Journal of Plant Stress Physiology 2026, 12: 86-97
https://doi.org/10.25081/jpsp.2026.v12.9785

Review Article

Decoding plant resilience: Molecular mechanisms and regulatory strategies under abiotic stress: A review

Saleha Saeed*, Sami Ullah

Botany Department, University of Peshawar, Pakistan

(Received: October 27, 2025; Revised: October 14, 2026; Accepted: October 16, 2026; Published: November 13, 2026)

*Corresponding author: Saleha Saeed, E-mail: saleha362026@uop.edu.pk

Abstract

Abiotic stress refers to the detrimental influence of non-living environmental factors on plants, limiting their growth, development, and productivity. Stressors such as drought, salinity, and extreme temperatures often act simultaneously or interactively, imposing complex physiological and molecular challenges. Over time, plants have evolved intricate mechanisms to sense these adverse cues and modulate their metabolic and developmental programs to ensure survival and reproduction. This review synthesizes current findings on how plants perceive and respond to abiotic stress through coordinated signaling networks and regulatory cascades. Emphasis is placed on signal perception, transduction pathways, transcriptional and post-translational regulation, and the integration of stress responses with growth processes. In addition, we discuss recent progress in genetic and biotechnological strategies aimed at enhancing crop performance under stress conditions. Finally, the paper highlights how deeper insight into stress signaling can facilitate the development of resilient, high-yield crops and promote sustainable agricultural systems.

Keywords: Abiotic stress, Stress sensing, Signal transduction, Stress regulation, Plant adaptation

Introduction

Environmental conditions are a dominant determinant of plant growth and development, particularly for sessile organisms that cannot escape unfavorable surroundings (Zhang *et al.,* 2022b). Abiotic stress encompasses any adverse influence from non-living factors—such as drought, salinity, flooding, or temperature extremes—that disrupts normal physiological and biochemical processes (Zhang *et al.,* 2020, 2022b). These stresses alter gene expression, cell metabolism, and developmental patterns, leading to reduced yield and limited distribution of plant species across ecosystems (Zhang *et al.,* 2022b).

Among these factors, extreme temperature, water deficit, and saline soils are particularly damaging, often occurring together in natural environments (Zhang *et al.,* 2022b). Understanding how plants detect, transduce, and respond to these stressors has become a central focus in plant biology (Swain *et al.,* 2023). Research on stress-response signaling at molecular, cellular, and physiological levels provides compelling evidence for diverse and highly regulated adaptive mechanisms (Markham & Greenham, 2021).

Drought and salt stresses, for instance, impose osmotic imbalances that trigger the accumulation of inorganic and organic solutes, leading to ion toxicity, reactive oxygen species (ROS) buildup, plasma-membrane disruption, and damage to cellular structures (Praveen *et al.,* 2023). Non-adaptive changes under stress include protein misfolding and cell-wall deformation, whereas adaptive modifications enhance tolerance and recovery (Radha *et al.,* 2023). Hence, plant responses to abiotic stress represent a multilevel regulatory network involving sensing, signal transduction, transcriptional regulation, protein translation, and post-translational modifications (Dong *et al.,* 2022).

The rising global population and intensifying climate change further amplify the urgency to safeguard food security (Zhang *et al.,* 2022b). Abiotic stressors—particularly drought, salinity, and temperature extremes—constitute major constraints on global crop productivity (Zhang *et al.,* 2020). Despite advances in genetic engineering and molecular breeding, achieving durable stress tolerance in crops remains challenging (Radha *et al.,* 2023; Zhang *et al.,* 2023). One underlying reason is the trade-off between growth and stress defense, as plants often redirect energy and resources from growth toward protective responses (Swain *et al.,* 2023). However, emerging evidence suggests that growth inhibition under mild stress is not merely a consequence of energy shortage but an active, adaptive strategy that primes plants for future severe stress (Zhang *et al.,* 2022b; Praveen *et al.,* 2023).

Abiotic stress can be detected in various cellular compartments—such as the cell wall, plasma membrane, cytoplasm, mitochondria, chloroplasts, peroxisomes, endoplasmic reticulum, and nucleus—initiating cascades of molecular responses. Stress sensors relay signals through secondary messengers, including Ca^{2+}, ROS, and protein kinases, which subsequently regulate downstream gene expression. Over evolutionary time, plants have refined these systems to balance growth and survival, ensuring reproductive success under hostile conditions.

This review provides an integrated overview of the mechanistic basis of abiotic stress perception, signaling, and regulation in plants. It also examines emerging molecular and biotechnological approaches that enhance stress tolerance and explores how understanding cross-talk between growth and stress signaling can inform the development of resilient, high-yield crops for sustainable agriculture.

Stress sensing and regulatory mechanisms

Osmotic stress

Abiotic stresses such as high salinity and drought induce hyperosmotic conditions in plant cells, causing substantial challenges to water homeostasis and cellular integrity (Munns *et al.,* 2020). To survive these conditions, plants employ osmoregulation, a process that increases intracellular solute concentrations by accumulating inorganic ions and organic osmolytes. This adjustment reduces osmotic potential and enhances water retention capacity (Gong *et al.,* 2020).

Inorganic ions such as K^+, Na^+, and Ca^{2+}, along with compatible solutes like proline, betaine, soluble sugars, and polyols, play crucial roles in osmotic adjustment (Alpert, 2006; Munns *et al.,* 2020). For instance, in drought-stressed leaves of *naked fruitwood*, accumulation of proline, soluble sugars, and soluble proteins helps lower osmotic potential and improves drought tolerance (Carpenter *et al.,* 1990). As drought intensifies, proline levels continue to rise, while soluble protein content initially declines and then increases once soil moisture drops below 31.38% (Kishor *et al.,* 2005).

In rice (*Oryza sativa*), osmotic stress activates OSCA ion channels, enabling rapid Ca^{2+} influx into cells (Liu *et al.,* 2018; Maity *et al.,* 2019). Additionally, osmotic stress rapidly triggers activation of the SnRK2 family of protein kinases, which are key regulators of osmotic stress tolerance (Maszkowska *et al.,* 2021). Lipid-derived signals, such as sphingolipids and phosphatidic acid, also participate in osmotic stress signaling (Hou *et al.,* 2016).

Furthermore, plant cells synthesize osmoregulatory proteins that reduce cellular osmotic potential, minimize dehydration, and enhance stress resilience. Autophagy, a conserved degradation pathway mediated by ATG genes, also plays a central role in growth, development, and stress adaptation (Gatica *et al.,* 2019). Studies across several plant species have demonstrated that ATG gene families are vital for stress tolerance and cellular homeostasis under osmotic stress (Nguyen *et al.,* 2016; Izumi *et al.,* 2017; Lystad & Simonsen, 2019; Nakamura & Izumi, 2019; Young *et al.,* 2019).

Salinity stress

Soil salinity is one of the most pervasive abiotic stresses limiting global agricultural productivity. Elevated salt levels disrupt plant growth through osmotic stress, ion toxicity, and oxidative stress. In response, plants activate defense mechanisms that regulate stomatal movement, synthesize osmolytes, compartmentalize toxic ions, and scavenge excess ROS to minimize damage (Zhu, 2002).

Early osmotic signaling under salt stress induces stomatal closure, reducing water loss and enhancing tolerance to both drought and salinity (Lizana *et al.,* 2026). This process also improves the dynamic regulation of stomata under changing light intensities, optimizing photosynthetic efficiency (Zhang *et al.,* 2022c).

Plants counter ion toxicity by compartmentalizing Na^+ and Cl^- ions into vacuoles or vesicles while using compatible solutes for osmotic balance. In *Arabidopsis thaliana*, the SOS (Salt Overly Sensitive) signaling pathway plays a key role. Upon salt stress, AtCBL4/SOS3 in the roots perceives Ca^{2+} signals and activates the protein kinase AtCIPK24/SOS2, which phosphorylates the Na^+/H^+ antiporter SOS1 on the plasma membrane (Qiu *et al.,* 2002). SOS2 also likely phosphorylates Na^+/H^+ exchangers (AtNHX) on vesicle membranes, facilitating both Na^+ efflux and vacuolar sequestration (Qiu *et al.,* 2004). These coordinated actions maintain cytoplasmic ion homeostasis and a stable K^+/Na^+ ratio, which is essential for enzymatic activity and metabolic balance.

Additionally, Na^+ sequestration increases vacuolar osmotic pressure, promoting water uptake and alleviating dehydration. High salinity alters lipid membrane composition and cell wall organization through pectin–Ca^{2+} substitution, phenolic cross-linking, and ROS-mediated reinforcement (Zhu, 2016).

Recent evidence highlights the role of transcription factors in salt tolerance. For example, the IbBBX24–IbTOE3–IbPRX17 module in sweet potato enhances salt resistance by promoting ROS scavenging through peroxidase gene activation (Zhang *et al.,* 2022a). Understanding these molecular response modules provides valuable insights for developing salt-tolerant plant varieties.

Temperature stress

Temperature extremes—both high and low—severely affect plant metabolism, membrane stability, and protein function. Cold stress rapidly activates numerous transcription factors, notably CBF (C-repeat Binding Factors) from the AP2 family, which induce expression of cold-responsive (COR) genes (Chinnusamy *et al.,* 2007). Cold sensing involves alterations in membrane fluidity, cytoskeletal organization, and Ca^{2+} fluxes, triggering MAP kinase (MAPK) signaling pathways (Sangwan *et al.,* 2002). Several plasma membrane-localized Ca^{2+} channels act as primary cold sensors (Furuya *et al.,* 2013; Liu *et al.,* 2021; Manasa *et al.,* 2022; Rubab *et al.,* 2022).

In Arabidopsis, loss-of-function mutations in AtANN1, a Ca^{2+} transporter, significantly impair Ca^{2+} influx and reduce freezing tolerance (Liu *et al.,* 2021). Accumulation of CBF transcription factors stabilizes phytochrome B (phyB), enhancing freezing resistance (Jiang *et al.,* 2020).

In contrast, heat stress leads to protein misfolding and denaturation, activating the synthesis of heat shock proteins (HSPs), which function as molecular chaperones to refold denatured proteins and maintain proteostasis (Scharf *et al.,* 2012). HSPs are distributed across cellular compartments such as the cytoplasm, endoplasmic reticulum, and mitochondria (Lin *et al.,* 2001) and are grouped into five

families: HSP100, HSP90, HSP70, HSP60, and sHSPs (Wang *et al.,* 2004). Among these, HSP70 is the most abundant, with expression levels strongly influenced by temperature changes (Siddique *et al.,* 2008; Jung *et al.,* 2013; Augustine *et al.,* 2015; Guo, 2016; Li & Liu, 2019; Jiang *et al.,* 2021; Wang *et al.,* 2024).

In *Arabidopsis* seedlings, heat stress rapidly elevates HSP70 transcript levels (Lin *et al.,* 2001; Park & Seo, 2015), while in rice, HSP70 genes are upregulated within minutes at 40 °C (Du *et al.,* 2021). Misfolded proteins under heat stress interact with HSPs, releasing heat shock transcription factors (HSFs) that activate heat-responsive genes. The MAPK cascade, activated by altered membrane fluidity and Ca^{2+} signaling, further regulates HSP expression and enhances thermal tolerance (Sangwan *et al.,* 2002).

Interestingly, cold and heat stress share overlapping regulatory mechanisms involving membrane dynamics, MAPK signaling, phospholipid metabolism, nitric oxide (NO), proteasomal degradation, and ROS accumulation (Chinnusamy *et al.,* 2007). These shared pathways illustrate plants' ability to integrate environmental cues into coordinated adaptive responses.

Signal transduction under abiotic stress

Plant responses to adverse environmental conditions begin with precise signal perception, followed by the activation of diverse signal transduction pathways. These cascades rely on second messengers—such as calcium ions (Ca^{2+}), reactive oxygen species (ROS), nitric oxide (NO), phospholipids, and protein kinases—to amplify and coordinate cellular responses (Zhu, 2016). Once stress is perceived, these messengers transmit information to downstream effectors that regulate transcription, metabolism, and physiological adaptation (Zhang *et al.,* 2022b).

Calcium (Ca^{2+}) signaling

Abiotic stresses including cold, drought, and salinity share common cellular signatures—particularly osmotic stress and a rapid, transient increase in intracellular Ca^{2+} concentrations (Dong *et al.,* 2022; Zhang *et al.,* 2022b). Owing to its highly regulated cellular distribution, Ca^{2+} serves as a universal second messenger in plant stress signaling (Dong *et al.,* 2022). Its low cytosolic baseline level allows for swift, localized changes in response to environmental cues, which are decoded by numerous Ca^{2+}-binding proteins (Martí *et al.,* 2013).

Stress-induced Ca^{2+} signals vary in intensity, frequency, and spatial distribution, forming specific "calcium signatures" that encode distinct responses (Zhu, 2016). In *Arabidopsis*, osmotic stress can induce transient Ca^{2+} spikes within 15 seconds in guard cells (Dong *et al.,* 2022). These changes are sensed by calcium-binding proteins such as calmodulins (CaMs), calcineurin B-like proteins (CBLs), and calcium-dependent protein kinases (CDPKs or CPKs), which translate Ca^{2+} fluctuations into phosphorylation-based signaling events (Brandt *et al.,* 2015).

During salt stress, the SOS (Salt Overly Sensitive) pathway exemplifies this mechanism. In *Arabidopsis thaliana*, a stress-induced cytosolic Ca^{2+} signal is recognized by SOS3 (CBL4) or SCaBP8, which then interact with SOS2 (CIPK24) to activate Na^+/H^+ antiporters (SOS1) that expel excess sodium from the cytoplasm (Hrabak *et al.,* 2003) Plants also contain multiple CBL–CIPK complexes, each mediating specific Ca^{2+}-dependent stress responses and regulating ion transport proteins (Ma *et al.,* 2019). These dynamic networks underscore Ca^{2+}'s pivotal role in maintaining ionic and osmotic homeostasis during abiotic stress (Zhang *et al.,* 2022b).

Reactive Oxygen Species (ROS) signaling

Reactive oxygen species (ROS)—including superoxide anion (O_2^-), hydrogen peroxide (H_2O_2), hydroxyl radicals (OH•), and singlet oxygen ($^1O_2$)—are both damaging byproducts of stress and crucial signaling molecules in plant defense (Zhang *et al.,* 2022b). ROS are generated in multiple compartments such as chloroplasts, mitochondria, peroxisomes, and the plasma membrane through the action of NADPH oxidases (Rbohs).

Among these, RbohD and RbohF, located at the plasma membrane, play major roles in generating apoplastic ROS that activate Ca^{2+}-dependent and electrical signaling throughout the plant (Qi *et al.,* 2018). This "ROS wave" can propagate at rates up to 8 cm per minute in *Arabidopsis*, linking local stress perception to systemic signaling.

While excessive ROS can oxidize proteins, lipids, and nucleic acids, controlled ROS levels mediate essential processes such as retrograde signaling (from chloroplast to nucleus) and abscisic acid (ABA)–dependent stress signaling (Zhang *et al.,* 2022b). Thus, ROS function as versatile messengers that integrate environmental stress cues with cellular defense mechanisms.

Protein phosphorylation

Protein phosphorylation represents one of the most fundamental regulatory events in plant signal transduction under abiotic stress. Protein kinases and phosphatases modulate the activity of target proteins by reversible phosphorylation, allowing plants to fine-tune stress responses (Min *et al.,* 2019).

Members of the SnRK2 (Sucrose Non-Fermenting-1-Related Protein Kinase 2) family and PP2C (Type 2C Protein Phosphatase) family are critical regulators in multiple stress pathways, including ABA signaling, and are conserved across crops such as rice and maize (Min *et al.,* 2019). These kinases phosphorylate downstream targets such as transcription factors, plasma membrane anion channels (SLAC1) that control stomatal closure, and NADPH oxidases (RbohF) that mediate ROS generation (Geiger *et al.,* 2009, 2010).

Another key phosphorylation system is the MAP kinase (MAPK) cascade, which comprises MAP3K–MAP2K–

MAPK tiers and transmits signals from receptors to the nucleus. In *Arabidopsis*, the MEKK1–MKK2–MPK4 cascade is activated by cold-induced Ca^{2+} signals through the CRLK1 receptor-like kinase (Yang *et al.,* 2010; Wang *et al.,* 2020). Conversely, the MAP3K17/18–MKK3–MPK1/2/7/14 module functions downstream of SnRK2 kinases in ABA-mediated responses and operates largely independent of Ca^{2+} signaling (Zhao *et al.,* 2017).

These phosphorylation cascades illustrate how plants use hierarchical signaling networks to convert transient stress stimuli into stable physiological and genetic adaptations.

Abscisic Acid (ABA) signaling

Abscisic acid (ABA), often referred to as the "stress hormone," is a central regulator of plant responses to abiotic stress (Zhang *et al.,* 2022b). Derived from carotenoids (Zhang *et al.,* 2020), ABA controls processes such as seed maturation, dormancy, stomatal regulation, senescence, and growth inhibition under stress conditions (Ma *et al.,* 2009; Min *et al.,* 2019).

A major breakthrough in understanding stress signaling was the identification of ABA receptors and the elucidation of the PYR/PYL/RCAR–PP2C–SnRK2 signaling module (Melcher *et al.,* 2009). In this pathway, ABA binds to PYR/PYL/RCAR receptors, inducing a conformational change that enables binding to PP2C phosphatases (Park *et al.,* 2009; Wang *et al.,* 2013). This interaction inhibits PP2C activity, thereby releasing SnRK2 kinases from repression. Activated SnRK2s phosphorylate downstream targets such as ABF/AREB transcription factors, Rbohs (for ROS generation), and ion channels that mediate stomatal closure (Zhang *et al.,* 2020).

ABA signaling thus serves as a master regulatory hub, integrating environmental cues such as drought, salinity, and temperature into coordinated physiological and molecular responses. Its cross-talk with Ca^{2+} and ROS pathways ensures rapid stress perception and the fine-tuned activation of defense mechanisms essential for plant survival (Zhang *et al.,* 2020).

Regulation of abiotic stress responses

Plants rely on multiple layers of regulation—ranging from transcriptional to epigenetic control—to coordinate precise and efficient responses to environmental stress. These regulatory systems ensure rapid perception, signal integration, and physiological adaptation under fluctuating conditions (Zhang *et al.,* 2022b).

Transcriptional regulation

Abiotic stress triggers extensive transcriptional reprogramming that rebalances water and ion homeostasis and activates protective mechanisms, including osmoregulation, detoxification, and repair (Zhang *et al.,* 2022b). Genome-wide studies have identified numerous transcription factor (TF) families involved in these processes, such as NF-Y, WOX, WRKY, bZIP, and NAC, each orchestrating networks of stress-responsive genes.

Distinct transcriptional patterns often emerge depending on the stress type, but there is also significant overlap. Genes responsive to cold, drought, or salinity often encode components of MAPK cascades, Ca^{2+} signaling proteins, ROS metabolism enzymes, and proteins involved in apoptosis or degradation (Banerjee & Roychoudhury, 2017; Yang *et al.,* 2018; Nag *et al.,* 2021; Jang *et al.,* 2022; Praveen *et al.,* 2023).

A central regulator of abiotic stress transcription is abscisic acid (ABA), which induces phosphorylation-dependent cascades leading to gene activation. Many ABA-responsive genes contain a conserved *ABA-responsive element* (ABRE; ACGTGG/TC) in their promoters, while *ABA-independent pathways* are mediated by the *dehydration-responsive element* (DRE; TACCGACAT) (Narusaka *et al.,* 2003; Ma & Bohnert, 2007).

The CBF/DREB transcription factor family bridges these pathways:

- CBF1/2/3 genes primarily respond to cold stress, activating downstream cold-responsive (COR) genes.
- CBF4 and DREB2 respond mainly to osmotic and high-salinity stress (Yamaguchi-Shinozaki & Shinozaki, 2006).

Through these finely tuned networks, plants coordinate transcriptional activity to manage stress-specific and cross-tolerant responses that safeguard cellular function and promote survival.

Translational regulation

Translational control adds another vital layer of stress adaptation. Environmental stress often causes ribosome pausing, translation initiation blockades, and restructuring of ribosomal complexes (Merret *et al.,* 2015).

In *Arabidopsis*, high-temperature stress induces ribosomal stalling that leads to co-translational mRNA decay, primarily affecting transcripts that encode HSP70 chaperones (Merret *et al.,* 2013). This process involves the ribonuclease XRN4 and the RNA-binding protein LARP1, both essential for acclimation during prolonged heat exposure (Nguyen *et al.,* 2015). Interestingly, while XRN4 supports adaptation to chronic heat, it negatively regulates acute heat resistance by promoting the degradation of HSFA2, a major heat stress transcription factor (Merret *et al.,* 2017).

Under heat stress, translation initiation is inhibited, and mRNAs encoding ribosomal proteins are temporarily sequestered in stress granules. During recovery, these transcripts are released for rapid translation with the help of HSP101 chaperones (Chukka *et al.,* 2021). Mutations in translation initiation factors such as eIF5B reduce thermotolerance by disrupting this recovery mechanism.

Cold stress also influences translation. For example, the REIL2 gene regulates ribosome biogenesis and enhances cold tolerance, while chilling stress alters the association between chloroplast RNA-binding proteins (RBD1) and ribosomal RNAs, reducing chloroplast protein synthesis efficiency (Nishimura *et al.,* 2010; Yu *et al.,* 2020). Together, these findings emphasize that translation-level regulation is essential for balancing energy conservation and stress response during environmental fluctuations.

Post-translational regulation

Post-translational modifications (PTMs) fine-tune protein activity, localization, and stability under stress, enabling plants to respond within minutes of environmental change (Rodrigues *et al.,* 2013; Ding *et al.,* 2019; Willems *et al.,* 2019). These modifications include phosphorylation, ubiquitination, acetylation, and methylation, which modulate both signaling and structural proteins critical to stress adaptation.

Under osmotic and ABA stress, SnRK2 kinases phosphorylate transcription factors, transporters, and enzymes associated with ROS metabolism and osmolyte biosynthesis (Zhang *et al.,* 2020). Among SnRK2 isoforms, SnRK2.2, SnRK2.3, and SnRK2.6 (OST1) are strongly activated by ABA, while SnRK2.7 and SnRK2.8 are weakly induced. Mutants lacking SnRK2.2/3/6 show marked insensitivity to ABA during seed germination, seedling growth, and stomatal closure, underscoring their importance in ABA-mediated signaling (Wang *et al.,* 2013).

ABA effector proteins—such as bZIP transcription factors (ABI5, ABFs)—are phosphorylated by SnRK2s to regulate gene expression. Many ABA signaling events occur at the plasma membrane, where PYL receptors interact with C2-domain proteins to facilitate ion channel activation (e.g., SLAC1) and reduce transpiration during drought stress.

Recent phosphoproteomics analyses have identified multiple SnRK2 substrates associated with chloroplast function, flowering time regulation, chromatin remodeling, and RNA splicing. Moreover, SnRK2 activation intersects with MAP kinase (MAPK) cascades (e.g., MAP3K17/18–MKK3–MPK1/2/7/14), forming a multilayered phosphorylation network that ensures rapid and precise control of stress adaptation (Zhang *et al.,* 2020).

Epigenetic regulation

Epigenetic mechanisms are increasingly recognized as pivotal in controlling gene expression under abiotic stress. These include histone modifications, DNA methylation, and RNA-based regulation, which allow plants to establish both short-term and heritable stress responses.

Histone deacetylases (HDACs) and histone acetyltransferases (HATs) dynamically regulate chromatin accessibility. For example, HDA6 is essential for cold acclimation and freezing tolerance in Arabidopsis (To *et al.,* 2011; Chauhan *et al.,* 2021), while the HAT enzyme GCN5 promotes freezing resistance through histone acetylation. WD40-repeat proteins such as FVE and HOS15 contribute to chromatin remodeling and regulation of cold response genes (Chauhan *et al.,* 2021).

Noncoding RNAs (ncRNAs) also play significant roles. The long noncoding RNA SVALKA, located near the CBF1 locus, represses CBF1 transcription to fine-tune freezing tolerance (Chauhan *et al.,* 2021).

At the RNA modification level, N^6-methyladenosine (m^6A) is the most prevalent mRNA modification in eukaryotes and is crucial for mRNA stability and translation efficiency under stress (Yue *et al.,* 2015; Kindgren *et al.,* 2018). Components of the m^6A methyltransferase complex are upregulated during salt stress (Hu *et al.,* 2021), while RNA demethylases such as ALKBH9B and ALKBH10B modulate ABA signaling by altering mRNA methylation status (Shoaib *et al.,* 2021; Hou *et al.,* 2022).

YTH-domain proteins, which act as m^6A "readers," are induced under various stresses and phytohormone treatments (Tang *et al.,* 2021) Notably, ECT2, a cytoplasmic YTH protein, relocates to stress granules under heat stress, linking RNA methylation to translational control (Li *et al.,* 2014; Scutenaire *et al.,* 2018; Tang *et al.,* 2022).

Collectively, these findings underscore that epigenetic and post-transcriptional processes are not merely passive responses but active modulators of gene expression plasticity, enabling plants to adapt efficiently to recurring or prolonged abiotic stress.

Strategies to improve plant growth under stress

Despite substantial progress in identifying molecular mechanisms of stress tolerance, translating this knowledge into improved crop performance remains a key challenge. To mitigate the adverse effects of abiotic stress, researchers employ diverse strategies, including the exploitation of natural genetic variation, genetic engineering, chemical priming, and transcriptomic profiling. Together, these approaches aim to strengthen plant defense systems, enhance productivity, and promote sustainable agricultural practices.

Natural genetic variation

Natural genetic variation within and among plant species provides an invaluable resource for improving stress tolerance. Over evolutionary time, plants have accumulated allelic variations in genes involved in ion transport, hormone signaling, antioxidant defense, and osmolyte biosynthesis that confer differential stress responses (Munns *et al.,* 2012; Venkataraman *et al.,* 2021).

By screening natural populations and landraces, researchers can identify genotypes with inherent resilience to drought, salinity, or temperature extremes. These tolerant accessions can serve as parents in conventional breeding programs or be subjected to marker-assisted selection

(MAS) and genomic selection (GS) to accelerate trait introgression (Olías *et al.,* 2009).

For example, in rice (Oryza sativa), allelic diversity in the HKT1;5 gene modulates Na^+ exclusion efficiency, contributing to salt tolerance (Egea *et al.,* 2023). Similarly, Arabidopsis ecotypes adapted to different climatic zones exhibit variable expression of CBF transcription factors and associated cold tolerance levels (Wang *et al.,* 2021).

Exploring natural genetic variation not only identifies tolerance-associated alleles but also helps uncover novel regulatory mechanisms and adaptive pathways that may be transferable across species through modern biotechnological tools.

Genetic engineering and genome editing

Genetic engineering has provided direct means to manipulate plant stress responses by overexpressing or silencing specific genes that enhance tolerance. Early approaches focused on introducing single-gene traits, such as osmoprotectant biosynthesis (e.g., *P5CS* for proline accumulation) or antioxidant enzymes (*SOD, CAT, APX*) (Wang *et al.,* 2016). However, these modifications often provided limited protection because stress tolerance involves complex, multigenic interactions.

Recent advancements in CRISPR/Cas-based genome editing have revolutionized plant biotechnology, enabling precise modifications of stress-responsive genes and regulatory elements (Matsukura *et al.,* 2010). For instance, targeted mutagenesis of ABA receptor genes (PYR/PYL) has improved drought resistance without major yield penalties (Zhang *et al.,* 2018). Similarly, CRISPR editing of transcription factors such as DREB, NAC, and WRKY has resulted in enhanced tolerance to multiple stresses (Lou *et al.,* 2018).

Moreover, transcriptional activator-like effectors (TALEs) and CRISPR activation (CRISPRa) systems allow fine-tuned upregulation of beneficial genes, while RNA interference (RNAi) and CRISPR interference (CRISPRi) enable suppression of negative regulators. Integrating these tools with transcriptomic and metabolomic datasets provides a powerful platform for designing crops with improved stress adaptability and yield stability under adverse environments (Verma *et al.,* 2023).

Chemical priming

Chemical priming involves treating plants with small molecules that "train" their defense systems to respond more effectively to future stress events. Primed plants display faster and stronger activation of defense mechanisms upon exposure to stress, a phenomenon often associated with stress memory (Abdallah *et al.,* 2015).

Priming agents include phytohormones (ABA, SA, JA, and ethylene), osmoprotectants (proline, glycine betaine, trehalose), and ROS modulators (ascorbic acid, hydrogen peroxide, nitric oxide donors) (Das *et al.,* 2022). For instance, salicylic acid (SA) enhances antioxidant enzyme activities and membrane stability under salinity and drought, whereas hydrogen peroxide functions as a low-dose signal that activates systemic acquired tolerance (Nguyen *et al.,* 2018).

Emerging evidence also supports the use of nanoparticles and biostimulants as priming agents. Nanoparticles of zinc, silica, and titanium dioxide can modulate ROS signaling and improve photosynthetic efficiency under stress (Gurmani *et al.,* 2013). Similarly, natural compounds such as melatonin and chitosan induce stress-related gene expression and boost cellular antioxidant capacity (Sripinyowanich *et al.,* 2013).

Chemical priming is a cost-effective, eco-friendly approach that complements genetic methods, offering short-term protection and enhanced resilience during critical developmental stages.

Transcriptome and multi-omics approaches

Comprehensive transcriptome profiling and integrative "omics" studies have greatly advanced our understanding of abiotic stress responses. Transcriptomic analyses identify key regulatory genes, noncoding RNAs, and signaling networks that orchestrate stress adaptation (Bulgakov *et al.,* 2019).

For instance, high-throughput RNA sequencing (RNA-Seq) in rice and maize has revealed thousands of differentially expressed genes under drought and heat stress, including those involved in photosynthesis, secondary metabolism, and hormone signaling (Liu *et al.,* 2019). Similarly, proteomic and metabolomic studies uncover dynamic changes in enzyme activity and metabolite accumulation that provide biochemical insights beyond transcriptional data (Sako *et al.,* 2021).

Integrating multi-omics datasets allows the construction of gene regulatory networks (GRNs) that map interactions among transcription factors, signaling components, and metabolic pathways. These models help identify master regulators—such as SnRK2 kinases and NAC transcription factors—that serve as promising targets for genetic manipulation (Yuan *et al.,* 2021).

Ultimately, combining multi-omics data with machine learning and systems biology approaches will enable predictive modeling of plant stress responses, guiding both breeding and biotechnology strategies for developing climate-resilient crops (Gour *et al.,* 2022).

Future perspectives and conclusion

Global climate change continues to intensify the frequency and severity of abiotic stresses such as drought, salinity, and extreme temperatures. These challenges pose a serious threat to agricultural productivity and global food security. Although substantial progress has been made in deciphering the molecular and physiological mechanisms of

stress perception and tolerance, integrating this knowledge into field-level crop improvement remains a major scientific and technological frontier.

Future research must focus on bridging molecular insights with agronomic applications by leveraging advances in genomics, transcriptomics, proteomics, and metabolomics. High-throughput screening and multi-omics integration will help identify novel stress-responsive genes and regulatory hubs, offering precise targets for genome editing and marker-assisted breeding (Liu *et al.,* 2022).

Moreover, cross-talk among signaling pathways—including Ca^{2+}, ROS, ABA, and MAPK networks—should be explored to unravel how plants prioritize responses under combined or sequential stresses. Understanding these interactions will aid in developing multi-stress-tolerant genotypes rather than varieties that respond to individual stress types (Mofatto *et al.,* 2016).

The emerging field of epigenetic memory also holds great promise. By uncovering how DNA methylation, histone modification, and RNA-based regulation contribute to stress imprinting, researchers may design crops capable of "remembering" previous stress encounters and responding more effectively upon re-exposure (Badhan *et al.,* 2018).

In addition, expanding research on beneficial soil microbes, such as plant growth–promoting rhizobacteria (PGPR) and mycorrhizal fungi, will be crucial for sustainable resilience. These symbiotic relationships enhance nutrient uptake, modulate hormone signaling, and prime plants for stress tolerance without genetic modification.

Finally, translating laboratory findings into practical agricultural systems requires interdisciplinary collaboration between molecular biologists, breeders, soil scientists, and climate modelers. Integrating biotechnology with precision agriculture, supported by data-driven decision-making, can accelerate the creation of crops capable of thriving in rapidly changing environments.

In conclusion, understanding the complex regulatory and signaling networks that govern plant responses to abiotic stress is vital for the future of sustainable agriculture. By combining cutting-edge molecular research with ecological and agronomic innovation, it will be possible to design resilient crop systems that maintain productivity and ensure food security in the face of global environmental challenges.

Acknowledgement

We are highly acknowledged to Department of Botany, University of Peshawar for providing all facilities regarding this work.

Funding

No funding was given by any source to conduct this study but this study is a part of Phd degree of Saleha Saeed for which Botany Department, University of Peshawar, Pakistan provided the laboratory facilities.

Author contributions

Saleha Saeed collects all the data for review paper and compiles it and Dr. Sami Ullah revision on it. All authors approved the final manuscript.

References

Abdallah, N. A., Prakash, C. S., & McHughen, A. G. (2015). Genome editing for crop improvement: Challenges and opportunities. *GM Crops & Food, 6*(4), 183-205. https://doi.org/10.1080/21645698.2015.1129937

Alpert, P. (2006). Constraints of tolerance: why are desiccation-tolerant organisms so small or rare?. *Journal of Experimental Biology, 209*(9), 1575-1584. https://doi.org/10.1242/jeb.02179

Augustine, S. M., Cherian, A. V., Syamaladevi, D. P., & Subramanian, N. (2015). *Erianthus arundinaceous* HSP70 (*EaHSP70*) acts as a key regulator in the formation of anisotropic interdigitation in sugarcane (*Saccharum* spp. hybrid) in response to drought stress. *Plant and Cell Physiology, 56*(12), 2368-2380. https://doi.org/10.1093/pcp/pcv142

Badhan, S., Kole, P., Ball, A., & Mantri, N. (2018). RNA sequencing of leaf tissues from two contrasting chickpea genotypes reveals mechanisms for drought tolerance. *Plant Physiology and Biochemistry, 129*, 295-304. https://doi.org/10.1016/j.plaphy.2018.06.007

Banerjee, A., & Roychoudhury, A. (2017). Abscisic-acid-dependent basic leucine zipper (bZIP) transcription factors in plant abiotic stress. *Protoplasma, 254*, 3-16. https://doi.org/10.1007/s00709-015-0920-4

Brandt, B., Munemasa, S., Wang, C., Nguyen, D., Yong, T., Yang, P. G., Poretsky, E., Belknap, T. F., Waadt, R., Alemán, F., & Schroeder, J. I. (2015). Calcium specificity signaling mechanisms in abscisic acid signal transduction in *Arabidopsis* guard cells. *eLife, 4*, e03599. https://doi.org/10.7554/eLife.03599.001

Bulgakov, V. P., Wu, H.-C., & Jinn, T.-L. (2019). Coordination of ABA and chaperone signaling in plant stress responses. *Trends in Plant Science, 24*(7), 636–651. https://doi.org/10.1016/j.tplants.2019.04.004

Carpenter, J. F., Crowe, J. H., & Arakawa, T. (1990). Comparison of solute-induced protein stabilization in aqueous solution and the frozen and dried states. *Journal of Dairy Science, 73*(12), 3627-3636. https://doi.org/10.3168/jds.S0022-0302(90)79065-0

Chauhan, D. K., Yadav, V., Vaculík, M., Gassmann, W., Pike, S., Arif, N., Singh, V. P., Deshmukh, R., Sahi, S., & Tripathi, D. K. (2021). Aluminum toxicity and aluminum stress-induced physiological tolerance responses in higher plants. *Critical Reviews in Biotechnology, 41*(5), 715-730. https://doi.org/10.1080/07388551.2021.1874282

Chinnusamy, V., Zhu, J., & Zhu, J. K. (2007). Cold stress regulation of gene expression in plants. *Trends in Plant Science, 12*(10), 444-451. https://doi.org/10.1016/j.tplants.2007.07.002

Chukka, P. A. R., Wetmore, S. D., & Thakor, N. (2021). Established and emerging regulatory roles of eukaryotic translation initiation factor 5B (eIF5B). *Frontiers in Genetics, 12*, 737433. https://doi.org/10.3389/fgene.2021.737433

Das, D., Singha, D. L., Paswan, R. R., Chowdhury, N., Sharma, M., Reddy, P. S., & Chikkaputtaiah, C. (2022). Recent advancements in CRISPR/Cas technology for accelerated

crop improvement. *Planta, 255*, 109. https://doi.org/10.1007/s00425-022-03894-3

Ding, Y., Lv, J., Shi, Y., Gao, J., Hua, J., Song, C., Gong, Z., & Yang, S. (2019). EGR2 phosphatase regulates OST1 kinase activity and freezing tolerance in *Arabidopsis*. *The EMBO Journal, 38*, e99819. https://doi.org/10.15252/embj.201899819

Dong, Q., Wallrad, L., Almutairi, B. O., & Kudla, J. (2022). Ca^{2+} signaling in plant responses to abiotic stresses. *Journal of Integrative Plant Biology, 64*(2), 287-300. https://doi.org/10.1111/jipb.13228

Du, Q., Jiang, J., Chen, M., Ning, N., Reng, M., Li, X., & Xie, X. (2021). Cloning, expression analysis, and prokaryotic expression of rice heat shock protein HSP70 gene. *Journal of Plant Protection, 48*, 10.

Egea, I., Estrada, Y., Faura, C., Egea-Fernández, J. M., Bolarin, M. C., & Flores, F. B. (2023). Salt-tolerant alternative crops as sources of quality food to mitigate the negative impact of salinity on agricultural production. *Frontiers in Plant Science, 14*, 1092885. https://doi.org/10.3389/fpls.2023.1092885

Furuya, T., Matsuoka, D., & Nanmori, T. (2013). Phosphorylation of Arabidopsis thaliana MEKK1 via Ca^{2+} signalling as a part of the cold stress response. *Journal of Plant Research, 126*, 833-840. https://doi.org/10.1007/s10265-013-0576-0

Gatica, D., Hu, G., Zhang, N., Williamson, P. R., & Klionsky, D. J. (2019). The Pat1-Lsm complex prevents 3' to 5' degradation of a specific subset of *ATG* mRNAs during nitrogen starvation-induced autophagy. *Autophagy, 15*(4), 750-751. https://doi.org/10.1080/15548627.2019.1587262

Geiger, D., Scherzer, S., Mumm, P., Marten, I., Ache, P., Matschi, S., Liese, A., Wellmann, C., Al-Rasheid, K. A. S., Grill, E., Romeis, T., & Hedrich, R. (2010). Guard cell anion channel SLAC1 is regulated by CDPK protein kinases with distinct Ca^{2+} affinities. *Proceedings of the National Academy of Sciences of the United States of America, 107*(17), 8023-8028. https://doi.org/10.1073/pnas.091030107

Geiger, D., Scherzer, S., Mumm, P., Stange, A., Marten, I., Bauer, H., Ache, P., Matschi, S., Liese, A., Al-Rasheid, K. A. S., Romeis, T., & Hedrich, R. (2009). Activity of guard cell anion channel SLAC1 is controlled by drought-stress signaling kinase-phosphatase pair. *Proceedings of the National Academy of Sciences of the United States of America, 106*(50), 21425-21430. https://doi.org/10.1073/pnas.0912021106

Gong, Z., Xiong, L., Shi, H., Yang, S., Herrera-Estrella, L. R., Xu, G., Chao, D.-Y., Li, J., Wang, P.-Y., Qin, F., Li, J., Ding,Y., Shi, Y., Wang, Y., Yang, Y., Guo, Y., & Zhu, J. K. (2020). Plant abiotic stress response and nutrient use efficiency. *Science China Life Sciences, 63*, 635-674. https://doi.org/10.1007/s11427-020-1683-x

Gour, P., Kansal, S., Agarwal, P., Mishra, B. S., Sharma, D., Mathur, S., & Raghuvanshi, S. (2022). Variety-specific transcript accumulation during reproductive stage in drought-stressed rice. *Physiologia Plantarum, 174*(1), e13585. https://doi.org/10.1111/ppl.13585

Guo, M. (2016). *Expression analysis and functional study of heat stress-related genes in pepper*. Doctoral Dissertation, Northwest A&F University.

Gurmani, A. R., Bano, A., Ullah, N., Khan, H., Jahangir, M., Flowers, T. J. (2013). Exogenous abscisic acid (A.B.A.) and silicon (Si) promote salinity tolerance by reducing sodium (Na^{+}) transport and bypassing flow in rice (*Oryza sativa* indica). *Australian Journal of Crop Science, 7*(9), 1219-1226.

Hou, N., Li, C., He, J., Liu, Y., Yu, S., Malnoy, M., Mobeen Tahir, M., Xu, L., Ma, F., & Guan, Q. (2022). MdMTA-mediated m^6A modification enhances drought tolerance by promoting mRNA stability and translation efficiency of genes involved in lignin deposition and oxidative stress. *New Phytologist, 234*(4), 1294-1314. https://doi.org/10.1111/nph.18069

Hou, Q., Ufer, G., & Bartels, D. (2016). Lipid signalling in plant responses to abiotic stress. *Plant, Cell & Environment, 39*(5), 1029-1048. https://doi.org/10.1111/pce.12666

Hrabak, E. M., Chan, C. W. M., Gribskov, M., Harper, J. F., Choi, J. H., Halford, N., Kudla, J., Luan, S., Nimmo, H. G., Sussman, M. R., Thomas, M., Walker-Simmons, K., Zhu, J. K., & Harmon, A. C. (2003). The Arabidopsis CDPK-SnRK superfamily of protein kinases. *Plant Physiology, 132*(2), 666-680. https://doi.org/10.1104/pp.102.011999

Hu, J., Cai, J., Park, S. J., Lee, K., Li, Y., Chen, Y., Yun, J. Y., Xu, T., Kang, H. (2021). N^6-methyladenosine mRNA methylation is essential for salt stress tolerance in Arabidopsis. *The Plant Journal, 106*, 1759-1775. https://doi.org/10.1111/tpj.15270

Izumi, M., Ishida, H., Nakamura, S., & Hidema, J. (2017). Entire photodamaged chloroplasts are transported to the central vacuole by autophagy. *The Plant cell, 29*(2), 377-394. https://doi.org/10.1105/tpc.16.00637

Jang, Y.-H., Park, J.-R., Kim, E.-G., & Kim, K.-M. (2022). *OsbHLHq11*, the Basic Helix-Loop-Helix transcription factor, involved in regulation of chlorophyll content in rice. *Biology, 11*(7), 1000. https://doi.org/10.3390/biology11071000

Jiang, B., Shi, Y., Peng, Y., Jia, Y., Yan, Y., Dong, X., Li, H., Dong, J., Li, J., Gong, Z., Thomashow, M. F., & Yang, S. (2020). Cold-induced CBF-PIF3 interaction enhances freezing tolerance by stabilizing the phyB thermosensor in *Arabidopsis*. *Molecular Plant, 13*(6), 894-906. https://doi.org/10.1016/j.molp.2020.04.006

Jiang, L., Hu, W., Qian, Y., Ren, Q., & Zhang, J. (2021). Genome-wide identification, classification and expression analysis of the *Hsf* and *Hsp70* gene families in maize. *Gene, 770*, 145348. https://doi.org/10.1016/j.gene.2020.145348

Jung, K.-H., Gho, H.-J., Nguyen, M. X., Kim, S.-R., & An, G. (2013). Genome-wide expression analysis of *HSP70* family genes in rice and identification of a cytosolic *HSP70* gene highly induced under heat stress. *Functional & Integrative Genomics, 13*, 391-402. https://doi.org/10.1007/s10142-013-0331-6

Kindgren, P., Ard, R., Ivanov, M., & Marquardt, S. (2018). Transcriptional read-through of the long non-coding RNA *SVALKA* governs plant cold acclimation. *Nature Communications, 9*, 4561. https://doi.org/10.1038/s41467-018-07010-6

Kishor, P. B. K., Sangam, S., Amrutha, R. N., Laxmi, P. S., Naidu, K. R., Rao, K. R. S. S., Rao, S., Reddy, K. J., & Sreenivasulu, N. (2005). Regulation of proline biosynthesis, degradation, uptake, and transport in higher plants: Its implications in plant growth and abiotic stress tolerance. *Current Science, 88*(3), 424-438.

Li, D., Zhang, H., Hong, Y., Huang, L., Li, X., Zhang, Y., Ouyang, Z., & Song, F. (2014). Genome-wide identification, biochemical characterization, and expression analyses of the YTH domain-containing RNA-binding protein family in *Arabidopsis* and rice. *Plant Molecular Biology Reporter, 32*, 1169-1186. https://doi.org/10.1007/s11105-014-0724-2

Li, J., & Liu, X. (2019). Genome-wide identification and expression profile analysis of the *Hsp20* gene family in barley (*Hordeum vulgare* L.). *PeerJ, 7*, e6832. https://doi.org/10.7717/peerj.6832

Lin, B.-L., Wang, J.-S., Liu, H.-C., Chen, R.-W., Meyer, Y., Barakat, A., & Delseny, M. (2001). Genomic analysis of the Hsp70 superfamily in *Arabidopsis thaliana*. *Cell Stress and*

Chaperones, 6(3), 201-208. https://doi.org/10.1379/1466-1268(2001)006<0201:gaoths>2.0.co;2

Liu, Q., Ding, Y., Shi, Y., Ma, L., Wang, Y., Song, C., Wilkins, K. A., Davies, J. M., Knight, H., Knight, M. R., Gong, Z., Guo, Y., & Yang, S. (2021). The calcium transporter ANNEXIN1 mediates cold-induced calcium signaling and freezing tolerance in plants. *The EMBO Journal, 40*(2), e104559. https://doi.org/10.15252/embj.2020104559

Liu, Q., Wang, F., Shuai, Y., Huang, L., & Zhang, X. (2022). Integrated analysis of single-molecule real-time sequencing and next-generation sequencing eveals insights into drought tolerance mechanism of *Lolium multiflorum*. *International Journal of Molecular Sciences, 23*(14), 7921. https://doi.org/10.3390/ijms23147921

Liu, X., Wang, J., & Sun, L. (2018). Structure of the hyperosmolality-gated calcium-permeable channel OSCA1.2. *Nature Communications, 9*, 5060. https://doi.org/10.1038/s41467-018-07564-5

Liu, X.-L., Zhang, H., Jin, Y.-Y., Wang, M.-M., Yang, H.-Y., Ma, H.-Y., Jiang, C.-J., & Liang, Z.-W. (2019). Abscisic acid primes rice seedlings for enhanced tolerance to alkaline stress by upregulating antioxidant defence and stress tolerance-related genes. *Plant and Soil, 438*, 39-55. https://doi.org/10.1007/s11104-019-03992-4

Lizana, C., Wentworth, M., Martinez, J. P., Villegas, D., Meneses, R., Murchie, E. H., Pastenes, C., Lercari, B., Vernieri, P., Horton, P., & Pinto, M. (2006). Differential adaptation of two varieties of common bean to abiotic stress: I. Effects of drought on yield and photosynthesis. *Journal of Experimental Botany, 57*(3), 685-697. https://doi.org/10.1093/jxb/erj062

Lou, D., Wang, H., & Yu, D. (2018). The sucrose non-fermenting-1-related protein kinases SAPK1 and SAPK2 function collaboratively as positive regulators of salt stress tolerance in rice. *BMC Plant Biology, 18*, 203. https://doi.org/10.1186/s12870-018-1408-0

Lystad, A. H., & Simonsen, A. (2019). Mechanisms and pathophysiological roles of the ATG8 conjugation machinery. *Cells, 8*(9), 973. https://doi.org/10.3390/cells8090973

Ma, L., Ye, J., Yang, Y., Lin, H., Yue, L., Luo, J., Long, Y., Fu, H., Liu, X., Zhang, Y., Wang, Y., Chen, L., Kudla, J., Wang, Y., Han, S., Song, C.-P., & Guo, Y. (2019). The SOS2-SCaBP8 complex generates and fine-tunes an AtANN4-dependent calcium signature under salt stress. *Developmental Cell, 48*(5), 697-709.e5. https://doi.org/10.1016/j.devcel.2019.02.01

Ma, S., & Bohnert, H. J. (2007). Integration of *Arabidopsis thaliana* stress-related transcript profiles, promoter structures, and cell-specific expression. *Genome biology*, *8*(4), R49. https://doi.org/10.1186/gb-2007-8-4-r49

Ma, Y., Szostkiewicz, I., Korte, A., Moes, D., Yang, Y., Christmann, A., & Grill, E. (2009). Regulators of PP2C phosphatase activity function as abscisic acid sensors. *Science, 324*(5930), 1064-1068. https://doi.org/10.1126/science.1172408

Maity, K., Heumann, J. M., McGrath, A. P., Kopcho, N. J., Hsu, P.-K., Lee, C.-W., Mapes, J. H., Garza, D., Krishnan, S., Morgan, G. P., Hendargo, K. J., Klose, T., Rees, S. D., Medrano-Soto, A., Saier Jr., M. H., Piñeros, M., Komives, E. A., Schroeder, J. I., Chang, G., & Stowell, M. H. B. (2019). Cryo-EM structure of OSCA1.2 from *Oryza sativa* elucidates the mechanical basis of potential membrane hyperosmolality gating. *Proceedings of the National Academy of Sciences of the United States of America, 116*(28), 14309-14318. https://doi.org/10.1073/pnas.1900774116

Manasa, S. L., Panigrahy, M., Panigrahi, K. C. S., & Rout, G. R. (2022). Overview of plant cold stress regulation. *The Botanical Review, 88*, 359-387. https://doi.org/10.1007/s12229-021-09267-x

Markham, K. K., & Greenham, K. (2021). Abiotic stress through time. *The New Phytologist, 231*(1), 40-46. https://doi.org/10.1111/nph.17367

Martí, M. C., Stancombe, M. A., & Webb, A. A. R. (2013). Cell- and stimulus type-specific intracellular free Ca^{2+} signals in *Arabidopsis*. *Plant Physiology, 163*(2), 625-634. https://doi.org/10.1104/pp.113.222901

Maszkowska, J., Szymańska, K. P., Kasztelan, A., Krzywińska, E., Sztatelman, O., & Dobrowolska, G. (2021). The Multifaceted Regulation of SnRK2 Kinases. *Cells, 10*(9), 2180. https://doi.org/10.3390/cells10092180

Matsukura, S., Mizoi, J., Yoshida, T., Todaka, D., Ito, Y., Maruyama, K., Shinozaki, K., & Yamaguchi-Shinozaki, K. (2010). Comprehensive analysis of rice *DREB2*-type genes that encode transcription factors involved in the expression of abiotic stress-responsive genes. *Molecular Genetics and Genomics, 283*, 185-196. https://doi.org/10.1007/s00438-009-0506-y

Melcher, K., Ng, L.-M., Zhou, X. E., Soon, F.-F., Xu, Y., Suino-Powell, K. M., Park, S.-Y., Weiner, J. J., Fujii, H., Chinnusamy, V., Kovach, A., Li, J., Wang, Y., Li, J., Peterson, F. C., Jensen, D. R., Yong, E.-L., Volkman, B. F., Cutler, S. R., Zhu, J.-K.,… Xu, H. E. (2009). A gate-latch-lock mechanism for hormone signalling by abscisic acid receptors. *Nature, 462*, 602-608. https://doi.org/10.1038/nature08613

Merret, R., Carpentier, M.-C., Favory, J.-J., Picart, C., Descombin, J., Bousquet-Antonelli, C., Tillard, P., Lejay, L., Deragon, J.-M., & Charng, Y.-Y. (2017). Heat Shock Protein HSP101 affects the release of ribosomal protein mRNAs for recovery after heat shock. *Plant Physiology, 174*(2), 1216-1225. https://doi.org/10.1104/pp.17.00269

Merret, R., Descombin, J., Juan, Y.-T., Favory, J.-J., Carpentier, M. C., Chaparro, C., Charng, Y.-Y., Deragon, J. M., & Bousquet-Antonelli, C. (2013). XRN4 and LARP1 are required for a heat-triggered mRNA decay pathway involved in plant acclimation and survival during thermal stress. *Cell Reports, 5*(5), 1279-1293. https://doi.org/10.1016/j.celrep.2013.11.019

Merret, R., Nagarajan, V. K., Carpentier, M.-C., Park, S., Favory, J.-J., Descombin, J., Picart, C., Charng, Y.-Y., Green, P. J., Deragon, J.-M., & Bousquet-Antonelli, C. (2015). Heat-induced ribosome pausing triggers mRNA co-translational decay in *Arabidopsis thaliana*. *Nucleic Acids Research, 43*(8), 4121-4132. https://doi.org/10.1093/nar/gkv234

Min, M. K., Choi, E. H., Kim, J. A., Yoon, I. S., Han, S., Lee, Y., Lee, S., & Kim, B. G. (2019). Two clade A phosphatase 2Cs expressed in guard cells physically interact with abscisic acid signaling components to induce stomatal closure in rice. *Rice, 12*, 37. https://doi.org/10.1186/s12284-019-0297-7

Mofatto, L. S., Carneiro, F. de A., Vieira, N. G., Duarte, K. E., Vidal, R. O., Alekcevetch, J. C., Cotta, M. G., Verdeil, J. L., Lapeyre-Montes, F., Lartaud, M., Leroy, T., De Bellis, F., Pot, D., Rodrigues, G. C., Carazzolle, M. F., Pereira, G. A. G., Andrade, A. C., & Marraccini, P. (2016). Identification of candidate genes for drought tolerance in coffee by high-throughput sequencing in the shoot apex of different *Coffea arabica* cultivars. *BMC Plant Biology, 16*, 94. https://doi.org/10.1186/s12870-016-0777-5

Munns, R., James, R. A., Xu, B., Athman, A., Conn, S. J., Jordans, C., Byrt, C. S., Hare, R. A., Tyerman, S. D., Tester, M., Plett, D., & Gilliham, M. (2012). Wheat grain yield on saline soils is improved by an ancestral Na^+

transporter gene. *Nature Biotechnology, 30*(4), 360-364. https://doi.org/10.1038/nbt.2120

Munns, R., Passioura, J. B., Colmer, T. D., & Byrt, C. S. (2020). Osmotic adjustment and energy limitations to plant growth in saline soil. *The New Phytologist, 225*(3), 1091-1096. https://doi.org/10.1111/nph.15862

Nag, M., Lahiri, D., Garai, S., Mukherjee, D., & Ray, R. R. (2021). Regulation of β-amylase synthesis: a brief overview. *Molecular Biology Reports, 48*(9), 6503-6511. https://doi.org/10.1007/s11033-021-06613-5

Nakamura, S., & Izumi, M. (2019). Chlorophagy is *ATG* gene-dependent microautophagy process. *Plant Signaling & Behavior, 14*, 1554469. https://doi.org/10.1080/15592324.2018.1558679

Narusaka, Y., Nakashima, K., Shinwari, Z. K., Sakuma, Y., Furihata, T., Abe, H., Narusaka, M., Shinozaki, K., & Yamaguchi-Shinozaki, K. (2003). Interaction between two *cis*-acting elements, ABRE and DRE, in ABA-dependent expression of *Arabidopsis* rd29A gene in response to dehydration and high-salinity stresses. *The Plant Journal, 34*(2), 137-148. https://doi.org/10.1046/j.1365-313x.2003.01708.x

Nguyen, A. H., Matsui, A., Tanaka, M., Mizunashi, K., Nakaminami, K., Hayashi, M., Iida, K., Toyoda, T., Nguyen, D. V., & Seki, M. (2015). Loss of Arabidopsis 5'-3' Exoribonuclease AtXRN4 function enhances heat stress tolerance of plants subjected to severe heat stress. *Plant & Cell Physiology, 56*(9), 1762-1772. https://doi.org/10.1093/pcp/pcv096

Nguyen, H.-C., Lin, K.-H., Ho, S.-L., Chiang, C.-M., & Yang, C. M. (2018). Enhancing the abiotic stress tolerance of plants: from chemical treatment to biotechnological approaches. *Physiologia Plantarum, 164*(4), 452-466. https://doi.org/10.1111/ppl.12812

Nguyen, T. N., Padman, B. S., Usher, J., Oorschot, V., Ramm, G., & Lazarou, M. (2016). Atg8 family LC3/GABARAP proteins are crucial for autophagosome-lysosome fusion but not autophagosome formation during PINK1/Parkin mitophagy and starvation. *Journal of cell biology, 215*(6), 857-874. https://doi.org/10.1083/jcb.201607039

Nishimura, K., Ashida, H., Ogawa, T., & Yokota, A. (2010). A DEAD box protein is required for formation of a hidden break in Arabidopsis chloroplast 23S rRNA. *The Plant Journal, 63*(5), 766-777. https://doi.org/10.1111/j.1365-313X.2010.04276.x

Olías, R., Eljakaoui, Z., Li, J., De Morales, P. A., Marín-Manzano, M. C., Pardo, J. M., & Belver, A. (2009). The plasma membrane Na^+/H^+ antiporter SOS1 is essential for salt tolerance in tomato and affects the partitioning of Na^+ between plant organs. *Plant, Cell & Environment, 32*(7), 904-916. https://doi.org/10.1111/j.1365-3040.2009.01971.x

Park, C.-J., & Seo, Y.-S. (2015). Heat shock proteins: A review of the molecular chaperones for plant immunity. *The Plant Pathology Journal, 31*(4), 323-333. https://doi.org/10.5423/PPJ.RW.08.2015.0150

Park, S.-Y., Fung, P., Nishimura, N., Jensen, D. R., Fujii, H., Zhao,Y., Lumba, S., Santiago, J., Rodrigues, A., Chow, T. F. F., Alfred, S. E., Bonetta, D., Finkelstein, R., Provart, N. J., Desveaux, D., Rodriguez, P. L., McCourt, P., Zhu, J.-K., Schroeder, J. I.,… Cutler, S. R. (2009). Abscisic acid inhibits type 2C protein phosphatases via the PYR/PYL family of START proteins. *Science, 324*(5930), 1068-1071. https://doi.org/10.1126/science.1173041

Praveen, A., Dubey, S., Singh, S., & Sharma, V. K. (2023). Abiotic stress tolerance in plants: a fascinating action of defense mechanisms. *3 Biotech, 13*, 102. https://doi.org/10.1007/s13205-023-03519-w

Qi, J., Song, C.-P., Wang, B., Zhou, J., Kangasjärvi, J., Zhu, J.-K., & Gong, Z. (2018). Reactive oxygen species signaling and stomatal movement in plant responses to drought stress and pathogen attack. *Journal of Integrative Plant Biology, 60*(9), 805-826. https://doi.org/10.1111/jipb.12654

Qiu, Q.-S., Guo, Y., Dietrich, M. A., Schumaker, K. S., & Zhu, J. K. (2002). Regulation of SOS1, a plasma membrane Na^+/H^+ exchanger in Arabidopsis thaliana, by SOS2 and SOS3. *Proceedings of the National Academy of Sciences of the United States of America, 99*(12), 8436-8441. https://doi.org/10.1073/pnas.122224699

Qiu, Q.-S., Guo, Y., Quintero, F. J., Pardo, J. M., Schumaker, K. S., & Zhu, J.-K. (2004). Regulation of vacuolar Na+/H+ exchange in Arabidopsis thaliana by the salt-overly-sensitive (SOS) pathway. *Journal of Biological Chemistry, 279*(1), 207-215. https://doi.org/10.1074/jbc.M307982200

Radha, B., Sunitha, N. C., Sah, R. P., Azharudheen, T. P. M., Krishna, G. K., Umesh, D. K., Thomas, S., Anilkumar, C., Upadhyay, S., Kumar, A., Manikanta Ch, L. N., Behera, S., Marndi, B. C., & Siddique, K. H. M. (2023). Physiological and molecular implications of multiple abiotic stresses on yield and quality of rice. *Frontiers in Plant Science, 13*, 996514. https://doi.org/10.3389/fpls.2022.996514

Rodrigues, A., Adamo, M., Crozet, P., Margalha, L., Confraria, A., Martinho, C., Elias, A., Rabissi, A., Lumbreras, V., González-Guzmán, M., Antoni, R., Rodriguez, P. L., & Baena-González, E. (2013). ABI1 and PP2CA phosphatases are negative regulators of Snf1-related protein kinase1 signaling in *Arabidopsis*. *The Plant Cell, 25*(10), 3871-3884. https://doi.org/10.1105/tpc.113.114066

Rubab, S., Talha, J., Sadam, H., Sunny, A., Misbah, N., Hina, Z., Saurabh, P., Jyoti, C., Manzer, H. S., & Chen, P. (2022). Calcium homeostasis and potential roles to combat environmental stresses in plants. *South African Journal of Botany, 148*, 683-693. https://doi.org/10.1016/j.sajb.2022.05.038

Sako, K., Nguyen, H. M., & Seki, M. (2021). Advances in chemical priming to enhance abiotic stress tolerance in plants. *Plant & Cell Physiology, 61*(12), 1995-2003. https://doi.org/10.1093/pcp/pcaa119

Sangwan, V., Örvar, B. L., Beyerly, J., Hirt, H., & Dhindsa, R. S. (2002). Opposite changes in membrane fluidity mimic cold and heat stress activation of distinct plant MAP kinase pathways. *The Plant Journal, 31*(5), 629-638. https://doi.org/10.1046/j.1365-313x.2002.01384.x

Scharf, K.-D., Berberich, T., Ebersberger, I., & Nover, L. (2012). The plant heat stress transcription factor (Hsf) family: structure, function and evolution. *Biochimica et Biophysica Acta (BBA) - Gene Regulatory Mechanisms, 1819*(2), 104-119. https://doi.org/10.1016/j.bbagrm.2011.10.002

Scutenaire, J., Deragon, J. M., Jean, V., Benhamed, M., Raynaud, C., Favory, J. J., Merret, R., & Bousquet-Antonelli, C. (2018). The YTH domain protein ECT2 is an m^6A reader required for normal trichome branching in *Arabidopsis*. *The Plant Cell, 30*(5), 986-1005. https://doi.org/10.1105/tpc.17.00854

Shoaib, Y., Hu, J., Manduzio, S., & Kang, H. (2021). Alpha-ketoglutarate-dependent dioxygenase homolog 10B, an N^6-methyladenosine mRNA demethylase, plays a role in salt stress and abscisic acid responses in *Arabidopsis thaliana*. *Physiologia Plantarum, 173*(3), 1078-1089. https://doi.org/10.1111/ppl.13505

Siddique, M., Gernhard, S., von Koskull-Döring, P., Vierling, E., & Scharf, K. D. (2008). The plant sHSP superfamily: five new members in *Arabidopsis thaliana* with unexpected properties.

Cell Stress and Chaperones, 13(2), 183-197. https://doi.org/10.1007/s12192-008-0032-6

Sripinyowanich, S., Klomsakul, P., Boonburapong, B., Bangyeekhun, T., Asami, T., Gu, H., Buaboocha, T., & Chadchawan, S. (2013). Exogenous ABA induces salt tolerance in indica rice (*Oryza sativa* L.): The role of *OsP5CS1* and *OsP5CR* gene expression during salt stress. *Environmental and Experimental Botany, 86*, 94-105. https://doi.org/10.1016/j.envexpbot.2010.01.009

Swain, R., Sahoo, S., Behera, M., & Rout, G. R. (2023). Instigating prevalent abiotic stress resilience in crop by exogenous application of phytohormones and nutrient. *Frontiers in Plant Science, 14*, 1104874. https://doi.org/10.3389/fpls.2023.1104874

Tang, J., Yang, J., Duan, H., & Jia, G. (2021). ALKBH10B, an mRNA m^{6}A Demethylase, modulates ABA response during seed germination in *Arabidopsis*. *Frontiers in Plant Scienc*e, *12*, 712713. https://doi.org/10.3389/fpls.2021.712713

Tang, J., Yang, J., Lu, Q., Tang, Q., Chen, S., & Jia, G. (2022). The RNA N^6 -methyladenosine demethylase ALKBH9B modulates ABA responses in *Arabidopsis*. *Journal of Integrative Plant Biology, 64*(12), 2361-2373. https://doi.org/10.1111/jipb.13394

To, T. K., Nakaminami, K., Kim, J.-M., Morosawa, T., Ishida, J., Tanaka, M., Yokoyama, S., Shinozaki, K., & Seki, M. (2011). *Arabidopsis* HDA6 is required for freezing tolerance. *Biochemical and Biophysical Research Communications, 406*(3), 414-419. https://doi.org/10.1016/j.bbrc.2011.02.058

Venkataraman, G., Shabala, S., Véry, A.-A., Hariharan, G. N., Somasundaram, S., Pulipati, S., Sellamuthu, G., Harikrishnan, M., Kumari, K., Shabala, L., Zhou, M., & Chen, Z.-H. (2021). To exclude or to accumulate? Revealing the role of the sodium HKT1;5 transporter in plant adaptive responses to varying soil salinity. *Plant Physiology and Biochemistry, 169*, 333-342. https://doi.org/10.1016/j.plaphy.2021.11.030

Verma, V., Kumar, A., Partap, M., Thakur, M., & Bhargava, B. (2023). CRISPR-Cas: A robust technology for enhancing consumer-preferred commercial traits in crops. *Frontiers in Plant Science, 14*, 1122940. https://doi.org/10.3389/fpls.2023.1122940

Wang, P., Hsu, C.-C., Du, Y., Zhu, P., Zhao, C., Fu, X., Zhang, C., Paez, J. S., Macho, A. P., Tao, W. A., & Zhu, J.-K. (2020). Mapping proteome-wide targets of protein kinases in plant stress responses. *Proceedings of the National Academy of Sciences of the United States of America, 117*(6), 3270-3280. https://doi.org/10.1073/pnas.1919901117

Wang, P., Xue, L., Batelli, G., Lee, S., Hou, Y.-J., Van Oosten, M. J., Zhang, H., Tao, W. A., & Zhu, J. K. (2013). Quantitative phosphoproteomics identifies SnRK2 protein kinase substrates and reveals the effectors of abscisic acid action. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(27), 11205-11210. https://doi.org/10.1073/pnas.1308974110

Wang, Q., Sun, W., Duan, Y., Xu, Y., Wang, H., Hao, J., Han, Y., & Liu, C. (2024). Genome-wide identification and expression analysis of HSP70 gene family under high-temperature stress in lettuce (*Lactuca sativa* L.). *International Journal of Molecular Sciences, 26*(1), 102. https://doi.org/10.3390/ijms26010102

Wang, W., Vinocur, B., Shoseyov, O., & Altman, A. (2004). Role of plant heat-shock proteins and molecular chaperones in the abiotic stress response. *Trends in Plant Science, 9*(5), 244-252. https://doi.org/10.1016/j.tplants.2004.03.006

Wang, X., Wang, H., Liu, S., Ferjani, A., Li, J., Yan, J., Yang, X., & Qin, F. (2016). Genetic variation in *ZmVPP1* contributes to drought tolerance in maize seedlings. *Nature Genetics, 48*, 1233-1241. https://doi.org/10.1038/ng.3636

Wang, Z., Hong, Y., Li, Y., Shi, H., Yao, J., Liu, X., Wang, F., Huang, S., Zhu, G., & Zhu, J.-K. (2021). Natural variations in *SlSOS1* contribute to the loss of salt tolerance during tomato domestication. *Plant Biotechnology Journal, 19*(1), 20-22. https://doi.org/10.1111/pbi.13443

Willems, P., Horne, A., Van Parys, T., Goormachtig, S., De Smet, I., Botzki, A., Van Breusegem, F., & Gevaert, K. (2019). The plant PTM viewer, a central resource for exploring plant protein modifications. *The Plant Journal, 99*(4), 752-762. https://doi.org/10.1111/tpj.14345

Yamaguchi-Shinozaki, K., & Shinozaki, K. (2006). Transcriptional regulatory networks in cellular responses and tolerance to dehydration and cold stresses. *Annual Review of Plant Biology, 57*, 781-803. https://doi.org/10.1146/annurev.arplant.57.032905.105444

Yang, T., Ali, G. S., Yang, L., Du, L., Reddy, A. S. N., & Poovaiah, B. W. (2010). Calcium/calmodulin-regulated receptor-like kinase CRLK1 interacts with MEKK1 in plants. *Plant Signaling & Behavior, 5*(8), 991-994. https://doi.org/10.4161/psb.5.8.12225

Yang, X., He, K., Chi, X., Chai, G., Wang, Y., Jia, C., Zhang, H., Zhou, G., & Hu, R. (2018). *Miscanthus* NAC transcription factor MlNAC12 positively mediates abiotic stress tolerance in transgenic Arabidopsis. *Plant science, 277*, 229-241. https://doi.org/10.1016/j.plantsci.2018.09.013

Young, P. G., Passalacqua, M. J., Chappell, K., Llinas, R. J., & Bartel, B. (2019). A facile forward-genetic screen for Arabidopsis autophagy mutants reveals twenty-one loss-of-function mutations disrupting six ATG genes. *Autophagy, 15*(6), 941-959. https://doi.org/10.1080/15548627.2019.1569915

Yu, H., Kong, X., Huang, H., Wu, W., Park, J., Yun, D. J., Lee, B. H., Shi, H., & Zhu, J. K. (2020). STCH4/REIL2 confers cold stress tolerance in *Arabidopsis* by promoting rRNA processing and CBF protein translation. *Cell Reports, 30*(1), 229-242.e5. https://doi.org/10.1016/j.celrep.2019.12.012

Yuan, L., Zheng, Y., Nie, L., Zhang, L., Wu, Y., Zhu, S., Hou, J., Shan, G. L., Liu, T. K., Chen, G., Tang, X., & Wang, C. (2021). Transcriptional profiling reveals changes in gene regulation and signalling transduction pathways during temperature stress in wucai (*Brassica campestris* L.). *BMC Genomics, 22*, 687. https://doi.org/10.1186/s12864-021-07981-9

Yue, Y., Liu, J., & He, C. (2015). RNA N^6-methyladenosine methylation in post-transcriptional gene expression regulation. *Genes & Development, 29*(13), 1343-1355. https://doi.org/10.1101/gad.262766.115

Zhang, H., Liu, S., Ren, T., Niu, M., Liu, X., Liu, C., Wang, H., Yin, W., & Xia, X. (2023). Crucial abiotic stress regulatory network of NF-Y transcription factor in plants. *International Journal of Molecular Sciences, 24*(5), 4426. https://doi.org/10.3390/ijms24054426

Zhang, H., Wang, Z., Li, X., Gao, X., Dai, Z., Cui, Y., Zhi, Y., Liu, Q., Zhai, H., Gao, S., Zhao, N., & He, S. (2022a). The IbBBX24-IbTOE3-IbPRX17 module enhances abiotic stress tolerance by scavenging reactive oxygen species in sweet potato. *New phytologist, 233*(3), 1133-1152. https://doi.org/10.1111/nph.17860

Zhang, H., Zhao, Y., & Zhu, J.-K. (2020). Thriving under stress: How plants balance growth and the stress response. *Developmental Cell, 55*(5), 529-543. https://doi.org/10.1016/j.devcel.2020.10.012

Zhang, H., Zhu, J., Gong, Z., & Zhu, J.-K. (2022b). Abiotic stress

responses in plants. *Nature Reviews Genetics, 23*, 104-119. https://doi.org/10.1038/s41576-021-00413-0

Zhang, J., Zhang, H., Srivastava, A. K., Pan, Y., Bai, J., Fang, J., Shi, H., & Zhu, J. K. (2018). Knockdown of rice MicroRNA166 confers drought resistance by causing leaf rolling and altering stem xylem development. *Plant Physiology, 176*(3), 2082-2094. https://doi.org/10.1104/pp.17.01432

Zhang, Y., Kaiser, E., Li, T., & Marcelis, L. F. M. (2022c). NaCl affects photosynthetic and stomatal dynamics by osmotic effects and reduces photosynthetic capacity by ionic effects in tomato. *Journal of Experimental Botany, 73*(11), 3637-3650. https://doi.org/10.1093/jxb/erac078

Zhao, C., Wang, P., Si, T., Hsu, C.-C., Wang, L., Zayed, O., Yu, Z., Zhu, Y., Dong, J., Tao, W. A., & Zhu, J. K. (2017). MAP kinase cascades regulate the cold response by modulating ICE1 protein stability. *Developmental Cell, 43*(5), 618-629. e5. https://doi.org/10.1016/j.devcel.2017.09.024

Zhu, J.-K. (2002). Salt and drought stress signal transduction in plants. *Annual Review of Plant Biology, 53*, 247-273. https://doi.org/10.1146/annurev.arplant.53.091401.143329

Zhu, J.-K. (2016). Abiotic stress signaling and responses in plants. *Cell, 167*(2), 313-324. https://doi.org/10.1016/j.cell.2016.08.029