CellPress

Review

The Role of MAPK Modules and ABA during Abiotic Stress Signaling

Axel de Zelicourt,[1,3] Jean Colcombet,[2,3] and Heribert Hirt[1,2,*]

To respond to abiotic stresses, plants have developed specific mechanisms that allow them to rapidly perceive and respond to environmental changes. The phytohormone abscisic acid (ABA) was shown to be a pivotal regulator of abiotic stress responses in plants, triggering major changes in plant physiology. The ABA core signaling pathway largely relies on the activation of SnRK2 kinases to mediate several rapid responses, including gene regulation, stomatal closure, and plant growth modulation. Mitogen-activated protein kinases (MAPKs) have also been implicated in ABA signaling, but an entire ABA-activated MAPK module was uncovered only recently. In this review, we discuss the evidence for a role of MAPK modules in the context of different plant ABA signaling pathways.

Trends

Abiotic stresses impact average yield in agriculture by more than 50% globally.

Since ABA is a key regulator of abiotic stress responses, an understanding of its functioning at the molecular level is essential for plant breeding. Although the ABA core signaling pathway has been unraveled, several downstream events are still unclear.

MAPKs are involved in most plant developmental stages and in response to stresses. Several members of the MAPK family were shown to be directly or indirectly activated by the ABA core signaling pathway.

Recent evidence shows that the complete MAP3K17/18-MKK3-MPK1/2/7/14 module is under the control of ABA, whose members are under the transcriptional and post-translational control of the ABA core signaling pathway.

Abiotic Stress Responses of Plants

Abiotic stresses, such as drought, salinity, or temperature variation, impair the productivity of all major crops and constitute the primary cause of crop loss worldwide, reducing average yields by more than 50% globally [1,2]. These environmental stresses influence plant yield and quality by affecting various cellular and whole-plant processes [2,3]. For example, salinity and drought, two major causes of environmental stress, reduce the availability of water necessary for basic cellular functions and maintenance of turgor pressure. The osmotic shock caused by these stresses reduces carbon assimilation and photosynthesis in particular. Abiotic stresses also induce reactive oxygen species (ROS) production, causing irreversible cell and tissue damage and ultimately contributing to reduced growth, fertility, and premature senescence [4].

To counter the detrimental effects of environmental stresses, plants have evolved adaptation mechanisms or specific growth habits to avoid stress [5,6]. Their responses are dynamic and comprise both reversible and irreversible changes, including adjustments of membrane systems, modifications of the cell wall architecture, and changes in cell division [7–9]. In addition, the production of compatible solutes (e.g., proline or raffinose) helps to stabilize proteins and cellular structures and/or maintain cell turgor, and reduce excess levels of ROS [4,6,10,11]. Abiotic stress responses are also under epigenetic [12,13] and transcriptional regulation, which massively modify gene expression, including genes involved in the synthesis of osmoprotectants, detoxifying enzymes, transporters, and regulatory proteins, such as protein kinases, phosphatases, and transcription factors [4,14,15].

ABA Is Perceived by a Core Signaling Module

One of the early events following the perception of abiotic stress is the local biosynthesis of **ABA** (see Glossary) [16], which is then transported throughout the plant to adapt physiological processes to the prevailing stress conditions. For example, drought, which is first sensed at the root level, triggers ABA production, which is then transported to the upper parts of the plant

[1]4700 King Abdullah University of Sciences and Technology, KAUST, Thuwal 23955-6900, Saudi Arabia
[2]Institute of Plant Sciences Paris Saclay, INRA-CNRS-UEVE, Orsay 91405, France
[3]These authors contributed equally to this work.

*Correspondence:
heribert.hirt@kaust.edu.sa (H. Hirt).

to reduce water transpiration, the most obvious part of the response being the **stomatal** pore closure.

After several decades of research, characterization of the core ABA signaling pathway was achieved in 2009. The pathway was shown to primarily perceive and transmit the hormone stimulus to activate downstream events [17–19]. This core module comprises three protein classes: the ABA receptor *per se*, named Pyrabactin Resistance/Pyrabactin resistance-like/Regulatory Component of ABA Receptor (PYR/PYL/RCAR); negative regulators of the Protein Phosphatase 2C (PP2C) group A family; and the positive regulators SNF1-Related Protein Kinases type 2 (SnRK2s) (Figure 1). In the absence of ABA, SnRK2s are continuously inactivated by PP2Cs, which dephosphorylate the kinase activation loop and, therefore, prevent the SnRK2 protein kinases from phosphorylating their targets. Upon ABA binding, PYR/PYL/RCAR receptors undergo a conformational change that allows the binding of the catalytic site of PP2Cs [20]. In turn, ABA-induced inhibition of PP2Cs leads to SnRK2 autophosphorylation and activation [21]. It is now clear that this module of three proteins is the main ABA-sensing mechanism of the plant. Each class of protein is encoded by small multigenic families, whose members are largely functionally redundant. Single mutants of PYR/PYL/RCAR receptors have a weak or no phenotype, while triple and higher-order mutants of the gene family show low or no sensitivity in germination and root growth responses to ABA [22,23]. The overexpression of *PYL5*, *PYL8*, or *PYL9* alone suffices to produce enhanced ABA responses and drought resistance in *Arabidopsis* [18,24,25]. PP2C mutants have been identified during different genetic screens and, for several years, only very strong gain-of-function alleles, such as *abi1-1* (*abi1*^{G180D}) or *abi2-1*

Glossary

Abscisic acid (ABA): a major phytohormone involved in seed maturation, plant development, and response to abiotic stresses.

Mitogen-activated protein kinase (MAPK): signaling kinases present in all eukaryotes and involved in cell function and response to stimuli.

Stomata: plant pore comprising two guard cells mainly found on the leaf abaxial face, involved in gas exchange between the plant and its environment; used as entry point for many plant pathogens.

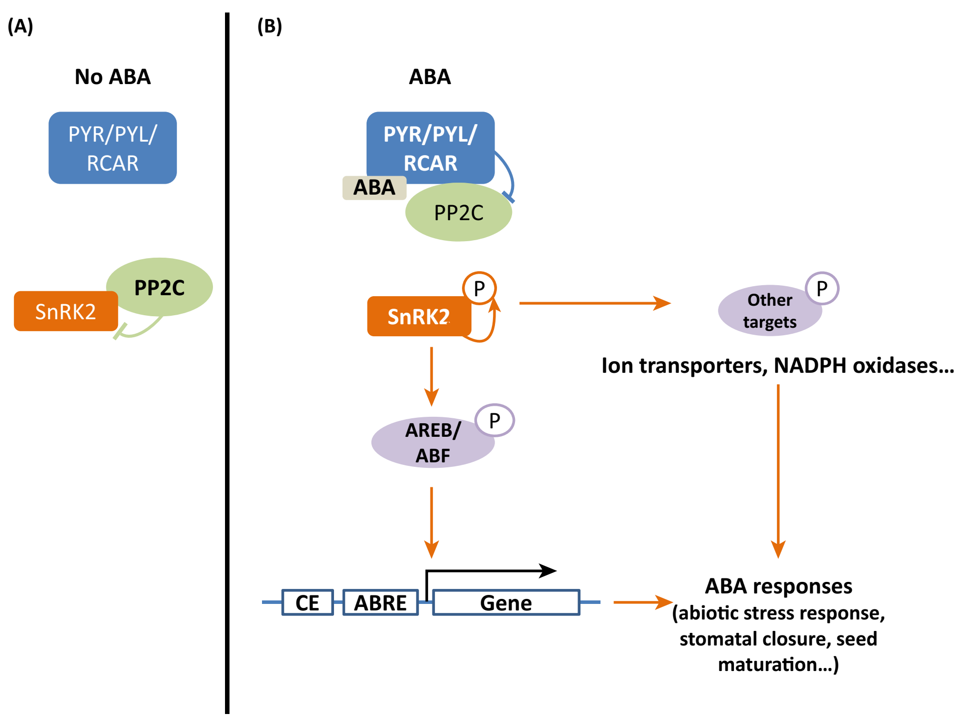

Figure 1. The Core Abscisic Acid (ABA) Signaling Module Comprises Three Main Components. (A) In the absence of ABA, the ABA receptors are inactivated and Protein Phosphatase 2C (PP2C) proteins inhibit SNF1-Related Protein Kinases type 2 (SnRK2) proteins. (B) In the presence of ABA, the ABA receptors PYR/PIL/RCAR proteins bind to ABA and in turn inhibit PP2C activity, allowing the activation of SnRK2s through autophosphorylation. Activated SnRK2s then phosphorylate their downstream targets, such as the AREB/ABF transcription factors, which bind to the ABRE *cis*-element and modulate gene expression. They can also phosphorylate other proteins, such as ion channels and NADPH oxidases. Together, these events lead to the establishment of the ABA response.