



Cellular Dynamics: Cellular Systems in the Time Domain

Plant cells are the fundamental building blocks of growth and development. For each cell type, the size, shape, and mechanical properties of the cell wall are customized for particular physiological functions (Szymanski and Cosgrove, 2009; Winship et al., 2011). The morphogenesis of highly polarized cell types such as trichoblasts and pollen tubes is internally programmed and occurs largely in the absence of a neighbor. Most cell types differentiate in the context of a tissue. Therefore, their growth and shape change can operate at larger spatial scales to influence tissue- and organ-level processes. Because plant cells grow symplastically and are mechanically coupled to their neighboring cells, growth properties and information flow within and between tissues can feed back on and influence cell behaviors. Plant cells are also metabolically specialized. Within a single tissue or organ, cell types can differ greatly in terms of how central metabolism is fueled, the types of metabolites that accumulate, and where in the cell they are stored.

Despite the structural and biochemical diversity of different cell types, their cell biology and development can be considered as a similar set of integrated systems-level processes. For example, the metabolic activity and energy status of a cell varies as a function of light levels or developmental stage. The biosynthesis and transport activities of the cytosol and endomembrane systems are integrated with metabolism over time. Cellular systems are also integrated across wide spatial scales. Proteins and protein complexes at the approximately 10- to 100-nm scale can use the cytoskeleton to position organelles and organize the cytoplasm at the approximately 1- to 10- μ m spatial scale, to influence cell behaviors. Discovering and unraveling the complexity of these multiscale systems level interactions is a grand challenge in plant research. In recent years, progress has been rapid and is being driven in large part by the widespread use of multi-channel quantitative time-lapse imaging. Using this approach, it is possible to create a spatial and temporal coordinate system in which multiple parameters can be measured and cross-correlated, and the effects of mutations or other experimental manipulations can be more deeply analyzed.

GROWTH STRATEGIES AND BIOMECHANICS

This Focus Issue includes *Updates* that broadly cover recent discoveries in the field of cell biology and can serve as an important resource for research and classroom instruction. The *Updates* section of the issue

begins with two articles that describe recent discoveries on the biomechanics and control mechanisms of cells that employ either a diffuse growth (Cosgrove, 2018) or tip growth mechanism (Bascom et al., 2018). Quantitative multivariate live cell imaging enables the creation of computational models that predict the mechanics of morphogenesis. In the *Update* by Bidhendi and Geitmann (2018), the impact of recent papers that use finite element computational modeling to analyze cell morphogenesis is reviewed.

CYTOSKELETON: CELLULAR ORGANIZATION AND FUNCTION

Growing plant cells use the cytoskeleton to organize the cytoplasm and pattern the cell wall to define the roadways for intracellular transport and influence the mechanical properties of the cell wall. The cortical microtubule cytoskeleton is tightly associated with the plasma membrane and can dictate the patterns of cellulose synthesis in the cell wall (Wasteneys and Ambrose, 2009). Determining how microtubules are patterned at cellular spatial scales is an active area of research and is covered in a research *Update* in this issue (Elliott and Shaw, 2018b). The Focus Issue also contains a research article describing new types of cortical microtubule arrays that were discovered using spatial and temporal analysis of microtubule polymerization patterns in light-grown hypocotyl cells (Elliott and Shaw, 2018a). Long-term time-lapse imaging and cross-correlation analyses of leaf epidermal pavement cell shape and microtubule organization were used to reveal unexpected temporal and spatial variability of cortical microtubules during the process of lobe formation in pavement cells (Belteton et al., 2018). This issue also contains important new discoveries on the genetic control of microtubule arrays that position the cell division plane (Mir et al., 2018) and a plant-specific Kinesin (KinG) that uses microtubule-based transport to affect intercellular transport of a developmental regulatory protein (Spiegelman et al., 2018). The actin cytoskeleton also is required for the growth of cells that employ either tip or diffuse growth mechanisms. However, it has been difficult to assign particular functions to specific actin arrays in the cell because they are often short-lived, widely distributed, and highly variable with respect to their spatial organization in the cell. The *Update* by Szymanski and Staiger (2018) focuses on recent discoveries that advance our understanding of how particular actin filament arrays influence growth and organelle clustering in polarized cell types. In this issue, quantitative live cell imaging and biophysical modeling of organelle diffusion was used to demonstrate an important role for actin filaments in locally increasing vesicle concentration at the

¹Address correspondence to szymandb@purdue.edu.
www.plantphysiol.org/cgi/doi/10.1104/pp.17.01777

apex of tip-growing moss protonema (Bibeau et al., 2018). A major research question in the transport and morphogenesis field is centered on understanding how myosin motors are dynamically coupled to actin filament roadways and cargo. The structure and regulation of plant myosin motors is the subject of a timely *Update* from the Nebenführ lab (Ryan and Nebenführ, 2018).

ORGANELLES

Endoplasmic Reticulum: Morphology and Function

The endomembrane system, plastids, and mitochondria compose an interdependent population of organelles that compartmentalize the biosynthetic and metabolic activities of the cell. The Cell Dynamics Focus Issue contains numerous *Updates* and research articles that analyze the biogenesis and function of many of the major plant organelles. For example, the endoplasmic reticulum (ER) consists of a highly dynamic network of membrane sheets and tubules that runs throughout the cytoplasm. The synthesis, quality control, and trafficking of various macromolecules originates in the ER, and is therefore critical for plant growth, development, and stress responses (Stefano and Brandizzi, 2018). This *Update* discusses the dynamics of ER morphology and how this changes under different conditions and throughout development. Recent findings on the function of the cytoskeleton and ER membrane-shaping proteins are presented. In this issue, Sun and Zheng (2018) present a detailed structure-function analysis of the RHD3, an ER membrane fusion factor. The article describes the importance and mechanism of RHD3 dimerization and how it influences ER network structure. Oil or lipid bodies are present in many cell types and are derived from the ER. Control of the size and morphology of oil bodies and the role of oil body membrane proteins in both oil body formation and oil body breakdown during seed germination are described in an *Update* (Shimada et al., 2018). The interaction between oil bodies and peroxisomes is discussed as an example of the dynamics of organelle interactions.

Endocytosis, Early Endosomes, and the trans-Golgi Network

Endocytosis is the process by which plasma membrane lipids and proteins, and soluble apoplastic proteins, are packaged and internalized within clathrin-coated vesicles. The cellular control of endocytosis has been controversial in plants, and in this issue Reynolds et al. provide an authoritative *Update* on the recent advances in this field (Reynolds et al., 2018). Phosphatidylinositol (PI) 3-phosphate (PI3P) is a minor phospholipid that has been implicated in the trafficking of endocytic cargo in plants (Schink et al., 2013).

The trans-Golgi network (TGN) not only is a sorting station for cargo en route to the plasma membrane, but also functions as an early endosome, receiving endocytic vesicles from the plasma membrane. Therefore, the TGN is the convergence site for multiple trafficking pathways. Cargo from each of these pathways has to be correctly sorted at the TGN for transport on to the appropriate destination. An *Update* discusses recent work on the biogenesis of the TGN from the Golgi, the specialization of distinct TGN domains for sorting via different pathways, and role of the TGN in cell wall synthesis and cytokinesis (Rosquete et al., 2018).

Chloroplasts and Mitochondria

Chloroplasts and mitochondria are critical organelles for photosynthesis and respiration, respectively. This Focus Issue highlights the cell biology of their division and their membrane connectivities. The *Update* from Chen et al. describes our recent understanding of chloroplast division machineries (Chen et al., 2018). In bacteria, cell division involves only a single FtsZ protein that forms polymers that mark and generate the division site. In this issue, the Osteryoung group demonstrates that photosynthetic organisms encode a second FtsZ isoform and that plastid division involves the polymerization of FtsZ heteropolymers during chloroplast division (TerBush et al., 2018). Another interesting aspect of chloroplasts is their unique protruding structures, termed “stromules,” that extend from the outer chloroplast membrane. The imaging techniques to visualize and analyze stromules in the context of interorganelle communication and environmental response is reviewed (Hanson and Hines, 2018). Although chloroplasts respond to external abiotic signals, such as blue light-regulated chloroplast relocation in mesophylls, how chloroplast morphologies are affected by biotic signals is poorly understood. A research article by Jin et al. (2018) moves the field forward by using electron tomography and 3D construction of chloroplasts in virus-infected *Nicotiana* cells, and reveals cytoplasmic invaginations at outer envelopes as the site of virus replication. Similar to chloroplasts, mitochondria also proliferate by division of preexisting organelles. However, they are much more dynamic because of a highly active “fusion” system that chloroplasts do not possess. This fusion system plays a fundamental role in exchanging mitochondrial genetic information, as mounting evidence now indicates that a majority of mitochondria exist without DNA. Arimura (2018) reviews mitochondrial fusion and fission systems in plant cells, with emphasis on the interorganelle mitochondrial DNA exchange.

Cellular Responses to Stress

Fundamentally important cellular processes such as gene expression (see *Updates* Daszkowska-Golec [2018] and Chantarachot and Bailey-Serres [2018]) and vesicle trafficking respond to adverse conditions. Autophagy is a vesicle trafficking process in which organelles and

macromolecules are transported in autophagosomes to the vacuole for degradation, often as a response to stress. An *Update* by Soto-Burgos et al. discusses recent advances in our understanding of how the autophagy pathway is activated by a variety of stress conditions, and also the mechanisms by which membrane remodeling and dynamics contributes to the formation of autophagosomes (Soto-Burgos et al., 2018). Peroxisomes are specialized for oxidation reactions during fatty acid catabolism, reactive oxygen species scavenging, and photorespiration. Peroxisomes not only emerge from budding ER membranes but also proliferate by division. Kao et al. provide a comprehensive *Update* in which peroxisome biogenesis as well as metabolic reactions are reviewed (Kao et al., 2018). Environmental stress is known to cause proliferation of peroxisomes, but the mechanisms by which this occurs are unknown. An article by Frick and Strader shows that MAP KINASE17 (MPK17) controls the number of peroxisomes via the peroxisome division factor PMD1, with an increase in peroxisome number in *mpk17* mutants (Frick and Strader, 2018). Both MPK17 and PMD1 were shown to be required for proliferation of peroxisomes upon salt stress, in a process requiring actin polymerization. MPK17 therefore defines a new pathway for the regulation of peroxisome number, particularly as a response to stress conditions. The nucleus usually receives attention because of its importance in controlling gene expression in response to developmental or positional cues. The nuclear envelopes and nuclear pore complexes are important components of the nuclear periphery and help to define nuclear structure. Knowledge about how the structure of the nucleus is generated and how it responds to developmental and biotic/abiotic signals is described in the *Update* by Groves et al. (2018). The issue also contains an article that analyzes how nuclear position is controlled during root hair differentiation (Nakamura et al., 2018).

CLOSING REMARKS

Sophisticated live cell imaging pipelines are being used to quantitatively analyze organelle, cytoskeletal, and cell wall systems (often in parallel). These imaging-centric approaches, empowered further by solid genetics and biochemistry, are providing mechanistic insight into how cells control their division and morphogenesis across wide spatial and temporal scales. The field is learning more about how cellular systems allow the plant to respond adaptively to abiotic and biotic stress. Collectively, these discoveries are providing a knowledge base that can enable the engineering of improved crops with specified architectural traits or stress tolerances. There are likely to be increasing opportunities to use different types of computational modeling techniques to define specific targets and efficient strategies for cellular engineering (Zuñiga et al., 2018). As more of the proteins and cellular activities that control cellular

phenotypes become known, there are new opportunities to use rapidly evolving superresolution and light sheet microscopy technologies (see *Update* by Komis et al. [2018]). Protein complexes and cellular dynamics can be analyzed at spatial and temporal resolutions far beyond what has been previously achieved. An important remaining challenge is centered on learning how small GTPases and other signaling molecules coordinate diverse cellular activities during plant growth and development (see *Update* by Feiguelman et al. [2018]). In the coming years, it will be interesting to see the extent to which new imaging technologies and computational methods accelerate the rate at which the control modules of the cell are revealed.

Dan Szymanski¹
Monitoring Editor

Diane Bassham
Monitoring Editor

Teun Munnik
Monitoring Editor

Wataru Sakamoto
Monitoring Editor

LITERATURE CITED

Arimura S (2018) Fission and fusion of plant mitochondria, and genome maintenance. *Plant Physiol* 176: 152–161

Bascom CS Jr, Hepler PK, Bezanilla M (2018) Interplay between ions, the cytoskeleton, and cell wall properties during tip growth. *Plant Physiol* 176: 28–40

Belteton SA, Sawchuk MG, Donohoe BS, Scarpella E, Szymanski DB (2018) Reassessing the roles of PIN proteins and anticlinal microtubules during pavement cell morphogenesis. *Plant Physiol* 176: 432–449

Bibeau JP, Kingsley JL, Furt E, Tüzel E, Vidali L (2018) F-actin mediated focusing of vesicles at the cell tip is essential for polarized growth. *Plant Physiol* 176: 352–363

Bidhendi AJ, Geitmann A (2018) Finite element modeling of shape changes in plant cells. *Plant Physiol* 176: 41–56

Chantarachot T, Bailey-Serres J (2018) Polysomes, stress granules, and processing bodies: a dynamic triumvirate controlling cytoplasmic mRNA fate and function. *Plant Physiol* 176: 254–269

Chen C, MacCready JS, Ducat DC, Osteryoung KW (2018) The molecular machinery of chloroplast division. *Plant Physiol* 176: 138–151

Cosgrove DJ (2018) Diffuse growth of plant cell walls. *Plant Physiol* 176: 16–27

Daszkowska-Golec A (2018) Emerging roles of the nuclear cap-binding complex in abiotic stress responses. *Plant Physiol* 176: 242–253

Elliott A, Shaw SL (2018a) Microtubule array patterns have a common underlying architecture in hypocotyl cells. *Plant Physiol* 176: 307–325

Elliott A, Shaw SL (2018b) Update: plant cortical microtubule arrays. *Plant Physiol* 176: 94–105

Feiguelman G, Fu Y, Yalovsky S (2018) ROP GTPases structure-function and signaling pathways. *Plant Physiol* 176: 57–79

Frick EM, Strader LC (2018) Kinase MPK17 and the peroxisome division factor PMD1 influence salt-induced peroxisome proliferation. *Plant Physiol* 176: 340–351

Groves NR, Biel AM, Newman-Griffis AH, Meier I (2018) Dynamic changes of plant nuclear organization in response to environmental and developmental signals. *Plant Physiol* 176: 230–241

Hanson MR, Hines KM (2018) Stromules: probing formation and function. *Plant Physiol* 176: 128–137

Jin X, Jiang Z, Zhang K, Wang P, Cao X, Yue N, Wang X, Zhang X, Li Y, Li

D, et al (2018) Three-dimensional analysis of chloroplast structures associated with virus infection. *Plant Physiol* **176**: 282–294

Kao YT, Gonzalez KL, Bartel B (2018) Peroxisome function, biogenesis, and dynamics in plants. *Plant Physiol* **176**: 162–171

Komis G, Novák D, Ovecčka M, Šamajova O, Šamaj J (2018) Advances in imaging plant cell dynamics. *Plant Physiol* **176**: 80–93

Mir R, Morris VH, Buschmann H, Rasmussen CG (2018) Division plane orientation defects revealed by a synthetic double mutant phenotype. *Plant Physiol* **176**: 418–431

Nakamura M, Claes AR, Grebe T, Hermkes R, Viotti C, Ikeda Y, Grebe M (2018) Auxin and ROP GTPase signaling of polar nuclear migration in root epidermal hair cells. *Plant Physiol* **176**: 378–391

Reynolds GD, Wang C, Pan J, Bednarek SY (2018) Inroads into internalization: five years of endocytic exploration. *Plant Physiol* **176**: 208–218

Rosquete MR, Davis DJ, Drakakaki G (2018) The plant trans-Golgi network: not just a matter of distinction. *Plant Physiol* **176**: 187–198

Ryan JM, Nebenführ A (2018) Update on myosin motors: molecular mechanisms and physiological functions. *Plant Physiol* **176**: 119–127

Schink KO, Raiborg C, Stenmark H (2013) Phosphatidylinositol 3-phosphate, a lipid that regulates membrane dynamics, protein sorting and cell signalling. *BioEssays* **35**: 900–912

Shimada TL, Hayashi M, Hara-Nishimura I (2018) Membrane dynamics and multiple functions of oil bodies in seeds and leaves. *Plant Physiol* **176**: 199–207

Soto-Burgos J, Zhuang X, Jiang L, Bassham DC (2018) Dynamics of autophagosome formation. *Plant Physiol* **176**: 219–229

Spiegelman Z, Lee CM, Gallagher KL (2018) KinG is a plant-specific kinesin that regulates both intra- and intercellular movement of SHORT-ROOT. *Plant Physiol* **176**: 392–405

Stefano G, Brandizzi F (2018) Advances in plant ER architecture and dynamics. *Plant Physiol* **176**: 178–186

Sun J, Zheng H (2018) Efficient ER fusion requires a dimerization and a C-terminal tail mediated membrane anchoring of RHD3. *Plant Physiol* **176**: 406–417

Szymanski DB, Cosgrove DJ (2009) Dynamic coordination of cytoskeletal and cell wall systems during plant cell morphogenesis. *Curr Biol* **19**: R800–R811

Szymanski D, Staiger CJ (2018) The actin cytoskeleton: functional arrays for cytoplasmic organization and cell shape control. *Plant Physiol* **176**: 106–118

TerBush AD, MacCready JS, Chen C, Ducat DC, Osteryoung KW (2018) Conserved dynamics of chloroplast cytoskeletal FtsZ proteins across photosynthetic lineages. *Plant Physiol* **176**: 295–306

Wasteneys GO, Ambrose JC (2009) Spatial organization of plant cortical microtubules: close encounters of the 2D kind. *Trends Cell Biol* **19**: 62–71

Winship LJ, Obermeyer G, Geitmann A, Hepler PK (2011) Pollen tubes and the physical world. *Trends Plant Sci* **16**: 353–355

Zuñiga C, Levering J, Antoniewicz MR, Guarnieri MT, Betenbaugh MJ, Zengler K (2018) Predicting dynamic metabolic demands in the photosynthetic eukaryote *Chlorella vulgaris*. *Plant Physiol* **176**: 450–462