



OPEN ACCESS

EDITED AND REVIEWED BY
Simon Gilroy,
University of Wisconsin-Madison,
United States

*CORRESPONDENCE

Muhammad Asim
✉ asim.ktk91@aup.edu.pk
Yan Zhang
✉ zhangyan03@caas.cn

RECEIVED 07 September 2023

ACCEPTED 22 September 2023

PUBLISHED 04 October 2023

CITATION

Asim M, Zhang Y and Liu W (2023)
Editorial: Cooperation of gene regulatory
networks and phytohormones in cell
development and morphogenesis.
Front. Plant Sci. 14:1290538.
doi: 10.3389/fpls.2023.1290538

COPYRIGHT

© 2023 Asim, Zhang and Liu. This is an
open-access article distributed under the
terms of the [Creative Commons Attribution
License \(CC BY\)](#). The use, distribution or
reproduction in other forums is permitted,
provided the original author(s) and the
copyright owner(s) are credited and that
the original publication in this journal is
cited, in accordance with accepted
academic practice. No use, distribution or
reproduction is permitted which does not
comply with these terms.

Editorial: Cooperation of gene regulatory networks and phytohormones in cell development and morphogenesis

Muhammad Asim^{1,2*}, Yan Zhang^{1*} and Wenwen Liu³

¹Key Laboratory of Tobacco Biology and Processing, Ministry of Agriculture and Rural Affairs, Tobacco Research Institute, Chinese Academy of Agricultural Sciences, Qingdao, China, ²National Key Laboratory of Plant Molecular Genetics, CAS Center for Excellence in Molecular Plant Sciences, Institute of Plant Physiology and Ecology, Chinese Academy of Sciences, Shanghai, China, ³CAS Key Laboratory of Biofuels, Shandong Provincial Key Laboratory of Synthetic Biology, Qingdao Institute of Bioenergy and Bioprocess Technology, Chinese Academy of Sciences, Qingdao, Shandong, China

KEYWORDS

morphogenesis, phytohormones, cell growth, genes, gene regulatory network (GRNs), transcription factors

Editorial on the Research Topic

Cooperation of gene regulatory networks and phytohormones in cell development and morphogenesis

The cooperation between gene regulatory networks (GRNs) and phytohormones in cell development and morphogenesis represents a cornerstone of plant developmental biology. The interaction between these two biological systems governs many aspects of plant growth and differentiation, helping to shape the architecture of plants in response to various environmental and internal signals (Van den Broeck et al., 2020). GRNs consist of transcription factors (TFs), target genes, and other regulatory elements that coordinate the expression of genes in response to developmental cues and refer to the complex web of gene interactions that determine when and where individual genes are activated or repressed (Huang and Kauffman, 2009). This Frontiers in Plant Science virtual Research Topic on the “Cooperation of Gene Regulatory Networks and Phytohormones in Cell Development and Morphogenesis” consists of five publications, including two reviews and three original research articles.

1 Insights into GRNs and phytohormones

Thousands of genes are expressed in a cell and work together to maintain the cell's fitness, function, and survival. To provide the optimal functional result, each gene must be expressed at the proper time and suitable levels, manipulated by GRNs (Davidson and Levine, 2008). The regulation of genes' expression is incredibly strong. For instance, the genes involved in cell development in a particular cell type vary very little from one to another; however, some gene expression is highly variable: their levels are noisy and are

different from cell to cell and individual to individual. This can greatly benefit physiological responses to outside cues and stresses (Macneil and Walhout, 2011). Phytohormones are organic compounds, and their small amount affects plant growth and development (Davies, 2010). Some of the most well-known phytohormones include auxins, cytokinins, gibberellins, ethylene, abscisic acid, and JA. These hormones can stimulate or inhibit growth, mediate cellular differentiation, and contribute to the plant's response to environmental stimuli (Vaishnav et al., 2023). It is the cooperation of GRNs and phytohormones that inhibits cell development and morphogenesis.

To briefly outline recent technological progress made to elucidate GRNs in plants, such as the techniques that allow us to characterize physical interactions in GRNs in plants and to analyze their regulatory consequences, combining genome-wide experimental approaches with mathematical modeling allows us to obtain deeper insights into key regulatory interactions and the combinatorial control of important plant processes. About 15 years ago, the availability of high-throughput gene expression data made it possible to predict large-scale GRNs. Many different ways have been explored (Madhamshettiwar et al., 2012). Yao et al. identified the essential genes regulating rhizome axillary bud regrowth in perennial rice by trend analysis of expressed genes at different time periods and co-expression network creation through transcriptome sequencing technology. With the build-up of the connection between biology and other disciplines, modeling these networks is a big challenge that needs to be resolved. (Mishra et al., 2018). Yu et al. employed the “single-pole dual-control (SDPC)” competitive mechanism in plants to explain plant development and microbial infection. Furthermore, gene networks show how groups of genes work together to complete tasks. To comprehend the underlying biological process and its molecular system, targeted manipulation lets us investigate gene regulatory relationships (Kaufmann and Chen, 2017).

The cis-regulatory genomic DNA regions in or around their target genes are directly bound with TFs to regulate gene expression, which can raise or decrease downstream target expression. Other regulators include the transcriptional cofactor that interacts with the TFs physically, chromatin, or components of the basal transcriptional machinery; RNA-binding portions that interact with mRNAs and regulate the translation or mRNA stability; and the mRNAs that inhibit the mRNA stability by hybridizing to the sequence within their mRNA targets (Macneil and Walhout, 2011). GRNs have garnered attention and various statistical inference methods from gene expression data in recent years. Feng et al. found that *Halostachys caspica* pathogenesis-related protein 10 (HcPR10) acts as a cytokinin reservoir because its crystal structure showed a trans-zeatin riboside (cytokinin) deep in its cavity with a conserved conformation and protein–ligand interactions. Despite their popularity, GRNs have been misunderstood, so this current Research Topic studied the GRN more closely, notably by discussing their meaning, their coherence across network inference techniques, ensemble approaches, GRN evaluation, the estimated number of GRNs, and their use in diverse application domains. The discussion has brought greater comprehension of the questions and necessary steps to utilize

GRNs in a clinical context and personalize medicine. Through synthetic network biology, such investigations revealed the transcriptional processes that generate strong vs. stochastic gene expression and their effects on phenotypic robustness and variability. Here, we explored the topological features and transcriptional and phenotypic outputs of GRNs in development and organismal physiology.

2 Cooperation in cell development

The interaction between GRNs and phytohormones plays a pivotal role in cell development:

2.1 Cell division

Hormones such as cytokinins promote cell division, while others such as abscisic acid might inhibit it (El-Showk et al., 2013). The stem cell population in the shoot apical meristem (SAM) is maintained by cytokinin. The two distinct cytokinin-dependent pathways, CLAVATA (CLV)-dependent and CLV-independent, control WUS levels (Gordon et al., 2009). High levels of cytokinin signaling in Arabidopsis cause ectopic *WUSCHEL* (*WUS*) expression and influence neighboring cells' stem cell fate (Lee et al., 2019). *WUS* directly represses the transcription of several two-component ARABIDOPSIS RESPONSE REGULATOR genes (*ARR5*, *ARR6*, *ARR7*, and *ARR15*), which act in the negative-feedback loop of cytokinin signaling (Leibfried et al., 2005). These data imply that cytokinin is adequate for the induction of *WUS* and the determination of stem cell fate. GRNs determine the expression of genes that are vital for the cell cycle in response to these hormonal signals. As a non-canonical AUXIN RESPONSE FACTOR (*ARF*), *ARF3/ETTIN* (*ETT*) mediates auxin responses to orchestrate multiple developmental processes during the reproductive phase. GRNs respond to hormone cues by regulating cell cycle genes. The *ARF3/ETT* modulates auxin responses to coordinate reproductive development, according to recent findings by Fu et al. It is stated that *ARF3* maintains dynamic SAM non-autonomously. Regarding the temporal aspect, the term “cell differentiation” may also refer to the development of the unicellular organism for the origin of different growth stages and division cycles or the phases in which this cycle is interrupted (Differentiation and Plant, 1964). These antagonistic interactions between *CLV* and *WUS* are tightly integrated with hormone function, demonstrating the role of GRNs and phytohormones in cell division regulation.

2.2 Cell differentiation

GRNs and phytohormones have a hand in differentiating cells into various tissue types. For instance, the balance between auxin and cytokinin determines whether a cell differentiates into root or shoot tissue. Plants and other eukaryotic use sophisticated gene expression processes to regulate development, environmental

response, and cellular homeostasis. Plants generate new organs throughout their lifespan due to the pluripotent stem cell population, unlike mammals. Cell differentiation relies on the TFs, which form the GRNs with the basic cofactors and posttranslational regulators for specialized developmental activities (Kaufmann and Chen, 2017). The activities around DNA are controlled by hormones and chemicals, which decide what is transcribed and what is ignored. The body and nearby cells determine the variables that affect a cell from birth to death (Satterlee et al., 2020). For instance, the pancreas or thyroid may release hormones involved in cellular growth. These TFs directly impact the proteins that transcribe DNA, ultimately producing functioning proteins and more cells. However, when cells congress, they build up communication with one another so there is no more space. Thus, this interaction process between hormones and GRNs on cell differentiation is involved in plant growth and development, including meristem function, vascular development, stress responses, and senescence (Satterlee et al., 2020).

2.3 Cell expansion

Hormones such as gibberellins promote cell elongation. GRNs will mediate the expression of genes vital for cellular elongation in response to gibberellin signals. Jasmonic acid (JA) promotes potato tuber formation, reducing the leaf primordial length, meristem enlargement, and cell expansion (Naturales, 2003). Proper root development requires ROS homeostasis, which regulates cell proliferation and differentiation at root tips. Plant roots collect significant quantities of ROS; when this unbalances, the plant cannot adapt to environmental changes and dies. Moreover, ROS controls cell expansion and cell processes such as root hair formation and lateral root development (Mase and Tsukagoshi, 2021). Auxin is involved in cell enlargement and proliferation. During the process of tuberization, auxin in potato plant dynamics affects tuber initiation by stimulating its biomass and increasing tuberization (Aksenova et al., 2012). IAA transport from shoot to root and the stolon is necessary for tuberization (Sergeeva et al., 1994). *StYUC-like 1* expression increases at stolon tips during tuberization (Bachem, 2013). GA targets DELLA degradation in each elongation zone tissue to stimulate root development, which regulates over 100 transcription factors to integrate environmental signals. GA conjugation to GID1, its soluble receptor, increases GID1-GA and DELLA protein interaction, changing their ubiquitin in-proteasome route (Yoshida et al., 2014). GA-GID1-DELLA complexity alters independently of GA presence or absences. Without GA, DELLA conjugates to the protein complex and inhibits the TF, whereas in the presence of GA, GID1 triggers DELLA and TFs (Ariizumi et al., 2008). The DELLA protein may have coordinated multiple developmental programs throughout green lineage evolution by generating co-gene expression in different species. Thus, DELLA recruitment in the gibberellin signaling pathways may have expanded their role in different processes (Briones-moreno et al., 2017).

3 Cooperation in morphogenesis

Morphogenesis, the process that gives a plant its shape, is also governed by the interaction of GRNs and phytohormones:

The constant increase in evolution leads to the complexity of the regulatory mechanism and the plants' developmental process. Throughout their lifetime, plants undergo various morphological and developmental changes. Gene expression is the primary mechanism of development regulation (Kaufmann and Chen, 2017). It is controlled by other regulators that collectively make a network, integrating the environmental constraints and coordinating various developmental programs via GRNs (Kaufmann and Chen, 2017). As previously mentioned, GRNs are a series of regulatory factors that interact among themselves and with other regulators to control the levels of the mRNA and proteins to specify temporal and special patterns (Gene regulatory networks, 2005).

3.1 Organ formation

Plant hormone interactions produce complicated regulatory circuits that regulate new meristem growth. They collaborate with GRNs to control genes related to the development of roots, flowers, and fruits (Meitzel et al., 2021). Although many peptides and receptors have been discovered, most are one-way positive signal pathways. Only a few examples regulate the signal routes antagonistically (Lee and De, 2016). However, Yu et al. proposed that antagonistic competitive signaling pathways in plants adopt a "SPDC" competing mode. In plant developmental biology, polarity establishment is the core issue related to organ morphogenesis. Previous research has defined leaf polarity on a three-dimensional spatial axis based on the relative position of the leaf primordium and SAM to examine leaf polarity development (Bowman, 2000). Several studies showed that auxin is the primary regulator of the apical dominant. It is synthesized in the shoot tip and carried down the stem, suppressing the development of the lateral root buds (Kieffer et al., 2010). The regeneration of axillary buds is mainly involved in cell division, tissue differentiation, and organogenesis of the apical meristem (Petra, 2012).

To address these issues, Yao et al. examined axillary bud development trends before and after apical spike removal in perennial rice (PR23) and annual rice (Chugeng28). Annual rice axillary buds at high nodes expanded quicker than others. Through transcriptome sequencing analysis by Yao et al., the PR23 rhizome buds' global gene expression patterns at compression nodes that developed 1, 3, 4, and 5 days following apical spike removal were evaluated. Moreover, Yao et al. concluded that this research shed light on the differences between the auxiliary bus regeneration pattern of the perennials and annual rice and gave them intricate regulatory networks that are present during the regeneration of rhizome axillary buds in perennial rice. Auxin regulates gene expression by regulating the activity of ARFs via Aux/IAA pathways (Calderón Villalobos et al., 2012). Flowering plants

undergo four life stages: embryonic development, vegetative growth, reproductive growth, and senescence. The reproductive growth stage is a crucial period for plant fitness and is of significant importance from the biologists' and breeders' points of view (Alvarez-buylla et al., 2010). Genetic and phylogenetic analyses show that most of the *arf* single mutants display no obvious phenotypes, confirming the functional redundancy in the ARF family (Okushima et al., 2005). However, *arf3* mutation disrupts meristem homeostasis, floral determinacy, patterning formation, gynoecium morphogenesis, ovule development, and self-incompatibility (Su et al., 2018).

These findings showed that ARF3 uniquely functions in the auxin signaling and developmental process. To further elaborate on the importance, Fu et al. stated that auxin is involved practically in every aspect of plant growth and development. A recent study showed that ARF3 governs the dynamics of SAM maintenance in a non-cell autonomously. This showed the hierarchical regularity mechanism of ARF3 in the developmental process during the plant's reproductive process. To specify the primordium density in the principle zone, ARF5 directly activates the auxin transporters PIN FOMRMED 1 (PIN1), the floral meristem identity gene LEAFY (LFY), the organ size regulatory genes AINTEGUMENTA (ANT) and AINTEGUMENTA-LIKE 6 (AIL6), and the abaxial identity gene FILAMENTOUS FLOWER (FIL) (Wakeel et al., 2018). Furthermore, HcPR10-mediated traits, including bolting, faster flowering, higher branch number, and siliques per plant, are substantially linked with transgenic Arabidopsis cytokinin levels. HcPR10 expression patterns are temporally associated with plant cytokinin levels.

3.2 Tissue patterning

The formation of vascular tissues, epidermis, and other plant tissues is controlled by the coordinated action of hormones and GRNs. Leaves are one of the vegetative parts of the plant that are crucial for plant growth and development. The PIN proteins control auxin transport throughout various periods of plant development and have been thoroughly documented in various plant species (Ullah et al., 2021). Chen et al. have examined that *BpPIN3* regulates the expression of the auxin response-related genes and the polar transport of the auxin to alter the polar shape of the proximal and distal axes of the birch leaves. In addition, plant hormones such as ethylene and GAs regulate sex determination in monoecious plants and other factors. In cucumber (*Cucumis sativus* L.), GAs are necessary for developing the male flower. Cucumber plants treated with GA and the control plants' shoot apices were transcriptionally analyzed to give evidence that GA regulates sex determination via both ethylene-dependent and ethylene-independent mechanisms (Zhang et al., 2017).

According to Feng et al., plants create PRs responding to abiotic and biotic stressors. A large intracellular PR-10 family has over 100 members (Xu et al., 2014). PR-10 genes, including reproductive and vegetative tissue, are expressed everywhere in plants, indicating their crucial involvement in growth and development (Liu and Ekramoddoullah, 2018). Furthermore, HcPR10 in *Halostachys*

casipica mainly accumulates in vascular tissue, where plant hormones translocate for large distances.

3.3 Response to environment

Plant hormones play a crucial role in interpreting environmental signals (detected by receptors) and inducing developmental programs through different interconnected pathways.

Environment signals (light, gravity, microbial infection) may modify the plant's form. Phytohormones mediate these reactions, and GRNs govern gene expression that supports morphological transformation. Unlike mammals, plants create organs throughout their life cycle, even beyond embryonic development. This is possible because plants possess a small group of pluripotent stem cells in their meristems. The SAM plays a key role in forming all of the aerial structures of plants, including FMs. The FMs subsequently give rise to the floral organs containing reproductive structures.

The study on the model plant Arabidopsis has shown the importance of TFs and secreted peptides in meristem activity. Recent advances in genomic, transcriptomic, imaging, and modeling technologies have allowed us to study the interaction between TFs, secreted peptides, and plant hormones (Lee et al., 2019). Phytotropins, plasma membrane photoreceptors proteins in flowering plants, perceive blue light and trigger a phototropic response (Sakamoto and Briggs, 2002). Phototropins (PHOT1 and PHOT2) govern the stomatal opening, leaf expansion, stem inhibition, and the blue-light response (Christie, 2007). Another phototropism protein is ROOT PHOTOTROPISM 2 (RPT2). Mutations in the RPT2 cause defective phototropic response under intense blue light (Sakai et al., 2000). Gravity guides major plant structures, including the directional development of the primary root via auxin gradients that are disrupted when the roots depart from the vertical as a gravity sensor (Ferland and Paul, 2016). The vertical roots deliver PIN3/7 proteins evenly to the plasma membrane on all cell sides for the symmetrical auxin distribution to the lateral cap. When the plants are reoriented in the gravity response, these proteins immediately re-localize to the statocytes' lower sides, forcing auxin to the lower flank of the root caps (Bittner et al., 2022). The transcytosis delocalization of the PIN3 and PIN7 portions to the bottom of the statocytes is induced by gravity. It requires small GTPases of the ADP-ribosylation factor type and GNOM-type GDP/GTP exchange factors (GEFs) (Mohanasundaram and Pandey, 2022).

Auxin regulates plant growth and development, including cell division, elongation, and differentiation, tissue shape, and functions. Despite rosette leaves and other SAM products, auxin biosynthesis, transport, and signaling mutants have bare inflorescences without flowers (Banasiak and Biedro, 2019). Canonical ARF (class A), MONOPTEROS (MP), regulates auxin signaling, such as ARF5 regulating gene expression to determine meristematic and primordium fate signaling (Rademacher and Mo, 2011). Yu et al. claimed that plant growth and pattern formation depend on the diffusible signals and the location cues in this Research Topic, which activates the intracellular downstream components via cell surface receptors that direct cells to adapt specific fates for optimal functions and maintain biological fitness. For instance, Yu et al.

proposed that the “SPDC” competitive mode exists in microbial infection. The paracrine and autocrine signaling chemicals compete to bind receptors or receptor complexes, activate antagonistic molecular pathways, and precisely control plant growth.

In conclusion, the symbiotic relationship between GRNs and phytohormones is paramount for the complex orchestration of plant development and morphogenesis. Understanding this intricate dance can offer insights into plant development, crop improvement, and sustainable agriculture practices.

Author contributions

MA: Conceptualization, Writing – original draft, Writing – review & editing. YZ: Conceptualization, Funding acquisition, Writing – review & editing. WL: Writing – review & editing.

Funding

This study was funded by the National Natural Science Foundation of China (32301737), and the Agricultural Science and Technology Innovation Program of Chinese Academy of Agricultural Sciences (ASTIP-TRIC-ZD05).

References

- Aksenova, N. P., Konstantinova, T. N., Golyanovskaya, S. A., Sergeeva, L. I., and Romanov, G. A. (2012). Hormonal regulation of tuber formation in potato plants. *Russian J. Plant Physiol.* 59, 451–466. doi: 10.1134/S1021443712040024
- Alvarez-buylla, A. E. R., Benítez, M., Corvera-poiré, A., Cador, Á. C., Folter, S., Buen, A. G. De, et al. (2010). Flower development. *Arabidopsis Book* 8, 2–57. doi: 10.1199/tab.0127
- Ariizumi, T., Murase, K., Sun, T., and Steber, C. M. (2008). Proteolysis-independent downregulation of DELLA repression in arabidopsis by the gibberellin receptor GIBBERELLIN INSENSITIVE DWARF1. *Plant Cell* 20 (9), 2447–2459. doi: 10.1105/tpc.108.058487
- Roumeliotis, E., Kloosterman, B., Oortwijn, M., Visser, R. G., and Bachem, C. W. (2013). The PIN family of proteins in potato and their putative role in tuberization. *Front. Plant Sci.* 19 (4), 524. doi: 10.3389/fpls.2013.00524
- Banasiak, A., and Biedro, M. (2019). Ontogenetic changes in auxin biosynthesis and distribution determine the organogenic activity of the shoot apical meristem in pin1 mutants. *Int. J. Mol. Sci.* 20 (1), 180. doi: 10.3390/ijms20010180
- Bittner, A., Cie, A., Gruden, K., Lukan, T., Mahmud, S., and Teige, M. (2022). Organelles and phytohormones : a network of interactions in plant stress responses. *Review J. Exp. Bot.* 73 (21), 7165–7181. doi: 10.1093/jxb/erac384
- Bowman, J. L. (2000). Axial patterning in leaves and other lateral organs. *Curr. Opin. Genet. Dev.* 10 (4), 399–404. doi: 10.1016/S0959-437X(00)00103-9
- Briones-moreno, A., Hernández-garcía, J., Vargas-chávez, C., Romero-campero, F. J., Romero, J. M., Valverde, F., et al. (2017). Evolutionary analysis of DELLA-associated transcriptional networks. *Front. Plant Sci.* 25 (8), 626. doi: 10.3389/fpls.2017.00626
- Calderón Villalobos, L. I. A., Lee, S., De Oliveira, C., Ivetaç, A., Brandt, W., Armitage, L., et al. (2012). A combinatorial TIR1/AFB-Aux/IAA co-receptor system for differential sensing of auxin. *Nat. Chem. Biol.* 8 (5), 477–485. doi: 10.1038/nchembio.926
- Christie, J. M. (2007). Phototropin blue-light receptors. *Annu. Rev. Plant Biol.* 58, 21–45. doi: 10.1146/ANNUREV.ARPLANT.58.032806.103951
- Davidson, E. H., and Levine, M. S. (2008). Properties of developmental gene regulatory networks. *Proc. Natl. Acad. Sci. U.S.A.* 105 (51), 20063–20066. doi: 10.1073/pnas.0806007105
- Davies, P. J. (2010). The plant hormones: Their nature, occurrence, and functions. *Plant Horm. Biosynth. Signal Transduct. Action!*, 1–15. doi: 10.1007/978-1-4020-2686-7_1/COVER
- El-Showk, S., Ruonala, R., and Helariutta, Y. (2013). Crossing paths: Cytokinin signalling and crosstalk. *Dev.* 40 (7), 1373–1383. doi: 10.1242/dev.086371
- Ferl, R. J., and Paul, A. (2016). The effect of space flight on the gravity-sensing auxin gradient of roots : GFP reporter gene microscopy on orbit. *NPJ Microgravity* 21 (2), 15023. doi: 10.1038/npjmgrav.2015.23
- Davidson, E., and Levin, M. (1965). Plant cell differentiation. *Annu Rev Plant Physiol* 2 (16), 119–140. doi: 10.1073/pnas.0502024102
- Gordon, S. P., Chickarmane, V. S., Ohno, C., and Meyerowitz, E. M. (2009). Multiple feedback loops through cytokinin signaling control stem cell number within the Arabidopsis shoot meristem. *Proc. Natl. Acad. Sci. U.S.A.* 106 (38), 16529–16534. doi: 10.1073/pnas.0908122106
- Huang, S., and Kauffman, S. A. (2009). Complex complex gene regulatory networks – from structure to biological observables: cell fate determination. *Encycl. Complex. Syst. Sci.*, 1180–1213. doi: 10.1007/978-0-387-30440-3_79
- Kaufmann, K., and Chen, D. (2017). From Genes to Networks: Characterizing Gene-Regulatory Interactions in Plants. *Methods Mol. Biol.* 1629, 1–11. doi: 10.1007/978-1-4939-7125-1
- Kieffer, M., Neve, J., and Kepinski, S. (2010). Defining auxin response contexts in plant development. *Review Curr. Opin. Plant Biol* 13 (1), 12–20. doi: 10.1016/j.pbi.2009.10.006
- Lee, J. S., and De, I. (2016). Fine-Tuning development through antagonistic peptides : an emerging theme. *Trends Plant Sci.* 21 (12), 991–993. doi: 10.1016/j.tplants.2016.10.003
- Lee, Z. H., Hirakawa, T., and Yamaguchi, N. (2019). The roles of plant hormones and their interactions with regulatory genes in determining meristem activity. *Int. J. Mol. Sci.* 20 (16), 4065. doi: 10.3390/ijms20164065
- Leibfried, A., To, J. P. C., Busch, W., Stehling, S., Kehle, A., Demar, M., et al. (2005). WUSCHEL controls meristem function by direct regulation of cytokinin-inducible response regulators. *Nature* 438 (7071), 1172–1175. doi: 10.1038/nature04270
- Liu, J., and Ekramoddoullah, A. K. M. (2018). regulation, and function in response to biotic and abiotic stresses The family 10 of plant pathogenesis-related proteins: Their structure, regulation, and function in response to biotic and abiotic stresses. *Physiol. Mol. Plant Pathol.* 68 (1), 3–13. doi: 10.1016/j.pmp.2006.06.004
- Macneil, L. T., and Walhout, A. J. M. (2011). Gene regulatory networks and the role of robustness and stochasticity in the control of gene expression. *Genome Res* 21 (5), 645–657. doi: 10.1101/gr.097378.109.21

Acknowledgments

We would like to thank all the authors of the articles published in this Research Topic for their contributions, the reviewers and editors for their help in evaluating the manuscripts, and the members of the editorial office for their managerial support.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher’s note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

- Madhamshettiwar, P. B., Maetschke, S. R., Davis, M. J., Reverter, A., and Ragan, M. A. (2012). Gene regulatory network inference : evaluation and application to ovarian cancer allows the prioritization of drug targets. *Gene regulatory network inference : evaluation and application to ovarian cancer allows the prioritization of drug targets. Genome Med.* 4 (5), 41. doi: 10.1186/gm340
- Mase, K., and Tsukagoshi, H. (2021). Reactive oxygen species link gene regulatory networks during Arabidopsis root development. *Front. Plant Sci.* 27 (12), 660274. doi: 10.3389/fpls.2021.660274
- Meitzel, T., Radchuk, R., Mcadam, E. L., Thorm, I., Feil, R., Munz, E., et al. (2021). Trehalose 6-phosphate promotes seed filling by activating auxin biosynthesis. *New Phytol.* 229 (3), 1553–1565. doi: 10.1111/nph.16956
- Mishra, S., Kumar Satapathy, S., and Mishra, D. (2018). Enhanced gene ranking approaches using modified trace ratio algorithm for gene expression data. *Inform. Med. Unlocked* 5 (2), 39–51. doi: 10.1016/B978-0-12-816356-6.00004-5
- Mohanasundaram, B., and Pandey, S. (2022). Effect of environmental signals on growth and development in mosses. *J. Exp. Bot.* 73 (13), 4514–4527. doi: 10.1093/jxb/erac138
- Naturales, D. C. (2003). Exogenously applied jasmonic acid induces changes in apical meristem morphology of potato stolons. *Ann. Bot.* 91 (7), 915–919. doi: 10.1093/aob/mcg098
- Okushima, Y., Overvoorde, P. J., Arima, K., Alonso, J. M., Chan, A., Chang, C., et al. (2005). Functional genomic analysis of the AUXIN RESPONSE FACTOR gene family members in Arabidopsis thaliana : unique and overlapping functions of ARF7 and ARF19. *Plant Cell* 17 (2), 444–463. doi: 10.1105/tpc.104.028316.2
- Petra, J. (2012). A novel putative auxin carrier family regulates intracellular auxin homeostasis in plants. *Nature* 485 (7396), 119–122. doi: 10.1038/nature11001
- Rademacher, E. H., and Mo, B. (2011). A cellular expression map of the Arabidopsis AUXIN RESPONSE FACTOR gene family. *Plant J.* 68 (4), 597–606. doi: 10.1111/j.1365-3113X.2011.04710.x
- Sakai, T., Wada, T., Ishiguro, S., and Okada, K. (2000). RPT2 : A signal transducer of the phototropic response in Arabidopsis. *Plant Cell* 12 (2), 225–236. doi: 10.1105/tpc.12.2.225
- Sakamoto, K., and Briggs, W. R. (2002). Cellular and subcellular localization of phototropin 1. *Plant Cell* 14, 1723–1735. doi: 10.1105/tpc.003293.Phot1
- Satterlee, J. W., Strable, J., and Scanlon, M. J. (2020). Plant stem-cell organization and differentiation at single-cell resolution. *Proc. Natl. Acad. Sci. U.S.A.* 117 (52), 33689–33699. doi: 10.1073/pnas.2018788117
- Sergeeva, L. I., Mach, I., Konstantinova, T. N., Golyanovskaya, S. A., Eder, J., and Zaltsman, O. O. (1994). Morphogenesis of potato plants in vitro. II. endogenous levels, distribution, and metabolism of IAA and cytokinins. *J. Plant Growth Regul.* 13, 147–152. doi: 10.1007/BF00196379
- Stange, L. (1965). Plant cell differentiation. *Annu. Rev. Plant Physiol.* 2 (16), 119–140. doi: 10.1073/pnas.0502024102
- Su, Z., Zhao, L., Zhao, Y., Li, S., and Won, S. (2018). The THO Complex Non-Cell-Autonomously Represses Female Germline Specification through the TAS3-ARF3 Module. *Curr. Biol.* 27 (11), 1597–1609. doi: 10.1016/j.cub.2017.05.021
- Ullah, Z., Asim, M., Shi, S., and Khan, R. (2021). Cloning and functional analyses of NtPIN1a promoter under various abiotic stresses in Nicotiana tabacum. *Pak. J. Bot* 54 (2), 429–438. doi: 10.30848/PJB2022-2(12)
- Vaishnav, D., Chowdhury, P., Vaishnav, D., and Chowdhury, P. (2023). Types and function of phytohormone and their role in stress. *Plant Abiotic Stress Responses Tolerance Mechanisms* doi: 10.5772/intechopen.109325
- Van den Broeck, L., Gordon, M., Inzé, D., Williams, C., and Sozzani, R. (2020). Gene regulatory network inference: connecting plant biology and mathematical modeling. *Front. Genet.* 25 (11), 457. doi: 10.3389/fgene.2020.00457
- Wakeel, A., Ali, I., Raza, A., Minjie, K., and Sakila, W. (2018). Involvement of histone acetylation and deacetylation in regulating auxin responses and associated phenotypic changes in plants. *Plant Cell Rep.* 37 (1), 51–59. doi: 10.1007/s00299-017-2205-1
- Xu, P., Jiang, L., and Wu, J. (2014). Isolation and characterization of a pathogenesis-related protein 10 gene (GmPR10) with induced expression in soybean (Glycine max) during infection with Phytophthora sojae. *Mol. Biol. Rep.* 41 (8), 4899–4909. doi: 10.1007/s11033-014-3356-6
- Yoshida, H., Hirano, K., Sato, T., Mitsuda, N., Nomoto, M., Maeo, K., et al. (2014). DELLA protein functions as a transcriptional activator through the DNA binding of the INDETERMINATE DOMAIN family proteins. *Proc. Natl. Acad. Sci. U.S.A.* 111 (21), 7861–7866. doi: 10.1073/pnas.1321669111
- Zhang, Y., Zhao, G., Li, Y., Mo, N., Zhang, J., and Liang, Y. (2017). Transcriptomic Analysis Implies That GA Regulates Sex Expression via Ethylene-Dependent and Ethylene-Independent Pathways in Cucumber (Cucumis sativus L.). *Front. Plant Sci.* 19 (8), 10. doi: 10.3389/fpls.2017.00010