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The combined mechanisms of the reverse fountain and the reflected flow provide for self-organization and maintenance of the root apical meristem

The phytohormone auxin is critical for patterning and morphogenesis in plants. In plant roots, auxin maxima coincide with the sites of the root apical meristem (RAM) initiation and functioning. By today, the two main mechanisms of the auxin distribution formation in the root tip were proposed. The reverse fountain mechanism is based on a specific RAM structure in which each cell has a specified set of directions of auxin efflux. A stable location of the auxin maximum in silico is provided for by a reflux of auxin from the basipetal flow back to the acropetal flow all along the meristem, which transports auxin in a loop. The reflected flow mechanism is based on the auxin-dependent regulation of auxin acropetal flow: low auxin concentrations activate the transcription of PIN1 genes, whereas the high concentrations induce degradation of PIN1 proteins [2]. The mechanism explains self-organization of the auxin distribution pattern in an array of functionally identical cells acquiring cell type specialization due to auxin regulation of the level of PIN1 proteins in these cells. We suggested that the reverse fountain and the reflected flow mechanisms are complementary in root development. In particular, only the reflected flow mechanism operates at the very early stages of root development. At later developmental stages, an anatomical structure forms and provides for the functioning of the reverse fountain mechanism that serve for more robust maintenance of the auxin maximum in the RAM. However, the reflected flow mechanism does not disappear, revealing itself if RAM structure is disrupted or the environment changes. To test the hypothesis we combined both mechanisms in 2D mathematical model. This model describes (1) auxin flow from the shoot; (2) auxin synthesis that is positively regulated by auxin itself; (3) irreversible loss of auxin (degradation); (4) auxin diffusion, providing for an isotropic distribution in the root; synthesis and degradation depending on auxin concentration of (5) PIN1, (6) PIN2, (7) PIN3; (8) active auxin transport mediating by PINs proteins; (9) growth and division of root cells. Two cell types are considered in the 2D model: central cylinder and epidermis. For the central cylinder cells the processes (1-5,7-9) are considered and described as in [2]. For the epidermal cells the processes (2-4,6-9) are considered. As auxin transporters carry out different, often redundant, functions in specialized tissues, we introduced to the model some simplifications. Only three auxin carriers are considered: PIN1 transports auxin acropetally, PIN2 mediates basipetal auxin flow as well as lateral transport from basipetal back to

acropetal flow, PIN3 regulates auxin redistribution in the root cap. Thus, PIN proteins have the following locations in the cells: PIN1 is localized at the basal side of the central cylinder cells, PIN2 at the lateral internal and apical sides of the epidermal cells and PIN3 at all sides of potentially all cells. For the processes (1,3-5,8-9) the parameter values were taken from [2]. Other parameters were estimated so that: (1) PIN2 is expressed predominantly in epidermal cells with low auxin level; (2) PIN3 expression domain is localized in the zone of high auxin level; (3) auxin synthesis rates are high in the cells with high auxin level. With this set of parameters and initial uniform auxin distribution, the model provides steady-state auxin distribution pattern that agree well with the experimental data. The mechanism of auxin distribution self-organization found in the resulting stationary solutions is the following. At the first step, auxin maximum is generated in the central cylinder cell array at the distance from the root end under the reflected flow mechanism. As a result, the zone of high auxin level in the root tip is organized where PIN3 and auxin synthesis rate are high. Second, the PIN3-mediated auxin redistribution is switched on in the root tip, and auxin moves to PIN2-mediated basipetal flow in epidermis. Third, As PIN2 is localized on the lateral internal cell sides in epidermis, the reflux of auxin from the basipetal flow back to the acropetal flow starts to work. Finally, the auxin gradient associated with the maximum is formed under the reverse fountain mechanism which finishes formation of auxin distribution pattern. In numerical experiments we showed that the 2D model reveals both the robustness to the developmental processes from the reverse fountain mechanism [1] and the plasticity to the environment changes from the reflected flow mechanism [2]. Based on these advantages the 2D model gave new predictions about the positional information in root patterning that can be checked in the experiments. The 2D model of auxin distribution in root can be a powerful tool for investigation of root development in silico.

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