Mathematical study for the mechanism of vascular and spot patterns by auxin and pin dynamics in plant development

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HIGHLIGHTS

- We studied possible mechanisms to explain diversity of morphogen patterns in plant.
- We showed that the classic auxin flux model cannot produce the diversity of patterns.
- We studied two reasonable modifications of classic model and analyzed their dynamics.
- Auxin-dependent PIN degradation is candidate mechanism to explain pattern diversity.

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ABSTRACT

Inhomogeneous distribution of auxin is essential in various differentiation processes of plant development. Auxin transfer between cells by efflux carrier protein called PINFORMED (PIN) has been considered to be responsible for inhomogeneous distribution of auxin. Two major types of auxin distribution patterns are "spot" patterns and "passage" patterns, which are responsible for determining the position of the primordia of a leaf or flower in shoot apical meristem and formation of leaf veins, respectively.

In this study, we studied the pattern formation of auxin distribution mediated by polarization of PIN using mathematical methods. We developed several different models which show possible interaction mechanisms between auxin and PIN on 2-dimentional hexagonal cellular lattice, (1) Basic auxin flux model, (2) auxin-dependent PIN degradation model and (3) auxin self-feedback model.

We analyzed these models by numerical calculation and mathematical analysis. From intensive numerical calculations under different conditions, we found that some models show three different types of pattern formations in dynamics, (a) homogeneous, (b) passage and (c) spot pattern depending on parameter condition. We analyzed these models mathematically using approximation of 1-dimensional periodic space. We determined the conditions that passage and spot patterns are generated in each model, respectively. After these analyses, we propose possible mechanisms by which plants switch passage and spot patterns in different organs by small modification.

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1. Introduction

Understanding dynamics of pattern formations in biological systems has been important and challenging problems in modern biology. In many biological systems, we do not understand fundamental mechanisms for the spontaneous pattern generation or those

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for the regulation of diversity of patterns, despite the accumulation of experimental knowledge of the systems. One such example is the pattern formation of auxin distribution in plant. Auxin is a plant hormone that works in many developmental processes and growth phases, and it acts as a morphogen and regulates differentiation. The diffusive substance, auxin, forms characteristic distribution patterns in plant tissue. This pattern formation links directly to plant morphogenesis (Vanneste and Friml, 2009).

Plants have different auxin patterns in different organs. The auxin distribution patterns observed in plant tissue are classified into two types: "spot" patterns and "passage" patterns. Spot

patterns are observed when the primordium of a leaf and flower are formed in the shoot apical meristem (SAM) (Benková et al., 2003). Cell divisions and growth occur repeatedly in these meristems, and auxin plays an important role in their induction: the primordia form from spots where the auxin concentration is high. Arrangements of these spots show higher-order pattern known as phyllotaxis. Another example of a spot pattern is observed in the formation of lateral roots (Benková et al., 2003; Dubrovsky et al., 2008). As the other type of pattern, the passage pattern, or streak with high auxin concentration, is observed in leaves (Mattsson et al., 1999; Sieburth, 1999; Scarpella et al., 2006). Passages form a network structure, which then become the veins of a leaf. Because the leaf veins are networks for the transport of nutrition, defects in their structure are a matter of life and death for the plant. Both spot and passage network auxin patterns are observed in a single, individual plant. It has driven the researchers in the theoretical field to speculate that the diversity of the auxin pattern formations in different organs in plants can be explained by a single mechanism (Stoma et al., 2008; Merks et al., 2007).

In addition to auxin itself, an auxin efflux-carrier-protein called PINFORMED (PIN) are necessary in order to form characteristic auxin patterns (Okada et al., 1991). The pattern formation of auxin distribution is believed to be an emergent phenomenon produced by the interaction between auxin and PIN. In fact, many experimental data have discovered that the auxin pattern formation is largely dependent on the intracellular distribution of PIN (Mattsson et al., 1999; Sieburth, 1999; Scarpella et al., 2006). Although the interaction between auxin and PIN is considered to be important for auxin pattern formation, the specific mechanism of the interaction is still unclear. Moreover, the mechanism for the diversity of pattern formation is unknown. In order to understand and discuss the single mechanism to produce different patterns, we propose mathematical models that can produce both passage and spot patterns by a single model.

One of the major approaches for understanding auxin pattern formation is mathematical models based on canalization hypothesis, which thus exploit an assumption of positive feedback between auxin flux and PIN localization (Sachs, 1981, 1991, 2000; Mitchison, 1980, 1981; Feugier et al., 2005; Fujita and Mochizuki, 2006a,b). The expected developmental process of the auxin transport path by the mechanism is as follows: PIN is localized in plasma membrane and pumps out auxin from a cell. Once the auxin begins to flow in one direction, the flux in that direction will increase even more. A series of mathematical models have shown that the canalization and its derived flux-dependent mechanisms can indeed form venation-like patterns, including linear veins, branching patterns (Feugier et al., 2005; Fujita and Mochizuki, 2006a,b), and even closed loops and networks (Rolland-Lagan and Prusinkiewicz, 2005; Feugier and Iwasa, 2006). Some studies could generate auxin peaks by integrating additional assumption (Stoma et al., 2008; Walker et al., 2013). They assumed special cells whose auxin degradation rate is set to much higher than other cells. By this assumption, they obtained the auxin peaks where auxin concentration of the cell is higher than the surrounding cells. By this mechanism, the special cell has to be determined by unknown mechanism a priori. From these previous researches, it has been considered that it is difficult to produce auxin peaks by only canalization hypothesis without introducing artificial assumption. In the following, however, we consider mechanisms by which spots which have high auxin concentration are spontaneously realized as a steady state of ODEs without any additional assumption.

There is another class of model for auxin pattern formation, the auxin concentration-based model, which is based on different interaction mechanism between auxin and PIN (Reinhardt et al., 2003; Jönsson et al., 2006; Smith et al., 2006; Merks et al., 2007; Sahlin et al., 2009). The model was proposed to explain the phyllotactic patterns of auxin. It assumes that PIN proteins accumulate on the side of the cell that faces the neighboring cell with the highest auxin concentration. The study showed that the auxin concentration-based model can produce spot and stripe patterns. Before our study, the auxin concentration-based model has been a single possible model that can produce spot patterns. However, we found another possible mechanism producing spot patterns by giving a modification to the standard interpretation of canalization hypothesis.

In this study, we studied possible mechanisms by which plants switch passage and spot patterns in different organs. We developed several different models which show different molecular interactions between auxin and PIN on 2-dimentional hexagonal cellular lattice. From numerical and mathematical analysis, we examined the conditions of these models for generating three different types of pattern formations in dynamics, (a) homogeneous, (b) passage and (c) spot pattern. We found that both passage and spot patterns can be generated based on two mathematical models depending on the parameter values. However, in one of the models it is impossible to switch passage and spot patterns by changing parameter values. From these analyses, we discuss possible mechanisms by which plants switch passage and spot patterns in different organs.

In Section 2, we analyze the capacity for pattern formation of the auxin flux-based model. As a specific representation of this model, we adopt a mathematical model studied by Fujita and Mochizuki (2006b) and call it "basic auxin flux model" in this study. We clarify that the basic auxin flux model can produce passage pattern but not spot patterns by mathematical analysis. The basic auxin flux model was previously shown to explain the mechanism to produce vein-like pattern successfully (Fujita and Mochizuki, 2006b). There are some studies for vein-like patterns based on different mathematical modeling. Walker et al. (2013) used two mathematical models regarding PIN dynamics. One is the model that cell walls do not compete for PIN. This model can produce vein-like pattern, but the auxin concentration of the vein is lower than other tissues (Feugier et al., 2005). This is not consistent with the experimental observation in real plant. Auxin vein has higher concentration than other tissues (Uggla et al., 1996; Avsian-Kretchmer et al., 2002; Mattson et al., 2003). The other model is that cell membranes compete for PIN, which is the important property shared between our basic auxin flux model and (Walker et al., 2013). In Section 3, we give modifications to the basic auxin flux model to produce spot patterns in addition to passage patterns and then obtain two new models, "Auxin-dependent PIN degradation model" and "Auxin self-feedback model". In Sections 4 and 5, we study the features of these modified models with numerical calculation and mathematical analysis. In Section 6, we demonstrate that these modified models can generate realistic patterns by using special lattice shape and growth domain. Finally, through the comparison between two modified models, we discuss the mechanism that can produce the diversity of auxin pattern formation.

2. Results

2.1. The capacity for pattern formation of the basic auxin flux model

2.1.1. Model of the basic auxin flux model

The basic auxin flux model is written as a dynamics of auxin concentration in cells and that of PIN concentration among cell membranes. A plant tissue is modeled by a two dimensional arrangement of hexagonal cells, where each cell is identified by a regular numbers (i). Each edge of a cell is identified by k (Fig. 1),