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In nature, a variety of patterns, such as the galaxy and the snowflake, are found on a wide range of spatiotemporal scales, and they are generated in a self-organizing manner. Particularly in living organisms, such self-organization of spatiotemporal patterns is both remarkable and essential. Therefore, we aim to elucidate the mechanism of generation and control of self-organized patterns in living systems with a particular focus on plants using both mathematical and computational approaches.

I. Spatial regulation of resource allocation in response to nutritional availability

It is critical for living organisms to appropriately allocate resources among its organs, or within a specific organ, because available resources are generally limited. For example, in response to the nutritional environments of their soil, plants regulate resource allocation in their roots in order to plastically change their root system architecture (RSA), so they can efficiently absorb nutrients (Figure 1A). However, it is still not understood why and how RSA is adaptively controlled. Therefore, we modeled and investigated the spatial regulation of resource allocation by focusing on RSA in response to nutrient availability, and provided analytical solutions to the optimal strategy in the case of simple fitness functions (Fujita et al., J. Theor. Biol. 2020). First, we showed that our model could explain the experimental evidence indicating that root growth is maximized at the optimal nutrient concentration under homogeneous conditions. Next, we extended our model to incorporate the spatial heterogeneity of nutrient availability. This extended model revealed that growth suppression by systemic control is required for adaptation to high nutrient conditions, whereas growth promotion by local control is sufficient for adaptation to low-nutrient environments (Figure 1B). This evidence indicates that systemic control can be evolved in the presence of excessive amounts of nutrition, consistent with the 'N-supply' systemic signal that is observed experimentally. Furthermore, our model can also explain various experimen-



Figure 1. (A) Root growth in the homogeneous availability of nitrogen nutrition. (B) Schematic representation of the spatial regulation of the optimal resource allocation in response to nutrient availability. (left) In the low nutrient availability, the optimal root density is promoted by nutrient through local control (blue arrows). (right) By contrast, in addition to local control, is suppressed through systemic control (denoted in red) under high nutrient availability.

tal results using nitrogen nutrition, and provides a theoretical basis for understanding the spatial regulation of adaptive resource allocation in response to nutritional environment.

II. Phyllotaxis pattern formation

Phyllotaxis, the beautiful geometry of plant-leaf arrangement around the stem, has long attracted attention from researchers of biological-pattern formation. Many mathematical models, as typified by those of Douady and Couder (alternate-specific form, DC1; more generalized form, DC2), have been proposed for phyllotactic patterning, mostly based on the notion that a repulsive interaction between leaf primordia spatially regulates primordium initiation. In the framework of DC models, which assume that each primordium emits a constant power that inhibits new primordium formation, and that this inhibitory effect decreases with distance, the major (but not all) types of phyllotaxis can be manifested as a stable pattern. Orixate phyllotaxis, which has a tetrastichous alternate pattern with a four-cycle sequence of the divergence angle, is an interesting example of an unaddressed phyllotaxis type. We examined DC models regarding the ability to produce orixate phyllotaxis and found that model expansion through the introduction of primordial agedependent changes of the inhibitory power is essential for the establishment of orixate phyllotaxis (Yonekura et al., PLoS Comput. Biol. 2019). The simulation results obtained using the expanded version of DC2 (EDC2) fitted well the natural distribution of phyllotactic patterns. Our findings imply that changing the inhibitory power is generally an important component of the phyllotactic patterning mechanism.

Publication List:

[Original papers]

- Fujita, H., Hayashi-Tsugane, M., and Kawaguchi, M. (2020). Spatial regulation of resource allocation in response to nutritional availability. J. Theor. Biol. 486, 110078. doi: 10.1016/j.jtbi.2019.110078
- Tokumoto, Y., Hashimoto, K., Soyano, T., Aoki, S., Iwasaki, W., Fukuhara, M., Nakagawa, T., Saeki, K., Yokoyama, J., Fujita, H., and Kawaguchi, M. (2020). Assessment of plant characteristics of *Polygala paniculata* (Polygalaceae) for evolutionary studies of legume-rhizobia symbiosis. J. Plant Res. *133*, 109-122. doi: 10.1007/s10265-019-01159-x
- Yonekura, T., Iwamoto, A., Fujita, H., and Sugiyama, M. (2019). Mathematical model studies of the comprehensive generation of major and minor phyllotactic patterns in plants with a predominant focus on orixate phyllotaxis. PLoS Comput. Biol. 15, e1007044. doi: 10.1371/ journal.pcbi.1007044