



Crosstalk among plant growth regulators and signaling molecules during biotic and abiotic stresses: molecular responses and signaling pathways

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Abstract

Key message Plant stress responses are extremely sophisticated which implicate changes at the cellular, physiological and transcriptome levels by activating specific gene expression related to the challenges faced by plants.

In natural ecosystems, plants are subjected to a variety of biotic interactions (bacteria, viruses, fungi, insects, and nematodes) and abiotic (such as drought, metal/metalloid, salinity, temperature) factors, which can cause stress for plants. Sometimes plants are subjected to these stressors concurrently, which results in the alteration of different physiological traits and thus exacerbate the ability of plants to survive. Due to multifactorial environmental stress, plants have evolved diverse strategies to respond to stress; various signals are coordinated for these responses. These diverse adaptation strategies allow plants to survive in diverse environmental conditions (Shalak et al. 2021). It is crucial to recognize how the different response mechanisms to these stresses interplay with each other, and identify the crosstalk cascades which shift the feedback from one pathway to another (Ku et al. 2018). The signaling pathways of various phytohormones are meshed in a complicated network, giving plants an immense regulatory power to quickly adjust to their environment and exploit limited resources for development, and adaptation. For crops, these responses must be effective for economic (crop yield) purposes (Pieterse et al. 2012). In recent times, there has been a rising significance in elucidating the role of phytohormone-like growth regulators

and other signaling molecules in plant adaptation and tolerance mechanisms against environmental stresses.

Plant hormones play crucial roles in regulating various development processes such as seed germination, flowering, senescence, and dormancy. They also activate adaptive responses induced by external stimuli such as abiotic and/or biotic stresses. While auxins, gibberellins, cytokinins, brassinosteroids and strigolactones have been established as the major developmental growth regulators in plants, salicylic acid (SA), jasmonates (JA), ethylene and abscisic acid (ABA) and are linked to stress regulation (Verma et al. 2016). Apart from these, recently discovered natural plant growth substances that have phytohormone-like regulatory roles are polyamines (e.g., putrescine, spermidine, and spermine), neurotransmitters (serotonin, melatonin, dopamine, acetylcholine and gamma-amino butyric acid), gasotransmitters (nitric oxide, hydrogen sulfide, and carbon monoxide). Calcium sensors are usually considered as the primary response to different environmental stimuli to activate downstream signaling pathways. ABA is the major phytohormone regulating stress responses, and for this purpose it collaborates with SA and JA signaling pathways. This collaboration in turn helps to allocate resources for attenuating the impacts of abiotic stress. GTP-binding proteins (G-proteins) comprising of structurally and functionally diverse proteins are often involved in carrying out the signal transduction in these pathways (Roychoudhury et al. 2021).

A novel paradigm suggests the multidimensional role of ABA in pathogen response, where it depends on the time and magnitude of the infection (Lievens et al. 2017). This model suggests that there are three different stages of pathogen infection. To begin with, ABA triggers stomatal closure, enhancing the resistance against pathogen invasion,

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and consequently has a significant impact on the defence response. In this stage, as the effects of JA, SA, and ethylene pathways are not yet required so ABA antagonizes these pathways to save resources (Atkinson et al. 2012). In the second stage, strengthening of cell walls is done post-invasion, this process is facilitated by ABA during fungal invasion, while suppressed during bacterial invasion. In the third stage, pathogen-associated molecular patterns (PAMPs) induce ethylene, SA, and JA, and various cascades to control wide range of compounds that help in defense. Certain genes induced by ABA-like *ATAF1* and *ERD15* have been recognized as switches that may be involved in activation of ABA-dependent biotic stress responses by compromising abiotic responses (Ton et al. 2009; Lievens et al. 2017).

TFs (transcription factors) are of vital significance in allowing specificity in plant responses against different stressors. Their manoeuvring delivers precise prospects for generating multiple stress resilience by controlling a broad array of downstream events (Xu et al. 2011). MYC2, a basic helix–loop–helix transcription factor is key to the communication between abiotic and biotic stress signalling, which acts as a positive regulator of defence genes triggered by JA, but suppresses those that are induced by integrated ethylene/JA signalling (Anderson et al. 2004; Pieterse et al. 2009). Besides, MYC2 has also been reported as a major suppressor of the SA pathways (Laurie-Berry et al., 2006). Furthermore, it has been reported to be induced by ABA, with its mutants showing lack of ABA-responsive gene expression and transgenic plants overexpressing *MYC2* showing increased ABA sensitivity (Abe et al. 2003). Thus, multifunctional MYC2 may operate as a regulatory hub within ABA controlled biotic stress biochemical cascade (Asselbergh et al. 2008; Pieterse et al. 2009). Various ethylene response factors have been reported to be activated by ethylene under a number of abiotic stresses, such as those caused by salinity and heat, with these response factors showing differential regulation depending upon the type of stress (Klay et al. 2018). Drought, salinity and osmotic stresses rapidly activate the sucrose non-fermenting 1-related kinases (SnRK2) family of serine/threonine kinases. Osmotic stress triggers all 10 SnRK2s except SnRK2.9 in *Arabidopsis*, with SnRK2.2/3/6/7/8 showing activation via ABA as well (Boudsocq et al. 2004). In spite of the fact that ABA-mediated SnRK2 activation mechanism has been explained, how osmotic shock triggers the kinases is not fully understood. In *Arabidopsis*, *OSCA1* (reduced hyperosmolality-induced calcium increase 1) encodes an intrinsic protein which forms hyperosmolality-gated calcium-permeable channel. *OSCA1* is regarded as a putative sensor for hyper-osmotic stress, with loss of function *OSCA1* mutants displaying a conserved calcium spike as compared with wild type plants when under osmotic stress inducing agents like mannitol and sorbitol (Yuan et al. 2014).

Substantial advancement has been made in untangling different signaling cascades involved in conferring abiotic stress resilience to the plants. It has largely become possible due to accessibility of several omics approaches such as transcriptomics, proteomics and genomics analyses (Liu et al. 2014). Expression of stress related genes, signal perception and transduction constitute the basic signaling pathway for any given abiotic stress (Pérez-Clemente et al. 2013). The mitogen-activated protein kinase (MAPK) pathways and calcium dependent protein kinase (CDPK) pathways are found to mediate plant stress responses (Huang et al. 2012), with MAPK acting as a pivotal convergence point for many signaling pathways conveying the stress signals to downstream effectors like transcription factors via phosphorylation to reprogram transcriptome and metabolome. Moreover, miRNAs (microRNAs) are very short endogenous regulatory RNAs that govern gene expression at the post-transcriptional level by mRNA degradation in plants. Furthermore, miRNAs have also been found to be involved in numerous abiotic (e.g., salinity, drought, cold, and mineral nutrient deficiency) and biotic (e.g., viral and bacterial pathogenesis) stress responses. The high-throughput tools and techniques may be beneficial in providing genome-wide identification of stress-related miRNAs under various abiotic stresses. Also, RNA interference (RNAi) mediated by miRNAs might be helpful in developing transgenic crop plants with improved resistance against abiotic and biotic stress responses (Kumar 2014).

Keeping in mind the significant role of phytohormones, plant growth regulators and signaling molecules during abiotic and biotic stress events, the second volume of this special issue is intended to elucidate the molecular mechanisms that collaborate in a complex regulatory network. The present volume includes several research and review articles evaluating kinase cascades, transcription factors, and reactive oxygen species, which are the key elements of signaling crosstalk, together with gene expression regulation and miRNA targeting. The identification of master regulators connecting abiotic and biotic stress response pathways is critical to the development of stress-tolerant crops. Furthermore, the engineering of phytohormone-biosynthetic pathways could also prove to be an exciting prospect for researchers developing crops with improved resistance that are also nutritionally efficient. This becomes even more important due to escalation in the intensity of various stress factors making plant survival even more challenging. We hope that the present volume will add a new dimension in these areas of research and will largely benefit the scientific community in pushing the investigations forward.

Author contribution statement TA drafted the Editorial while AR provided valuable suggestions.

Declarations

Conflict of interest The authors declare that there is no conflict of interest.

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