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A Cellular Automaton Model of Morphogenesis in *Arabidopsis thaliana**

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Abstract—Development of organisms is a very complex process in that a lot of gene networks of different cell types are to be integrated. Development of cellular automata that model the morphodynamics of different cell types is the first step in understanding and analyzing the regulatory mechanisms that underlie the developmental gene networks. We have developed a model of a cellular automaton that simulates the embryonic development of the shoot meristem in *Arabidopsis thaliana*. The model adequately describes the basic stages in the development of this organ in wild type and mutants.

Key words: cellular automaton, mathematical model, development of shoot meristem, period of division
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INTRODUCTION

Postembryonic development of the above- ground part of higher plants depends on the expression of apical shoot meristem, a dynamic structure that forms foliage, flowers, and stem. The apical shoot meristem is formed at the earliest stages of embryogenesis. Furthermore, the functioning of the promeristem triggers the development of the germ layers, and at that time a complex meristem structure is being formed (Fig. 1) [1]. The cells of the apical and basal parts have different gene expression patterns in a 16-cell-like embryo. No further development of embryos is possible without shoot meristems, or at least their apical parts [2].

A cellular automaton [3] was developed to model the development of shoot meristems of the *Arabidopsis thaliana* in embryogenesis. Modeling covered the initiation of meristem, the formation of its complex structure and functioning. Here the embryo is described as a two-dimensional array of cells, the rates of division of which depend on the cellular environment. The cells in the model can receive and, depending on the cell type, produce signals that can be received by other cells in the model. The biological meaning of a signal is the concentration of certain diffusing substances, morphogens, which have a specific influence on the cell.

METHODS AND ALGORITHMS

The model assumes that the state and the division rate of an individual cell depend on the influence of signals that are coming from other cells of the embryo. In

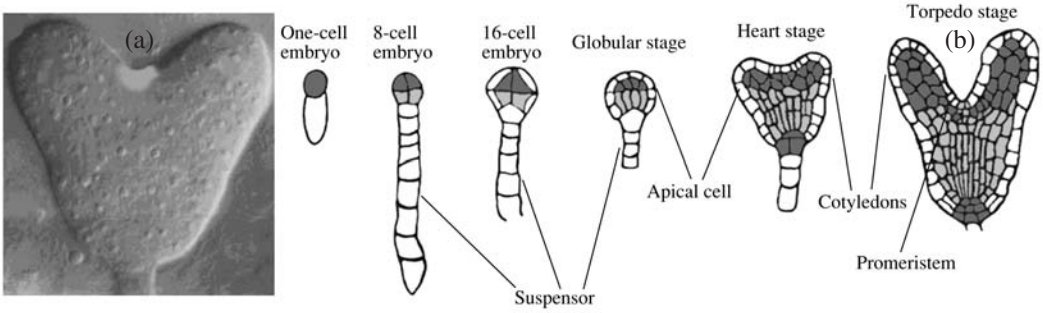

Fig. 1. (a) Directions of the model's hypothetical signal distributions in heart-stage embryo tissues: *ES* is *External Signal*, *SS* is *Stem Signal*, *SD* is *Signal of Differentiation*, and *BS* is *Basal Signal*. (b) Developmental stages of a plant embryo, indicating organs and tissues significant to the model.

* This article was translated by the authors.

the model, we use four biologically meaningful signals, which unambiguously simulate the morphodynamics of cellular tissues at the generally accepted level of abstraction (Fig. 1).

All the cells in the model embryo plant can be classed according to the type of the signal they produce:

(1) *Null.* These cells neither produce any signal nor divide.

(2) *NullEx*. Cells of the epidermis layer. They produce *ES* (*External Signal*) and are represented around the entire perimeter of the embryo. They do not divide, but we had them surround the embryo in the model.

(3) *NullSus*. Cells of the suspensor. They produce *BS* (*Basal Signal*) and are confined to the lower part of the embryo. There are two NullSus cells in the model.

(4) *Lateral*. These cells imitate "differentiated" cells, which produce *SD* (*Signal of Differentiation*).

(5) *Promeristem*. Cells of the embryo meristem. These cells produce *SS* (*Stem Signal*) and are confined to the upper part of the embryo. During development, they change into *L2meristem* and *L3meristem* type cells.

(6) *Transit*. Cells near the meristem. They also produce *SD*, but have the highest rates of division.

(7) *L2meristem*. Cells of the meristem in the second layer (counting from epidermis) of the upper part of the embryo. These cells produce *SS*.

(8) *L3meristem*. Cells one layer down from *L2meristem*. These cells produce *SS*.

Each cell has a set of internal parameters to characterize its state:

(1) *Type*. Cell type.

(2) *ES0*, *BS0*, *SS0*, *SD0* are the values of the signals produced by the cell.

(3) *ES*, *BS*, *SS*, *SD* are the values of the signals accepted by the cell.

(4) K_{ij} is the characteristic of cell state at position (i, j) calculated as the ratio of *SS* to *SD*. At the current point of time, the cell is influenced in the state characterized by the parameter $K_{ij} = \dfrac{StemSignal_{ij}}{DifferentSignal_{ij}}$.

(5) T_{ij} is the period of cell division, which depends on the current K_{ij}.

(6) Tp_{ij} is the number of iterations after the last division of the cell at position (i, j). We calculate the overall influence of all the cells on the cell at position (i, j) by the following formulas:

$$ES_{ij} = \alpha_{ij}^{E} \sum ES0_{km} e^{-\frac{n}{R_E}},$$

$$BS_{ij} = \alpha_{ij}^{B} \sum BS0_{km} e^{-\frac{n}{R_B}},$$

$$SS_{ij} = \alpha_{ij}^{S} \sum SS0_{km} e^{-\frac{n}{R_S}},$$

$$SD_{ij} = \alpha_{ij}^{D} \sum SD0_{km} e^{-\frac{n}{R_D}}.$$

The summation is performed over all the cells of a particular tissue, including the epidermis and the suspensor; (k, m) is the position of the cell assessed for its influence; $n = |k - i| + |m - j|$ where i, j are the considered cell coordinates, k, m are the affected cell coordinates; R_B, R_S, R_D are the constants that characterize penetrance for *ES*, *BS*, *SS* and *SD* respectively; α_{ij}^{B}, α_{ij}^{S}, α_{ij}^{D} are the constants that characterize the sensitivity of the cell to a certain type of signal, depending only on the type of the cell.

The qualitative behavior of the function T_{ij} is shown in Fig. 2 according to the biological position.

As can be seen in Fig. 2, the embryo meristem cells (*Promeristem*, *L2meristem*, *L3meristem*) in the tissue divide slower than others; the *Transit* cells divide very quickly; the rates of division of the *Lateral* cells are medium. At K_{cr}, the period of division becomes infinite and the cells will not divide anymore. At the threshold value K_1, the *Promeristem* cells divide into *L2meristem* and *L3meristem*. This dependence was revealed using the function $f(x) = \dfrac{1}{1 + e^{\frac{x - \mu}{\sigma}}}$, where x is value of K_{ij}, μ equals critical values of K_{ij} and σ equals 0.1. If T_{ij} is not an integer, the function T_{ij} is rounded in accordance with the standard rules. To ascertain whether or not a cell is undergoing division, Tp_{ij} and T_{ij} are compared. At the next iteration, the value Tp_{ij} is increased by one for each non-dividing cell. If $Tp_{ij} > T_{ij}$, division into two daughter cells is ascertained. For each daughter cell, Tp_{ij} is equal to zero. Note that if T_{ij} increases more rapidly than Tp_{ij}, the cell will not divide.

RESULTS

The cellular automaton adequately describes the developmental morphodynamics of *Arabidopsis thaliana* shoot meristems in embryogenesis (Fig. 3).

Varying the parameters of the cell automaton, we have successfully modeled the following mutations described in the literature:

(a) The meristem does form but cannot cope with auxin flowing in from the germ layers, and so it differentiates. This leads to the formation of joined germ layers, and plant development stops [4].

(b) The meristem does form, and so do germ layers, but no regulation is exerted on the meristem cell population. As a result, the meristem cells differentiate and the meristem zone shrinks [1, 5].

Visualization of the cellular automaton (Fig. 4) allows simulating the process of development.

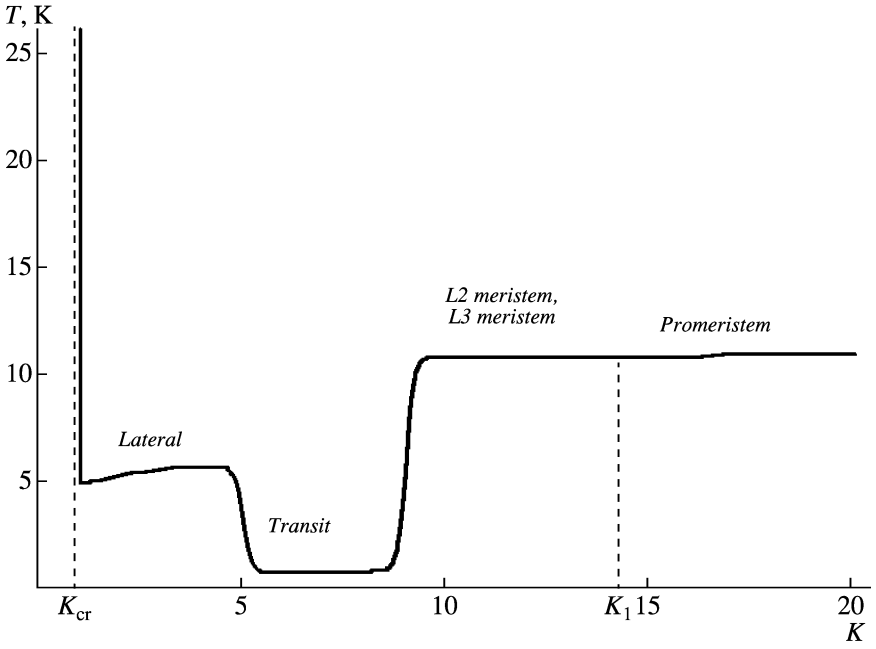

Fig. 2. Dependence of division periods on parameter *K* for different cell types.

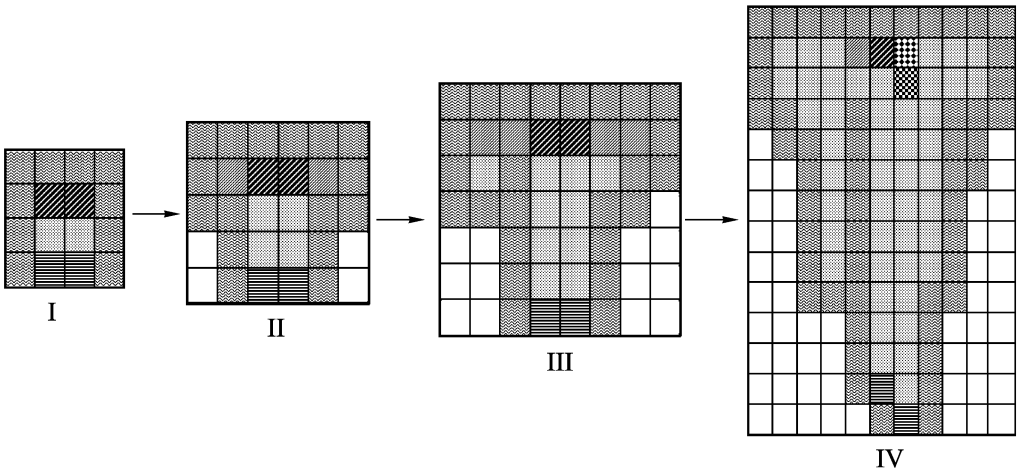

Fig. 3. Developmental stages of a plant embryo modeled by the cell automaton: I, 16-cell embryo (— *NullEx*, —*Promeristem*, —*Lateral*, —*NullSus*); II, globular stage (—*Transit*, —*Null*); III, heart stage (not new cell types); IV, torpedo stage (—*L2meristem*, —*L3meristem*).

DISCUSSION

Designing a cellular automaton that simulates the morphodynamics of embryo development under the influence of signals produced by different embryonic cells is the first step in modeling the process of development in general and in modeling the gene network for morphogenesis in particular. The formation of plant meristems in embryogenesis is characterized by a combination of avalanchine development of differentiating tissue and steady development of its stem cells. Both processes were modeled in the cellular automaton. Thus, we offer a tool not only for predicting the dynamics of the division process and the cell differentiation process, but also for examining how real mutations influence the system. In the future work, we plan that sophistication of characteristic cell definitions will be added for a more adequate description. We also plan to use the cellular automaton to investigate the development of primary shoot meristem in embryogenesis under different initial parameters of the model, which would help discern the most significant factors for the behavior of the dynamic system. The graphical visualization of the model will make it much more convenient for biologists.

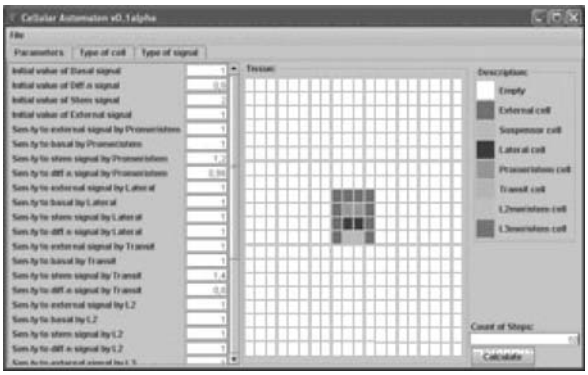

Fig. 4. Visualization of the cellular automaton.

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