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## Abiotic Stress Signaling in Plants – An Overview

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### Abstract

Abiotic stress factors [such as salinity, water availability (less or excess water), temperature extremes (freezing, cold, or high), metal/metalloids, nutrient stress, etc.] are basically severe menaces to the global agriculture, restricting the crop plants from reaching their full genetic potential and causing significant yield losses worldwide. In general, stresses are complex and multigenic traits that affect the plant performance significantly by reducing the growth, development, and, finally, the yield. To counteract the adverse effect of the stressors, plants have evolved efficient defense mechanisms by manipulating their tolerance potential through integrated molecular and cellular responses. To face the environmental challenges in the form of various abiotic stresses, perception of stress signals as well as their transduction is a very crucial step for switching on adaptive responses to ensure the survival of plants. Therefore, understanding the physiological and molecular aspects of plant functions under stressful conditions, for example, the activation of cascades of molecular networks (perception of stress signals, transducers, transcription regulators, target stress related genes and metabolites), is desirable. Recent studies have revealed that understanding signal perception and its transduction is crucial for engineering stress tolerance in crop plants. This chapter appraises recent literature on stress signaling and stress responses in plants.

### 1.1

#### Introduction

Environmental insults in the form of various abiotic stress factors (salinity, water availability (less or excess water), temperature extremes (freezing, cold, or high), metal/metalloids, nutrient stress, etc.) are basically severe menaces to global agriculture, which restrict the crop plants to reach their full genetic potential and cause significant yield losses worldwide. The changing climatic conditions are further enhancing the severity of abiotic stress, making them even worse.

It has been estimated that salinity and/or drought significantly affects >10% of agriculturally cultivable land, which leads to ~50% reduction in crop productivity globally [1–3]. Stresses are complex and multigenic traits that affect the plant performance significantly by reducing the growth, development, and, ultimately, the final produce. To counteract the adverse effect of environmental insults, plants have evolved efficient defense mechanisms by manipulating their tolerance potential through integrated molecular and cellular responses. In general, the defense machinery involves the activation of stress-inducible genes and their products, which are either functional or regulatory in nature to ascertain direct stress tolerance or through the downstream signal transduction pathway. It is well established that certain stress hormones such as abscisic acid (ABA) also play a pivotal role in the mediation of stress responses in plants. However, plants respond to various stresses through ABA-independent and ABA-dependent pathways [3]. Therefore, it is desirable to understand the physiological and molecular aspects of plant functions under stressful conditions: for example, the activation of cascades of molecular networks (perception of stress signals, transducers, transcription regulators, target stress-related genes, and metabolites). Employing genetic engineering techniques to overcome the load of abiotic stress factors seems to be a promising tool [4]. The present article on abiotic stress signaling in plants focuses on stress signaling and stress responses in plants.

## 1.2

### **Perception of Abiotic Stress Signals**

Being sessile, plants have to encounter various environmental insults. For their survival, plants have evolved comprehensive defense mechanisms that help them to tolerate stresses through physical adaptation and/or by means of integrated molecular and cellular responses. To face the environmental challenge in the form of various abiotic stresses, perception of stress signals and their transduction is a very crucial step for switching on adaptive responses to ensure the survival of plants. Recent studies have revealed that understanding signal perception and its transduction is crucial for engineering stress tolerance in crop plants.

## 1.3

### **Abiotic Stress Signaling Pathways in Plants**

In nature, tolerance and survival of plants are achieved by their capacity to make their responses flexible to environmental cues. In turn, the plant stress response flexibility is governed by the signaling pathways, interwoven at cellular and molecular levels [5]. In fact, the perception of abiotic stress initiates the signals that trigger downstream signaling processes and transcription controls and notify parallel pathways [1, 6]. In the signal transduction pathway, as a first step, perception of the signal is performed by receptors/sensors such

as phytochromes, histidine kinases, receptor-like kinases, G-protein-coupled receptors, hormones). Second, the generation of secondary signaling molecules such as inositol phosphatase, reactive oxygen species (ROS), and abscisic acid (ABA) is accomplished. Subsequently, the secondary molecule-mediated modulation of intracellular  $\text{Ca}^{2+}$  level takes place, which in turn causes the initiation of protein phosphorylation cascades (i.e., mitogen-activated protein kinase (MAPK), calcium-dependent protein kinase (CDPK), protein phosphatase, SOS3/protein kinase S, etc.), transcription factors (TFs), and stress-responsive genes [7, 8]. Nevertheless, in order to genetically engineer stress tolerance traits in plants, a good understanding of both the endpoints and the specificity of the signaling pathways is necessary [9–11]. Considering the basic concepts and the recent breakthroughs, the following subsections briefly provide an overview of the significance of ROS, TFs, calcium and calcium-regulated proteins, and MAPK cascades in signaling pathways in abiotic-stressed plants.

### 1.3.1

#### Reactive Oxygen Species

ROS and its reaction products are among the most significant second messengers that actively participate in stress signal transduction [8]. ROS and its reaction products have been credibly evidenced to play a significant role in cell signaling, redox-sensing mechanisms, and plant survival under abiotic stresses [12–16]. ROS can help plants in their acclimatization/tolerance to stress as well as in signaling. A number of workers [17–22] have considered  $\text{H}_2\text{O}_2$  as an active signaling molecule in plants, where a variety of cellular responses are accomplished due to redox-sensing-mediated  $\text{H}_2\text{O}_2$  accumulation. Though little information is available on ROS-mediated induction of the redox-sensing mechanisms and the associated signaling pathways, the contribution of ROS-induced signaling in the activation of defense genes and subsequent stress tolerance/specific acclamatory responses has been widely accepted [23–27]. The role of ROS-caused lipid peroxidation products [17, 28] and of alkoxy radicals and peroxy radicals [29] in the activation of genes has also been reported. Researchers including [30–32] provided the clues in support of  $\text{H}_2\text{O}_2$  as a central metabolite and diffusible signal that has the capacity to induce a number of defense genes. Reports are also available on the signaling role of ROS in systemic acclimation to photooxidative stress [18, 30, 33, 34] and chilling stress [18, 35].  $\text{H}_2\text{O}_2$  and  $\text{O}_2^-$  are involved in the signaling events that lead to the variation of the transcript levels of Cu/Zn-SOD in pea (*Pisum sativum*) plants under Cd stress [36]. Information on the  $\text{H}_2\text{O}_2$ -mediated enhanced stress tolerance is also available [37–41].  $\text{H}_2\text{O}_2$  originating from apoplastic polyamine oxidase has been evidenced to play a role in balancing the plant response between stress tolerance and cell death [42]. Relationship between ABA-regulated stomata closure and the generation of  $\text{H}_2\text{O}_2$  has also been observed [43]. Involvement of  $\text{H}_2\text{O}_2$  in signal transduction events as a result of its role in the modulation of proline level was reported by Yang *et al.* [44] in maize (*Zea mays*) seedlings. Recently,  $\text{H}_2\text{O}_2$  pretreatment was evidenced to increase

enzymatic and nonenzymatic antioxidants in four *Digitalis* species (*D. lamarckii*, *D. trojana*, *D. davisiana*, *D. cariensis*) [45]. Information regarding the dynamics and specificity of ROS signaling, the significance of ROS as signaling molecules in cells, and the integration of ROS with other signaling pathways within and across different cells can be found elsewhere [46].

### 1.3.2

#### Transcription Factors

TFs are regulatory proteins and are among the major master regulators of abiotic stress responses in plants [47, 48]. In principle, to tolerate potential stress impacts, plants first recognize stress cues and subsequently transduce the signals to activate adaptive responses and regulate stress-related genes mainly at the transcriptional level [10, 49]. Nevertheless, ~7% of the plant genome-coding sequences, comprising mainly TFs, are immediate-early abiotic stress-responsive genes [50, 51]. TF-mediated regulation of plant signaling and regulatory pathways of stress adaptation have been widely reported [52]. Devotion of a large portion of genome capacity to transcription has been evidenced in plants [53]. Owing to the involvement of TFs in almost all biological processes, TFs have been considered significant for the generation of stress-tolerant crops [54]. TF genes fall under large gene families such as APETALA 2/ethylene-responsive element-binding factor (AP2/ERF), HSE, basic leucine zipper (bZIP), myelocytomatosis oncogene (MYC)/myeloblastosis oncogene regulon (MYB), nuclear factor Y (NFY), NAC, WRKY, Cys2His2, MADS-box, and zinc finger. Literature is full of information on the regulatory role of the previous TF gene families in the expression of stress-responsive genes [54–56].

NAC family TFs are TFs containing the NAC domain, namely, NAM (no apical meristem), ATAF1-2, and CUC2 (cup-shaped cotyledon) [57, 58]. Hu *et al.* [59] reported the exhibition of a highly conserved N-terminal DNA-binding domain and a diversified C-terminal domain in NAC family TFs. In Arabidopsis, Tran *et al.* [60] identified the cis element of NAC TF (NAC-recognized sequence (NACRS)). Rice and Arabidopsis were reported to harbor, respectively, 149 and 106 NAC family TFs [61, 62]. The role of NAC family TFs in the modulation of plant abiotic stress responses has been reported in a number of plants including rice (ONAC045 [63]; OsNAC5, OsNAC6 [64], and OsNAC10 [65]; Arabidopsis (ANAC019, ANAC055, ANAC072 [60]); Brassica (BnNAC [66]); and soybean (GmNAC2, GmNAC3, and GmNAC4 [67]). More than 10 groups of bZIP TFs were reported in Arabidopsis [68], and most of them were reported to play a central role in ABA signaling [69, 70]. Reports on the significance of bZIP TFs as regulators of plant stress responses are available [71–75]. WRKY TFs compose one large family of regulatory proteins in plants and are grouped into three based on the number of WRKY domains and the features of the associated zinc finger-like motif [76]. Information is also available on the origin of WRKY TFs in eukaryotes and expansion in plants [77] and plant abiotic stress responses and immunity [70, 78–82]. In particular, WRKY-mediated ABA signal transduction has been

extensively reported in plants [70, 83]. The significance of Cys2His2 zinc finger (C2H2 ZF) TFs [84–86], NFY [87, 88], dehydration-responsive element (DRE)/C-repeat (CRT) proteins [89, 90], and dehydration-responsive element binding (DREB) and APETALA2/ethylene-responsive (AP2/EREBP) TFs [91, 92] in plant responses to environmental stress factors has also been extensively reported.

### 1.3.3

#### Calcium and Calcium-Regulated Proteins

Calcium ion ( $\text{Ca}^{2+}$ ) is among the many chemicals involved in plant growth and development as well as in signal transduction pathways. In plant stress signal transduction pathway,  $\text{Ca}^{2+}$  serves as a very important ubiquitous second messenger and regulates many physiological processes [93–96]. Environmental cues such as cold [41] and water and heat stress [97, 98] were earlier reported to  $\text{Ca}^{2+}$  levels.  $\text{Ca}^{2+}$  channels, pumps, and exchangers (carriers) control the plant  $\text{Ca}^{2+}$  homeostasis maintenance under a variety of stimuli through the regulation of diverse  $\text{Ca}^{2+}$  transport systems [8, 96, 99]. In addition, reduction in  $\text{Ca}^{2+}$  mobility, localization, and spatial concentration elevations are facilitated by the abundance of buffering calcium-binding proteins, also known as  $\text{Ca}^{2+}$  sensors [100, 101].  $\text{Ca}^{2+}$  sensor groups, namely, sensor relays (proteins such as calmodulin (CaMs), calcineurin B-like (CBL)) and sensor responders, that is, sensor protein kinases (such as CDPKs, calcium and calmodulin-dependent protein kinases (CCaMKs)) lack any intrinsic enzymatic activity, directly activated upon  $\text{Ca}^{2+}$  binding, decode cellular  $\text{Ca}^{2+}$  signals, and transmit the  $\text{Ca}^{2+}$ -induced modification to target proteins [93, 96, 99, 102]. In soybean, DeFalco *et al.* [103] reported the coding of many  $\text{Ca}^{2+}$  sensors by multiple genes that are induced by stresses. Luan *et al.* [104] and Yang and Poovaiah [105] reported touch-, cold-, heat shock-, or salinity-mediated induction of both CaMs and CMLs. Stress-dependent role of CaM3 has been evidenced in plants, where both a negative role of CaM3 in cold signaling and positive regulation of salt tolerance due to GmCaM4 can be evidenced in the same plant such as Arabidopsis [106, 107]. Majority of putative CaM-binding protein genes (CaMBPs) identified in Arabidopsis (about 100 numbers) belong to multigene families, and some of them are induced by salinity, drought, or cold [108]. In higher plants, there exists a relationship between  $\text{Ca}^{2+}$  signaling and blue light receptor phototropin-mediated regulation of plant growth and development [109] and the sucrose-signaling pathway [110].

### 1.3.4

#### MAPK Cascades

The MAPK cascade is one of the major significant stress signaling pathways for intra- and extracellular signal transduction in plants where it connects diverse receptors/sensors to cellular and nuclear responses [111, 112]. In MAPK cascades, a series of subfamilies (i.e., MAP4K, MAP3K, MAP2K, MAPK) are sequentially activated as a result of different environmental stimuli that in turn cause

the activation of TFs, phospholipases or cytoskeletal proteins, microtubule-associated proteins, and the expression of specific sets of genes [113–117]. In contrast to the occurrence of only three large families (i.e., ERK, JNK, p38 family) in animals, a large family exists in plant MAPK cascades. For example, in *Arabidopsis* genomes, MAPK nomenclature has already identified a unified nomenclature of four classes of MAPK, namely, 23 MAPKs, 10 MAP2Ks, 80 MAP3Ks, and 10 MAP4K [118–120]. A high substrate specificity is known in the MAPK cascade, where the regulation of signaling location, specificity, and duration of MAPK is performed by scaffolding proteins and MAPK phosphatases [121]. The role of MAPK in plant immunity has been accepted [122], where a variety of (abiotic) stress responses were reported to be involved in MAPK signaling [114, 123]. In addition to the role of cold, salinity, and drought [124–130], Cd and Cu have also been reported to induce the activation of MAPK [131–133].

#### 1.4

#### Conclusions, Crosstalks, and Perspectives

A complicated interplay of signaling cascade is adopted by abiotic-stressed plants in order to perceive, amplify, and transmit stress signals and, finally, to trigger stress responses. ROS, TFs,  $\text{Ca}^{2+}$  and  $\text{Ca}^{2+}$ -regulated proteins, and MAPK cascades have been credibly evidenced to play a significant role in plant abiotic stress signaling pathways. There exists a high integration between ROS signaling with hormonal signaling networks processing and transmitting environmental stresses [46, 134, 135]. Hormonal signals are also known to induce changes in cytosolic  $\text{Ca}^{2+}$  [136]. In the context of  $\text{H}_2\text{O}_2$  homeostasis in plants, in particular, CaM may induce  $\text{H}_2\text{O}_2$  production (by activating NAD kinase) [137] and may also induce  $\text{H}_2\text{O}_2$  detoxification by activating the catalase AtCat3 [138]. The activation of MAPK in plants has also been reported to be elicited by  $\text{H}_2\text{O}_2$  [139–144]. Nevertheless, involvement of  $\text{Ca}^{2+}$ -dependent MAPK pathways in signaling of abiotic stress in plant cells is also known [145]. Though much has been achieved in the context of plant abiotic stress signaling pathways, efforts should be made with the aid of powerful molecular tools, including transcriptome and proteome analyses, to get more insights into molecular mechanism(s) underlying ROS and  $\text{Ca}^{2+}$  sensing and signal transduction. Additionally, the research on abiotic stress signaling pathways will be benefited by shedding more light on the interplay between  $\text{Ca}^{2+}$  and MAPK signaling pathways.

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