



PREFACE

Regulatory networks in plant growth and development

# Towards a next step of the research of regulatory networks in plant growth and development

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Plants properly coordinate growth and development through a complex system that fundamentally underlies thousands of genes in the plant genome. As the numbers of possible relationships between genes are almost unlimited, it is challenging to elucidate one particular regulatory mechanism, no matter how important. This complex combination of connections eventually displays an organized character, designated as a network. Networks can represent many different types of data, such as protein–protein and protein–metabolite interactions. When the network consists of genes, it is referred to as a genetic network, whereas when components interact with each other and with other cellular constituents to govern the gene expression levels of mRNA and proteins, it is labelled a gene regulatory network (GRN) (de Luis Balaguer et al. 2017; Mejia-Guerra et al. 2012).

This special issue on “Regulatory networks in plant growth and development” is based on a JPR international symposium held during the 81st Annual Meeting of the Botanical Society of Japan that took place in Tokyo (Japan), September 8–10, 2017. This conference provided an overview of cutting-edge topics that covered the broad perspectives of regulatory networks in plant growth and development. Results on various aspects of plant research were presented, namely on epidermal differentiation, hypocotyl elongation, secondary metabolism, phyllotaxis, and hormone signaling.

Plant growth requires well-coordinated cell division and expansion. These events involve a key factor, expansin, of which the function is essential for cell wall expansion. Ilias et al. (2019) presented a detail analysis of the genome-wide effects of the expansin function. Cell expansion in a dark-grown hypocotyl is initially slow, where after it is followed by a rapid hypocotyl elongation. The transition from cell wall biogenesis to structural organization has been proposed to coincide with this fast elongation phase between day 3 and day 5. Ilias et al. (2019) used transgenic *Arabidopsis thaliana* lines for a time-course analysis of hypocotyl growth. They obtained a gene expression dataset that will further benefit the identification of regulatory networks involved in the accelerated hypocotyl growth as well as of networks perturbed by either suppression or overexpression of the expansin gene.

Plants produce various amounts of metabolites, in particular, secondary (also called specialized) metabolites. More than 200,000 secondary metabolites have been reported to date, consisting of various types of compounds, such as terpenoids, alkaloids, and phenolics (Verpoorte and Memelink 2002; Zwenger and Basu 2008). The synthesis of secondary metabolites often requires the coordinated expression of multigene families that encode enzymes needed for different enzymatic steps. Moreover, transcription factors play a key role in the GRN of such synthetic pathway. Steroidal glycoalkaloids (SGAs) and nicotine are secondary metabolites found in some *Solanaceae* species. A group of jasmonate-responsive ETHYLENE RESPONSE FACTOR (ERF) transcription factors regulate the production of SGAs in this family. Shoji and Hashimoto (2019) reported on the predominant role of the JASMONATE RESPONSE FACTOR (JRE), one of the ERF transcription factors in the SGA regulation. They demonstrated that such a regulatory system occurs in different species within the *Solanaceae* family and discussed the altered regulation of the downstream biosynthetic gene QUINOLINATE

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PHOSPHORIBOSYL TRANSFERASE2 (QPT2) due to promoter mutations.

Although the elucidation of the coordinated regulation of a metabolic pathway in fruit is interesting from a prospective applications point of view, it still remains unclear. Jamaluddin et al. (2019) analyzed the transcriptome of papaya (*Carica papaya*), one of the most nutritional fruits and studied the effects of *DE-ETIOLATED1* (*DET1*) gene suppression in embryogenic callus. A transcriptomic analysis of immature zygotic embryos transformed with a constitutive expressing hairpin *DET1* construct (hp*DET1*) to repress the *DET1* gene expression revealed transcriptome-wide relationships between the light-regulated and secondary metabolite biosynthetic pathways in papaya.

Plants are exposed to various biotic and abiotic environmental factors, such as light, temperature, drought, flooding, nutrient shortage, chemicals, herbivores, and microorganisms. As plants are sessile, they can only survive by adapting to their environment. To this end, they must sense the environmental factors and coordinate their biological processes for an adequate response by, on the one hand, producing secondary metabolites and, on the other hand, regulating organ growth and development. Therefore, metabolic and developmental pathways are often coregulated. In Arabidopsis, the formation of a trichome, a hair-shaped organ that develops from epidermal cells, and the synthesis of anthocyanin that accumulates in epidermal cells coexist, suggesting that their GRNs are related. Kengo Morohashi presented a systems approach based on the inducible system of the *GLABRA3* gene that is a basic helix-loop-helix (bHLH)-type transcription factor involved in both trichome formation and anthocyanin biosynthesis in Arabidopsis and found that the accountable GRN consisted of an incoherent feed forward loop. Furthermore, Arai et al. (2019) reported on a *AtGL3* homolog in *Marchantia polymorpha* (liverwort), designated *MpBHLH12*. Transcriptomic analysis with transgenic *M. polymorpha* lines revealed that the activity of *MpBHLH12* might differ from that of *AtGL3*, despite their high amino acid sequence similarity.

Moreover, perception of different signals and integration into appropriate responses are essential elements of the living cell and require robust, but adaptable, biochemical networks. These networks are largely composed of proteins that can interact, move to specific cellular locations, be modified or be degraded. The integration of these events often triggers activation or inactivation of transcription factors, inducing or repressing thousands of genes. To coordinate these regulatory networks, plants employ not only gene products, but also small molecules, such as plant hormones. Brassinosteroid signal transduction pathway shares signaling components with the signaling pathway that controls stomatal development in the leaf epidermis (Gudesblat et al. 2012; Khan et al. 2013; Kim et al. 2012). Eugenia Russinova

reported that the incorporation of these shared components into distinct macromolecular complexes through scaffolding molecules ensures their localization to different cellular compartments and provides specificity (Houbaert et al. 2018).

In plants, the aerial organs are generated from the shoot apical meristem according to robust spatiotemporal patterns that control the shoot primary architecture, known as phyllotaxis. Results from modeling approaches and laboratory experiments have demonstrated that the auxin distribution dynamics allows reiterative organogenesis at the shoot apex. Other hormones, such as cytokinins, are also implicated in the regulation of the spatiotemporal patterns of organ initiation at the shoot apical meristem. Teva Vernoux discussed recent results from both modeling and imaging approaches that provided insights into the regulation mechanism of phyllotaxis.

Thanks to the symposium and recent advances on the GRN research, we realized that a network can consist of unlimited nodes and that its structure is flexible. Therefore, nested networks, such as a network of networks, could possibly exist. Even when a GRN appears in a particular biological event, it still just starts a next endeavor of building high-ordered GRNs. Considering the quick development of artificial intelligence in the computational biology field, computational analysis becomes a more powerful approach to infer a meta-GRN with such complicated structures (Haque et al. 2019). However, when the meta-GRN can be implied by experimental and/or computational approaches, it remains static, in contrast to a living organism, in which the GRN should be “alive”. A next step in this research should be to integrate time into a dynamic GRN that would more plausibly reflect genuine biological processes. In the future, we should predict outcomes (phenotypes) based on dynamic meta-GRNs of plants and eventually develop beneficial crops for agriculture and human well-being.

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