





Back to the roots: A focus on plant cell biology

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Defining plant cell biology—especially in multicellular organisms—is not an easy task as it encompasses diverse tissues, organs, and ultimately the whole organism and its interaction with the environment. Events taking place at cellular scale are a consequence of molecular mechanisms that drive myriad processes occurring within and between single cells and their compartments. Perhaps, for this reason, it is fitting that *The Plant Cell* publishes in a broad range of topics. In this Focus Issue, we go back to the “roots” of the journal, that gave it its name, and turn our attention to the many fascinating facets of plant cell biology. The 11 review papers and 11 original research articles in this issue exemplify the breadth of the field and highlight both established concepts and recent achievements.

Much has changed in the 33 years since *The Plant Cell* was founded in 1989. Although molecular techniques were well established, researchers still largely studied one gene at a time, using relatively crude assays such as RNA blots to quantify gene expression. Arabidopsis research was gaining traction, but researchers still lacked a complete genome sequence or knock-out libraries. Imaging tools and probes were, by today’s standards, relatively limited; a further 5 years would pass before GFP was developed as a fluorescent protein reporter. Today’s research tools provide extraordinary insights into cell structure and function that were unimaginable in 1989, but also have opened new research avenues such as the ability to view cellular dynamics in real time in living cells and address questions about the roles of stochasticity and emergent properties in cell biology. Thus,

we felt it was time to provide readers with an up-to-date view of plant cell biology.

This Focus Issue has two types of review papers: a set of eight traditional review papers, as well as three reviews that each are a collection of vignettes contributed by several authors. In the first of the vignette-style reviews, [Kang et al. \(2022\)](#) offer visual insight into the structures that compose plant cells, and present open questions related to plant cell structure. In the [Cheung et al. \(2022\)](#) review, seven eminent plant cell biologists offer first-hand narratives of several seminal discoveries that helped shape the field. Lastly, in [Roeder et al. \(2022\)](#), experts in a range of areas within the field of plant cell biology formulate important outstanding questions to inspire future investigation.

The remaining reviews cover a broad range of topics at both subcellular and supracellular scales. [Gu and Rasmussen \(2022\)](#) provide an extensive overview of the cell biology underlying primary cell wall biosynthesis. [Codjoe et al. \(2022\)](#) focus on how plant cells sense and respond to physical forces through the mechanobiology of the walls, plasma membrane, and protoplast. Plant cells consist of many internal membrane structures, and [Aniento et al. \(2022\)](#) discuss the endomembrane trafficking processes that organize, maintain, and remodel these internal membrane structures. A notable aspect of the organization of plant cells and their membranes is the ability to define polar membrane domains. [Ramalho et al. \(2022\)](#) present an overview of the processes underlying plant cell polarity and its evolution. For any multicellular plant, cell division must be connected to

growth and cell identity. Sablowski and Gutierrez (2022) describe the mechanisms that control cell cycle progression, cell growth, and cell fate. Zuch et al. (2022) integrate many of the elements in each of these reviews in a developmental context: the leaf epidermis. They discuss how cell division plane, cell cycle, cell polarity, and growth are coordinated to arrive at an organized multicellular structure. Since the development of molecular biology, genomics, and transgenesis, many cell biology studies have used flowering plant models such as tobacco and *Arabidopsis*. However, many of the developmental processes in flowering plants are derived from ancestral processes in early land plants. Naramoto et al. (2022) discuss the insights gained and open questions in using the bryophytes *Physcomitrium patens* and *Marchantia polymorpha* as models. The plant cell biology field has developed with the advent of methodologies that allow visualizing molecules and structures, and their dynamics. Colin et al. (2022) discuss the development of methodologies that enable present and future plant cell biologists to obtain a quantitative and dynamic view of plant cells.

Besides insightful and inspiring review papers, the Focus Issue contains 11 original research articles, of which two are Breakthrough Reports. These two Breakthrough Reports present crisp, shorter studies that are of exceptional novelty, or that open new avenues of investigation. Duncombe et al. (2022) describe the use of structured illumination microscopy (SIM) to track *Arabidopsis* Cellulose Synthase A (CESA) particle movement in the plasma membrane. This super-resolution approach provides new insight into the particle density and velocity, as well as their variation. Hacker et al. (2022) used a strategy revolving around CRISPR/Cas mutant analysis to identify the proteins in *Arabidopsis* that mediate the repair of DNA breaks and DNA-protein crosslinks induced by stalled topoisomerase 2 cleavage complexes. While this mechanism was suspected to exist in plants, its components had not yet been discovered.

The nine regular original research articles in this Focus Issue span a range of topics at different levels of cellular organization. Noack et al. (2022) describe the identification and characterization of a protein complex that acts as a scaffold to target the *Arabidopsis* PI4 kinase alpha1 to membrane nanodomains. Genetic analysis demonstrates a central role of this complex, which thus controls local membrane composition, in gametophyte and sporophyte development. Chang et al. (2022) present an extensive cell biological and genetic analysis of the *Physcomitrium* family of COPII coat proteins belonging to the Sec23 and Sec24 families. Within the Sec23 family, different isoforms have unique localization and functions related to endomembrane trafficking, secretion, and growth and development. The same COPII coat protein complex is linked to PI3P and autophagy in *Arabidopsis* by Kim et al. (2022). In this study, the FYVE2 PI3P-binding protein is found to interact both with the COPII regulator SAR1, and with the ATG18A autophagy protein. Ma et al. (2022) report the formation of membrane

nanodomains compartments containing Remorin proteins upon pathogen perception in *Arabidopsis*. Remorin in these clusters appears to undergo condensation, an example of liquid–liquid phase separation. Through interaction, Remorin concentrates the Formin protein, which causes local Actin nucleation. In a second paper from the same team, Minh Tran et al. (2022) report that outer membrane vesicles from the pathogenic bacterium *Xanthomonas campestris* can fuse with the plasma membrane in *Arabidopsis*, thus modifying host cell membrane properties. To complete a set of papers on organelles and endomembrane compartments, Liu et al. (2022) report an analysis of the FtsZ protein which is involved in chloroplast division. The authors show that weak membrane association through a newly identified protein motif, coupled to protein polymerization, is sufficient for membrane tethering and function. De Jaeger-Braet et al. (2022) used live imaging of male meiocytes in *Arabidopsis* under normal and heat stress conditions to follow progression of meiosis. Their study revealed the existence of a previously unknown checkpoint that is sensitive to heat stress. Finally, two papers report on aspects of stomatal development and function. Yang et al. (2022a) reveal an interesting link between cuticle formation and stomatal patterning in *Arabidopsis*. Analysis of the transcription factor MYB16 revealed that its downregulation by the SPCH transcription factor is necessary to prevent excess cuticle formation and clustering of stomata. Yang et al. (2022b) describe the analysis of the *Arabidopsis* stomatal closure-related Actin-binding protein1 (SCAB1). This protein binds the membrane phospholipid PI3P and thereby controls its ability to oligomerize. As such, membrane PI3P influences Actin bundling during ABA-induced stomatal closure.

Beyond this set of papers in the Focus Issue, a larger collection of papers in the area of cell biology, published ~1 year before or after this issue, will be bundled into a Focus Collection. This Focus Issue, together with the Focus Collection, showcases past and present insights, victories, and successes in this research field. The field has progressed immensely in the past decades, and we wonder what the next 33 years have in store. If one thing has become clear, it is that scientific progress, and thereby the development of a research field, is difficult to predict. Who would have predicted the concepts and findings reported in this Focus Issue 33 years ago? A key element of surprise is the development of new technologies that bring new boundaries into view, and challenges of which previously we were unaware. It seems biology has gotten much more complex, and yet we are also increasingly able to manage this complexity through computational approaches, including artificial intelligence. This latter development is also removing the shackles inherent to the limitations of the human mind in grasping complexity and thinking non-linearly. Perhaps the field of cell biology will be revolutionized by the computer sciences? We leave it to future Focus Issues to tell that story.

References

- Aniento F, Sánchez de Medina Hernández V, Dagdas Y, Rojas-Pierce M, Russinova E** (2022) Molecular mechanisms of endomembrane trafficking in plants. *Plant Cell* **34**: 146–173
- Chang M, Wu S-Z, Ryken SE, O'Sullivan JE, Bezanilla M** (2022) COPII Sec23 proteins form isoform-specific endoplasmic reticulum exit sites with differential effects on polarized growth. *Plant Cell* **34**: 333–350
- Cheung AY, Cosgrove DJ, Hara-Nishimura I, Jürgens G, Lloyd C, Robinson DG, Staehelin LA, Weijers D** (2022) A rich and bountiful harvest: key discoveries in plant cell biology. *Plant Cell* **34**: 53–71
- Codjoe JM, Miller K, Haswell ES** (2022) Plant cell mechanobiology: greater than the sum of its parts. *Plant Cell* **34**: 129–145
- Colin L, Martin-Arevalillo R, Bovio S, Bauer A, Vernoux T, Caillaud M-C, Landrein B, Jaillais Y** (2022) Imaging the living plant cell: from probes to quantification. *Plant Cell* **34**: 247–272
- De Jaeger-Braet J, Krause L, Buchholz A, Schnittger A** (2022) Heat stress reveals a specialized variant of the pachytene checkpoint in meiosis of *Arabidopsis thaliana*. *Plant Cell* **34**: 433–454
- Duncombe SG, Grama Chethan S, Anderson CT** (2022) Super-resolution imaging illuminates new dynamic behaviors of cellulose synthase. *Plant Cell* **34**: 273–286
- Gu Y, Rasmussen CG** (2022) Cell biology of primary cell wall synthesis in plants. *Plant Cell* **34**: 103–128
- Hacker L, Dorn A, Enderle J, Puchta H** (2022) The repair of topoisomerase 2 cleavage complexes in *Arabidopsis*. *Plant Cell* **34**: 287–301
- Kang B-H, Anderson CT, Arimura S, Bayer E, Bezanilla M, Botella MA, Brandizzi F, Burch-Smith TM, Chapman KD, Dünser K, et al.** (2022) A glossary of plant cell structures: current insights and future questions. *Plant Cell* **34**: 10–52
- Kim JH, Lee HN, Huang X, Jung H, Otegui MS, Lic F, Chung T** (2022) FYVE2, a phosphatidylinositol 3-phosphate effector in *Arabidopsis*, interacts with COPII machinery to control autophagosome formation. *Plant Cell* **34**: 351–373
- Liu X, An J, Wang L, Sun Q, An C, Wu B, Hong C, Wang X, Dong S, Guo J, et al.** (2022) A new type of amphiphilic motif at the C-terminus of FtsZ1 facilitates chloroplast division. *Plant Cell* **34**: 419–432
- Ma Z, Sun Y, Zhy X, Yang L, Chen X, Miao Y** (2022) Membrane nanodomains modulate formin condensation for actin remodeling in *Arabidopsis* innate immune responses. *Plant Cell* **34**: 374–394
- Minh Tran T, Chng C-P, Pu X, Ma Z, Han X, Liu X, Yang L, Huang C, Miao Y** (2022) Potentiation of plant defense by bacterial outer membrane vesicles is mediated by nanodomain assembly. *Plant Cell* **34**: 395–418
- Naramoto S, Hata Y, Fujita T, Kyojuka J** (2022) The bryophytes *Physcomitrium patens* and *Marchantia polymorpha* as model systems for studying evolutionary cell and developmental biology in plants. *Plant Cell* **34**: 228–246
- Noack LC, Bayle V, Armengot L, Rozier F, Mamode-Cassim A, Stevens FD, Caillaud M-C, Munnik T, Mongrand S, Pleskot R, et al.** (2022) A nanodomain-anchored scaffolding complex is required for the function and localization of phosphatidylinositol 4-kinase alpha in plants. *Plant Cell* **34**: 302–332
- Ramvalho JJ, Jones VAS, Mutte S, Weijers D** (2022) Pole position: how plant cells polarize along the axes. *Plant Cell* **34**: 174–192
- Roeder AHK, Otegui MS, Dixit R, Anderson CT, Faulkner C, Zhang Y, Harrison MJ, Kirchhelle C, Goshima G, Coate JE, et al.** (2022) Fifteen compelling open questions in plant cell biology. *Plant Cell* **34**: 72–102
- Sablowski R, Gutierrez C** (2022) Cycling in a crowd: coordination of plant cell division, growth, and cell fate. *Plant Cell* **34**: 193–208
- Yang S-L, Tran N, Tsai M-Y, Ho C-MK** (2022a) Misregulation of MYB16 expression causes stomatal cluster formation by disrupting polarity during asymmetric cell divisions. *Plant Cell* **34**: 455–476
- Yang Y, Zhao Y, Zheng W, Zhao Y, Zhao S, Wang Q, Bai L, Zhang T, Huang S, Song C, et al.** (2022b) Phosphatidylinositol 3-Phosphate Regulates SCAB1-Mediated F-Actin Reorganization during Stomatal Closure in *Arabidopsis*. *Plant Cell* **34**: 477–494
- Zuch DT, Doyle SM, Majda M, Smith RS, Robert S, Torii KU** (2022) Cell biology of the leaf epidermis: fate specification, morphogenesis and coordination. *Plant Cell* **34**: 209–227