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Response of Abiotic Stress through Signaling in Plants: A Review

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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Review Article

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Abstract

This review explores the key components of abiotic stress signaling, including stress perception, secondary messengers like calcium ions and reactive oxygen species (ROS), and the central role of phytohormones such as abscisic acid (ABA). Abiotic stress is the adverse effect of any abiotic factor on a plant in a given environment, affecting its growth and development. Abiotic stresses, such as

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low or high temperature, deficient or excessive water, high salinity, heavy metals, and ultraviolet radiation, are hostile to plant growth and development, leading to great crop yield penalty worldwide. Abiotic stresses such as drought, salinity, extreme temperatures, and nutrient deficiencies adversely affect plant growth and productivity. Plants have evolved sophisticated signaling mechanisms to perceive, respond, and adapt to these environmental challenges. Plants respond to these stresses through intricate signaling networks that integrate external stimuli and coordinate adaptive responses. Key signaling pathways involve phytohormones like abscisic acid (ABA), salicylic acid (SA), jasmonic acid (JA), and ethylene, which regulate gene expression and physiological processes. Additionally, secondary messengers such as reactive oxygen species (ROS), calcium ions (Ca^{2+}), and nitric oxide (NO) play crucial roles in stress perception and signal transduction. Cross-talk between these signaling pathways ensures a robust response, enabling plants to maintain homeostasis, activate stress-specific genes, and promote survival. The dynamic cross-talk between signaling pathways enables plants to integrate multiple stress signals, while transcriptional and post-transcriptional regulation fine-tune stress responses. Emerging insights into epigenetic modifications reveal their role in stress memory, providing an adaptive advantage. These signaling networks offer promising targets for genetic engineering and crop improvement to enhance resilience against abiotic stresses. Understanding the intricacies of these mechanisms is crucial for developing sustainable agricultural practices in the context of climate change.

Keywords: Abiotic stress; signaling; phytohormones; epigenetic modifications; reactive oxygen.

1. Introduction

The responses of plants to stress factors are extremely elaborate. These responses occur at multiple levels, ranging from alterations in the molecular processes to structural changes in both the underground and aboveground parts of plants. The development of a comprehensive response to stress by plants is preceded by the activation of an effective system of signals (Nykiel et al., 2023). Plants are constantly exposed to various abiotic stresses, including drought, salinity, extreme temperatures, heavy metals, and oxidative stress. These stresses adversely affect plant growth, development, and productivity (Yamaguchi-Shinozaki and Shinozaki, 2006; Zhu, 2016). Plants have evolved mechanisms to sense these environmental challenges and make adjustments to their growth in order to survive and reproduce. In this review, we summarized recent studies on plant stress sensing and its regulatory mechanism, emphasizing signal transduction and regulation at multiple levels (Zhang et al., 2023). To survive and adapt, plants have evolved intricate signaling mechanisms that allow them to perceive stress signals, transmit these signals within cells, and initiate appropriate physiological and molecular responses (Kaur and Asthir, 2017; Yang et al., 2021). Recent progress in our understanding of the molecular mechanisms underlying the responses of plants to abiotic stresses emphasizes their multilevel nature; multiple processes are involved, including sensing, signalling, transcription, transcript processing, translation and post-translational protein modifications. This improved knowledge can be used to boost crop productivity and agricultural sustainability through genetic, chemical and microbial approaches (Liu et al., 2024). Abiotic stress signaling begins with the perception of stress. Plants use specialized receptors and sensors located on the plasma membrane, cytoplasm, or organelles to detect environmental changes (Zhang et al., 2022). Key components involved in stress perception include, Receptor-like kinases (RLKs) which detect extracellular signals like osmotic changes or salt ions, ion channels also perceive ionic imbalances caused by stresses such as salinity or drought and reactive oxygen species (ROS) serve as both a signal and a stress byproduct, triggering downstream responses (Takahashi et al., 2020; Skalak et al., 2021). Once a stress signal is perceived, it is transduced through a series of interconnected pathways involving secondary messengers, protein kinases, and transcription factors (Tahir et al., 2020). Major components include *viz*., calcium ions (Ca^{2+}) which spike transiently in response to stress and the spatiotemporal pattern of these spikes acts as a stress-specific signal. Reactive oxygen species (ROS) also act as signaling molecules, modulating stress responses through redox-sensitive pathways and nitric oxide (NO) plays a role in modulating antioxidant defences and other stress responses. Phytohormones like abscisic acid (ABA), ethylene, salicylic acid (SA), jasmonic acid (JA), and gibberellins regulate specific stress responses (Farooq et al., 2009, Prasad et al., 2011). Protein Kinase Cascades such as Mitogen-Activated Protein Kinases

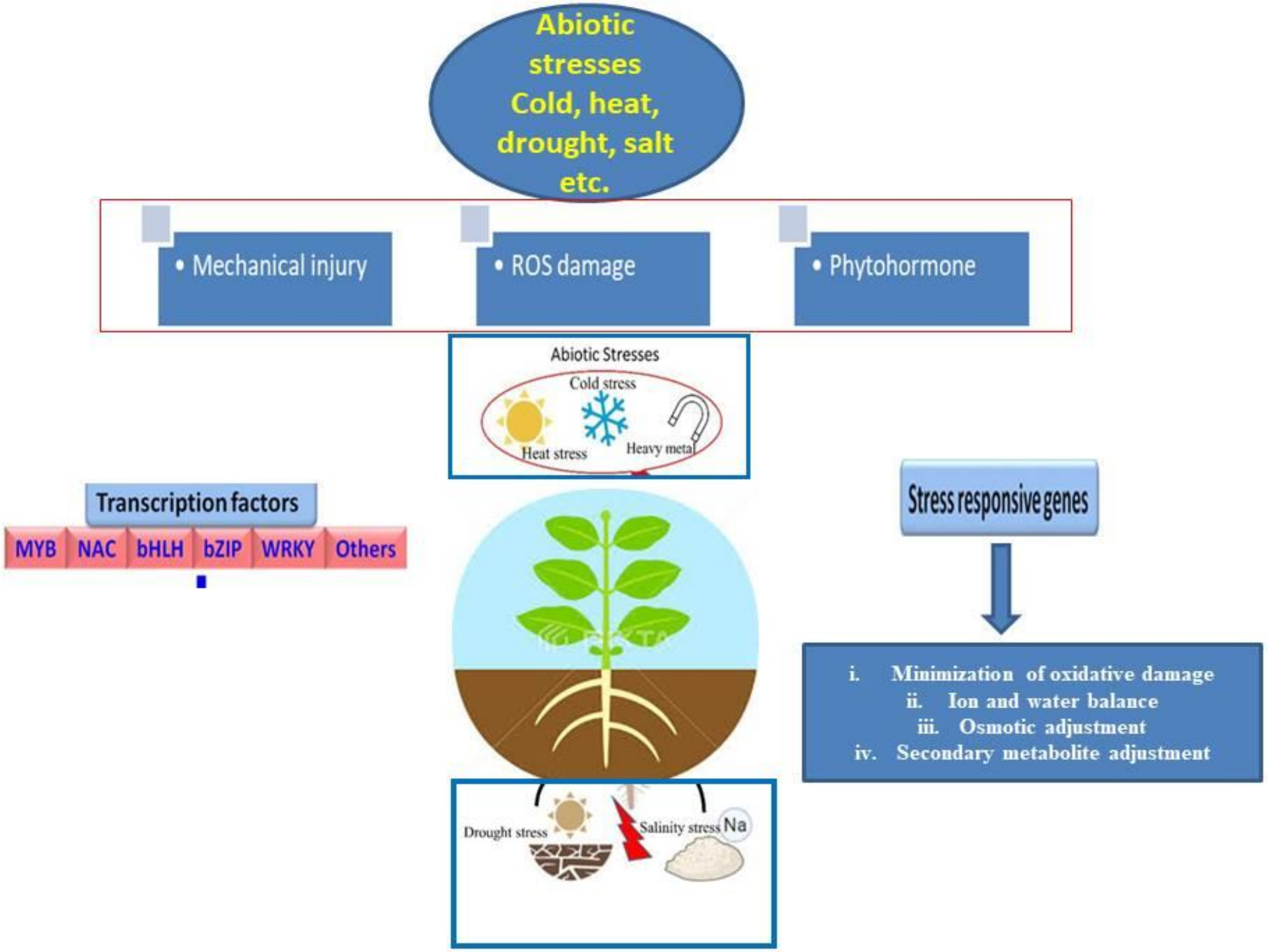

Fig. 1. Abiotic stress response in plants

(MAPKs) phosphorylate downstream targets, amplifying stress signals. Calcium-dependent protein kinases (CDPKs) interpret Ca^{2+} signals and activate specific responses (Pandey, 2020). SNF1-related protein kinase 2 (SnRK2) is central regulator of ABA-mediated responses (Hirt, 1997; Mizoguchi et al., 1996; Williams et al., 2019). Transcription factors regulate stress-responsive gene expression. Some key families include: DREB (Dehydration-responsive element-binding) proteins that regulate drought and cold stress responses. NAC and WRKY families: Modulate oxidative and abiotic stress tolerance. bZIP (Basic Leucine Zipper) which is involved in ABA-dependent signaling (Singh and Chamovitz, 2019). Signal transduction leads to the activation of stress-responsive genes, which encode: Protective proteins such as heat-shock proteins (HSPs), late embryogenesis abundant (LEA) proteins and dehydrins. Enzymes for detoxification acts as antioxidant enzymes like superoxide dismutase (SOD), catalase (CAT), and peroxidases (POD) to mitigate ROS damage (Junsheng et al., 2018). Osmoprotectants produces synthesis of proline, glycine betaine, and trehalose helps maintain cellular osmotic balance (Nimma et al., 2017). Phytohormones play a critical role in coordinating stress responses. For instance, ABA is a central regulator of drought and salinity responses, modulating stomatal closure and gene expression, ethylene mediates responses to oxidative and hypoxic stress and SA and JA are involved in cross-talk between biotic and abiotic stress responses (Schwarz and Bauer, 2020). Stress signals often propagate systemically to initiate a long-term adaptation which includes epigenetic modifications viz., DNA methylation, histone modifications, and chromatin remodeling alter gene expression patterns to adapt to stress (Muhammad et al., 2022). Systemic acquired acclimation (SAA) transmits signals to distant tissues to prepare them for potential stress. Abiotic stress signaling pathways often overlap, allowing plants to mount integrated responses to multiple stresses. For example, ROS production triggers Ca^{2+} signaling, and vice versa, creating feedback loops (Sierla et al., 2016; Junsheng et al., 2018). Hormonal cross-talk like ABA, SA, and ethylene pathways interact to fine-tune stress responses (Zandalinas et al., 2020). Abiotic stress signaling in plants is a complex and dynamic process involving precise sensing, signal transduction, and response activation (He et al., 2018; Scott and Ron, 2020). These pathways ensure that plants adapt to environmental changes while maintaining growth and reproduction. A deeper understanding of these mechanisms can inform strategies to develop stress-resilient crops and enhance agricultural productivity (Nishiyama et al., 2013; Osakabe et al., 2014) (Fig. 1).

2. Key Signaling Pathways are

Stress Perception and Early Signaling Events: Plants detect abiotic stress through specialized receptors located on the cell membrane, such as receptor-like kinases (RLKs) and ion channels. These receptors sense external stimuli and trigger intracellular signaling cascades. For instance, in response to drought, osmotic stress is perceived, leading to the activation of calcium ion channels, generating calcium signatures that act as secondary messengers. Similarly, salinity stress is sensed by membrane proteins such as the Salt Overly Sensitive (SOS) pathway components (Mori and Schroeder, 2004).

Role of Hormones in Stress Signaling: Plant hormones like abscisic acid (ABA), ethylene, jasmonic acid (JA), and salicylic acid (SA) play critical roles in abiotic stress signaling. ABA is central to drought and salt stress responses, mediating stomatal closure and regulating stress-responsive gene expression (Narusaka et al., 2003). The interplay of ABA with other hormones like gibberellins (GAs) and auxins fine-tunes the plant's growth versus stress tolerance trade-off.

Reactive Oxygen Species (ROS) and Antioxidant Networks: Abiotic stress often results in the overproduction of ROS, which acts as both damaging agents and signaling molecules. Controlled ROS production by NADPH oxidases like RBOHs and their scavenging by antioxidant systems (e.g., superoxide dismutase, catalase) ensures a balanced response (Mittler et al., 2011). ROS-mediated signaling activates transcription factors such as WRKYs and NACs, which regulate stress-responsive genes (Camejo et al., 2016).

Cross-Talk between Pathways: One of the most fascinating aspects of abiotic stress signaling is the cross-talk between pathways (Singh et al., 2016). Calcium signaling, ROS, and phytohormones often interact, creating a complex network that enables plants to prioritize and integrate multiple stress responses. For instance, calcium- and ROS-mediated signaling converge on MAPK (mitogen-activated protein kinase) cascades, amplifying stress signals and ensuring effective responses (Hai et al., 2020).

Transcriptional and Post-Transcriptional Regulation: Stress-responsive transcription factors, including DREB (Dehydration-Responsive Element-Binding), bZIP (basic leucine zipper), and MYB, regulate the expression of stress-protective genes. Additionally, small RNAs and RNA-binding proteins play significant roles in post-transcriptional regulation, fine-tuning gene expression during stress adaptation. Translation initiation is blocked under heat stress and mRNAs encoding ribosomal proteins (RP) are first stored. During the process of recovery, mRNAs are released and translated rapidly to resume translation, which is dependent on the chaperone protein HSP101 (Merret et al., 2017).

Epigenetic Modifications and Memory: It is evidence that epigenetic regulators, particularly histone deacetylases, are involved in the transcriptional regulation of COR genes (Chauhan et al., 2021). Recent studies highlight the importance of epigenetic modifications such as DNA methylation, histone modifications, and chromatin remodeling in abiotic stress responses. These modifications can create stress memory, enabling plants to respond more robustly to subsequent stress events. In Arabidopsis, RNA demethylase ALKBH9B and ALKBH10B were demonstrated to modulate ABA response via regulating the mRNA m6A level (Shoaib et al., 2021; Tang et al., 2021).

3. Application of Abiotic Stress Signalling in Crop Improvement

Abiotic stress signaling plays a crucial role in crop improvement by enhancing plant resilience to environmental stresses such as drought, salinity, temperature extremes, and nutrient deficiencies. By understanding and manipulating the molecular and physiological responses of plants to these stresses, scientists can develop stress-tolerant crop varieties with improved yield and sustainability. Abiotic stress signaling is applied in crop improvement are illustrated below.

3.1 Genetic Engineering and Biotechnology

- **Transgenic Approaches:** Genes related to stress tolerance (e.g., DREB, HSPs, NHX1) are introduced into crops to enhance their ability to withstand drought, heat, or salinity.
- **CRISPR-Cas9 Gene Editing:** Precise modifications in stress-responsive genes help in developing stress-tolerant plants (Tahir et al., 2020).

3.2 Marker-Assisted Breeding (MAB)

- Identifying and using molecular markers linked to stress-tolerance genes speeds up breeding programs to develop resilient crop varieties. Example: Salt-tolerant rice varieties developed using Saltol QTL (Quantitative Trait Locus) (Muhammad et al., 2022).

3.3 Hormonal Regulation for Stress Adaptation

- **Abscisic Acid (ABA):** Enhances drought and salinity tolerance by regulating stomatal closure and gene expression. Salicylic Acid and Jasmonic Acid Improve plant defense against oxidative stress (Merret et al., 2017).

3.4 Microbial and Biostimulant Applications

- Plant Growth-Promoting Rhizobacteria (PGPR) and mycorrhizal fungi enhance nutrient uptake and stress resistance. Silicon and proline applications improve plant tolerance to drought and salinity (Narusaka et al., 2003).

3.5 Omics Approaches for Stress-Resilient Crops

- **Genomics**: Identifies stress-responsive genes for breeding programs.
- **Proteomics and Metabolomics:** Understand stress-responsive proteins and metabolites involved in plant defense mechanisms (Williams et al., 2019).

3.6 Climate-Smart Agriculture

Development of stress-resilient crops like drought-tolerant maize and heat-resistant wheat ensures food security under changing climate conditions (Yang et al., 2021).

Table 1. Applications of abiotic stress signaling in different crops

Abiotic Stress	Signaling Pathway	Mechanism of Action	Application in Crop Improvement
Drought	Abscisic Acid (ABA)	Stomatal closure, osmotic adjustment, activation of stress-responsive genes	Development of drought-resistant crops with enhanced water-use efficiency (e.g., transgenic rice, wheat)
Salinity	Salt Overly Sensitive (SOS) Pathway	Ion homeostasis, exclusion of Na^+, production of osmoprotectants	Breeding and genetic engineering of salt-tolerant crops like salt-resistant rice and wheat
Heat Stress	Heat Shock Proteins (HSPs)	Protein stabilization, prevention of aggregation, repair of damaged proteins	Developing thermotolerant crops like heat-resistant wheat and maize
Cold Stress	CBF (C-repeat Binding Factor) Pathway	Upregulation of cold-responsive genes (COR), membrane stabilization	Engineering cold-tolerant crops such as winter wheat and cold-resistant tomatoes
Flooding/Hypoxia	Ethylene and ROS Signaling	Formation of aerenchyma, induction of anaerobic metabolism, scavenging of ROS	Breeding submergence-tolerant rice varieties (e.g., SUB1 rice)
Nutrient Deficiency	Phosphate Starvation Response (PHR)	Enhanced root architecture, phosphate transporter activation	Development of nutrient-efficient crops with improved uptake efficiency
Heavy Metal Toxicity	Metallothioneins, Phytochelatins	Detoxification by chelation, sequestration of metals into vacuoles	Engineering heavy metal-tolerant crops for phytoremediation and safe food production

4. Practical Applications

Understanding signaling pathways in abiotic stress responses has practical implications for agriculture. Genetic engineering and breeding strategies targeting key components like transcription factors, ROS regulators, and hormone biosynthesis genes have shown promise in developing stress-resilient crops.

5. Conclusion

Abiotic stress signaling in plants is a highly dynamic and integrated process involving diverse molecular players. Advances in systems biology, genomics, and proteomics are enhancing our understanding of these networks, paving the way for innovative strategies to improve plant resilience to environmental stresses. However, further research is needed to unravel the intricate cross-talk mechanisms and translate laboratory findings into field applications effectively. This review underscores the importance of signaling in plant adaptation to abiotic stress to address global food security.

Disclaimer (Artificial Intelligence)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of this manuscript.

Competing Interests

Authors have declared that no competing interests exist.

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