Asynchronous cell division model for morphogenesis of plant leaves

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Introduction

In order to describe the developmental process of plants, we have to consider various factors (Taiz and Zeiger, 2002). Many models of morphogenesis have been proposed so far, and each of them shed a light on a certain aspect of the complicated phenomena.

Map L-system extends the concept of the L-system on the planar network (Prusinkiewicz and Lindenmayer, 1990). This model is based on a symbol dynamics driven by a set of rewriting rules similar to its original system (Lindenmayer, 1968). It successfully describes the developmental process of fern gametophytes etc., however, the argument for each rule is a segment of cell wall, and therefore even a simple developmental process requires an artificial set of rules. Also, it deals with only the topological connectivity and neglects the mechanical interaction among cells.

The context-sensitive cell system is a model in which rules operate on cells, not on cell walls (Fracchia, 1996). The orientation of the division plane is determined by concentration gradient of the morphogen calculated by the reaction-diffusion equation. Both the above two models are synchronous.

Some asynchronous models have been proposed to capture the development of phyllotaxis (Smith, et al., 2006)(Jönsson, et al., 2006). In these models, asynchrony is realized by the following mechanism. Cells are assumed to expand at constant speed. A cell divides when its size reaches the constant threshold. If they divide unequally, the length of time before the next division will be different. The orientation of division plane is determined by geometry of the cell polygon (Smith, et al., 2006) or determined at random (Jönsson, et al., 2006).

In this paper, we propose a new model to give a general framework to describe varieties of developmental processes of plant leaves. Our model possesses the following three features: asynchronous cell division, explicitly described determination rules for the cell division plane, and inter-cellular mechanical interactions. Although cell division is synchronous in early stage of embryogenesis, it must be described as asynchronous process in later development. The determination rules are given as functions of the cell type (internal state of the cell) and the types of the neighboring cells. This is important because vegetable cells are usually surrounded by rigid cell walls that prevent cell migration, thus the local connectivity is almost determined at the time of cell division. The inter-cellular mechanical interactions distort the network among cells whenever the cells divide or expand, eventually leading to the reconfiguration of the network. In the asynchronous cell division model, the rearrangement may cause instability, e.g. the resultant morphology may become sensitive to the order of activation. Therefore we think it is essential to study the mechanism of development of multi-cellular organisms.

Model

In this model, cells are represented as nodes with discrete internal states. Each cell is connected to neighbors via "link"s. Linked cells can refer to each other's state.

There are two sets of rules that interact each other: cellular rules and physical rules.

The cellular rules represent state transition or cell division. Updated state and direction of cell division is defined by current states of itself and linked cells (Fig. 2). State transition and division are executed asynchronously. These rules are described in a uniform manner, thus it is easy to build modular and hierarchical rule set for complex morphology.

The physical rules rearrange the connectivity network among cells. Each cell has the same mass, and its position is defined on two-dimensional space. Linked cells are connected by springs and dampers. If the distance between neighboring cells becomes shorter than a constant threshold value, they are connected by a new link. Links can be disengaged or locally rearranged (by Delaunay flip (de Berg, et al., 2000)) when the distortions of the spring-mass-damper networks exceeds a threshold (Fig. 3).

Fig. 4 shows the morphogenesis of fern leaves generated by our model. The venation pattern of the leaf was obtained mainly by the cellular rules. Cells that compose the segments of the vein are produced by division at the tip. The length of each segment is determined by counting the number of cell divisions, and at the predefined interval, branches are generated. At the same time, additional cells grow around the vein segments. Interaction between the cellular rules and the physical rules make the vein structure stable under the asynchronous activation of rules. We have conducted several simulations from different random seeds and obtained slightly different patterns (Fig. 4 c)).

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Set initial network
Put all the cell IDs in queue Q in random order
While Q is not empty do {
    Pick a cell C from Q
    Apply cellular rules to cell C
    Relaxation of spring-mass-damper network
    Apply physical rules to all cells
}
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Fig. 1. Simulation procedure of proposed model. For asynchronous update, we introduce a random cell cycle. The cellular rules are applied just once in a cycle in random order. When a cellular rule applied, the physical rules are immediately applied to all cells.

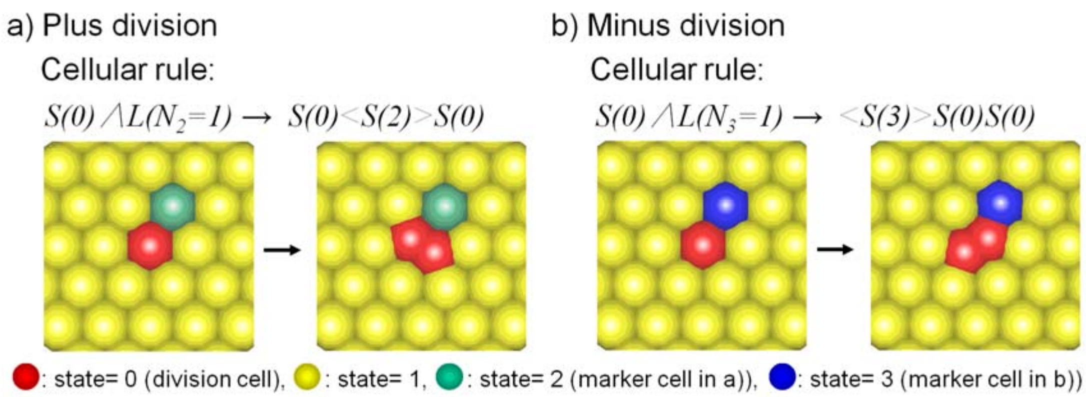

Fig. 2. Determination of the division direction by the cellular rule. The division procedure is as follows: (1) Select a "marker" cell from the linked cells according to the left-hand side of the rule. (2) Divide the cell according to the right-hand side of the rule. (a) Plus division: Both of the new cells connect to the marker cell. (b) Minus division: one of the new cells connects to the marker cell.

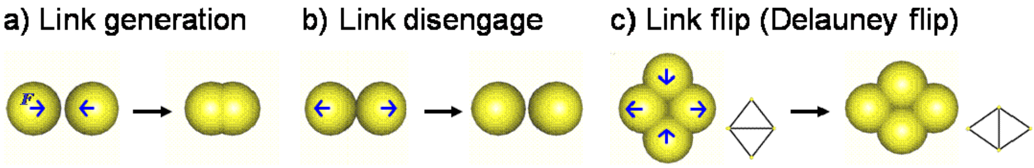

Fig. 3. Physical rules. A) Link generation: If the distance between neighboring cells becomes shorter than a constant threshold, they are connected by a new link. B) Link disengage: If the distance between neighboring cells becomes longer than a constant threshold, they are disengaged. C) Link flip: Links are rearranged by Delaunay flip to release the distortion energy in the network.

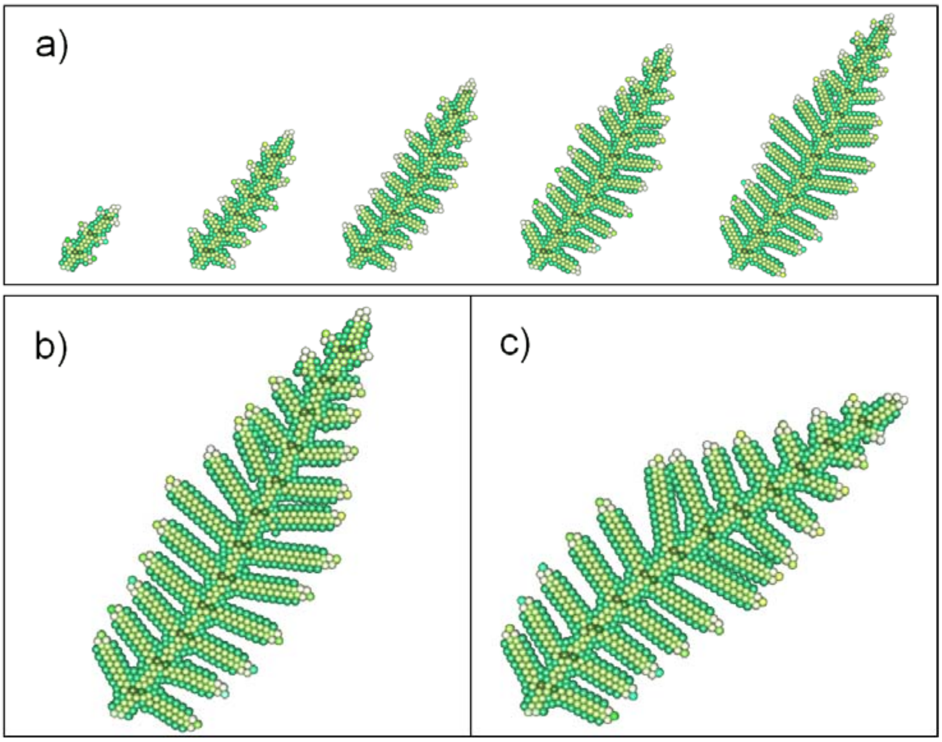

Fig. 4 The morphogenesis of fern leaves generated by the model. a) Snapshots from the simulated growth process (100, 300, 500, 700 and 900 cells). b) A close-up of a pattern when the number of cells reaches 1000. c) A close-up of a pattern by different random seed. Colors represent the internal states.

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