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Current Opinion in Plant Biology

Computational modeling of epidermal cell fate determination systems

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Cell fate decisions are of primary importance for plant development. Their simple 'either-or' outcome and dynamic nature has attracted the attention of computational modelers. Recent efforts have focused on modeling the determination of several epidermal cell types in the root and shoot of Arabidopsis where many molecular components have been defined. Results of integrated modeling and molecular biology experimentation in these systems have highlighted the importance of competitive positive and negative factors and interconnected feedback loops in generating flexible yet robust mechanisms for establishing distinct gene expression programs in neighboring cells. These models have proven useful in judging hypotheses and guiding future research.

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Current Opinion in Plant Biology 2013, **16**:5–10

This review comes from a themed issue on **Growth and development**

Edited by **Michael Scanlon** and **Marja Timmermans**

For a complete overview see the Issue and the Editorial

Available online 1st January 2013

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http://dx.doi.org/10.1016/j.pbi.2012.12.003

Introduction

Recent advances in computing power and software, combined with the wealth of new information generated by traditional and large-scale molecular biological research, have led to increased interest in the application of computational and mathematical modeling in biology [1–3]. Advantages to applying a computational modeling approach are many: they can provide insight into nonintuitive, unpredictable, or complex systems, they can enable multi-component processes to be systematically untangled, they can predict the existence of new elements or mechanisms, and they can be used to test hypotheses.

One area of plant biology where computational modeling has already had a significant impact is cell fate determination. The goal here is to define the mechanism that generates a stable molecular difference between neighboring cells (sometimes referred to as 'symmetry breaking'); typically envisioned as a dynamic process with a simple 'either/or' outcome amenable to modeling. This process can often be subdivided into two stages, one that initiates the difference (either intrinsically and/or in response to extrinsic factors) and another that stably amplifies the difference (often via feedback loops) to ensure the adoption of distinct fates.

Here we focus on applications of computational modeling to gain insight into the problem of cellular pattern formation in the root hair, trichome, and stomatal developmental systems of Arabidopsis. We focus on the most recent findings, emphasizing the lessons learned and fruitful areas for further exploration.

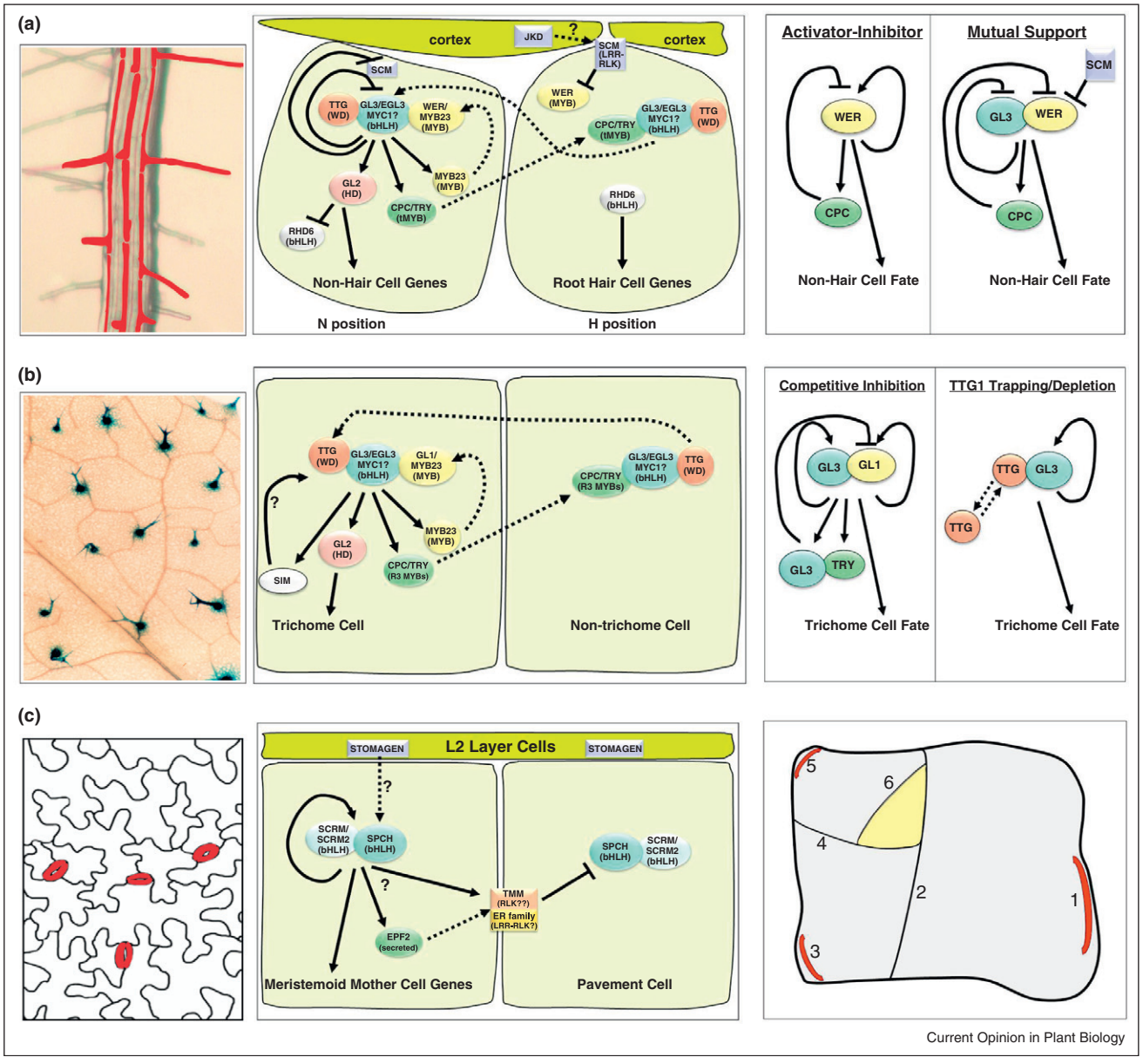
Root hair patterning

Root-hair cells and nonhair cells are patterned in rows within the Arabidopsis root epidermis, with columns of root-hair cells interspersed with columns of nonhair cells (recently reviewed in [4,5]). Central to the cell fate choice is the type of trimeric MYB–bHLH–WD protein complex that accumulates within a developing root epidermal cell. A complex including the WEREWOLF (WER) MYB together with the GLABRA3 (GL3) or ENHANCER OF GLABRA3 (EGL3) bHLHs and the TRANSPARENT TESTA GLABRA (TTG) WD protein promotes nonhair gene expression and represses root-hair gene expression. An alternative inactive complex with WER replaced by a small R3 MYB protein, such as CAPRICE (CPC) or TRIPTYCHON (TRY), lacks the transcriptional activity of the functional WER complex so that cells accumulating this complex adopt the hair cell fate (Figure 1**(A)**). An array of experimental evidence indicates that the WER MYB and the R3 MYBs compete for binding to the N-terminal region of the bHLHs [6•,7], including a recent study that defines important residues and demonstrates that two amino acid substitutions are sufficient to convert the WER to a CPC-like function [8•].

Given the presumed importance of the competitive MYB interactions, there has been great interest in understanding how these two types of MYBs differentially accumulate during epidermis development. A fascinating aspect of this problem is that transcription of the R3 MYB genes is promoted by the WER complex, effectively generating a negative feedback loop. Further, the R3 MYBs are capable of moving intercellularly, presumably through plasmodesmata, to affect complex formation in neighboring cells.

The dynamic aspect of this problem has attracted modeling efforts, largely derived from classic 'reaction-diffusion' mechanisms of Turing [9] and elaborated by

Figure 1



Summary of the three cell fate determination systems in Arabidopsis. Common colors indicate components that appear similar in structure or function between the systems or models. Solid lines indicate gene regulation; dotted lines represent protein movement/signaling. **(A)** Root Hair Patterning. Left: Root hair cells (red) occur in files. Center: Molecular genetic diagram of root epidermal cell determination. Right: Activator–Inhibitor Model — The basic activator–inhibitor model generates concentration differences between a self-promoting activator and a more-mobile inhibitor. Mutual Support Model — This model has interlocking loops, but lacks a direct self-activation loop. **(B)** Trichome Patterning. Left: Trichomes (GUS stained) distributed on an Arabidopsis leaf. Center: Molecular genetic summary of the trichome determination network. Right: Competitive Inhibition Model — TRY mediates inhibition of the activating complex via binding to GL3. Trapping/Depletion Model — The mobile TTG tends to move into developing trichome cells and is trapped in the nucleus by GL3 binding. **(C)** Stomatal Patterning. Left: Tracing of pavement cells and stomatal complexes (guard cells in red) on an Arabidopsis leaf. Center: Speculative diagram for determination of meristemoid mother cells and pavement cells from unspecified protodermal cells. Right: Model for regulating orientation of asymmetric MMC divisions via postmitotic redistribution of BASL (red), adapted from [39••]. Numbers indicate the order of events.

Meinhardt and colleagues [10,11], which show that stable patterns of substance concentrations can be generated from a uniform field provided simple rules are followed (including local self-enhancement and long-range inhibition; see Box 1 for background information). In one of the first models of the root hair system, appropriate patterns of WER and CPC accumulation could be generated from an activator–inhibitor-based model, so long as a

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