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Counting what counts: the importance of quantitative approaches to studying plant cell biology

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The Haswell lab aims to identify the molecular and cellular mechanisms by which molecules and cells sense and respond to physical forces. At the moment they are focused on elucidating the structure, function, regulation, and evolution of multiple families of mechanosensitive ion channels in the green lineage. Their work has revealed roles for membrane-based mechanoperception in organelle dynamics, pollen development, and abiotic/biotic stress response.

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The Dixit lab studies the cytoskeletal mechanisms underlying plant cell morphogenesis. Currently the lab is focused on how microtubule tip-binding and severing proteins regulate the dynamics and organization of the cortical microtubule cytoskeleton and how motor proteins contribute to cell wall deposition. The lab is also working on developing new techniques to study how plant cells sense and respond to mechanical stimuli.

When asked to edit the 2018 Cell Biology issue of Current Opinion in Plant Biology, we quickly agreed to focus it on the topic of 'quantitative cell biology'. The plant cell biology field has grown increasingly focused on quantitative analyses as part of the push to dissect the molecular mechanisms underlying basic cellular activities. In a sense, this movement is the natural progression of a maturing field. While the traditional trifecta of genetics, biochemistry and cell biology have revealed the key molecular components of the plant cell, new quantitative approaches are allowing us to determine how interactions between these components in time and space shape the form and function of cells.

We wished to highlight this trend for a number of other reasons. Simply put: if seeing is believing, then measuring is knowing. Measurements enable us to go beyond the simple what, where and when questions to address how often, in what order, and to what degree. Quantitative approaches also facilitate reproducibility and are particularly important for the many cellular processes that are driven by stochastic events. One could argue that conclusions drawn from these approaches are more uniform and universal than from qualitative observations. Finally, measurements of parameters lay the groundwork for computational and mathematical models, which are fast becoming indispensable tools for mechanistic studies of complex cell biological processes.

Arguably, the grand challenge of our field is to fully describe every aspect of a plant cell. To meet this challenge, we need to study the **parts of the cell,** the **things cells and cell parts do**, and we need to create the right **tools and model systems** in which to do so. We must understand the contribution of both molecular factors and physical properties such as diffusion, volume, concentration, kinetics, and force. Below, we outline how these themes play out in the articles collected for this issue.

The parts of a cell

Knowing the molecular components and their dynamics are key steps towards fully describing a cell. Six contributions to this issue address how quantitative approaches have enabled new insights into the ultrastructure and dynamics of key cellular structures in plants. The strong cellulosic wall surrounding plant cells is a remarkably complex and dynamic structure that determines plant growth and mechanics. Cosgrove discusses how different surfaces of cellulose microfibrils might lead to the assembly of a poly-lamellate cell wall structure that can withstand turgor-driven tensile stress and puts forth the idea that slippage of cellulose microfibrils rather than their lateral separation may be more limiting for cell growth. Land

plants construct elaborate microtubule architectures despite the absence of centrosomes which nucleate and spatially organize microtubules in animal cells. By comparing bipolar spindle formation and orientation in the angiosperm *Arabidopsis thaliana*, liverwort *Marchantia polymorpha* and moss *Physcomitrella patens*, Yi and Goshima reveal how plants have evolved morphologically different types of cytoplasmic microtubule organizing centers which nonetheless consist of evolutionarily conserved molecular components as their animal counterparts. Mitosis culminates with the physical separation of the daughter cells by a cell plate whose construction relies on a microtubule-based structure called the phragmoplast. By analogy to automobile engines, Smertenko posits a four-stroke process consisting of different sets of molecular players to explain the sequence of events that power the outward expansion of the phragmoplast. Organelles also dynamically change shape but the relationship between organelle morphology and function remains largely unclear. Erickson and Schattat tackle the intriguing and controversial plastid stromules, which are dynamic protrusions of plastid membrane and stroma that are widely observed and can be provoked by both biotic and abiotic stresses. They discuss potential models for how these tubules are produced and conclude that the most likely explanation is pulling of the plastid membrane by motor proteins and cytoskeletal filaments. The functional significance of organelle dynamics is highlighted by Rosquete and Drakakaki who emphasize the role of the *trans*-Golgi network in both biotic and abiotic stress responses by describing molecular mechanisms that regulate vesicle trafficking through the secretory and endocytic pathways to potentially affect the localization of sensory and effector proteins involved in stress responses. The well-being of cells also depends on mechanisms that get rid of unwanted or damaged cytoplasmic contents. Ding et al. describe the role of autophagy in this process including the well-studied process of macroautophagy which involves the formation of a double-membrane cup-like structure for selectively degrading cytoplasmic material and the more poorly understood process of microautophagy in which selected cargo are engulfed by the vacuole.

What cells do

Cell biologists also want to understand how these cell parts work together dynamically during the life of a cell and the life of a plant. Three contributions to this issue explore different approaches to understanding how the final 3-dimensional form of a tissue or organ is created. Eng and Sampathkumar use recent investigations into the shape of leaf epidermal cells to explain how the microtubule cytoskeleton directs cell shape and is itself controlled by both biochemical and mechanical properties. The interplay between biochemical and mechanical signals is also highlighted by Marsollier and Ingram, who describe the complex reciprocal communication between invading and invaded tissues during lateral root emergence, embryo development, and pollen tube growth. While researchers continue to reveal the factors required for dependable cell and tissue development, stochasticity also plays an important role in plant morphogenesis. Serra et al. explain how heterogeneous growth at multiple scales can produce mechanical stresses that feedback to control decisions such as cell fate and growth arrest. All of these contributions describe how quantitative microscopic and biophysical methods and computational approaches have facilitated the recent jumps in our understanding of plant biomechanics and morphogenesis.

Tools and model systems

As quantitative cell biologists, we must both ask important questions and develop the model systems and tools that make it possible to find the answers. Three contributions to this collection illustrate the value of employing diverse model systems that span the green lineage. Umen promotes the use of the green alga *Chlamydomonas reinhardtii* to study the process and regulation of cell division. This unicellular organism propagates through a process called multiple fission and recent systems-level genetic and transcriptomic experiments have revealed the key role played by cyclin-dependent kinases in this process. Reski explains that the moss *Physcomitrella patens* is an excellent model system for the study of a wide range of cell biological questions, and its simple body plan and haploid genetics make quantitative analyses straightforward. A survey of recent discoveries that have been made in this system is presented, including the evolution of desiccation-tolerant characteristics, the transition from tip growth to 3-dimensional growth, and the identification of organellar protein networks. A third article in this issue features guard cells, the stomata-forming cell pairs that control water and gas exchange in the aerial portion of the plant. How guard cell opening is regulated by hormones, water potential, and H_2O_2 in a range of model systems has been intensively studied. Hedrich and Shabala propose that the guard cells of halophytes, naturally salt-tolerant species, provide a fascinating comparison to other plants and lay out a roadmap to further developing this future model system.

Microscopy remains an indispensable tool for cell biology, capable of generating high-resolution quantitative information in three-dimensional space and in time. Advances in imaging technology, image analysis, and new methods for labeling desired components in living cells have greatly enhanced our ability to quantitatively characterize complex processes such as the trafficking and behavior of cell wall-synthesizing enzymes and matrix polysaccharides, as described by Anderson. For many quantitative cell biologists, one of the most exciting developments in recent years has been the development of genetically encoded fluorescent biosensors, as they allow the non-invasive visualization and quantification of dynamic cellular events. Hilleary et al. describe the rapidly expanding

array of plant biosensors and present a set of best-practices for their use. Biosensors are just one way in which scientists can now indirectly visualize membrane transport in plants, and Geisler outlines the ways in which direct substrate detection, reporters, sensors, and transporter level, localization, or activity are used to monitor and study membrane transport in plant cells. Our understanding of membrane transport would also benefit from a structural understanding of the transporters involved, according to Hrmova and Gilliham. They explain the insights gained from these types of studies into salinity and boron toxicity tolerance. Finally, Sparkes illustrates the power of optical tweezer technology to hold or change the location of organelles and to directly measure the forces acting on them.

Most articles in this issue address the need for counting what counts and the techniques to do so across the many length and time scales relevant to plant growth and development. Many also illustrate the power of modeling to explain data and to uncover the mechanisms driving-specific cellular activities. Together, we hope that this collection will clearly demonstrate to the reader that we are indeed on the path to a complete computational description of a plant cell. The cell biology community is doing all the 'things that count' in this pursuit—articulating the fundamental questions, understanding the parts of the cell and what cells do, and developing the quantitative tools and appropriate model systems.