



Editorial overview: Toward deciphering the molecular basis of plant phenotypic plasticity

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Anna Stepanova did her PhD work in the Joseph Ecker lab at the University of Pennsylvania and the Salk Institute for Biological Studies and her postdoctoral training with Jose Alonso at North Carolina (North Carolina) State University. She is currently an Associate Professor of Plant Biology and Genetics. Her primary research interests center around plant hormones, specifically the mechanisms of ethylene signal transduction, auxin biosynthesis, hormonal pathway crosstalk, and translational regulation of hormone responses. In her work, Anna is employing classical and molecular genetics, genomics and synthetic biology in *Arabidopsis* and tomato to decipher the mechanisms governing plant adaptation and phenotypic plasticity.

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Hong Qiao earned her PhD from the Institute of Genetics and Developmental Biology, China and did her postdoctoral work with Joseph Ecker at the Salk Institute for Biological Studies. She is currently an Associate Professor of Molecular Biosciences. Her research focuses on the study of chromatin remodeling and the establishment of the specificity of gene expression in response to hormones and stress factors. Dr. Qiao's interdisciplinary program combines genetic, genomic, proteomic, molecular, biochemical and bioinformatics approaches to develop a validated mechanistic model that accurately describes the interplay between hormone signaling pathways and stress responses.

Plant development is a continuous process that starts with embryogenesis and the formation of the primary plant body and continues post germination with the stereotypical production of new organs (roots, leaves, branches, and flowers). The fundamental processes governing plant growth are regulated by the network of interactions between internal developmental signals and external environmental cues that drive the phenotypic plasticity and shape adaptive responses of plants. The crosstalk between different signals and pathways is delineated by the rigid framework of organism's genetics and mediated by dynamic modifications in the epigenome that lead to changes in gene expression and ultimately in plant physiology and morphology. Our comprehension of the molecular network of interacting pathways orchestrating plant development in ever-changing environments is continuously evolving. In the current issue, we feature 25 individual snapshots of the state-of-the-art in select areas of plant developmental biology, plant hormones, environmental responses, gene regulation, and technological innovations.

Plant development

The life cycle of a plant involves pre-programmed progression through a series of developmental stages that in higher plants include embryogenesis, seed germination, formation of above-ground (shoots, branches and leaves) and below-ground (primary and secondary roots) vegetative organs, flowering, fruit development and seed set. A thorough understanding of these processes is important not only from the basic science perspective but is also paramount to our ability to combat the consequences of climate change and improve crop resilience and yield to feed the world's growing population.

Leaves are the major photosynthetic organs that harvest the energy of sunlight and fix CO₂ from the atmosphere to provide the plant with organic carbon for biomass accumulation. Leaf shape and plant canopy architecture are key morphological traits determining the efficiency of light capture. [Strable and Nelissen](#) take a deep dive into the genetic basis of maize leaf development and review what is known about the molecular factors and plant hormonal signals controlling spatiotemporal patterning and growth of these essential organs, defining leaf shape and angle, and ultimately dictating maize canopy architecture. CO₂ enters the leaves via specialized gated cells known as stomata that regulate gas exchange, water

balance, leaf temperature, nutrient transport, and pathogen entry. [Spiegelhalder and Raissig](#) highlight recent findings on the development and functional differentiation of kidney-shaped and dumbbell-shaped guard cells of the stomata and discuss how stereotypical morphogenetic processes shape these highly specialized, essential cells.

The transition from vegetative growth to flowering is a critical developmental process that needs to be well-timed for optimal plant fertility. [Freytes et al.](#) revisit the long-standing question of flowering time control and take another look at the role of light cues and the circadian clock in the regulation of key flowering pathway genes, such as *CONSTANS* and *FLOWERING TIME*, and their interactors at the transcriptional and post-transcriptional level. Flower fertility is dictated by both male and female components. Female gametes are produced in the ovules, and male gametes are formed in the anthers. [Yang and Tucker](#) review the process of ovule development and the suite of the genetic factors and developmental signals that regulate ovule number, underscoring the importance of this critical trait to seed yield and suggesting the possibility of targeted manipulation of key regulators of this pathway as a promising strategy to boosting plant productivity. [Huang et al.](#) summarize the key genetic regulators and mechanisms in the early stages of male germline development, as well as discuss the ‘one-bus-two-passengers’ model of double fertilization in plants, highlighting the passive roles of the sperm cells during pollen tube delivery.

Upon flower pollination, the highly regulated processes of seed development and fruit ripening take center stage. Successful seed set is not only key to plant sexual reproduction but is also extremely important from the agricultural productivity and crop yield perspective. [Alizadeh et al.](#) summarize how transcriptional regulation during seed maturation helps shape major seed traits, describe recent literature on the integration of transcriptional activation and repression of seed maturation genes, and brainstorm potential future research directions to further our understanding of the transcriptional network of seed maturation. Similarly, fruit ripening is not only essential for seed dispersal and plant propagation but is also a central agriculturally relevant process. [Brumos](#) overviews the dynamic interactions between multiple hormones, transcription factors, and epigenetic modifications that together form a complex regulatory network controlling the expression of ripening-related genes. Some promising new methodologies are discussed that can be leveraged to further dissect the ripening process.

Plant hormones

Phytohormones are small regulatory molecules that not only control diverse physiological and developmental

processes and plant acclimation to abiotic and biotic stresses but also serve as effective communication signals within and among plants or between plants and other organisms. In this issue, several plant hormones receive the spotlight. [Park et al.](#) take a deep dive into a single protein family of ACC synthases catalyzing the rate-limited step in the biosynthesis of hormone ethylene. Post-translational control of these remarkable proteins is re-examined in response to a variety of environmental and developmental signals to regulate ethylene production and tip the balance between plant growth and stress responses. [Yoneyama and Brewer](#) describe the genetic basis of biosynthesis of another plant hormone, strigolactone, and argue how the unusually high structural diversity of these important growth regulators, with over 30 strigolactones known in plants, comes into play as both internal and secreted signals that are leveraged by parasitic plants to detect host plant presence. [Wu et al.](#) summarize current advances in gibberellic acid signaling focusing on DELLA-dependent and independent pathways and their role in the regulation of plant growth and metabolic adaptations to changes in nitrogen availability. Possible breeding strategies for future sustainable agriculture and a new Green Revolution are discussed. [Bunsick et al.](#) integrate a series of recent findings in the area of gibberellin and strigolactone signaling to propose that focusing on output regulators of signaling cascades helps to explain how the plethora of hormone responses can arise from the same core pathway.

[Anfang and Shani](#) present a timely compilation of recent findings in the area of hormone transport. Subcellular, cell-to-cell and long-distance hormone movement for a variety of growth regulators is considered, and the role of local hormone sinks in triggering or preventing hormone-mediated responses is discussed, offering a new perspective on controlling plant hormone responses. Finally, [Willoughby and Nimchuk](#) take a careful look at the intercellular communication via peptide hormones of the CLE family in plant development, focusing on both WUSCHEL-dependent and independent mechanisms of CLE signaling in shoots and roots and the integration of the CLE pathway with that of hormone auxin.

Gene regulation

Regulation of gene expression takes place at several levels, from transcription to splicing, transcript stability, translation, and protein turnover. Other processes such as RNA export from the nucleus to the cytoplasm, RNA and protein localization, modification and folding also control gene expression. In plants, methylation of the N6-position of adenosine (m6A) affects multiple aspects of mRNA metabolism. Herein, [Shao et al.](#) provide a literature overview of the recent progress in dissecting the roles of m6A in plants and linking this RNA modification

with developmental control and stress responses. Similarly, post-translational modifications of proteins alter protein folding, activity, interactions and stability. [Kong et al.](#) examine the effects of post-translational modifications on the activity of the pattern recognition receptor complexes and discuss how protein phosphorylation and ubiquitination act in concert to ensure a rapid, proper, and robust immune response.

[Castellano and Merchante](#) focus their manuscript on the regulation of protein synthesis, highlighting the features that distinguish translational control in plants from that in animal systems and describing what is known about plant-specific, non-canonical translation initiation complexes and the molecular mechanisms of their regulation. To counterbalance protein production, protein turnover serves as a critical factor in the control of gene expression at the protein level. [Clavel and Dagdas](#) [COPLBI-D-21-00048R1 accepted] discuss the latest insights into protein degradation in the context of the organelle quality control pathways triggered in response to stress upon the accumulation of misfolded proteins in the endoplasmic reticulum, chloroplast, or mitochondria. Targeted degradation of defective components enables plants to deal with otherwise dire consequences of acute stress.

Another exciting area in the study of gene regulation is the coordination of gene expression between genomes in the plant. Plastid-to-nucleus retrograde signaling is a suite of molecular means of communication between plastidic and nuclear genomes in plants that among other things enable the production of stoichiometric quantities of dually encoded heteromeric proteins. Herein, [Calderon and Strand](#) revisit the topic of retrograde signaling from the plastids, approaching this long-standing question from the evolutionary perspective and providing some novel yet still speculative interpretations for the fragmentary data available in the field to date.

Environmental responses

This issue also includes a small sample of articles that examine the effect of abiotic factors. For example, plants often face specific nutrient limitations, such as iron deficiency, which trigger adaptive responses that enable the plant to maximize the uptake and/or redistribute the needed molecule. [Gratz et al.](#) examine the interplay between iron uptake under iron-deficient conditions and the secondary messengers, calcium and reactive oxygen species. Mechanistic aspects of how these signaling intermediates affect the levels of iron-acquisition proteins and their regulators are discussed.

Light quality is another important environmental factor that regulates plant development. [Kathare and Huq](#) examine the effect of light on RNA processing and

provide a summary of what is known about light-mediated changes in the patterns of pre-mRNA splicing. The review highlights the latest strive to fill in the knowledge gap between extensive transcriptomic work that implicates phytochromes in light-driven alternative splicing and the still limited mechanistic understanding of such regulation. Finally, photoperiod is a highly predictable signal for seasonal change. Many organisms have photoperiod-measuring systems that optimize physiology and development during different seasons. [Gendron et al.](#) [COPLBI-D-21-00041R1] summarize the latest insights into the connection between the photoperiod and plant metabolism, review the role of starch in the daily allocation of nutrients and discuss how photoperiod affects this allocation to maintain photostasis, that is, proper balance between the light and CO₂ input, organic carbon output and the sink tissue demand, throughout the year.

Technological innovations

State-of-the-art technologies accelerate scientific discovery and open new avenues for tackling pressing questions in plant biology. In this issue, four diverse yet connected areas of plant sciences propelled by the latest technological breakthroughs are described. [Shojaee et al.](#) review the recent developments and applications of single-cell sequencing technologies in plants to shed light on how cellular phenotypes emerge as a result of selective transcription at different developmental stages, in various tissues or in response to different cues. [Huang et al.](#) [COPLBI-D-21-00043] write about the technological innovations in targeted gene expression manipulation in plants and describe how synthetic biology is coming into the spotlight offering new exciting tools to control gene activity not only through the generation of synthetic, stimulus-responsive promoters and engineered transcription factors, but also via targeted regulation of mRNA and protein stability and protein synthesis. [Zemlyanskaya et al.](#) summarize the latest bioinformatics and machine learning approaches that can be leveraged to make sense of the vast amount of genomic and transcriptional data and limited protein-DNA interaction datasets in plants to shed light on the cis-regulatory code governing gene expression. Finally, [Elmore et al.](#) highlight recent methodological advances in functional proteomics and discuss applications of these technologies toward studying plant–pathogen interactions and ultimately using that knowledge to develop more disease-resistant crops.

Concluding remarks

The field of cell signaling and gene regulation in the study of plant development and adaptive responses is a diverse and exciting area of research. There are far too many relevant topics that fall under the theme of plant phenotypic plasticity that we would have liked to highlight in this issue but were not able to accommodate

because of space limitations. We hope that the selection of the invited articles that made it into this issue provides a representative palette of ‘flavors’ for the types of research this field covers, and we are looking forward to see the continuous progression of these areas of plant science in the future.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could

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