Creating Complex Patterns from Simple Developmental Rules

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Iterative developmental processes as discrete dynamical systems

Many developmental processes in plants involve the iteration of simple geometrical rules. Examples of such processes are the initiation of lateral organs at the shoot apical meristem and the division of cells during tissue growth. A powerful way to study these iterative developmental processes is to recast them as discrete dynamical systems. In this context, development is fully determined by specifying the initial state of the system and the set of geometrical rules to be applied to evolve the system in time. L-systems are also dynamical systems that typically involve rewriting rules applied to strings of characters instead of geometrical rules applied in space. *The foremost motive to formulate developmental processes as L-systems or geometrical dynamical systems is to allow one to study systematically the morphogenetic potential of a specific set of developmental rules*. Although similar in their approach, geometrical dynamical systems offer one important advantage over L-systems – they operate directly on 2-D or 3-D space. This feature allows greater flexibility to capture complex developmental processes. We illustrate our approach with an analysis of cell division patterns in plant tissues.

Cell geometry in growing tissue layers

The development of the wide array of cell patterns in plants has attracted a lot of attention from biologists (e.g. Lück et al. 1988; Nakielski 1999; Barlow and Lück 2004). Historically, two main rules have been recognized for the division of plant cells. Sachs' Rule stipulates that cells divide such that the two daughter cells are of equal size. Errera's Rule of cell division stipulates that new cell walls behave like soap films (Errera 1888). A consequence is that new walls take the configuration of least possible area subject to some constraints. These constraints are that new walls have constant curvature and meet older walls at right angle.

These two simple geometrical rules were used to explain rather complex division patterns (Thompson 1942). Figure 1A shows the cellular pattern of the glandular trichomes located on the adaxial leaf surface of the Venus flytrap (*Dionaea muscipula*). The trichomes are made of a single cell layer atop a short stalk. The cell pattern is definitely intricate but offers, upon inspection, a few suggestive symmetries. We owe to D'Arcy Thompson the first detailed explanation for the development of this pattern. His argument is based on Sachs' and Errera's rules which, together, lead to a characteristic sequence of divisions (Fig. 1B-F). An initial circular cell is first divided along one of its diameter (Fig. 1C) and then at right angle from the first plane of division (Fig. 1D). These two rounds of radial division fulfill the division rules stated above and lead to the four nearly equivalent quadrants seen in Fig. 1A. The third round of cell division is the most revealing since there are more than one division plane that seem plausible. The most natural inclination would be to divide the cell along the bisecting radial line as in the previous two rounds of division (Fig. 1G, upper right quadrant). This new wall, however, would not meet at 90˚ with older walls. Alternatively, the cell could divide periclinally (Fig. 1G, lower right quadrant). This division seems promising but it is not the shortest wall compatible with both Sachs and Errera's Rules. The shortest possible division plane is anticlinal and culminates in the formation of asymmetric daughters cells (Fig. 1E). It is this division that is observed most frequently in glandular trichomes (Fig. 1A).

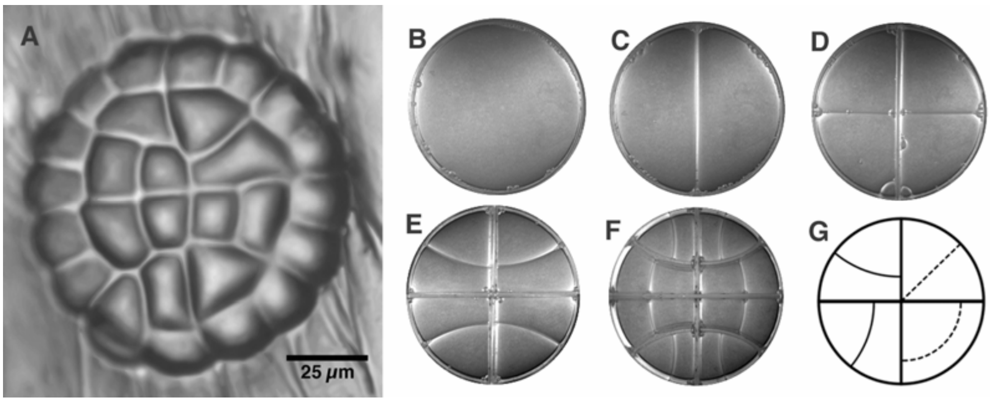

Figure 1: Cell patterning in glandular trichomes. A) Fully developed glandular trichome from the adaxial leaf face of the Venus flytrap. B) - F) Sequential subdivision of a circular dish with soap bubbles. New walls are assumed to rigidify after formation and serve as a fixed template for the next division. G) Possible wall positions for the third round of cell division. The dashed lines indicate divisions that are not compatible with Sachs and Errera's Rules while the solid lines represents the two geometries that fulfill the two rules and are observed in Nature. (From Dumais 2007)

The ability of these geometrical rules to predict several rounds of cell division indicates that they capture a fundamental aspect of the mechanism of cell division in these structures. Patterns akin to the one just described were first studied by Berthold (1886) who reported them from various algal species. Errera's rule was also verified in fern protonemata (Miller 1980, Cooke and Paolillo 1980). The rules, therefore, may be quite general.

Although the predictions made with the geometrical rules can be quite robust, we have also found some exceptions. For example, our observations of glandular trichomes reveal that approximately 15% of the divisions in the third round are of the periclinal type instead of the anticlinal type predicted by the application of Sachs and Errera's Rules. This result has led us to reformulate Errera's Rule such that all walls of constant curvature and right-angle contact are considered. It is then possible, with a simple geometrical argument, to predict what proportion of each division types should be observed. We have found that the 85:15 ratio of anticlinal versus periclinal walls can be predicted by assuming a random selection of the plane of division followed by minimization of the wall area to conform, locally, to Errera's Rule. The simple modification has increased tremendously the predictive power of the geometrical model.

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