

Growth and development: from genes to networks and a mechanistic understanding of plant development

Editorial overview

Michael Scanlon and Marja Timmermans

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Michael Scanlon

Department of Plant Biology, Cornell University, 413 Mann Library, Ithaca, NY 14853, USA
e-mail: mjs298@cornell.edu

Mike Scanlon's research group is focused on shoot apical meristem function, utilizing classical genetics alongside comparative genomic analyses of meristem and leaf development. Recent work has focused on transcriptomic analyses of maize shoot meristem ontogeny, and evolutionary-developmental studies of shoot apical function in structurally diverse meristems from model land plants.

Marja Timmermans

Cold Spring Harbor Laboratory, 1 Bungtown Road, Cold Spring Harbor, NY 11724, USA

Marja Timmermans' research group studies axial patterning of lateral organs, with a particular focus on the role of small regulatory RNAs as mobile instructive signals in this process. Her lab also investigates the molecular mechanisms that regulate stem cell homeostasis in the shoot and that distinguish indeterminate cells within the shoot apical meristem from their differentiating derivatives. Their latest work in this area focuses on the epigenetic repression of stem cell regulators during organogenesis.

Over the past twenty to thirty years, genetic screens in a variety of plant species have yielded a wide array of developmental mutants whose analyses have greatly enhanced our understanding of plant morphogenesis. The field has matured to the point where complex gene regulatory networks (GRNs) comprising signal transduction pathways, transcription factors, small RNAs and downstream target genes are becoming clearer for an ever-increasing number of developmental processes. Yet, a detailed, step-by-step understanding of the molecular mechanisms that give rise to stem cell organization, organogenesis, and differentiation in plant tissues is still lacking. With unparalleled recent advances in the areas of genomics, digital imaging and computational biology, the technology is now in place to enable the use of systems biological approaches toward unraveling the molecular mechanisms of plant growth and development at the whole organ level. In this issue of *Current Opinion in Plant Biology*, new technological advances in the study of plant development are presented within seventeen reviews of this new paradigm and its application to address longstanding, fundamental questions in plant biology.

Computational and mathematical models investigate developmental principles at the systems level. When combined with molecular genetic experimentation, such theoretical approaches have proven extremely useful in testing plausible models and in guiding future research. Modeling can provide insights into non-intuitive behavior of networks or systems, and predict the existence of additional network components, not unlike the way theoretical physics predicted the existence of the Higgs boson and other yet to be identified particles. The power of such integrated approaches is illustrated nicely in the article by [Ryu](#) and colleagues, which highlights recent advances in our understanding of the patterning mechanisms underlying epidermal cell fate specification in the root and shoot of *Arabidopsis*. Epidermal patterning is an especially tractable subject for modeling because many of the GRNs impacting leaf and root epidermal development are well described. Results from computer modeling emphasize the importance of competitive positive and negative regulators and interconnected feedback loops in generating flexible yet robust cell fate patterns.

In the article '*Dynamic models of epidermal patterning as an approach to plant eco-evo-devo*', [Alvarez-Buylla](#) and colleagues elaborate on this theme. They describe computer modeling of epidermal patterning in *Arabidopsis* as a robust experimental system to explore the effects of ecological parameters on the evolution of plant development. A merging of ecology, evolution and developmental biology, Eco-Evo-Devo investigates the impact of variations in environmental stimuli on the evolution of epigenetic and gene regulatory

networks that control developmental and morphological plasticity. Epidermal patterning is an especially tractable subject for Eco-Evo-Devo modeling, not only because many of the GRNs involved are well described, but also because the epidermal phenotypes are developmentally plastic, and current models can be predictive of such morphological variation following perturbation of specific epigenetic, genetic, and/or hormonal parameters. [Alvarez-Buylla](#) summarizes current research into the GRNs and hormonal interactions regulating epidermal patterning, and presents a convincing justification of the use of this plastic developmental system for modeling Eco-Evo-Devo.

Another research area where computational and mathematical modeling has been applied successfully is in plant hormone signaling. While our knowledge on the topologies of hormone signaling networks had increased tremendously in recent years, it remained difficult to predict the dynamic properties of these signaling networks. In their review, [Vernoux](#) and colleagues highlight recent studies that use modeling approaches to describe how hormone signals are converted into specific outputs and how spatiotemporal regulation of hormone signaling contributes to pattern formation and modulates plant growth.

The availability of *in vivo* imaging techniques and other quantitative approaches are instrumental in the design of accurate computational models. [Routier-Kierzkowska and Smith](#) review the latest advances in the development of techniques to quantitatively investigate the mechanical properties of plant tissues at the cellular level. Morphogenesis reflects the coordinated growth of individual cells mediated via localized changes in the cell wall. As such, the control of growth and morphogenesis by hormone and other signaling networks ultimately requires the coordinated regulation of mechanical properties in individual cells. Micro-indentation and nano-indentation techniques are now being used to measure cell wall elasticity, viscosity and plasticity at the cellular level. As discussed in this review, differences in such mechanical properties, for instance, exist between the central and peripheral zones of the shoot apical meristem and likely contribute to the organogenic potential of these meristem regions.

The article by [Sappl and Heisler](#) discusses the latest innovations toward marrying computer modeling with live imaging, which is an especially synergistic combination of tools toward understanding plant development. His review presents state-of-the-art technology to counteract photodamage, an ever-present problem during live-imaging of fluorescently labeled proteins, and strategies for *in vivo* imaging of intracellular proteins with increasing specificity and resolution are reviewed. Studies analyzing the effects of intracellular mechanical signals on plant

development, and research into how localized cell perturbations affect development of neighboring cells and tissues are all being conducted in a live setting.

A number of precise techniques, such as biochemical and affinity purification, cell sorting and microsurgery, genetic subtraction and laser-microdissection have enabled transcriptomic analyses of single, isolated, plants cells. The use of these innovative approaches is proving to be especially useful in studies of the angiosperm female gametophyte, which over the course of plant evolution has been reduced to just eight cells that nonetheless exhibit remarkably diverse and specific functions. In their article '*Cells specific expression profiling of rare celltypes as exemplified by its impact on our understanding of female gametophyte development*', [Grossniklaus](#) and co-authors update recent advances in our understanding of cell-specific gene expression and intercellular signaling within the Arabidopsis female gametophyte. These technologies are easily adaptable for comparative studies of gametophyte evolution in non-model species.

A high-resolution cell type and temporal mRNA expression atlas has been generated also for the Arabidopsis root. The relatively simple organization of the Arabidopsis root with distinct cell types arranged in concentric rings and developmental time revealed along cell files has made this organ a preferred model for systems biology studies. High-throughput tools also in proteomics, metabolomics, and on the interactome have been applied extensively to the Arabidopsis root. The article by [de Lucas and Brady](#) reviews how this wealth of information has been used to develop GRNs that describe how genes, transcripts, proteins, and metabolites are inter-connected to drive cell fate specification and differentiation. These studies reveal general properties of robust GRNs, including complex feedback or feedforward loops and extensive combinatorial interactions in gene regulation.

Mobile signals allow cell-to-cell communication to provide positional information for cell fate specification, to coordinate GRNs across multiple cells, and to alter these networks in response to environmental change. The spectrum of mobile signals is diverse, including diffusible proteins, hormones, mRNAs, miRNAs, and secreted peptides. The article by [Yamada and Sawa](#) describes diverse roles of peptide signals in development, highlighting recent studies describing the nature of biologically active peptide signals, how these are perceived, and the cell-type dependent read-outs these generate. Biochemical approaches have proven particularly important in these studies and have revealed essential modifications on biologically active signaling peptides.

Molecular mechanisms generating robustness at the organismal level are discussed in the review by [Lempe](#) and colleagues. Robustness in this sense refers to the plant's

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