

Mathematical modeling of hormonal regulation of the plant root tip structure

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The plant root tip is a convenient object to study the stem cell niche organization. The tip contains columella and the meristem zone (MZ), which consists of the quiescent center (QC), the proliferation domain and the transition domain (Fig. 1A). In the MZ mitotically inactive cells of the QC are surrounded by proliferating cells, losing their ability to divide at a certain distance from the QC. Plant hormones auxin and cytokinin play an important role in regulation of the MZ pattern, but the mechanisms maintaining the structure in dynamics remain unknown.

Auxin and cytokinin are the antagonists in regulation of cell divisions (Dello Ioio *et al.*, 2007). Auxin induces cell divisions in the MZ, while cytokinin promotes cell differentiation in the transition domain. Treatments by exogenous cytokinin as well as increase of its endogenous synthesis lead to root growth inhibition and reduction of the proliferation domain in the MZ. Decrease in the cytokinin levels leads to an opposite effect (Kuderova *et al.*, 2008). According to the data on the cytokinin-sensitive reporter activity (Zürcher *et al.*, 2013), cytokinin level is high in the transition domain of the MZ and in columella.

Auxin gradient is a key factor that locates the stem cells niche in the root meristem and maintains its size (Sabatini *et al.*, 1999). The auxin maximum is generated in the QC and columella by PIN auxin carriers (Grieneisen *et al.*, 2007). By regulation of *PINs* transcription and PIN proteins polarization and degradation, auxin creates its own gradient (Mironova *et al.*, 2010, 2012).

In this work, we propose a mathematical model that summarizes the experimental data on distribution of auxin and cytokinin along the root tip and their role in cell cycle regulation. We suggest a baseline mechanism of the root tip structure formation (columella, proliferation and transition domains) with auxin and cytokinin gradients only. The consistency and sufficiency of the mechanism were tested in the mathematical model. For this purpose, the mathematical model (Mironova *et al.*, 2010) was extended with the equations for cytokinin distribution and the rules for G1/S and G2/M transitions regulated by auxin and cytokinin.

The model describes cell dynamics in 1D cell array ($i=1, \dots, N$) along the central root axis (Fig. 1A). We assign a number 1 for the most distal cell in a root tip, the cell N is located in the transition domain. Stochastic grammar reactions describe events such as cell division or death, whereas continuous rules depict cell growth and movement and the active or passive transportation of signaling molecules between cells as well as dissipation of these molecules. We made two variants of the model: with constant number of cells (1) and with cell divisions (2).

For pattern distribution analysis of the morphogens we used a stationary solution of a model (1) with $N=20$. We adjusted the values of parameters so that during the model calculation the self-organization of auxin maximum in the 4th cell and two cytokinin maxima occurred – in the root tip and the root base (Fig. 1B).

Based on the proposed mechanism for cell cycle regulation we got the model (2) solution with dynamical cells number from $N=15$ to $N=50$. During calculation the model generates the auxin maximum in the 4th cell and keeps it there despite increase the number of cells. The same was observed for cytokinin, which patterning in the root tip was modelled here for the first time (Fig. 1C).

In the model solution we observed formation of three regions that vary by the cell status in the cell cycle. Fig. 1D shows that the columella cells are in the G1 phase, the cells in the transition domain are in G2, the cells in the proliferation domain can be in both phases. Such a distribution correlates well with the experimental data. These three subzones were maintaining through the calculation, which indicates the consistency and sufficiency of the proposed mechanism for the MZ patterning.

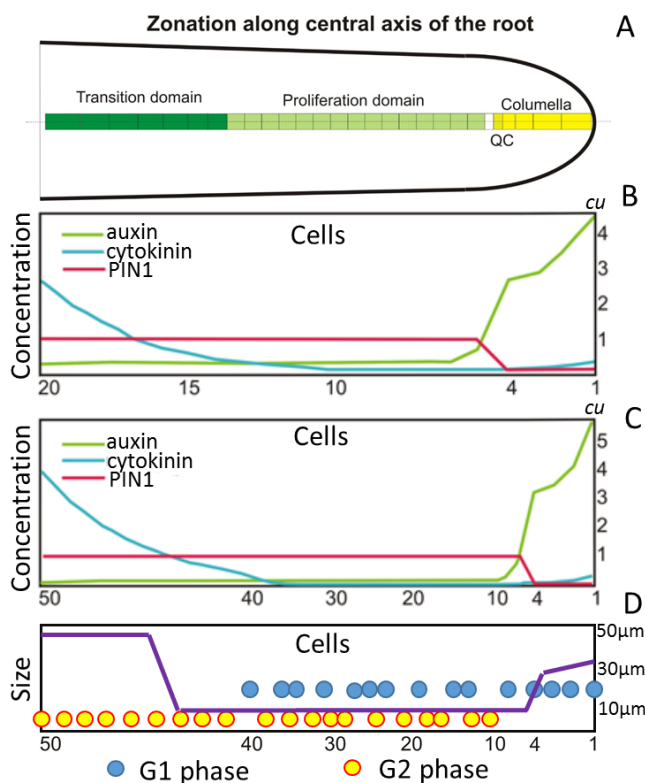


Figure 1. A. Zonation of the root tip along the central axis. Yellow cells belong to columella, the white cell is the Quiescence center (QC), the light green cells are in the proliferation domain, the dark green cells belongs to the transition domain. **B.** The steadystate solution of the model (1) for $N=20$. **C.** The model (2) solution, after the cell array grew $N=15$ to $N=50$. **D.** The size and the cell cycle phase of the cells in the solution (C.)

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