Plant Stress Responses

Edited by

Muhammad Waseem, Pingwu Liu and Guangsheng Yang

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2025

Ethics International Press, UK

British Library Cataloguing in Publication Data

A catalogue record for this book is available from the British Library

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ISBN (Hardback): 978-1-80441-830-7
ISBN (Ebook): 978-1-80441-831-4

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Preface

Plants continuously face a variety of environmental challenges—ranging from drought, salinity, cold, and heat to attacks by pathogens—that threaten their growth, development, and productivity. As climate change intensifies, the frequency and severity of these stressors are increasing globally, making it essential to understand the intricate molecular, biochemical, and physiological mechanisms that govern plant stress responses. This book, *Plant Stress Responses*, is a collective effort of distinguished scientists and early-career researchers to provide an in-depth exploration of how plants perceive, transduce, and adapt to both abiotic and biotic stresses.

The opening chapter by **Dr. Muhammad Kaleem** and co-authors lays the theoretical foundation of plant stress biology, focusing on *Signal Perception and Transduction*. It highlights the critical role of calcium signaling, transcription factors, and hormonal crosstalk in coordinating responses to temperature extremes, drought, salinity, and pathogen invasion. The authors also discuss how pattern recognition receptors (PRRs) and NBS-LRR proteins activate plant immune responses through pattern-triggered and effector-triggered immunity.

Building on this, **Dr. Tahira Noor** and her team contribute a highly relevant chapter on *Marker-Assisted Selection (MAS)* and its role in breeding for abiotic stress resilience. This chapter provides a clear overview of how molecular tools such as SSRs and SNPs have enhanced precision in selecting traits linked to stress tolerance in major crops like rice, wheat, and maize. It also introduces emerging techniques like genomic selection and high-throughput phenotyping that are reshaping crop improvement strategies.

The third chapter, *Metabolic Adjustments to Abiotic Stress Tolerance*, by **Tauqeer Ahmed Qadri** and colleagues, presents detailed mechanisms by which plants reprogram their metabolism to maintain cellular homeostasis. The accumulation of osmolytes such as proline and glycine betaine, the activation of antioxidant systems, and the regulation of energy pathways are emphasized, with real-world case studies demonstrating the success of metabolic engineering in improving crop tolerance.

The hormonal basis of stress adaptation is explored in *Hormonal Regulation of Abiotic Stress Responses*, where the authors dissect the signaling roles of abscisic acid (ABA), jasmonic acid (JA), salicylic acid (SA), ethylene, and cytokinins under various stresses. The chapter explains how these hormones interact, often antagonistically or synergistically, to balance growth and stress responses through key regulators like DELLA proteins and calcium signaling.

Salinity, a growing concern for global agriculture, is addressed in two chapters. **Dr. Ansa Asghar** and her team examine *Gene Expression Regulation Under Salinity Stress*, revealing how ion homeostasis, ROS signaling, and stress-responsive transcription factors are orchestrated to enhance tolerance. In *Salinity Stress: Adaptations and Tolerance Mechanisms*, the authors discuss structural and physiological adaptations such as sodium compartmentalization, the SOS signaling pathway, and the importance of omics technologies in understanding stress tolerance complexity.

Cold stress, another major abiotic factor, is analyzed in two interconnected chapters by **Ch. Aruna Kumari** and collaborators. The chapter on *Calcium Sensing Networks* illustrates how plants use calcium-binding proteins and transcription factors to mediate cold-responsive gene expression, while the subsequent chapter details the interplay between calcium signals and ABA in orchestrating cold stress responses.

The final chapter, *NBS-LRR Proteins: Key Players in Plant Immunity*, authored by **Dr. V. Ramya** and her team, emphasizes the structural, evolutionary, and functional diversity of resistance (R) genes. The chapter presents cutting-edge approaches such as RenSeq and CRISPR to engineer broad-spectrum resistance in crops and highlights the regulatory role of microRNAs in fine-tuning immune responses.

This book is the result of a collaborative spirit and scientific commitment among scholars from various institutes across Pakistan, India, Turkey, and beyond. Each chapter offers a unique perspective, collectively contributing to a comprehensive understanding of plant adaptation in the face of stress. We sincerely thank all the contributors for their scholarly work and dedication. Special appreciation goes to our institutions for supporting this endeavor, and to our families for their unwavering encouragement.

We hope that *Plant Stress Responses* will serve as an essential resource for researchers, postgraduate students, and educators in plant science, crop biotechnology, and environmental biology. We trust it will inspire future innovations aimed at developing resilient crops for sustainable agriculture.

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Chapter 1

Signal Perception and Transduction in Plant Stress Responses

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Abstract

Plant stress responses in adverse environmental conditions are important for the survival and productivity of plants. Abiotic stresses like extreme temperatures, salinity and drought interrupt the balance of water, ionic homeostasis and photosynthetic efficacy which result in agriculture losses. While the biotic stresses like pathogen infections initiate the immune responses. Plants adopt strategies and mitigate these stresses through signal perception and transduction pathways including secondary messengers, protein kinases and transcription factors. Hormonal interaction, particularly between jasmonic acid (JA), abscisic acid (ABA) and salicylic acid (SA) governs the regulatory response to concurrent stresses. The significance of stress memory and epigenetic modifications in promoting resilience is becoming more

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important. Drought and salinity impede osmotic equilibrium and photosynthesis, and thus making salinity osmoregulation a necessity. Pattern recognition receptors and nucleotide binding leucine rich repeat proteins are used in biotic stress techniques such as effector triggered immunity and pattern triggered immunity for immune system activation and detection of pathogens. Research that presents how genetic and molecular techniques can improve crops stress tolerance is demonstrated. In sum, this chapter shows the importance of understanding stress circumstances in which plants are living and provides valuable insights for stress resilient agriculture techniques.

Introduction

As the population demand rises and the climate changes, a global food security can only be achieved when we understand depth of plants working to strengths across various conditions. The stresses associated with these events have a great influence on growth, development and production of plants. To overcome these issues, plants evolved systems which allow signal transduction pathways (STP), able to perceive, transmit and unify stress signals that lead to adaptive response (Huang et al., 2012; Lata et al.,2015, Ahmad et al., 2022).

Because of plant sessility, they are continuously confronted with a variety of environmental stresses that is a difficult hurdle for their achievement and overall output. The main causes of agriculture losses worldwide are abiotic stressors (basically the future of agriculture losses) such as salt stress and temperature stress. Since these stresses often lead to osmotic imbalances, ion toxicity and oxidative damage on a cellular level, well built adaptive mechanisms to these stresses have to be generated (Huang et al., 2012). Complex signaling networks carried out immune responses to different biotic stresses, such as bacterial, viral, and fungal infections (Verma et al., 2013, Ahmad et al., 2024). This knowledge of these processes is important so that stress tolerant crops can be created and agricultural productivity improved in difficult situations. This redeems because primarily, abiotic stresses, such as drought, salt and extreme temperatures, disrupt the plant water balance and ionic homeostasis through specific and even associate signaling pathways. Salt Overly Sensitive (SOS) keeps the cellular homeostasis and participates in ion transport regulation. Salt Overly Sensitive (SOS) is known to be regulated in response to ionic stress, mostly through modulation of ion transport, thus it is a SOS pathway responsible for the inactivation of ionic stress, hence the preservation of cellular ion homeostasis (Chinnusamy et al., 2004). Similarly, the ICE-CBF-COR signalling cascade is triggered by the cold stress to change gene expression order to make the plants freezing tolerant (Xiong and Zhu, 2001, Ali et al., 2022).

Plants are in contact with biotic stressors by means of intricate relationships with other living things. Plants have developed sophisticated immune system that works in phases to detect and fight the illnesses. In the presence of both abiotic and biotic stimuli, the hormonal interactions, predominantly between ABA, JA and SA, are necessary to maintain plant development balance with defence systems (Ku et al., 2018). Plants sense signals in order to identify both interior and exterior stimuli necessary to produce adaptive responses necessary for life and growth. Many environmental cues are sensed by plants through a variety of receptors that respond to light, temperature, presence of pathogens and mechanical forces. Receptor-like kinases (RLKs) respond to a number of signals including pathogen defence systems; photoreceptors such as phytochromes are photoreceptors responsive to light to regulate growth (Batschauer, 1999).

Signal transduction systems are required for allowing plants to recognise and react to immediate stressors external. Sensors, secondary messengers, protein kinases and transcription factors are these mechanisms that coordinate a variety of biological processes that lead to stress adaptation. The calcium ions function as secondary messengers and play an important role in signalling pathways in stress response through calcium binding proteins such as Calmodulin (CaM). Modulation of downstream effectors is performed by these proteins to effect stress induced gene expression (Virdi et al., 2015). Cascades of mitogen activated protein kinase (MAPK) are the key for transduction of stress related signalling. The signalling proteins activate transcription factors in response to abiotic stresses (drought or salinity) and support such stress tolerant phenotypes (Nakagami et al., 2005, Asghar et al., 2024).

ABA is an essential modulator of plant reactions to abiotic stresses. In this way, via its signallig pathways, SnRK2kinases and PYR/PYL receptors, SnRK1 controls stomatal closure and gene expression. In order to modulate plant immunity, hormonal cross talk is essential. The antagonistic relationship between JA and SA pathways is the basis of effective pathogen immunity. This is because the nature of their interactions dictate how intense and specific the immune response is (Verma et al., 2016). Additionally, through MAPK pathways, reactive oxygen species (ROS) serve as both signal mediators of defence responses and harmful by-products (Huang et al., 2012). The same signalling components are used to integrate signals by MAPKs and by transcription factors. Through the combination of ABA and JA pathways, plants are able to focus on the difficult survival techniques needed to survive when the two types of stress occur simultaneously (Fujita et al., 2006, Haider et al., 2021).

Signal Perception

Two general classes of receptors activate the immune response in plants. First class they all share is cell surface pattern recognition receptors (PRRs) that detect the molecular signatures of pathogens (conserved pathogen associated molecular patterns [PAMPs]) and host (damage associated molecular patterns, DAMPs). This recognition mechanism activates pattern-triggered immunity (PTI) (Yu et al., 2017).Second group includes intracellular nucleotide-binding leucine-rich repeat receptors (NLRs) that recognize pathogen effectors directly or indirectly in the context of the plant cell act effectively and activate effector-triggered immunity (ETI) (Zhou and Zhang, 2020). While PRRs and NLRs exhibit variability in their structural architecture and subcellular localizations, they ultimately converge on common downstream defense pathways. Some of these mechanisms are Ca^{2+} influx; production of ROS; activation of mitogen-activated protein kinase (MAPK) signaling cascades; synthesis of defense-related hormones, such as ethylene and salicylic acid; generation of phytocytokines; and extensive transcriptional reprogramming (Ngou et al., 2022).

PTI and ETI are interconnected to each other and can positively reinforce each other (Ngou et al., 2021; Yuan et al., 2021).However, they show distinct response profiles. PTI responses are generally described by moderate and transient effects, while ETI mediates a more robust and long-lasting immune response, often coupled with a hypersensitive response (HR). HR is a localized programmed cell death that acts to restrict or kill pathogen. By dissociation of HR in terms of kinetics (HR is separated from apoptosis and changes in cellular viability) and genetics (HR is separated from apoptosis), it allows the separation of HR resistance and cellular apoptosis (Künstler et al., 2016).

Receptor-like kinases (RLKs)

Major elements of the immune response to pathogen associated molecular pattern (PAMPs) include PRRs, that are mostly constituted by RLKs and RLPs. Both types of the proteins are three folded sizes of molecular mass, possessing transmembrane regions as well as extracellular domain (ECD) and a cytoplasmic tail. The cytoplasmic tail of RLKs contains a kinase domain, whereas that of RLP has a shorter tail. For example, a well known is the leucine rich repeat receptor like kinase (LRR-RLK) Flagellin sensitive 2 (FLS2), that responds to bacterial PAMP fllg22 via its ECD. PEPR1 and PEPR2 aid in the identification of phytocytokines, such as Pep1 and related peptides, in Arabidopsis thaliana (Huffaker et al., 2006). RLCKs are integral signal intermediates downstream of PRRs, and receptors like cytoplasmic kinases (RLCKs). ACIK1 is an example of a PTI response that depends on Arabidopsis counterpart of tomato (BIK1, BOTRYTIS INDUCED KINASE 1). Raising the reactive oxygen species content for the immunological response depends on BIK1 to promote activation of respiratory burst oxidase homolog D (RBOHD) (Kadota et al., 2014; Liang and Zhou, 2018). A further function for BIK1 is in stomatal closure as well as general defence measures and BIK1 is also implicated in the induction of $Ca(2^+)$ channel activity, particularly cyclic nucleotide gated channels (Tian et al., 2019).

Ion channels

Ion channels are proteins that have been incorporated into the lipid bilayers of cellular membranes so that ions, in the absence of a gradient can be passively moved to communicate intracellular to extracellular environments through well-organized pore. All of these ion channels contribute to numerous physiological processes such as osmoregulation, movement, growth, signalling and the uptake of nutrients, in roots, as well as transport of these nutrients to aerial tissues through stems. Some immediate effects on ion channel activity occur while some factors, such as pH and Ca2+ also reside in the cytoplasm. Other factors, like interactions with kinases, phosphatases, or calmodulin, require post translational modifications of the channel protein or specific binding events to activate before they can affect channel activity, suggesting a more gradual regulatory mechanism. Exploration of ion channels in plants began with the identification of single-channel activity for potassium ions (K^+) in isolated guard cells (Schroeder et al., 1984).

G-protein coupled receptors (GPCRs)

Pharmacological studies from the late 1980s and early 1990s emphasized the pivotal role of G-protein signaling in plant systems (Fairley-Grenot and Assmann, 1991). However, much of our understanding of the molecular genetics underlying plant G-protein signaling stems from research on *Arabidopsis thaliana*. These proteins were initially characterized through gene cloning and expression analyses (Mason and Botella, 2001). Subsequent studies employing gene knockout and overexpression approaches for various components of the G-protein complex confirmed their essential roles in regulating numerous processes related to plant growth, development, and physiology. In Arabidopsis, the G-protein complex consists of one canonical Gα protein (GPA1), one Gβ protein (AGB1), and three Gγ proteins (AGG1, AGG2, AGG3). Detailed phenotypic analyses have revealed novel insights into the complexity of G-protein signaling in plants. Some responses follow conventional signaling mechanisms, where the knockout of either Gα or Gβ results in similar phenotypes. However, other responses exhibit greater complexity. For instance, specific traits like root biomass, stomatal density, and defense responses are antagonistically regulated by Gα and Gβ proteins. Additionally, some traits, such as silique morphology, are uniquely controlled by Gβ, while others such as leaf morphology, hypocotyl length, and responses to ABA display quantitative variations in their regulation (Wang et al., 2011).

Signal Transduction Pathways

Signal transduction mechanisms in plants are essential for their adaptation to various environmental stressors, such as low temperatures, water scarcity, high salinity, and mechanical disturbances. Distinct signalling pathways such as ICE-CBF-COR and Salt-Overly-Sensitive (SOS) facilitate the acclimatization of plants to cold and saline environments, respectively (Huang et al., 2011). Calcium ions and ROS serve dual roles as both harmful by-products and vital signaling molecules within the framework of stress responses (Xiong & Zhu, 2001).Mitogen-activated protein kinases (MAPKs) serve as important links between various stress response networks that increase plant tolerance to unfavorable environmental conditions (Nykiel et al., 2022). Additionally, the pathways that are responsive to ABA and the pathways which are non-responsive to ABA are crucial in mediating the responses to osmotic stress, thus combining the drought and salinity adaptation mechanisms (Solanke & Sharma, 2008). Plants can react appropriately to environmental stressors. This happens due to the unification of biotic and abiotic signalling pathways combined by hormones ABA, JA, and SA (Ku et al., 2018). Regulatory factors, such as the fast stress response element, have a significant impact on transcriptional reaction to mechanical and osmotic stress (Walley et al., 2007). By focusing on modifications in the signal transduction components, engineering strategies leverage this understanding of the pathways involved in stress responses to create crops that are resistant to stress (Xing & Jordan, 2000). Additionally, ion homeostasis and antioxidant defence systems under abiotic stress depend heavily on reactive oxygen specie signalling and hormone-to-hormone interactions (Kaur & Gupta, 2005, Haider et al., 2022).

The enzymes known as protein kinases are responsible for phosphorylation, a sort of post-translational modifications. The first phosphorylation of a target protein is necessary for its activation or inactivation. Significant types of protein kinases include: Mitogen-Activated Protein Kinases (MAPKs): In eukaryotes, the MAPK signaling pathways coordinate important cellular activities like proliferation, differentiation, and even stress responses. These pathways often involve a phosphorylation cascade that includes MAPK, MEK, and MEKK (Brown and Griendling, 2009). Calcium-Dependent Protein Kinases (CDPKs): Having their major occurrence in plant tissues, CDPKs transform calcium signals into cellular effects, playing an important role in pathogen defense, developmental and stress signaling (Wang et al., 2021). Plants respond to changes in the environment by altering the levels of phytohormones. In response to abiotic stress, ABA, JA, SA, and ethylene are produced. ABA stomata close during drought periods and induce drought resistance traits while JA and SA stimulate the plant to defend against biotic stresses (Adjei and Hidalgo, 2005).

Function of Transcription Factors under Stress Conditions

Activation of stress-responsive genes

Transcription factors are crucial in the regulation of stress response genes and modification of the stress response at the cellular level to environmental and physiological challenges. Some TFs like WRKY, NAC, DREB, and bZIP prominently engaged in specific gene activation when facing biotic and abiotic stresses. For example, the DREB (Dehydration Responsive Element-Binding) family binds DREB situated in the regulatory regions of stress-inducible genes, activating pathways to enable plant resilience under dehydration and cold stress (Sharma et al., 2015). Table 1.1 shows some of the precision diverse transcription factors from crops with varied biology that reduce the level of different stress types. Similarly, WRKY transcription factors are crucial in the defense response of plants by attaching to W-box sequences situated within the promoters of pathogenesis-related genes, consequently immune responses are activated during infections. The NAC family is fundamental for some responses connected with salinity, oxidative stresses, whereas bZIP factors control processes like sugar signaling, energy metabolism, and oxidative stress responses (Wang et al., 2021). Transcription factors help to strengthen and coordinate responses by integrating signals from the outside environment.

Transcription factors	Plants	Abiotic stress	References
ABF3	*Arabidopsis thaliana*	Drought	(Kang et al., 2002)
FtbZIP5	*Fagopyrum tataricum*	Salinity, Drought and oxidative	(Li et al., 2020)
FtbHLH2	*Fagopyrum tataricum*	Freezing	(Yao et al., 2018)
PebHLH35	*Populus euphratica*	Drought	(Dong et al., 2014)
OsNAC9	*Oryza sativa*	Drought	(Redillas et al., 2012)
TaRNAC1	*Triticum aestivum*	Drought	(Chen et al., 2018)
AhDREB1	*Arachis hypogaea*	Osmosis	(Zhang et al., 2018)
OsEREBP1	*Oryza sativa*	Drought, submergence	(Jisha et al., 2015)
GmERF3	*Glycine max*	Drought, Salinity, heat stress	(Zhang., et al. 2009)
OsMYB48-1	*Oryza sativa*	Salinity, Drought	(Xiong et al., 2014)
AtWRKY26	*Arabidopsis thaliana*	Heat	(Li et al., 2011)

Table 1.1 *Transcription factors that drive plant tolerance to abiotic stress.*

Epigenetic modifications during stress

Epigenetic modifications due to stressare important in precisely governing the expression of genes, which enable the organisms to adjust and survive in challenging environments. These changes include histone acetylation, DNA chromatin remodelling and chromatin remodelling, that could stimulate or hinder the genes that response to stress. For example, acetylation of histone at specific loci improves the availability of chromatin which enable transcription factors to fix more effectively and improves the development of stress responsive genes. In contrast methylation of DNA at the promoter sites could minimize non-essential processes maintaining important assets during stress conditions. Stress induced modifications normally target binding sites for the transcription factors like DREB, NAC and WRKY governing their function in a positive or negative way. Specifically, particular epigenetic changes can be inherited which result in a stress memory that could prepare plants or for future challenges (Ducibella and Fissore, 2008). This complex interaction of epigenetic modifications and transcription factors shows a complex regulatory mechanism which keeps the expression of genes stable in the face of alterations in the environment.

Drought stress and responses of plants

Drought conditions results in the decrease of water availability consequently decline in the turgor pressure occur that inhibits both photosynthetic processes and the long-distance transport of nutrients. For example severe drought, cellular desiccation incurs damage to membrane integrity and disrupts protein configurations, culminating in irreversible cellular impairment and subsequent cell mortality. In reaction to drought stress, plants deploy a diverse array of adaptive mechanisms (Levitt, 2015). Figure 1.1 shows the consequences of drought stress alongside the corresponding plant responses, which can be systematically divided into three principal strategies: escape, avoidance, and tolerance. Drought escape modifies the temporal framework of the life cycle, drought avoidance mitigates the loss of tissue water as soil moisture diminishes, and drought tolerance facilitates cellular viability under conditions characterized by low tissue water potential. Although the underlying mechanisms that govern drought escape exhibit variability across different species, this discourse primarily concentrates on avoidance and tolerance. Within the context of drought avoidance, stomata regulation assumes a pivotal role, whereas drought tolerance encompasses the activation of pathways for scavenging ROS, accumulation of protective compounds and augmented synthesis of compatible solutes (Zhang et al., 2022).

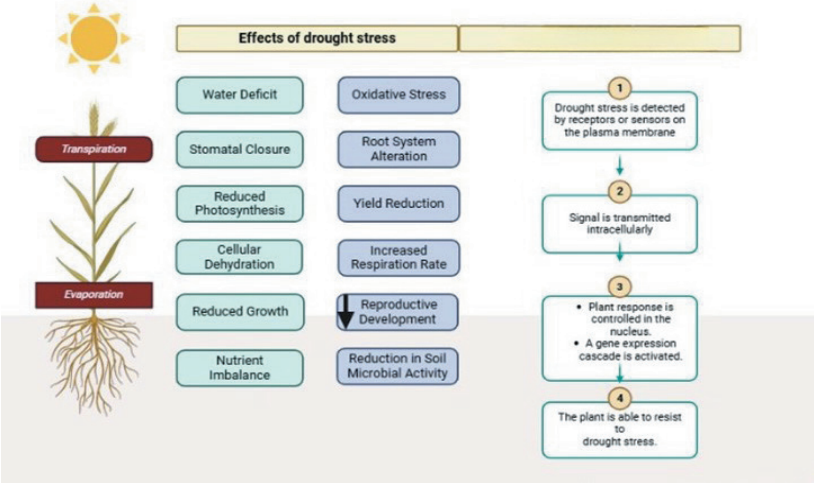

Figure 1.1 *Effects of drought stress and response of plants to drought stress.*

Photosynthetic response under drought stress

Carbon dioxide assimilation during the process of photosynthesis transpires through three principal pathways: the C4 pathway, the C3 pathway, and Crassulacean acid metabolism (CAM). In the ----context of drought stress, the C4 pathway exhibits a markedly superior efficiency in comparison to the C3 pathway. C4 plants are characterized by a distinctive Kranz anatomy, and their water use efficiency (WUE) is considerably elevated relative to that of C3 plants. During the shortage of water availability, C4 pathways assists in the increase of CO_2 assimilation there by promoting the higher synthesis of organic matter which results in the resilience of plants against early desiccation. In CAM plants opening of stomata primarily occur during the nocturnal hours, allowing the CO_2 uptake that is consequently changed into malic acid through the phosphoenolpyruvate carboxylase (PEPC) action and sequestered in the vacuoles. In the daylight, when the stomata are closed decarboxylation of stomata occurs and release of $CO_{2.}$ This CO_2 fixation mitigates the losses of transpiration that would otherwise follow the opening of the stomata during day time which addresses the inherent fight between the transpiration and CO_2 uptake under drought conditions. Various plants may demonstrate different pathways for environmental variables and assimilation can put a sufficient influence on the metabolism of carbon within plants. Modifications in the growth stages of plants, nutrient availability, growth conditions and bioregulators may precipitate changes in CO_2 fixation pathways. For example, high level of ABA in drought stress plants enhance the efficiency of C4 pathway. Similarly, C3 pathways has the potential to transition to CAM under stress conditions (Huber and Sankhla, 1976). Studies carried out by winter on *Mesembryanthemum crystallinum* L. (*Aizoaceae*) and different types of orchid species have shown that specific species showing adoptable photosynthetic phenotypes can alter their assimilation pathways in response to the changes in the environmental conditions. When salinity or drought stress is present, these species may switch to CAM, although under ideal circumstances, they typically operate in C3 mode (Silvera et al., 2005; Winter and Holtum, 2005, Ijaz et al., 2024).

ABA-mediated responses to drought

Phytohormones influence plant growth, development processes and strategies to adapt to the condition of environmental stress (Ali et al., 2024). Drought stress also greatly influences the synthesis of hormones that improve plant adaptation (Ismail et al., 2018). Drought causes a phytohormone secretion, that reduces stomatal closure, negative phototropism of roots, and osmotic balance (Lim et al., 2015). It increases ABA release thereby providing a plant with resistance to water constraint (Ng et al. 2014). In addition, under a series of optimal set of conditions, ABA is required for plant growth (Li et al., 2022). Additionally, ABA alters root shape and design, resulting in plant development patterns (Portola's et al., 2015). ABA also promotes leaf senescence, as demonstrated by the late-senescence phenotypes discovered in numerous ABA-deficient mutants (Passioura, 2007). In non-stressed situations, ABA coupled with increased CO_2 concentrations, induces partial or complete stomatal closure (Kim et al., 2010). Drought conditions increase ABA levels, which increases stomatal closure and reduces water loss from foliage (Hasan et al., 2021). Abscisic acid that accumulates as a reaction to drought conditions plays a pivotal role in modulating the expression of a multitude of genes, particularly those that are responsive to drought, which are essential for enhancing plant's resilience to drought stress (Fujita et al., 2011). Many transcriptomic investigations have demonstrated that 50% of the genes regulated by ABA are affected by drought stress. In Arabidopsis, approximately 245 genes have been identified (Seki et al., 2002). In rice, 43 of 73 genes related to stress response have been identified as being regulated by both ABA and drought stress (Rabbani et al., 2003).

Osmotic regulation under drought stress

Osmotic regulation is a fundamental physiological function that enables plants to lower their osmotic potential and survive in harsh situations like drought. In the presence of drought stress, osmotic control can be performed by three basic mechanisms: reduction of intracellular water, reduction of cellular volume, and increase in solute concentrations inside cells. Although these pathways function concurrently across various plant taxa, it is essential to acknowledge that not all botanical species possess the capacity for osmotic regulation. This phenomenon is conventionally perceived as the anticipatory modification of cellular constituents aimed at lowering osmotic potential via the augmentation of solute concentrations. Its main function is to decrease the water potential gradient between the cytosol and the extracellular medium to maintain water potential gradient for absorbing water when extracellular water potential is decreased. Osmotic regulation is essential to maintain turgor pressure for optimal cell development (Osakabe et al., 2014). Besides, it lends to maintaining stomatal conductance in marginal water deficit. This stability in tissues that are photosynthetically active ensures higher carbon dioxide's concentrations within the mesophyll intercellular gaps and prevents or reduces photosynthetic inhibition. Osmotic control also keeps cellular homeostasis and reduces the adverse effects of the external stress on biochemical, physiological and morphological processes such as cell proliferation, stomatal conductance and photosynthesis.

Osmotic control in plant systems depends, for the most part, on inorganic ions and organic osmotic solutes received from the surroundings. Amine derivatives such as polyamines and glycine betaine; amino acid derivatives especially proline, trehalose, mannitol, and fructans are organic osmotic solutes that affect the cytoplam's osmotic characteristics. These solutes are also small weight, high solubility and low toxicity. Together they ensure that the ideal osmotic pressure is maintained in order to keep cells from dissolving and proteins working as they should. Inorganic ion osmotic management is founded on the activity of ion transporters, like sodium ion, potassium ion and hydrogen ion pumps, at specific concentrations of inorganic ions within and outside the cell that also influence the term 'osmotic potential'. Ions can also cause variation in the cellular structure and function. Succulent xerophytes adapt well to the drought stress by their agglomeration of sodium ion. Potassium ion (K+) build up as well as free proline is critical for their xerophyte species subjected to drought stress (Wang et al., 2004). Investigations into osmotic regulators like proline (Pro), soluble sugars (SS), and glycine betaine (GB) have been in the rise. Certain studies suggest that the accumulation of proline functions as a defensive strategy against drought stress (Ashraf and Foolad, 2007). For instance, a notable increase in proline concentrations was documented in rice when the polyethylene glycol (PEG) concentration reached 30% (Patmi and Pitoyo, 2020). Under conditions of drought stress, the levels of osmotic regulating agents elevated, demonstrating a positive correlation with plant stress tolerance. Nevertheless, the extent of variation in osmotic regulators is species-dependent. For instance, Lanzhou lily enhances its drought resilience by manipulating osmotic regulation and levels of secondary metabolites, diminishing soluble sugars, polysaccharides, and fructose while increasing proline, glucose, and trehalose levels (Li et al., 2020). In *Maclura pomifera*, soluble carbohydrates such as sucrose, glucose, and fructose increased during the early stages of drought stress but then decreased after 22 days of severe drought. In drought conditions, osmotic regulators such as proline and mannitol respond more strongly (Khaleghi et al., 2019).

Inter-organ coordination in drought stress mitigation

Based on a wide variety of signaling molecules activated by alterations in environmental factors, higher plants have established complex inter-organ communication mechanisms. These signals travel through the vascular system to help coordinate stress responses across the entire plant. Phloem and xylem are two prominent vascular tissues that mediate inter-organ signaling. When drought stress occurs, decreasing water potential in their roots may reflect these conditions to insufficient soil water intake (Li et al., 202).

The water scarcity signal is transmitted from the roots to the leaves via the vascular system. The flow of calcium ions (Ca^{2+}), the decrease in turgor pressure, and the production of ROS are all crucial in detecting and dehydration stress within the vascular system and guard