}\, 2 \rightarrow \vec{C}_5[\overleftarrow{D}_6]_7\overleftarrow{E},$$

consistently divides edge A into segments C and E, although the markers inserted into walls 1 and 2 are different (Figure 2).

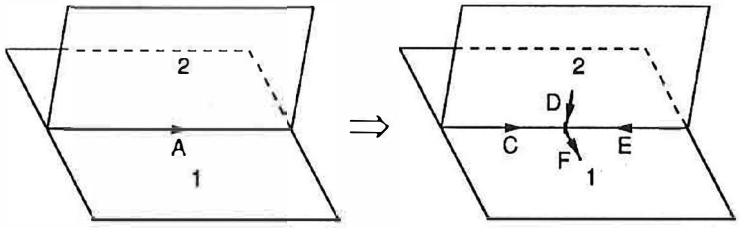


Figure 2: Example of consistent edge productions.

According to the above discussion, a *derivation step* in an mBPCOL-system consists of three phases.

1. Each edge in the cellwork is replaced by successor edges and markers using one or more productions in P. Note that if no production exists for an edge, the edge remains unchanged.

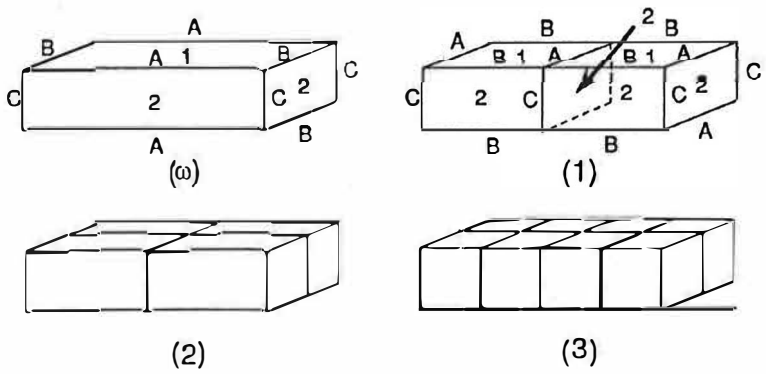
2. Each wall is scanned for matching markers. If a match inducing a consistent labeling of daughter walls is found, the wall is subdivided. The selection of matching markers is done by the system. Unused markers are discarded.

3. Each cell is scanned for a circular sequence of new division edges having the same wall label. If such a sequence is found, it is used to bound the new wall which will divide the cell into two daughter cells. If different possibilities exist, the edges are selected by the system.

A wall may be subdivided more than once as long as new division edges do not intersect and a consistent labeling of daughter walls is possible. In contrast, a cell may be divided only once in any derivation step.

For example, Figure 3 presents a three-dimensional cellwork L-system. In the first derivation step, production p_1 divides walls labeled 1, and production p_2 divides walls labeled 2. The inserted edges form a cycle that divides the cell with a new wall labeled 2. In the subsequent steps this process is repeated, generating a pattern of alternating division walls. Production p_3 introduces the necessary delay.

A more complex example is the construction of a Sierpiński tetrahedron, which is a three-dimensional extension of the Sierpiński gasket described in [16]. The cellwork L-system is given in Figure 4. It has been simplified by the addition of superscripts, for example A^i for $i = \{0, 1, 2\}$ replaces three edge labels (the total number of edge labels involved is 38). Also, productions without markers that



$$p_1 : \text{A} : 1 \rightarrow B_1[A_2]_1 B$$
$$p_2 : \text{A} : 2 \rightarrow B_2[C_2]_2 B$$
$$p_3 : \text{B} : * \rightarrow \text{A}$$

Figure 3: Example of a cellwork L-system.

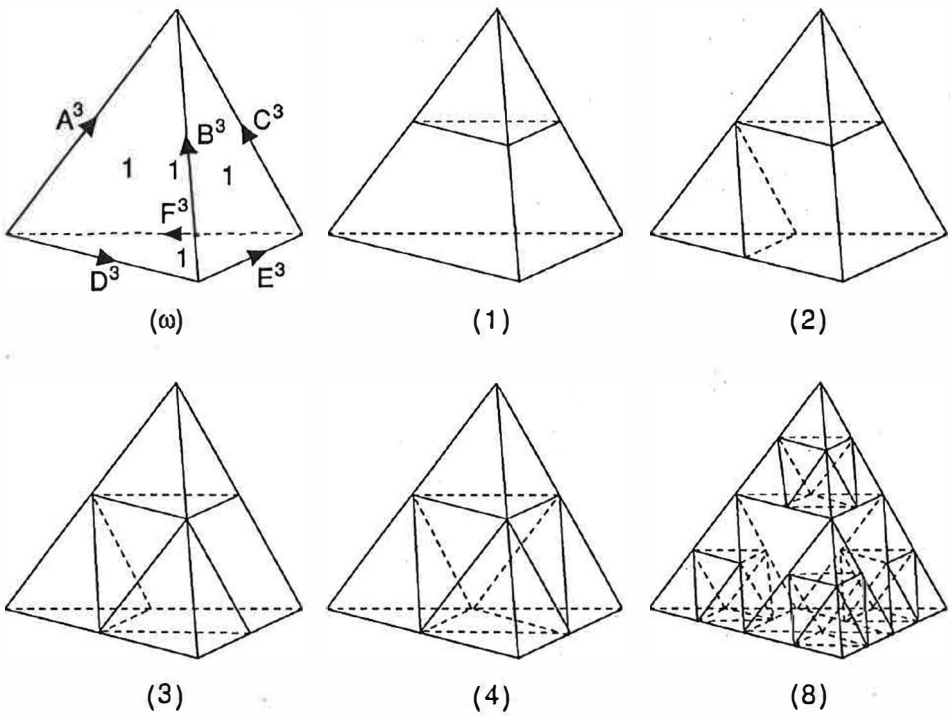
match those yielding markers for a particular edge are not shown. For example, production

$$p_{18} : \vec{d}^0 : 12 \rightarrow \vec{D}^1{}_1[\vec{B}^1{}_1]_2{}_1[\vec{E}^1{}_1]_2\vec{d}^1$$

yields markers for edge $\vec{d}^0$ contained in walls 1 and 2 and has matching production

$$m_{18} : \vec{d}^0 : 3 \rightarrow \vec{D}^1\vec{d}^1$$

which does not yield markers for walls labeled 3. Such matching productions are necessary to ensure the consistent replacement of edges. The productions in the cellwork L-system are applied as follows. Productions $p_1 - p_6$ are responsible for the first division (Figure 4(1)) which results in a new tetrahedron appearing at the top of the structure (given the orientation of the initial tetrahedron in (ω)). The next division (2) occurs at the left hand corner and is the result of productions p_{13}, p_{18} and p_{23}. The next two divisions ((3) and (4)) occur counterclockwise (viewed from the top) at the remaining corners. Division three results from the application of productions p_{15}, p_{19} and p_{21}, while the fourth division is determined by productions p_{16}, p_{22} and p_{25}. The remaining productions delay the modification of edge labels such that after four successive divisions, the initial tetrahedron is divided into four tetrahedrons having the same initial edge and wall labels, and a central octahedron which does not divide. The process is then repeated for each tetrahedron, as seen in derivation (8).



p_1 : $\vec{A}^3 : 1 \rightarrow \vec{a}^0{}_2[\overleftarrow{F}^0{}_1]_{1\,2}[\vec{D}^0{}_1]_1\vec{A}^0$

p_2 : $\vec{B}^3 : 1 \rightarrow \vec{b}^0{}_2[\overleftarrow{D}^0{}_1]_{1\,2}[\vec{E}^0{}_1]_1\vec{B}^0$

p_3 : $\vec{C}^3 : 1 \rightarrow \vec{c}^0{}_2[\overleftarrow{E}^0{}_1]_{1\,2}[\vec{F}^0{}_1]_1\vec{C}^0$

p_4 : $\vec{D}^3 : * \rightarrow \vec{d}^0$

p_5 : $\vec{E}^3 : * \rightarrow \vec{e}^0$

p_6 : $\vec{F}^3 : * \rightarrow \vec{f}^0$

p_7 : $\vec{A}^i : * \rightarrow \vec{A}^{i+1}$

p_8 : $\vec{B}^i : * \rightarrow \vec{B}^{i+1}$

p_9 : $\vec{C}^i : * \rightarrow \vec{C}^{i+1}$

p_{10} : $\vec{D}^i : * \rightarrow \vec{D}^{i+1}$

p_{11} : $\vec{E}^i : * \rightarrow \vec{E}^{i+1}$

p_{12} : $\vec{F}^i : * \rightarrow \vec{F}^{i+1}$

p_{13} : $\vec{a}^0 : 2 \rightarrow \vec{A}^1{}_1[\overleftarrow{B}^1{}_1]_{2\,1}[\overleftarrow{C}^1{}_1]_2$

p_{14} : $\vec{b}^0 : * \rightarrow \vec{b}^1$

p_{15} : $\vec{b}^1 : 2 \rightarrow \vec{B}^2{}_1[\overleftarrow{A}^2{}_1]_{3\,1}[\overleftarrow{C}^2{}_1]_2$

p_{16} : $\vec{c}^2 : 2 \rightarrow \vec{C}^3{}_1[\overleftarrow{A}^3{}_1]_{3\,1}[\overleftarrow{B}^3{}_1]_3$

p_{17} : $\vec{c}^i : * \rightarrow \vec{c}^{i+1}$

p_{18} : $\vec{d}^0 : 12 \rightarrow \vec{D}^1{}_1[\vec{B}^1{}_1]_{2\,1}[\vec{E}^1{}_1]_2\vec{d}^1$

p_{19} : $\vec{d}^1 : 12 \rightarrow {}_3[\vec{A}^2{}_1]_{1\,2}[\vec{F}^2{}_1]_1\vec{D}^2$

p_{20} : $\vec{e}^0 : * \rightarrow \vec{e}^1$

p_{21} : $\vec{e}^1 : 12 \rightarrow \vec{E}^2{}_1[\vec{C}^2{}_1]_{2\,1}[\vec{F}^2{}_1]_2\vec{e}^2$

p_{22} : $\vec{e}^2 : 12 \rightarrow {}_3[\vec{B}^3{}_1]_{1\,3}[\overleftarrow{D}^3{}_1]_1\vec{E}^3$

p_{23} : $\vec{f}^0 : 12 \rightarrow \vec{f}^1{}_2[\vec{C}^1{}_1]_{1\,2}[\vec{E}^1{}_1]_1\vec{F}^1$

p_{24} : $\vec{f}^1 : * \rightarrow \vec{f}^2$

p_{25} : $\vec{f}^2 : 12 \rightarrow \vec{F}^3{}_1[\vec{A}^3{}_1]_{3\,1}[\vec{D}^3{}_1]_3$

Figure 4: The Sierpiński tetrahedron.

2. DYNAMIC INTERPRETATION

Cellworks are topological objects without inherent geometric properties. In order to visualize them, some method for assigning geometric interpretation must be applied. Assuming the dynamic point of view, the shape of cells and thus the shape of the entire organism result from the action of forces. The unbalanced forces due to cell divisions cause the gradual modification of cell shapes until an equilibrium is reached. At this point, new cell divisions occur, and expansion resumes. The dynamic method is an extension of a similar approach used to model two-dimensional cell layers described by map L-systems [3, 4].

The dynamic interpretation method is based on the following assumptions:

- the structure is represented as a three-dimensional network of masses corresponding to cell vertices, connected by springs which correspond to cell edges,
- the springs are always straight and obey Hooke's law,
- for the purpose of force calculations, walls can be approximated by flat polygons,
- the cells exert pressure on their bounding walls; the pressure on a wall is directly proportional to the wall area and inversely proportional to the cell volume,
- the pressure on a wall is divided evenly between the wall vertices,
- the motion of masses is damped, and
- other forces are not considered.

The position of each vertex, and thus the shape of the structure, is computed as follows. As long as an equilibrium is not reached, unbalanced forces put masses in motion. The total force $\vec{F}_T$ acting on a vertex X is given by the formula:

$$\vec{F}_T = \sum_{e \in E} \vec{F}_e + \sum_{w \in W} \vec{F}_w + \vec{F}_d,$$

where $\vec{F}_e$ are forces contributed by the set of edges E incident to X, $\vec{F}_w$ are forces contributed by the set of walls W incident to X, and $\vec{F}_d = -b\vec{v}$ is a damping force. The forces $\vec{F}_e$ act along the cell edges and represent wall *tension*. The magnitude is determined by Hooke's law, $F_e = -k(l - l_0)$, where k is the spring constant, l is the current spring length, and l_0 is the rest length. The forces $\vec{F}_w$ are due to the

pressure exerted by the cells on their bounding walls. The total force of pressure exerted by a cell on a wall w has direction normal to w and is equal to $p \cdot A$, where p is the internal cell pressure and A is the wall area. The pressure p is assumed to be inversely proportional to the cell volume, $p \sim V^{-1}$, which corresponds to the equation describing osmotic pressure (with constant solute concentration and temperature). The area A of a wall is found by tesselating it into triangles and summing the areas of each triangle. The volume V of a cell is calculated by tesselating the cell into tetrahedra.

The force $\vec{F}_T$ acts on the mass at the cellwork vertex. Newton's second law of motion applies,

$$m\frac{d^2\vec{x}}{dt^2} = \vec{F}_T,$$

where $\vec{x}$ is the vertex position. If the entire structure has N vertices, we obtain a system of $2N$ differential equations,

$$m_i\frac{d\vec{v}_i}{dt} = \vec{F}_{T_i}\left(\vec{x}_1, \cdots, \vec{x}_N, \vec{v}_i\right), \qquad \frac{d\vec{x}_i}{dt} = \vec{v}_i,$$

where $i = 1, 2, \ldots, N$. The task is to find the sequence of positions $\vec{x}_1, \ldots, \vec{x}_N$ at given time intervals, assuming that the functions $\vec{F}_{T_i}$ and the initial values of all variables $\vec{x}_1^0, \ldots, \vec{x}_N^0$ and $\vec{v}_1^0, \ldots, \vec{v}_N^0$ are known. These initial values are determined as follows.

- Coordinates of the vertices of the starting cellwork are included in the input data for the simulation.
- Positions of existing vertices are preserved through a derivation step. New vertices partition the divided edges into segments of equal length. The initial velocities of all vertices are set to zero.

The system of differential equations with the initial values given above represents an *initial value problem.* It can be solved numerically using the *forward (explicit) Euler method* [2]. To this end, the differential equations are rewritten using finite increments $\Delta\vec{v}_i$, $\Delta\vec{x}_i$ and Δt,

$$\Delta\vec{v}_i^{\,k} = \frac{1}{m_i}\vec{F}_{T_i}\left(\vec{x}_1^{\,k}, \cdots, \vec{x}_N^{\,k}, \vec{v}_i^{\,k}\right)\Delta t, \qquad \Delta\vec{x}_i^{\,k} = \vec{v}_i^{\,k}\Delta t,$$

where the superscripts $k = 0, 1, 2, \ldots$ indicate the progress of time, $t = k\Delta t$. The position and velocity of a point i after time increment Δt are expressed as follows:

$$\begin{aligned} \vec{v}_i^{\,k+1} &= \vec{v}_i^{\,k} + \Delta\vec{v}_i^{\,k} \\ \vec{x}_i^{\,k+1} &= \vec{x}_i^{\,k} + \Delta\vec{v}_x^{\,k} \end{aligned}$$

The iterative computation of the velocities $\vec{v}_i^{k+1}$ and positions $\vec{x}_i^{k+1}$ is carried out for consecutive values of index k until all increments $\Delta\vec{v}_i^k$ and $\Delta\vec{x}_i^k$ fall below a threshold value. This indicates that the equilibrium state has been approximated to the desired accuracy. The next derivation step is then performed. A system of equations corresponding to the new cellwork topology is created, and the search for an equilibrium state resumes. In such a way, the developmental process is simulated as periods of continuous cell expansion, delimited by instantaneous cell divisions. Continuity of cell shapes during divisions is preserved by the rule which sets the initial positions of vertices. The dynamic method is illustrated by the example in the following section.

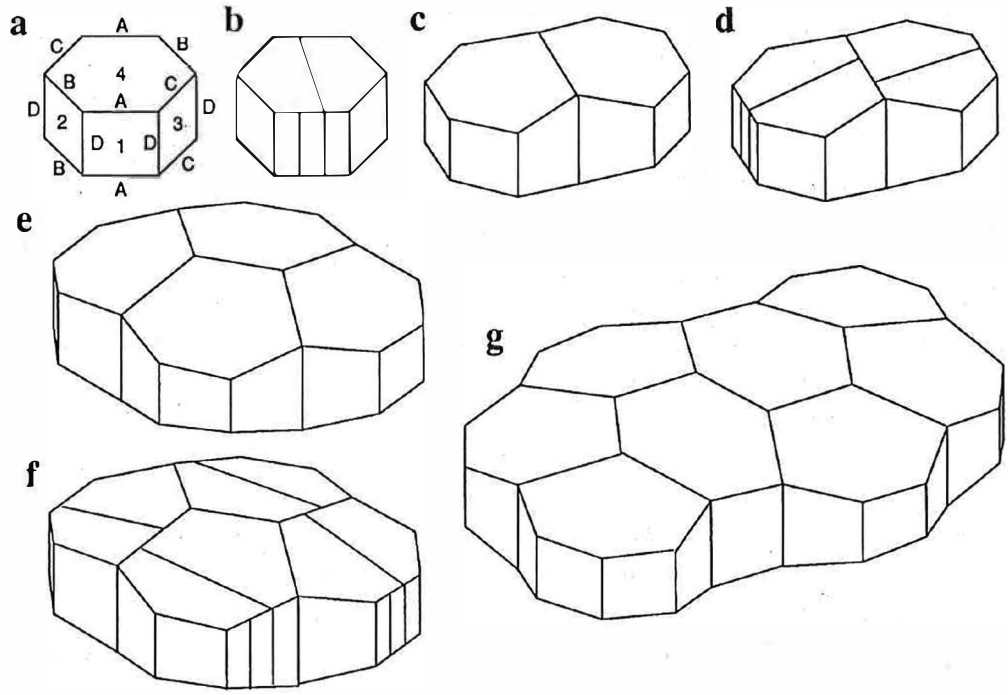
3. DEVELOPMENT OF EPIDERMAL CELLS

A division pattern that frequently occurs in epidermal cell structures is described by the cellwork L-system in Figure 5, based on a cyclic cellwork L-system developed by Lindenmayer [8]. Productions p_1, p_2, p_6 and p_7 are responsible for cell divisions, while the remaining productions change the states of edges for future divisions (delays). The resulting pattern consists of staggered divisions of sister cells such that all cells remain hexagonal and form a three-dimensional cell layer. The dynamic model for cellwork interpretation produces regular hexagonal cells without the specification of edge growth rates and exact division angles (as in [8]).

4. CONCLUSIONS

This paper presents a modeling method for three-dimensional cellular structures. Cell topology is captured by mBPCOL-systems, while the geometry results from a dynamic model that takes into account internal cell pressure and wall tension. The method is illustrated by a biological example.

The present formalism of cellwork L-systems imposes a restriction on how walls are allowed to subdivide. That is, a wall may subdivide more than once as long as the new division edges do not intersect. This will cause problems in the case where two neighbor cells divide in one derivation step along a shared wall such that the division edges of that wall cross each other. We are certain this case will arise many times while modeling three-dimensional biological structures. One solution to this problem is to introduce markers which themselves contain edge and marker labels into the cellwork L-system (hierarchical marker system). On



$$
\begin{aligned}
p_1 &: \; A:123 \;\rightarrow\; C_3[E_1\,]_2B_2[D_1\,]_3C \\
p_2 &: \; A:4 \;\rightarrow\; CB_4[F_1\,]_4C \\
p_3 &: \; B:* \;\rightarrow\; A \\
p_4 &: \; C:* \;\rightarrow\; B \\
p_5 &: \; E:* \;\rightarrow\; D \\
p_6 &: \; F:123 \;\rightarrow\; HGH \\
p_7 &: \; F:4 \;\rightarrow\; H_4[F_1\,]_4G_4[F_1]_4H \\
p_8 &: \; G:* \;\rightarrow\; F \\
p_9 &: \; H:* \;\rightarrow\; G
\end{aligned}
$$

Figure 5: Developmental sequence of epidermal cells: (a) The starting cellwork; (b), (d) and (f) cellworks immediately after cell divisions; (c), (e) and (g) the corresponding cellworks at equilibrium.

the other hand intersections could be detected at the geometric level resulting in the construction of new vertices at intersection points.

Double-wall cellwork L-systems have been proposed by the Lücks [13] for the modeling of plant meristems. It may be expected that, as in the two-dimensional case, three-dimensional double-wall systems have the advantage of being more convenient than single-wall systems when describing cell development, however, single-wall systems are simpler to implement. The translation of double-wall systems to single-wall systems may also parallel the two-dimensional case.

The dynamic method for determining cell shapes involves many arbitrary assumptions, such as equal distribution of pressure between the wall vertices, and reduction of wall tension to forces acting along the wall edges. It is tempting to introduce more sophisticated assumptions concerning physical properties of cells and their components. At this time we are not aware of biological observations which would provide a solid basis for such refinements.

The lack of data presents an obstacle to the modeling of three-dimensional structures using mBPCOL-systems. For example, we attempted to model the development of a root of *Azolla pinnata* presented in [5] and frequently quoted in biological literature, but the available description was too general to be captured in the form of an mBPCOL-system. Specifically, the development of the segments of the root could not be determined. Only the development of the outer surface of segments was distinguishable. Assuming such data was available, there is also the problem of inferring the cellwork L-system.

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