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Comprehensive Review

Molecular Mechanisms of Plant Adaptation to Abiotic Stress Under Changing Climates

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ABSTRACT:

Abiotic stresses, including drought, salinity, extreme temperatures, flooding, and nutrient deficiency, represent the most formidable constraints to global agricultural productivity, collectively accounting for more than 50% of yield losses in major crop species worldwide. The accelerating pace of climate change is predicted to intensify the frequency, severity, and co-occurrence of these stressors, posing unprecedented challenges to food security for a rapidly growing global population. Plants, as sessile organisms, have evolved an extraordinarily sophisticated and multilayered repertoire of molecular mechanisms to perceive, transduce, and respond to adverse environmental signals. These mechanisms span the entire spectrum of biological organization, from membrane-localized receptor kinases and second messenger cascades, through transcriptional reprogramming orchestrated by diverse families of transcription factors, to post-translational modifications, epigenetic remodeling, and non-coding RNA-mediated regulation. This review provides a comprehensive and integrative synthesis of the current understanding of the molecular mechanisms underpinning plant adaptation to abiotic stress in the context of changing climates. This review systematically examine stress perception and signal transduction, the roles of phytohormones particularly abscisic acid (ABA), jasmonic acid (JA), ethylene, and melatonin the functions of major transcription factor families including NAC, WRKY, AP2/ERF, bHLH, MYB, and HSF, the significance of post-translational modifications such as ubiquitination and SUMOylation, the emerging roles of epigenetic memory and stress priming, and the contributions of omics technologies and genome editing to crop improvement. Special attention is given to quantitative and statistical dimensions of these processes, as well as to the mathematical frameworks that describe stress response dynamics. The review concludes by identifying key knowledge gaps and future research priorities for engineering climate-resilient crops.

Keywords:
Abiotic stress, Climate change, Signal transduction, Transcription factors, Epigenetics, ABA signaling, Stress tolerance, Crop improvement

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1. Introduction

1.1 The Global Challenge of Abiotic Stress Under Climate Change

The intersection of rapid climate change and the imperative to sustain global food security represents one of the defining scientific and societal challenges of the twenty-first century. Abiotic stresses encompassing drought, high salinity, extreme heat, freezing temperatures, flooding, heavy metal toxicity, and nutrient deficiency are estimated to affect more than 90% of rural farmland at some point during the growing season **(Atak et al., 2023),** and collectively reduce the average yield of major crops by more than 50% **(Gandhi & Oelmüller, 2023; Sasi et al., 2018).** These losses are not uniformly distributed; they disproportionately affect smallholder farmers in tropical and subtropical regions, where the impacts of climate change are most acute **(Antoniou et al., 2017).**

Global warming and associated climatic perturbations are predicted to exacerbate the frequency and severity of abiotic stress events **(Lagiotis et al., 2023).** Extreme weather episodes, including intense rainfall, prolonged drought, and more frequent heat and cold waves, are becoming increasingly common **(Primo-Capella et al., 2022).** In the current state of global warming, the impact of abiotic stressors on crops has increased significantly and will only continue to rise **(Patel et al., 2023).** Some estimates suggest that ongoing global warming and climate change will further aggravate the effects of abiotic stressors on plants **(Atak et al., 2023).** The consequences for agricultural systems are profound: abiotic stresses lead to more than 50% of yield losses in most plant species **(Gandhi & Oelmüller, 2023)**, and the genetic basis of plant adaptation to abiotic stress remains poorly understood even in genomic model species such as rice **(Vigueira et al., 2016).**

Plants, by virtue of their sessile nature, cannot escape adverse environmental conditions and have therefore evolved a broad range of molecular mechanisms to respond to complex networks of environmental signals. These mechanisms activate multiple pathways, modulated by different responsive genes, which in some cases confer tolerance to the pressure exerted by stressor factors **(Ambrosino et al., 2020).** Understanding these mechanisms at the molecular level is not merely an academic exercise; it is a prerequisite for the rational engineering of stress-tolerant crops capable of sustaining productivity under the climatic conditions projected for the coming decades **(Moshelion & Altman, 2015).**

1.2 Scope and Organization of This Review

This review systematically examines the molecular mechanisms of plant adaptation to abiotic stress, with particular emphasis on developments reported through 2025. We begin with an overview of stress perception and early signal transduction, proceed through the major signaling cascades and transcriptional regulatory networks, address post-translational and epigenetic mechanisms, and conclude with a discussion of omics-enabled discoveries and biotechnological strategies for crop improvement. Throughout, we integrate quantitative and statistical data where available and highlight areas of nuance or disagreement in the literature. A summary of major abiotic stresses and their associated molecular responses is provided in Table 1.

Table 1. Major Abiotic Stress Types and Corresponding Molecular Responses

Abiotic Stress	Key Molecular Signals	Major Pathways	Representative Genes/Proteins	References
Drought	ABA accumulation, Ca^{2+} spikes	ABA signaling, stomatal regulation	PYR/PYL/RCAR, SnRK2, ABF	(Luo et al., 2018; Fidler et al., 2022)
Salinity	Ionic imbalance (Na^+/K^+), ROS	Ion transport, antioxidant defense	KUP transporters, SOD, APX	(Chakraborty et al., 2023; Hernández-Bueno et al., 2021)
Heat	Protein denaturation, ROS	Heat shock response	HSFs, HSPs	(Jin et al., 2020; Singh et al., 2019)
Cold	Membrane rigidity, Ca^{2+} influx	MAPK cascade, CBF pathway	CRLK1, CBF/DREB	(Li et al., 2017)
Flooding	Hypoxia, ethylene signaling	ERF-mediated transcription	ERFs, ACS genes	(Huang et al., 2025; Islam et al., 2020)
Nutrient deficiency	Metabolic imbalance	Hormonal + transcriptional regulation	PSTOL1, COR proteins	(Vigueira et al., 2016; Govta et al., 2024)

2. Stress Perception and Early Signal Transduction

2.1 Receptor-Like Kinases (RLKs) as Primary Stress Sensors

The perception of abiotic stress signals at the cell surface is a critical first step in the plant stress response. Receptor-like kinases (RLKs) constitute one of the largest gene families in plant genomes and serve as primary sensors of diverse environmental cues, hormonal signals, and stress stimuli **(Li et al., 2017)**. RLKs are characterized by an extracellular domain for ligand perception, a transmembrane domain, and an intracellular kinase domain for signal transduction **(Gandhi & Oelmüller, 2023)**. The RLK superfamily includes members such as leucine-rich repeat RLKs (LRR-RLKs), mannose-binding lectin RLKs (MRLKs), and lectin RLKs (LecRLKs), all of which have been shown to mediate cellular responses to various environmental cues **(Li et al., 2017).**

Despite the enormous size of the RLK family, only a handful of studies have shed light on the role of RLKs in abiotic stress responses and the potential mechanisms underlying RLK-mediated abiotic stress tolerance. A deeper understanding of kinase signaling cascades in responses to fluctuating environmental conditions such as drought, heat, cold, or salt is paramount to engineer stress-tolerant crops **(Gandhi & Oelmüller, 2023).** In rice, the LRR-RLK gene *FON1* increased drought tolerance of transgenic rice plants through phosphorylating key components of the ABA signaling pathway and activating the ABA signal**.** Another well-studied example is *CRLK1*, a calcium-regulated RLK, which modulated cold tolerance through phosphorylating MAP kinases in plants, promoted expression of cold stress response genes, and ultimately regulated plant adaptation to cold stress **(Li et al., 2017).**

The energy-dependent transmembrane receptor-like kinases (RLKs) also recognize priming elicitors and, when activated, regulate the transcription of abiotic stress defense genes **(Lagiotis et al., 2023).** This dual role in primary stress perception and stress memory underscores the centrality of RLKs in plant stress adaptation.

2.2 Calcium Signaling and Calcium-Dependent Protein Kinases (CPKs)

Calcium ions (Ca^{2+}) serve as universal second messengers in plant stress signaling, with transient increases in cytosolic Ca^{2+} concentration representing one of the earliest cellular responses to virtually all abiotic stresses. Calcium-dependent protein kinases (CPKs, also known as CDPKs) are a plant-specific family of serine/threonine kinases that directly sense Ca^{2+} signals through their calmodulin-like domain and transduce them into downstream phosphorylation events **(Atif et al., 2019).**

CPKs show their role against biotic and abiotic stress tolerance upon interaction with specific calcium signals. With respect to abiotic stresses, CPKs are involved in drought, salinity, heat, and cold stress response signaling by regulating ABA-responsive transcriptional factors and ion channel regulation. Some *Arabidopsis* CPKs (e.g., *CPK13*) is also involved in potassium ion (K^+) channel regulation and other ion transportation in guard cells. CPK11, induced by hydrogen peroxide (H_2O_2), regulates and controls the activity of superoxide dismutase (SOD) and ascorbate peroxidase (APX) production induced by the ABA signaling pathway. CPK activity confirmed by global expression analyses shows that several CPK members are expressed differentially under varying ABA, salinity, drought, and heat and cold levels. The change in the expression of CPK genes indicates the role of CPKs in plant adaptation against abiotic stress environments **(Atif et al., 2019).**

2.3 G-Protein Signaling

Heterotrimeric G-proteins, comprising Gα, Gβ, and Gγ subunits, are important components of plant stress signaling networks. The signaling mechanisms in plants during low and high temperature, drought, and salinity are different and yet related to each other, with G-proteins playing a role in integrating these diverse signals. In *Arabidopsis*, the G-protein coupled receptor GCR1 and the Gα subunit GPA1 mediate responses to multiple abiotic stresses. GCR1 acts as a negative regulator of GPA1-mediated ABA responses in *Arabidopsis* guard cells. In tobacco, transgenic lines overexpressing Gα and Gβ from pea revealed the role of Gα in salinity and high temperature stress response, while Gβ was linked to heat tolerance. Recent studies in *Arabidopsis* revealed that G-proteins are also involved in growth under salt stress, as well as cellular senescence and cell division in rice and maize **(Chakraborty et al., 2015).**

2.4 MAP Kinase Cascades

Mitogen-activated protein kinase (MAPK) cascades are evolutionarily conserved signal transduction modules that relay stress signals from the cell surface to the nucleus. The canonical MAPK cascade consists of a MAP kinase kinase kinase (MAPKKK), a MAP kinase kinase (MAPKK), and a MAP kinase (MAPK), operating in a sequential phosphorylation relay. The calcium-regulated RLK CRLK1 modulates cold tolerance through phosphorylating MAP kinases in plants **(Li et al., 2017)**, illustrating the integration of Ca^{2+} and MAPK signaling in stress responses. MAPK cascades are also activated by drought, salinity, and oxidative stress, and their outputs include the phosphorylation and activation of transcription factors that drive stress-responsive gene expression **(Gandhi & Oelmüller, 2023).**

2.5 Mathematical Framework for Signal Transduction Dynamics

The dynamics of stress signal transduction can be modeled mathematically using systems of ordinary differential equations (ODEs). In the case of a simplified two-component signaling system involving a receptor (R) and a response regulator (RR), the activation kinetics can be described as follows:

$$\frac{dR^*}{dt} = k_{\text{on}} S R - k_{\text{off}} R^*$$

$$\frac{dRR^*}{dt} = k_{\text{cat}} R^* RR - k_{\text{phos}} RR^*$$

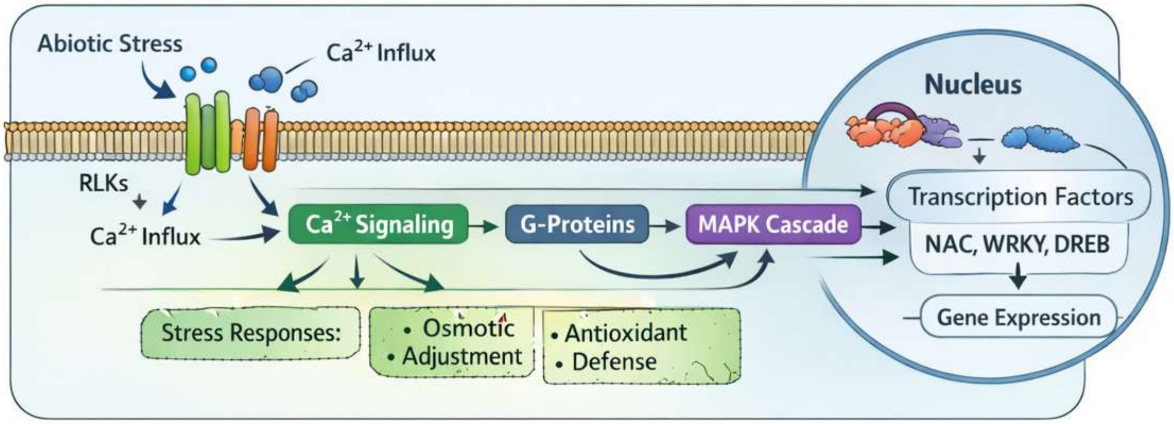
Here, S represents the concentration of the stress signal, R and R^* denote the inactive and active receptor concentrations, while RR and RR^* represent the inactive and active response regulator concentrations. The parameters k_{on} and k_{off} are the activation and deactivation rate constants, respectively, k_{cat} is the catalytic rate constant for response regulator phosphorylation, and k_{phos} is the dephosphorylation rate constant.

At steady state, the concentration of the active receptor is given by:

$$R^*_{\text{ss}} = \frac{k_{\text{on}} S R_{\text{total}}}{k_{\text{on}} S + k_{\text{off}}}$$

This mathematical framework demonstrates how the amplitude and duration of the stress signal (S) influence the magnitude of the downstream response. Additionally, feedback mechanisms, represented by k_{phos}, modulate the attenuation of the signal. This principle is particularly relevant to understanding the dose-dependent and time-dependent nature of plant stress responses, as observed in studies by **Atif et al. (2019)** and **Gandhi & Oelmüller (2023).** An integrated overview of stress perception and signal transduction pathways is illustrated in Figure 1.

Figure 1. Integrated Model of Abiotic Stress Signal Transduction



3. Phytohormone Signaling in Abiotic Stress Responses

3.1 Abscisic Acid (ABA): The Master Stress Hormone

Abscisic acid (ABA) is the central phytohormone mediating plant responses to abiotic stress, particularly drought, salinity, and cold **(Luo et al., 2018; Fidler et al., 2022).** ABA biosynthesis is rapidly induced by water deficit and other osmotic stresses, and the resulting increase in ABA concentration triggers a cascade of molecular events that collectively promote stress tolerance. Abiotic stress (such as cold, drought, salinity, and heat) results in strong increases in ABA level, and this accumulation promotes stress tolerance in various plant species. Exogenous ABA application has been shown to enhance plant abiotic stress tolerance through a series of physiological and biochemical changes **(Luo et al., 2018).**

3.1.1 The PYR/PYL/RCAR Receptor System

The molecular basis of ABA perception was elucidated with the discovery of the PYR/PYL/RCAR family of soluble ABA receptors. In many abiotic stresses, such as drought, salinity, or cold, the activation of many molecular mechanisms depends on the ABA content in the tissues. Endogenous changes in ABA concentration enable the initiation of a signaling cascade, the activation of which depends on the binding of ABA by appropriate receptor proteins **(Fidler et al., 2022).** Upon ABA binding, PYR/PYL/RCAR receptors inhibit type 2C protein phosphatases (PP2Cs), which in turn releases and activates SNF1-related protein kinase 2s (SnRK2s). Activated SnRK2s phosphorylate downstream targets including ABA-responsive element binding factors (ABFs/AREBs), which drive the expression of ABA-responsive genes.

The ABF/AREB/ABI5 family members are widely implicated in plant responses to abiotic stresses (e.g., drought, salinity, cold) and developmental regulations. *Arabidopsis* ABF/AREB/ABI5 gene expression is coordinately induced by light signals, ABA, and multiple abiotic stresses (drought, high salinity, and cold), forming a multi-layered stress response network. Beyond these signals, PmABFs in *Prunus mume* can also be activated by exogenous hormones (e.g., gibberellins, ethylene) and hypoxia stress, implying roles in broader physiological adaptation **(Zhang et al., 2025).**

3.1.2 ABA-Mediated Stomatal Regulation

One of the most critical responses to drought mediated by abscisic acid (ABA) is the regulation of stomatal aperture. When plants experience water deficit, ABA is perceived by guard cells, initiating a signaling cascade that leads to the activation of anion channels (such as SLAC1) and outward-rectifying K^+ channels (such as GORK). This results in the efflux of anions and K^+ from guard cells, causing water to exit the cells, reducing guard cell turgor, and ultimately leading to stomatal closure. This process minimizes water loss through transpiration and helps the plant conserve water during stress.

In Arabidopsis, the calcium-dependent protein kinase CPK13 plays a pivotal role in this regulatory network by inhibiting inward-rectifying K^+ channels (KAT1 and KAT2) in guard cells. By suppressing K^+ influx, CPK13 further promotes stomatal closure and exemplifies the integration of Ca^{2+} and ABA signaling pathways in guard cell function **(Atif et al., 2019).**

The quantitative relationship between stomatal conductance (g_s) and ABA concentration can be described by a Hill function:$g_s = g_{s,\max} \cdot \frac{K_d^n}{K_d^n + \mathrm{ABA}^n}$where:

- $g_{s,\max}$ is the maximum stomatal conductance in the absence of ABA,
- K_d is the ABA concentration at which conductance is reduced to half its maximum (reflecting sensitivity),
- n is the Hill coefficient, indicating the steepness and cooperativity of the response.

This sigmoidal dose-response model accurately captures how stomatal conductance decreases as ABA concentration increases and has been empirically validated across multiple plant species **(Fidler et al., 2022).**

3.1.3 ABA-Independent Stress Signaling

While ABA-dependent pathways are central to drought and osmotic stress responses, ABA-independent pathways also contribute significantly to stress tolerance. For example, SNAC3, a NAC transcription factor, functions as a positive regulator of drought, heat, and oxidative stress response through an ABA-independent pathway **(Yuan et al., 2019).** This highlights the complexity and redundancy of plant stress signaling networks.

3.2 Jasmonic Acid (JA) in Abiotic Stress Tolerance

Jasmonic acid (JA) and its bioactive conjugate jasmonoyl-isoleucine (JA-Ile) are lipid-derived phytohormones with well-established roles in biotic stress responses that have more recently been recognized as important regulators of abiotic stress tolerance **(Li et al., 2017).** JA regulates freezing tolerance controlled by the CBF pathway, where JAZ proteins physically interact with and inhibit ICE1 and ICE2 transcription factors to reduce expression of the cold regulon. Genetic analysis with various JA biosynthesis and response mutants has shown that JA is required for basal thermotolerance. JA also enhances salt stress tolerance in wheat by increasing antioxidant levels in order to reduce the effects of ROS stimulated by high salinity conditions **(Gonzalez et al., 2017).**

Recent studies have highlighted that JA plays an important role in the regulation of abiotic stress tolerance under osmotic stress conditions. JAs regulate gene expression involved in stress responses through up-regulating expression of antioxidant enzymes and eliciting plant secondary metabolism. In a global gene expression analysis of cassava seedlings, 50 differentially expressed genes (DEGs) associated with "response to JA stimulus" signaling pathways were significantly enriched under both cold and drought stress **(Li et al., 2017),** underscoring the broad relevance of JA signaling across multiple stress types.

3.3 Ethylene Signaling in Stress Adaptation

Ethylene is a gaseous phytohormone synthesized from methionine via the Yang cycle, with 1-aminocyclopropane-1-carboxylate (ACC) as the immediate precursor. The ACC synthase (ACS) gene family encodes the rate-limiting enzymes in ethylene biosynthesis and is differentially regulated by abiotic stresses. In cotton plants, the expression patterns of *GhACS10* and *GhACS12* change under various abiotic stresses, including cold, heat, drought, and salinity. In sugarcane, *ACS2* and *ACS3* respond to low-nitrogen stress by regulating ethylene biosynthesis, contributing to stress tolerance and sugar accumulation. These findings highlight the central role of ACS genes in regulating ethylene signaling in response to environmental stimuli **(Huang et al., 2025).**

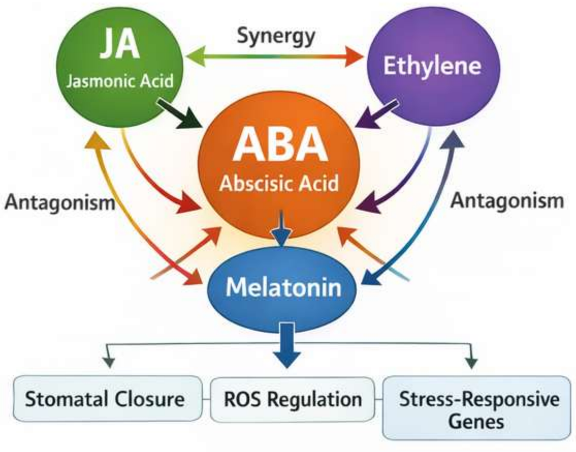
Ethylene-response transcription factors (ERFs) are key downstream effectors of ethylene signaling and have been shown to play important roles in regulating gene expression during submergence and other abiotic stresses **(Islam et al., 2020).** The AP2/ERF transcription factor family, which includes both DREB/CBF and ERF subfamilies, is one of the most extensively studied TF families in the context of abiotic stress **(Mosa et al., 2017).**

3.4 Melatonin as an Emerging Stress Regulator

Melatonin (N-acetyl-5-methoxytryptamine) has emerged as a pleiotropic molecule with diverse roles in plant stress response and growth regulation **(Gao et al., 2023; Antoniou et al., 2017).** An evolutionarily conserved molecule, melatonin participates in improving plant abiotic stress tolerance to cold, heat, high salinity, drought, heavy metals, waterlogging, global warming, and UV-B. It can regulate plant vegetative and reproductive growth, including seed germination, vegetative growth, root induction, tropism, photosynthesis, stem strength, leaf water/CO_2 exchange, root development, flowering, fruit quality, ripening, and senescence **(Gao et al., 2023).**

Melatonin systemically ameliorates drought stress-induced damage in *Medicago sativa* plants by modulating nitro-oxidative homeostasis and proline metabolism **(Antoniou et al., 2017).** Priming with melatonin is a rapidly emerging field in plant stress physiology and crop stress management, serving as an attractive alternate tool for improving plants' abiotic stress tolerance. Melatonin also alleviates fungal, bacterial, viral, phytophthora blight, and nematode diseases in plants by regulating plant immunity and pathogen pathogenicity **(Gao et al., 2023),** illustrating its role at the interface of abiotic and biotic stress responses. The interactions among major phytohormones in abiotic stress responses are summarized in Figure 2.

Figure 2. Phytohormone Crosstalk in Abiotic Stress Responses



4. Transcription Factor Networks in Abiotic Stress Responses

Transcription factors (TFs) are proteins that specifically bind to 5′ upstream DNA regions and ensure target gene expression at a certain time and space; they are vital for the normal development of an organism, as well as for routine cellular functions **(Zhang et al., 2017).** Some TFs interact with cis-elements in the promoter regions of several stress-related genes and thus up-regulate the expression of many downstream genes, resulting in the imparting of abiotic stress tolerance. Protein kinases and TFs correspond to the most regulated genes under abiotic stress, suggesting that cold and drought stress signal transduction pathways overlap at several points **(Li et al., 2017).** The following sections systematically review the major TF families involved in abiotic stress responses. The major transcription factor families involved in abiotic stress responses are summarized in Table 2.

Table 2. Key Transcription Factor Families in Abiotic Stress Tolerance

TF Family	Key Functions	Stress Types	Example Genes	References
NAC	Regulation of drought & oxidative stress genes	Drought, salinity, cold	ONAC066, SNAC3	(Yuan et al., 2019; Cao et al., 2017)
WRKY	W-box binding, stress gene activation	Drought, heat, salinity	OsWRKY45, WRKY53	(Zhang et al., 2017; Song et al., 2009)
AP2/ERF	DREB/CBF-mediated transcription	Cold, drought, heat	DREB2B	(Mosa et al., 2017)
HSF	Heat stress signaling, HSP regulation	Heat, oxidative stress	HSFA2	(Qiao et al., 2015; Singh et al., 2019)
bHLH	Gene regulation under stress	Drought	AtbHLH17	(Zhang et al., 2017)
MYB	Regulation of secondary metabolism	Drought, salinity	MYB TFs	(Fujita et al., 2011)
HD-Zip	Development + ABA signaling	Drought, salinity	HD-Zip TFs	(Patel et al., 2023)

4.1 NAC Transcription Factors

NAC (NAM, ATAF1/2, CUC2) domain proteins constitute the largest plant-specific transcription factor family and play important roles in plant development and regulation of abiotic stress tolerance. These proteins have received attention as major regulators in various stress signaling pathways and have been found to improve the abiotic stress tolerance of different crops through genetic engineering. As transcriptional factors, NAC domain proteins contain a highly conserved DNA-binding domain in the N-terminal and a diverse transcription activation or repression domain in the C-terminal.

Numerous NAC domain proteins from different crops have been reported to play a positive role in stress responsiveness and regulation of abiotic stress tolerance. For example, the pumpkin NAC transcription factor CmNAC1 significantly improves the tolerance of *Arabidopsis* to salt, drought, and cold stress, with ectopic expression (EE) lines showing better growth performance and higher survival ratios under stress conditions **(Cao et al., 2017).** In rice, the NAC transcription factor ONAC066 functions as a positive regulator of drought and oxidative stress response. Transgenic rice lines overexpressing stress-related NAC TFs exhibited significant improvement of abiotic stress tolerance under severe stress conditions without any adverse effect on yield, or even with yield increase, providing a promising potential for application of these stress-related NAC TFs in improvement of abiotic stress tolerance in crops.

Interestingly, ONAC095 negatively regulates drought response but oppositely acts as a positive regulator of cold response in rice, illustrating the context-dependent and sometimes opposing roles of individual NAC TFs in different stress responses. In most cases, ABA-mediated signaling pathways, stomatal movement, and root system architecture were found to be involved in NAC-mediated improvement of abiotic stress tolerance in transgenic plants **(Yuan et al., 2019).**

4.2 WRKY Transcription Factors

WRKY transcription factors are named for the conserved WRKYGQK amino acid sequence in their DNA-binding domain and bind with high affinity to the W-box cis-acting element ((C/T)TGAC(T/C)) in the promoters of stress-responsive genes Zhang et al., 2014). WRKY proteins are emerging as key regulators in abiotic stress defense responses. A majority of WRKY family members are differentially induced by drought, high salinity, cold, and heat. Many rice WRKY genes are inducible by drought, high salinity, cold, and heat stresses.

Overexpression of *OsWRKY45*, *OsWRKY11*, *TcWRKY53*, and *GmWRKY13/21/54* altered drought tolerance, dry heat tolerance, osmotic stress tolerance, and multiple abiotic stress tolerance of transgenic plants, respectively. Additionally, *LtWRKY21* was induced by drought and salinity stress, *CaWRKY1* protein was thought to function in cold adaptation, and *HvWRKY38* protein was involved in cold-, drought-, and ABA-responses. Overexpression of *OsWRKY08* improves osmotic stress tolerance in *Arabidopsis* **(Song et al., 2009).** In maize, WRKY transcription factors responding to Pb stress have been characterized, with TtWRKY28 up-regulated under oxidative stress. Over-expression of these TFs up-regulates downstream target genes and improves abiotic stress tolerance **(Zhang et al., 2017).**

4.3 AP2/ERF Transcription Factors

The AP2/ERF (APETALA2/Ethylene Response Factor) superfamily is one of the largest and most functionally diverse TF families in plants, encompassing the DREB (Dehydration-Responsive Element Binding), CBF (C-repeat Binding Factor), and ERF subfamilies. Abiotic stresses such as drought, salinity, cold, heat, and mechanical wounding regulate many genes, and this often occurs at the transcriptional level in which several genes are activated in response to different abiotic stresses. In the promoter regions, transcription factors interact with cis-elements of several stress-related genes, which leads to the upregulation of many downstream genes causing abiotic stress tolerance **(Mosa et al., 2017).**

The overexpression of Dehydration-Responsive Element-Binding Protein 2 (EsDREB2B), which exhibits transactivation activity of a GAL4-containing reporter, increases the tolerance to multiple abiotic stress factors including drought, salinity, cold, heat, heavy metals, and mechanical wounds in yeast **(Zhang et al., 2017).** Molecular characterization of two AP2/ERF transcription factor genes from Egyptian tomato cultivar (Edkawy) has revealed their roles in mediating responses to multiple abiotic stresses **(Mosa et al., 2017).**

4.4 Heat Shock Transcription Factors (HSFs)

Heat shock transcription factors (HSFs) are particularly involved in the heat stress response and are important regulators in the sensing and signaling of heat stress. Recent studies have also shown that HSFs are involved in plant growth and development, as well as in responses to other abiotic stresses such as cold, salt, and drought. In *Pyrus bretschneideri* and five other Rosaceae species, genome-wide identification revealed a large and diverse HSF family with members showing differential expression under multiple stress conditions **(Qiao et al., 2015).**

HSFA2 is associated with ABA-mediated heat stress tolerance in tall fescue and *Arabidopsis*. ABA can regulate the expression of several small HSPs (sHsps) in maize leaves when imposed to combined drought and heat stresses **(Singh et al., 2019).** Heat shock proteins (HSPs) are known as target genes for TFs responding to heat stress. Heat stress changes the way genes are involved in signaling pathways, as well as transcriptional control and the expression of heat shock proteins at the molecular level **(Jin et al., 2020).** In *Syzygium cumini*, the heat shock transcription factor (Hsf) regulates oxidative stress response by directly sensing reactive oxygen species (ROS) **(Chakraborty et al., 2023).**

4.5 bHLH and MYB Transcription Factors

Basic helix-loop-helix (bHLH) transcription factors are involved in diverse aspects of plant development and stress responses. TF AtbHLH17 is up-regulated under drought stress in *Arabidopsis*, and its over-expression up-regulates downstream target genes and improves abiotic stress tolerance **(Zhang et al., 2017).** The MYB (myeloblastosis) transcription factor family is one of the largest TF families in plants, with members involved in responses to drought, cold, salinity, and oxidative stress. MYB binding sites (MBS) are among the cis-regulatory elements identified in the promoters of stress-responsive genes.

4.6 HD-Zip Transcription Factors

The homeodomain-leucine zipper (HD-Zip) class of TFs has highly conserved homeodomain (HD) and leucine zipper (Zip) motifs. The HD-Zip class of TFs interacts with abscisic acid-regulated developmental networks, positioning them at the interface of developmental and stress-responsive signaling. HD-Zip TFs have been implicated in responses to drought, salinity, and other abiotic stresses, and represent potential targets for crop improvement **(Patel et al., 2023).**

4.7 Quantitative Aspects of Transcription Factor Networks

The transcriptional reprogramming of plants under abiotic stress is a remarkable phenomenon, characterized by the activation of complex regulatory networks involving transcription factors (TFs). These TFs play a pivotal role in modulating gene expression, enabling plants to adapt to environmental challenges such as drought, heat, and cold. For instance, in cassava seedlings subjected to cold and drought stress, global gene expression analysis revealed that protein kinases and TFs were among the most regulated genes, with 50 differentially expressed genes (DEGs) associated with "response to JA stimulus" signaling pathways significantly enriched under both stress conditions **(Li et al., 2017).** Similarly, transcriptome analyses in lentil under heat stress identified novel genes and regulatory networks linked to heat tolerance mechanisms **(Singh et al., 2019).** In rice, transcriptomic studies of seeds developing under heat stress uncovered critical heat-responsive genes involved in regulatory mechanisms **(Islam et al., 2020),** while meta-expression analyses under abiotic stress conditions identified 264 cold or heat stress-responsive plastid-related genes, illustrating the breadth of transcriptional reprogramming **(Rane et al., 2021)**.

The mathematical relationship between TF binding affinity and gene expression can be described using a thermodynamic model. For a gene regulated by a single TF, the binding site occupancy (θ) is given by:

$$\theta = \frac{\mathrm{TF}/K_d}{1 + \mathrm{TF}/K_d}$$

where TF represents the concentration of the transcription factor, and K_d is the dissociation constant for TF-DNA binding. The gene expression level can then be expressed as:

$$\begin{aligned} \text{Expression} &= \text{Basal} + \text{Max} \cdot \theta \\ &= \text{Basal} + \text{Max} \cdot \frac{\mathrm{TF}/K_d}{1 + \mathrm{TF}/K_d} \end{aligned}$$

Here, Basal is the basal expression level of the gene, and Max is the maximum inducible expression level. This model predicts that genes with lower K_d values (indicating higher TF binding affinity) will be more sensitively induced at lower TF concentrations. Such hierarchical activation of stress-responsive genes aligns with experimental observations, where genes with high-affinity TF binding sites are activated earlier or at lower stress levels. This quantitative framework provides valuable insights into the dynamics of transcriptional regulation during abiotic stress, highlighting the critical role of TFs in orchestrating plant stress responses **(Zhang et al., 2017).**

5. Post-Translational Modifications in Stress Signaling

5.1 Ubiquitination and the 26S Proteasome

Ubiquitination is a reversible post-translational modification in which ubiquitin, a 76-amino acid protein, is covalently attached to target proteins, typically marking them for degradation by the 26S proteasome. This system plays critical roles in regulating the abundance and activity of key stress signaling components. The ubiquitin-proteasome system (UPS) modulates the stability of transcription factors, signaling kinases, and hormone receptors, thereby controlling the amplitude and duration of stress responses **(Singh et al., 2022).**

5.2 SUMOylation and the SUMO Stress Response

Small ubiquitin-like modifier (SUMO) proteins are conjugated to target proteins in a process called SUMOylation, which modulates protein activity, localization, and interactions. Hyper-SUMOylation under acute heat, cold, high salinity, drought, oxidative stress, and nutrient deficiency marks the conserved SUMO stress response (SSR) in plants. SIZ1-mediated SUMOylation positively responds to salt and drought-induced osmotic stress; enhances metal stress tolerance and light signaling; and regulates N, P, and ROS homeostasis in plants. SUMOylation regulates heat stress positively at transcriptional, post-transcriptional, and translational levels.

The mutated AtSIZ1, a SUMO ligase, resulted in compromised tolerance to cold and drought, early flowering, and phosphate starvation symptoms, demonstrating the pleiotropic importance of SUMOylation in plant stress adaptation. The conservation of the SUMO stress response across diverse stress types suggests that SUMOylation serves as a general stress-responsive regulatory mechanism **(Singh et al., 2022).**

5.3 Phosphorylation Cascades

Protein phosphorylation is the most prevalent post-translational modification in stress signaling, with kinases and phosphatases acting as molecular switches that control the activity of signaling components **(Gandhi & Oelmüller, 2023).** CPKs phosphorylate ABA-responsive transcription factors and ion channels in response to Ca^{2+} signals **(Atif et al., 2019).** RLKs phosphorylate MAP kinases and other downstream effectors in response to stress perception **(Li et al., 2017)**. The interplay between phosphorylation and dephosphorylation events determines the net output of stress signaling cascades and the magnitude of the transcriptional response **(Atif et al., 2019).**

5.4 Cyclophilins and Protein Folding

Cyclophilins are peptidyl-prolyl cis-trans isomerases (PPIases) that catalyze the isomerization of peptide bonds preceding proline residues, facilitating protein folding and assembly. In plants, cyclophilin A (CyPA) was involved in signal transduction mechanisms regulating various abiotic stresses *via* phosphoprotein cascades, Ca^{2+}, and other secondary signaling molecules. A new class of cyclophilin, OsCyP-25, from rice (*Oryza sativa* L.) was upregulated in response to different abiotic stresses including salinity, cold, heat, and drought. The cyclophilin A homologue from *Piriformospora indica* (PiCyPA) is likely to be a part of the general cellular stress response to multiple abiotic stresses, which is conserved in prokaryotes, fungi, and plants **(Trivedi et al., 2013).**

6. Reactive Oxygen Species (ROS) Signaling and Antioxidant Defense

6.1 ROS as Stress Signals and Damaging Agents

Reactive oxygen species (ROS), including superoxide (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radicals (•OH), are produced as inevitable byproducts of aerobic metabolism and are generated in excess under virtually all abiotic stress conditions. Abiotic stresses that restrict CO_2 availability because of stomatal closure facilitate the generation of ROS molecules in chloroplasts. ROS serve a dual role: at low concentrations, they act as signaling molecules that activate stress-responsive gene expression; at high concentrations, they cause oxidative damage to proteins, lipids, and nucleic acids **(Sasi et al., 2018).**

The heat shock transcription factor (Hsf) in *Syzygium cumini* regulates oxidative stress response by directly sensing ROS **(Chakraborty et al., 2023),** illustrating the direct coupling between ROS levels and transcriptional responses. CPK11, induced by H_2O_2, regulates and controls the activity of SOD and APX production induced by the ABA signaling pathway **(Atif et al., 2019),** demonstrating the integration of ROS and Ca^{2+} signaling in antioxidant defense.

6.2 Antioxidant Enzyme Systems

Plants possess a sophisticated enzymatic antioxidant defense system comprising SOD, catalase (CAT), APX, glutathione reductase (GR), and peroxidases **(Hernández-Bueno et al., 2021).** To survive under conditions that consist of growing levels of abiotic stress, plants alter their metabolism by activating signal cascades and regulatory proteins such as transcription factors and heat shock factors, which activate and modify the antioxidant defense system. This response acts to help maintain homeostasis and synthesize and accumulate compatible solutes **(Patel et al., 2023).**

Peroxidases have been shown to enhance stress tolerance. A versatile peroxidase from the fungus *Bjerkandera adusta* confers abiotic stress tolerance in transgenic tobacco plants, demonstrating that heterologous expression of antioxidant enzymes can improve plant stress tolerance. Plants have a large number of peroxidase isozymes, which are encoded by multigenic families **(Hernández-Bueno et al., 2021).**

6.3 Glyoxalase System and Methylglyoxal Detoxification

Methylglyoxal (MG) is a cytotoxic byproduct of glycolysis that accumulates under abiotic stress conditions. The glyoxalase pathway, comprising glyoxalase I (Gly I) and glyoxalase II (Gly II), detoxifies MG using glutathione as a cofactor. Expression of glyoxalase genes, as well as enzyme activity, have been reported to be altered in response to various abiotic, biotic, hormonal, and chemical treatments. Overexpression of MG-detoxifying glyoxalase pathway provides significant abiotic stress tolerance by resisting the excess accumulation of MG in transgenic tobacco and tomato plants. Both glyoxalase enzymes and methylglyoxal level are considered as biomarkers for plant stress tolerance **(Islam & Ghosh, 2018).**

7. Osmotic Adjustment and Compatible Solute Accumulation

7.1 Proline and Other Osmolytes

Under osmotic and drought stress conditions, plants synthesize and accumulate a diverse array of low-molecular-weight organic solutes collectively termed compatible solutes or osmolytes that confer protection against cellular dehydration without disrupting normal metabolic functions **(Patel et al., 2023).** Among these, proline is perhaps the most extensively characterized; its rapid accumulation is orchestrated primarily through upregulation of the Δ^1-pyrroline-5-carboxylate synthetase (P5CS) pathway and concurrent suppression of proline dehydrogenase, resulting in substantial cytoplasmic proline pools that contribute to turgor maintenance and enzyme stabilization **(Zhang et al., 2014).** Beyond proline, glycine betaine synthesized *via* the choline oxidation pathway stabilizes thylakoid membranes and protects the photosynthetic apparatus under high-salinity and temperature stress, while trehalose and mannitol serve dual roles as osmoprotectants and reactive oxygen species (ROS) scavengers, collectively sustaining cellular redox homeostasis during prolonged stress exposure **(Antoniou et al., 2017).** The thermodynamic basis of osmotic adjustment is described by the van 't Hoff equation for osmotic potential:

$$\Psi_S = -(n/V) \cdot R \cdot T$$

where Ψ_S is the osmotic (solute) potential (MPa), n is the number of moles of solute, V is the volume of solvent (L), R is the universal gas constant (8.314×10^{-3} $\mathrm{L \cdot MPa \cdot mol^{-1} \cdot K^{-1}}$), and T is the absolute temperature (K). This relationship illustrates that increasing intracellular solute concentrations lowers Ψ_S, thereby maintaining a favorable water potential gradient for continued water uptake from the surrounding soil matrix. Importantly, the effectiveness of osmolyte-mediated adjustment is contingent not only on solute concentration but also on compartment-specific accumulation, with chloroplastic and cytosolic pools playing distinct protective roles **(Fidler et al., 2022).** Collectively, the coordinated induction of proline, glycine betaine, trehalose, and mannitol biosynthesis pathways represents a highly conserved and multifaceted adaptive strategy that underpins plant resilience to water-deficit environments, and their manipulation via genetic engineering or priming treatments holds considerable promise for improving crop performance under climate-change-associated abiotic stresses **(Patel et al., 2023).**

7.2 Betaine Synthesis

Another gene used to develop abiotic stress-tolerant crops is the betaine synthesis (*betA*) gene, derived from either *E. coli* or *Rhizobium meliloti*, which encodes choline dehydrogenase. Betaine accumulation contributes to osmotic adjustment and also protects macromolecular structures under stress conditions **(Patel et al., 2023).**

7.3 Ion Homeostasis Under Salinity Stress

Salinity stress imposes both osmotic and ionic stress on plants. The ionic component results from the accumulation of Na^+ and Cl^- ions to toxic levels in the cytoplasm. Plants maintain ion homeostasis through the activity of ion transporters and channels, including the KUP K^+ transporter family, which is involved in potassium deficiency and salt and drought stress response **(Chakraborty et al., 2023).** ABA-mediated signaling promotes the expression of ion transporters that exclude Na^+ from the cytoplasm or compartmentalize it in the vacuole. Research on rice seeds presoaked with ABA showed enhanced salinity tolerance through the suppression of Na^+ and Cl^- levels, lowering Na^+/K^+ ratios, as well as increasing soluble sugar content **(Luo et al., 2018).**

8. Non-Coding RNAs in Abiotic Stress Regulation

8.1 MicroRNAs (miRNAs)

MicroRNAs (miRNAs) are small (~21 nucleotide) non-coding RNAs that regulate gene expression post-transcriptionally by guiding the RNA-induced silencing complex (RISC) to complementary target mRNAs, resulting in their cleavage or translational repression **(Zhang et al., 2014; Patel et al., 2024).** Numerous miRNAs have been identified as potential targets for enhancing tolerance to abiotic stress, particularly cold, heat, salinity, and drought. For example, miRNAs were reported to be involved in tolerance against drought (miRNA156 and miR393), salt (miR319 and miR393), and temperature stress (miR9748, miR169, and miR1320) **(Patel et al., 2024).**

In potato, deep sequencing identified novel and conserved miRNAs related to drought stress, including miRNAs targeting WRKY transcription factors. WRKY transcription factors can bind with high affinity to the W-box cis-acting element, permitting signal transduction to regulate the expression of stress-related genes, resulting in plant stress tolerance **(Zhang et al., 2014).** In *Ammopiptanthus nanus*, conserved and lineage-specific miRNAs contributed to the cold stress response by regulating ROS homeostasis and stress signaling by negatively regulating the corresponding targets **(Zhu et al., 2023).**

8.2 Long Non-Coding RNAs (lncRNAs)

Long non-coding RNAs (lncRNAs) are transcripts longer than 200 nucleotides that lack significant protein-coding potential but play important regulatory roles in gene expression. Combined lncRNA and mRNA expression profiles identified lncRNA–miRNA–mRNA modules regulating the cold stress response in *Ammopiptanthus nanus*. *A. nanus* showed high levels of tolerance to drought, high salinity, high temperature, cold, and freezing stresses, and was used as an important material for studying the stress tolerance mechanism of woody plants. Researchers have carried out a number of studies using physiological and biochemical methods, transcriptomics, proteomics, and other omics techniques to analyze the abiotic stress tolerance mechanism and identify stress tolerance-related genes in *A. nanus* **(Zhu et al., 2023).**

8.3 Cell-Penetrating Peptides and miRNA Delivery

Cell-penetrating peptides (CPPs) offer a potential solution for improving plant tolerance to abiotic stress through the delivery of peptides and miRNAs. Several signaling peptides that play important roles in plant responses to abiotic stress have been identified and used to increase stress tolerance in plants. This emerging technology represents a novel approach to modulating stress-responsive miRNA levels in planta without the need for stable genetic transformation **(Patel et al., 2024).**

9. Epigenetic Mechanisms and Stress Memory

9.1 DNA Methylation

DNA methylation is a heritable epigenetic mark that plays important roles in regulating gene expression, transposon silencing, and genome stability. DNA methylation has been previously involved in the regulation of stress response genes, which may allow plants to transgenerationally adapt to stress conditions **(Lagiotis et al., 2023).** The intensity and duration of the abiotic stress stimulus (priming) can variably affect the intra

9.2 Histone Modifications

Histone modifications, including acetylation, methylation, phosphorylation, and ubiquitination, regulate chromatin accessibility and gene expression. Chromatin remodeling has been associated with a number of plant responses to abiotic signals, including cold, heat, drought, and salinity. Photon irradiance-dependent alterations in histone acetylation and global chromatin compaction have been recorded, illustrating the integration of light and stress signaling at the chromatin level. Since many developmental and environmental responses are known to be regulated by epigenetics, it is predicted that reprogramming of the epigenome will be a substantial factor in crop breeding and cultivar development **(Moshelion & Altman, 2015).**

9.3 Stress Priming and Epigenetic Memory

Stress priming refers to the phenomenon whereby a prior exposure to a mild or sublethal stress enhances the plant's ability to tolerate a subsequent, more severe stress. Climate change and global warming exacerbate abiotic stress incidents, which are predicted to become more frequent and severe within the century, posing a serious challenge for crop cultivation and production. To cope with such adverse environmental conditions, plants can reprogram their regular development at the expense of reproductive potential, favoring stress response mechanisms.

The overall molecular mechanism of priming-mediated responses against salt stress involves energy-dependent transmembrane receptor-like kinases (RLKs), which recognize the priming elicitors and, when activated, regulate the transcription of abiotic stress defense genes. In *Lolium perenne*, short-term epigenetic salt stress/recovery treatments could change the transcriptional response to subsequent abiotic stress, inducing transcriptional and metabolic changes and improving plants' stress response via inhibiting physiological damage (such as cell membrane stability and ROS) regulated by trainable genes **(Lagiotis et al., 2023)**. Abiotic stress might induce epigenetic changes as well, and epigenetic regulators might have an adaptive advantage although we must consider a negative impact on crop yield by preventing the plant from growing to its full potential **(Moshelion & Altman, 2015).**

10. Cross-Stress Signaling and Stress Crosstalk

10.1 Molecular Basis of Stress Crosstalk

Plants in natural environments are rarely exposed to a single abiotic stress in isolation; rather, they typically encounter multiple stresses simultaneously or sequentially **(Rane et al., 2021; Ambrosino et al., 2020).** The signal transduction genes and stress-tolerance genes often demonstrate overlapping functionalities when plants are subjected to abiotic stressors. For example, ethylene-response transcription factors and GA pathway regulators that are stress-responsive in heat stress were also reported to play important roles in regulating gene expression during submergence **(Islam et al., 2020).**

Global gene expression analysis of cassava seedlings revealed that cold and drought stress signal transduction pathways overlap at several points, with protein kinases and TFs corresponding to the most regulated genes. The important RLK group, which includes members like LRR-RLK, MRLK, and LecRLK, has been previously shown to be involved in mediating the cellular response to various environmental cues, hormonal signals, and stress perception **(Li et al., 2017).** The signaling mechanisms in plants during low and high temperature, drought, and salinity are different and yet related to each other **(Chakraborty et al., 2015).**

10.2 Chloroplast-Mediated Stress Responses

Chloroplasts are not only the sites of photosynthesis but also important sensors and integrators of abiotic stress signals. The metabolites synthesized in chloroplasts protect plants from abiotic and biotic stresses, including heat, cold, drought, salt, light, and pathogens. Through meta-expression analyses under abiotic stress conditions, 264 cold or heat stress-responsive plastid-related genes were identified in rice. The significance of the function of chloroplast-related genes in response to climate change has not been well studied in crops **(Rane et al., 2021),** representing an important knowledge gap.

10.3 Secondary Metabolites in Stress Adaptation

Secondary metabolites are produced and regulated in response to various abiotic and biotic stresses, and aid in better survival of the plants. In *Syzygium cumini*, various biotic and abiotic stress tolerance response genes displayed multiple signatures of adaptive evolution. Among the major genes with multiple signatures of adaptive evolution (MSA) involved in abiotic stress tolerance responses, ABF regulates the expression of ABA-responsive genes to provide salinity, drought, and osmotic stress tolerance; MPAO facilitates oxidative burst-mediated programmed cell death; KUP K^+ transporter family is involved in potassium deficiency and salt and drought stress response; and LOX confers abiotic (drought, salinity, etc.) and biotic stress tolerance **(Chakraborty et al., 2023).**

11. Omics Approaches to Dissecting Abiotic Stress Responses

11.1 Transcriptomics

Transcriptomic approaches, including microarray analysis and RNA sequencing (RNA-seq), have revolutionized our understanding of the global gene expression changes that occur during abiotic stress **(Ambrosino et al., 2020).** Transcriptome analysis may provide an overview of novel genes and regulatory networks linked with heat tolerance mechanisms in lentil **(Singh et al., 2019).** In rice seeds developing under heat stress, transcriptomic data-driven discovery revealed vital roles of heat-responsive genes in regulatory mechanisms **(Islam et al., 2020).** Comparative transcriptome analysis has uncovered different heat stress responses in heat-resistant and heat-sensitive jujube cultivars **(Jin et al., 2020).**

Bioinformatics resources for plant abiotic stress responses have expanded enormously in the omics era. Abiotic stresses, such as heat and cold, drought, salinity, and flooding, dramatically affect plant growth and crop yield, and extensive studies have been focused on understanding the molecular basis of abiotic stress response and the research for improved, productive plants adapted for stress tolerance **(Ambrosino et al., 2020).**

11.2 Genomics and Genome-Wide Association Studies (GWAS)

Genome-wide approaches have enabled the identification of quantitative trait loci (QTLs) and candidate genes associated with abiotic stress tolerance. The genetic basis of plant adaptation to abiotic stress remains poorly understood, even in genomic model species such as rice. Identification of stress tolerance genes is often limited to mutant lines or a relatively few individuals used in mapping populations, and wider analysis of natural allelic variants in cultivated and wild populations is rare **(Vigueira et al., 2016).**

In bread wheat, nitrogen deficiency tolerance was conferred by introgression of a QTL derived from wild emmer, with several candidate genes associated with abiotic stress identified within the QTL interval. These include genes encoding cold-regulated protein (COR) for plant adaptation to cold and drought stress tolerance, pentatricopeptide repeat proteins involved in resistance to abiotic stress including salinity, drought, and cold, and the HKMT protein that influences chromatin and DNA methylation under stress **(Govta et al., 2024)**.

Long-term balancing selection at the Phosphorus Starvation Tolerance 1 (*PSTOL1*) locus in wild, domesticated, and weedy rice (*Oryza*) illustrates how natural selection has shaped allelic diversity at stress tolerance loci. Abiotic stresses, such as drought, high salinity, and low soil nutrient levels, negatively impact crop production worldwide and are predicted to increase in coming decades due to climate change **(Vigueira et al., 2016)**.

11.3 Proteomics and Metabolomics

Proteomics and metabolomics provide complementary layers of information about the molecular responses to abiotic stress. Researchers have carried out a number of studies using physiological and biochemical methods, transcriptomics, proteomics, and other omics techniques to analyze the abiotic stress tolerance mechanism and identify stress tolerance-related genes **(Zhu et al., 2023).** Unraveling the genetic, epigenetic, transcriptomic, and metabolomic bases of stress tolerance mechanisms/traits is crucial for breeding climate-resilient or abiotic stress-tolerant crop varieties **(Rane et al., 2021).**

11.4 Genome Sequencing and Adaptive Evolution

Genome sequencing of *Syzygium cumini* (jamun) revealed adaptive evolution in secondary metabolism pathways associated with its medicinal properties and stress tolerance. Various biotic and abiotic stress tolerance response genes displayed multiple signatures of adaptive evolution in *S. cumini* **(Chakraborty et al., 2023).** High-throughput phenotyping and advances in bioinformatics allow researchers to screen for key genomic features that contribute to abiotic stress tolerance **(Patel et al., 2023).**

12. Biotechnological Strategies for Engineering Stress-Tolerant Crops

12.1 Transgenic Approaches

Transgenic technology has been widely used to overexpress stress-related genes in crop plants, with numerous examples of improved stress tolerance. A long list of transgenic plants with a myriad of exogenous genes has been shown to display improved tolerance to drought, salt, cold, heat, and oxidative stresses **(Hernández-Bueno et al., 2021).** Transgenic rice lines overexpressing stress-related NAC TFs exhibited significant improvement of abiotic stress tolerance under severe stress conditions without any adverse effect on yield, or even with yield increase **(Yuan et al., 2019).**

The betaine synthesis (*betA*) gene, derived from either *E. coli* or *Rhizobium meliloti*, which encodes choline dehydrogenase, has been used to develop abiotic stress-tolerant crops **(Patel et al., 2023)**. Overexpression of MG-detoxifying glyoxalase pathway provides significant abiotic stress tolerance by resisting the excess accumulation of MG in transgenic tobacco and tomato plants **(Islam & Ghosh, 2018).** A versatile peroxidase from the fungus *Bjerkandera adusta* confers abiotic stress tolerance in transgenic tobacco plants **(Hernández-Bueno et al., 2021).**

12.2 CRISPR/Cas9 and Genome Editing

CRISPR/Cas9 and related genome editing technologies offer unprecedented precision in modifying stress-related genes and regulatory elements. Climate change and extensive agriculture practice have provoked water scarcity, severe droughts, and soil salinity around the world; therefore, major efforts are required to improve abiotic stress tolerance in plants, either by classic genetics or genetic manipulation techniques using transgenic, CRISPR/Cas9, or oligonucleotide-directed mutagenesis tools **(Hernández-Bueno et al., 2021).** Methods of crop improvement and applications towards fortifying food security include CRISPR-based approaches targeting key genomic features that contribute to abiotic stress tolerance **(Patel et al., 2023).**

12.3 Marker-Assisted Selection and Conventional Breeding

Conventional breeding and marker-assisted selection (MAS) remain important tools for improving abiotic stress tolerance in crops. Seed companies are investing enormous effort into developing crops with higher tolerance to drought, heat, cold temperatures, and salinity. Recent studies have identified a large number of genetic and molecular networks underlying plant adaptation to adverse environmental growth conditions **(Moshelion & Altman, 2015)**. However, abiotic tolerance mechanisms in crop plants are limited and have largely failed to bridge the gap between theoretical research and crop breeding **(Rane et al., 2021).**

12.4 Grafting and Rootstock-Mediated Stress Tolerance

Grafting is widespread to improve plant performance in terms of yield, quality, and resilience to abiotic and biotic stresses. The use of tolerant rootstocks to different abiotic stresses, such as drought, salinity, and drastically rising or decreasing temperature, is becoming indispensable in this global climate change era. The influence of rootstocks on many scion biology aspects is well-established, and molecular aspects of root-to-shoot and/or shoot-to-root signaling events are starting to be known and show how grafting triggers differential responses between the scion and rootstock. Comparative transcriptomic analyses of citrus cold-resistant vs. sensitive rootstocks suggest a relevant role of ABA signaling in triggering cold scion adaptation **(Primo-Capella et al., 2022).** Current biotechnological approaches for improving abiotic stress tolerance are summarized in Table 3.

Table 3. Biotechnological Strategies for Enhancing Abiotic Stress Tolerance

Strategy	Mechanism	Example Application	Advantages	References
Transgenic overexpression	Introduce stress-responsive genes	NAC TF overexpression in rice	High specificity	(Yuan et al., 2019)
CRISPR/Cas9	Targeted genome editing	Editing stress-related loci	Precision breeding	(Hernández-Bueno et al., 2021)
Marker-assisted selection	QTL-based breeding	PSTOL1 introgression	Field applicability	(Vigueira et al., 2016)
Glyoxalase engineering	MG detoxification	Transgenic tobacco/tomato	ROS reduction	(Islam & Ghosh, 2018)
Antioxidant enzyme engineering	ROS scavenging	Peroxidase expression	Enhanced tolerance	(Hernández-Bueno et al., 2021)
Grafting	Rootstock-mediated signaling	Citrus cold tolerance	Non-GMO strategy	(Primo-Capella et al., 2022)

13. Crop-Specific Adaptations to Abiotic Stress

13.1 Cereals

Cereals, including rice, wheat, maize, and barley, are the most important food crops globally and are severely affected by abiotic stresses. The adaptation and tolerance of major cereals and legumes to important abiotic stresses have been extensively reviewed. In wheat, the chloroplast-localized membrane protein TaRCI has been characterized for its role in heat, drought, and salinity stress tolerance, and could be a potential candidate for gene manipulation for improving stress tolerance in crop plants **(Rane et al., 2021).** In rice, numerous stress-related genes and regulatory networks have been characterized, including NAC TFs, WRKY TFs, CPKs, and RLKs **(Atif et al., 2019; Song et al., 2009).**

13.2 Legumes

Legumes, including soybean, lentil, and *Medicago sativa*, are important sources of protein and are also severely affected by abiotic stresses **(Rane et al., 2021).** In soybean, genome-wide dissection and expression profiling of unique glyoxalase III genes revealed differential patterns of transcriptional regulation under abiotic stress **(Islam & Ghosh, 2018).** In lentil, transcriptome analysis identified novel genes and regulatory networks linked with heat tolerance mechanisms **(Singh et al., 2019).** Melatonin systemically ameliorates drought stress-induced damage in *Medicago sativa* plants by modulating nitro-oxidative homeostasis and proline metabolism **(Antoniou et al., 2017).**

13.3 Triticale and Other Cereals

Triticale has been found to tolerate some abiotic stress conditions better than other cereal species**.** For instance, triticale was reported to be more drought tolerant than durum wheat, and its salinity tolerance was better than wheat and even similar to barley. Some estimates suggest that over 90% of rural farmland was affected by abiotic stressors at some point during the growing season **(Atak et al., 2023),** underscoring the importance of developing stress-tolerant varieties of all major crops.

14. Integrative Models of Plant Stress Response

14.1 Systems Biology Approaches

The complexity of plant stress responses, involving thousands of genes, proteins, and metabolites interacting in dynamic networks, necessitates systems biology approaches for their comprehensive understanding. Plants display an amazing diversity and, owing to their sessile nature, they evolved a broad range of molecular mechanisms to respond to complex networks of environmental signals, which activate multiple pathways, modulated by different responsive genes. Bioinformatics resources for plant abiotic stress responses have expanded enormously in the fast-evolving omics era **(Ambrosino et al., 2020).**

14.2 Network Analysis and Gene Regulatory Networks

Gene regulatory network (GRN) analysis has been used to identify key regulatory hubs and modules in plant stress responses. Transcriptomic data-driven discovery of global regulatory features of rice seeds developing under heat stress revealed complex regulatory networks involving transcription factors, signaling kinases, and hormone pathways **(Islam et al., 2020).** A protein-to-protein interaction network analysis associated with high temperature stress is expected to provide the basis for studying molecular mechanisms by which chloroplasts will respond to different abiotic stresses under changing climatic scenarios **(Rane et al., 2021).**

14.3 Mathematical Modeling of Stress Tolerance

Mathematical modeling provides a quantitative framework for understanding and predicting plant stress responses. A general model for plant stress tolerance can be expressed using the Tolerance Index (TI), which quantifies the relative performance of plants under stress compared to optimal conditions:

$$TI = \frac{Y_{stress}}{Y_{control}} \times 100$$

where Y_{stress}represents plant yield (or any relevant performance metric) under stress conditions, and $Y_{control}$represents the corresponding yield under non-stress (control) conditions. This index provides a percentage-based measure of tolerance, with higher values indicating greater resilience.

To account for **multiple simultaneous stresses**, the model can be extended as follows:

$$TI_{combined} = \prod_{i=1}^{n} \left(\frac{Y_{stress,i}}{Y_{control}}\right)^{w_i}$$

where $n$is the total number of stress factors, $Y_{stress,i}$is the yield under the i-th stress condition, and $w_i$is the weight assigned to each stress based on its relative importance.

The weights allow differential contributions of individual stresses to the overall tolerance index.

More sophisticated models incorporate the dynamics of stress signaling, gene expression, and metabolic responses using systems of ODEs or stochastic differential equations (SDEs), enabling the prediction of stress tolerance phenotypes from molecular data (Atif et al., 2019; Gandhi & Oelmüller, 2023).

15. Future Perspectives and Research Priorities

15.1 Understanding Multi-Stress Responses

A major challenge for future research is to understand how plants respond to multiple simultaneous stresses, which is the condition most commonly encountered in agricultural settings **(Ambrosino et al., 2020).** The signal transduction genes and stress-tolerance genes often demonstrate overlapping functionalities when plants are subjected to abiotic stressors. Unraveling the genetic, epigenetic, transcriptomic, and metabolomic bases of stress tolerance mechanisms/traits is crucial for breeding climate-resilient or abiotic stress-tolerant crop varieties **(Rane et al., 2021).**

15.2 Translating Molecular Knowledge to Crop Improvement

Despite significant advances in understanding the molecular mechanisms of plant stress tolerance, abiotic tolerance mechanisms in crop plants are limited and have largely failed to bridge the gap between theoretical research and crop breeding. Some success has been achieved in understanding the crop tolerance mechanisms to abiotic stresses, and a few of them have been explored for crop improvement. Future research should focus on translating molecular knowledge into practical breeding strategies, leveraging the power of genomics, transcriptomics, and genome editing **(Patel et al., 2023; Moshelion & Altman, 2015).**

15.3 Epigenomics and Transgenerational Stress Memory

The role of epigenetic mechanisms in stress memory and transgenerational adaptation is an emerging and rapidly evolving field. DNA methylation has been previously involved in the regulation of stress response genes, which may allow plants to transgenerationally adapt to stress conditions. Future research should investigate the mechanisms by which stress-induced epigenetic changes are established, maintained, and erased, and how they contribute to adaptive evolution **(Lagiotis et al., 2023; Moshelion & Altman, 2015).**

15.4 Emerging Technologies

Emerging technologies, including single-cell transcriptomics, spatial transcriptomics, and advanced genome editing tools, offer new opportunities for dissecting the molecular mechanisms of plant stress responses at unprecedented resolution. Omics approaches have now been extensively studied and integrated to decipher the molecular mechanisms leading to abiotic stress tolerance in plants. Cell-penetrating peptides offer a potential solution for improving plant tolerance to abiotic stress through the delivery of peptides and miRNAs **(Patel et al., 2024)**, representing a novel and potentially transformative approach to crop improvement.

16. Conclusion

Plant adaptation to abiotic stress under changing climates is a complex, multilayered process involving the coordinated action of stress perception systems, signal transduction cascades, transcriptional regulatory networks, post-translational modifications, epigenetic mechanisms, and metabolic adjustments. Abiotic stresses collectively account for more than 50% of yield losses in major crop species, and the accelerating pace of climate change is predicted to intensify these losses. The molecular mechanisms reviewed here from RLK-mediated stress perception; and CPK-mediated Ca^{2+} signaling, through ABA, JA, ethylene, and melatonin signaling, to the transcriptional regulatory networks orchestrated by NAC, WRKY, AP2/ERF, HSF, and other TF families, and the post-translational regulatory layers of ubiquitination, SUMOylation, and phosphorylation, collectively constitute a sophisticated and highly integrated stress response system.

Epigenetic mechanisms, including DNA methylation, histone modifications, and non-coding RNA-mediated regulation, add further layers of complexity and provide mechanisms for stress memory and transgenerational adaptation. Omics technologies have dramatically accelerated the pace of discovery in this field, and biotechnological strategies including transgenic overexpression, CRISPR/Cas9 genome editing, and marker-assisted selection offer promising avenues for translating molecular knowledge into climate-resilient crops.

Despite these advances, significant knowledge gaps remain, particularly regarding the molecular basis of multi-stress responses, the mechanisms of transgenerational epigenetic inheritance, and the translation of laboratory findings to field-level crop improvement. Addressing these gaps will require integrated, interdisciplinary approaches combining molecular biology, systems biology, computational modeling, and plant breeding. The development of climate-resilient crops capable of sustaining productivity under the abiotic stress conditions projected for the coming decades is not merely a scientific challenge but an urgent societal imperative.

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