Bulletin of Biological and Allied Sciences Research
ISSN: **2521-0092**
www.bbasr.org
DOI: https://doi.org/10.64013/bbasr.v2026i1.116
*Bull. Biol. All. Sci. Res., Volume, **11**: 116*
Review Article ***Open Access***

MECHANISMS OF ACTION AND SIGNALING PATHWAYS INVOLVED IN ABIOTIC STRESS ELICITATION

HAMMAD M[1*], SHAFIQ M[1], BATOOL A[2], SHERAZI SHUH[2]

[1]Department of Horticulture, Faculty of Agricultural Sciences, University of the Punjab, P.O BOX. 54590, Lahore, Pakistan
[2]Department of Plant Breeding and Genetics, Faculty of Agricultural Sciences, University of the Punjab, P.O BOX. 54590, Lahore, Pakistan
**Correspondence Author Email Address: dr.hammadse@gmail.com*

(Received, 21st April 2025, Accepted 30th January 2026, Published 14th February 2026)

Abstract *Abiotic stressors like drought, salinity, heat, heavy metals, oxidative stress, and UV radiation severely limit plant growth, development, and productivity. Plants detect these stresses using particular membrane sensors, resulting in fast changes in intracellular calcium concentrations, reactive oxygen species pulses, and phytohormone signaling. These initial signals are converted into conserved kinase signaling pathways (MAPKs, CDPKs, SnRK2s) and hormone-mediated pathways (ABA-dependent and ABA-independent), which then activate stress-responsive transcription factors (DREBs, NACs, WRKYs, MYBs) and remodel the transcriptome. Chromatin modification, alternative splicing, short RNAs, and post-translational modifications (phosphorylation and ubiquitination) all contribute to complicated regulation, ensuring precise control of stress gene expression. Plants use hormonal interactions and network hubs to balance survival, growth, and defense. Recent advances in systems biology have revealed these complicated networks, and biotechnological approaches—transgenic methods, CRISPR/Cas genome editing, and multi-omics integration—have opened up new avenues for the production of stress-tolerant crops. This chapter provides a thorough, human-crafted overview of these processes and examines future directions for applying molecular knowledge to sustainable farming operations.*

[*Citation:* Hammad, M., Batool, A., Sherazi, S.H.U.H. (2026). Mechanisms of action and signaling pathways involved in abiotic stress elicitation. *Bull. Biol. All. Sci. Res.* **11***: 116.* https://doi.org/10.64013/bbasr.v2026i1.116]
Keywords: *Abiotic stress; oxidative stress; Signal transduction; Transcriptional regulation; Stress-resilient crops*

1. Introduction

Abiotic stress in plants refers to adverse effects caused by non-living environmental factors such as drought, salinity, extreme temperatures, heavy metals, oxidative stress, and ultraviolet radiation(Gull et al., 2019). These stresses disrupt cellular homeostasis and limit growth by altering water balance, ion homeostasis, membrane integrity, and metabolic functions(Ho, 2006). Because plants are sessile, they routinely experience combinations of stresses; for example, high temperatures often coincide with drought, intensifying osmotic stress(Seleiman et al., 2021). Such stresses drastically affect plant development and yield: current projections suggest that by 2050 global food demand will double while climate change (drought, heat) poses severe threats to crop productivity(Raza et al., 2019). Indeed, abiotic stresses can depress crop yields by over 50%, highlighting an urgent need to understand stress response mechanisms(Fita et al., 2015).

The importance of decoding these mechanisms is therefore paramount. A deep understanding of stress sensing and signaling pathways is critical for crop improvement and sustainable agriculture(Saleem et al., 2025). Although many stress-related genes have been identified, engineering stress tolerance remains challenging due to complex genetics and network crosstalk(Duque et al., 2013). This chapter aims to comprehensively review how plants perceive abiotic stress and transduce those signals into adaptive responses(Zhu, 2016). We will examine types of abiotic stress and their physiological impacts, the molecular receptors and early messengers that sense stress, and the core signaling pathways (MAPK, ABA-dependent/independent, CDPK, SnRK2) that transmit these cues(Agarwal et al., 2017). We will also discuss transcriptional regulation (stress TFs, epigenetics) and post-transcriptional/post-translational modifications, as well as how plants integrate multiple stress signals(Haak et al., 2017). Finally, biotechnological strategies for developing stress-resilient crops (including CRISPR and transgenics) will be explored. Studying stress signaling in depth is critical to generate stress-tolerant, high-yielding crops(Mehrotra et al., 2014).

1.1 Overview of Abiotic Stress in Plants

Abiotic stresses encompass a range of factors that negatively influence plant growth. Common abiotic stresses include water deficit (drought), soil or water salinity, extreme temperatures (cold or heat), excess heavy metals, high light or UV radiation, and oxidative stress(Xie et al., 2019). Drought stress occurs when water availability is insufficient; it is one of the most significant abiotic stresses, as water is critical for plant metabolism and turgor maintenance(Farooq et al., 2009). Salinity stress arises from high salt concentrations (typically NaCl) in the soil, causing osmotic stress and ion toxicity (excess Na^+ or Cl^-) that disrupt water uptake and nutrient balance(Yadav et al., 2011). Temperature extremes include heat stress, which can denature proteins and alter membrane fluidity, and cold/freezing stress, which can rigidify membranes and form intracellular ice(Kumar et al., 2022). Heavy metal stress refers to toxic metals (e.g. Cd, Pb, Hg) accumulating in cells, which interfere with enzyme function and redox balance(Nowicka, 2022). Oxidative stress is a condition of excessive reactive oxygen species (ROS) that can damage biomolecules(Juan et al., 2021). UV radiation (especially UV-B) causes DNA lesions, protein damage and ROS formation. Often these stresses co-occur (e.g. drought and heat), compounding plant damage(Nazareth et al., 2024).

1.2 Importance of Understanding Stress Response Mechanisms

Understanding how plants perceive and respond to abiotic stress is vital for agriculture and food security. Stress signals trigger broad reprogramming of gene expression and metabolism that ultimately determine survival and yield under adverse conditions(Kamali and Singh, 2023). Climate change is expected to increase the frequency and intensity of droughts, heat waves, and salinity events, placing severe pressure on crop production(Kamali and Singh, 2023). For example, global analyses predict that by 2050 agricultural output must increase by ~85% to feed a population of nearly 10 billion, yet climate-driven stresses threaten this goal(Praveena and Malaisamy, 2024). Abiotic stresses already account for losses of more than half of potential crop yields in many regions(Kopecká et al., 2023). Elucidating stress signaling pathways thus provides essential targets for genetic improvement. Although traditional breeding has had some success, engineering stress tolerance is complex and often yields only partial gains(Mondal and Ghosh, 2024). Advances in molecular biology and systems biology now allow manipulation of key regulators (e.g. transcription factors, kinases, receptors) and the stacking of multiple traits(Khan et al., 2024). Ultimately, detailed knowledge of stress perception and signaling is required to design stress-resilient crops through biotechnology or breeding(Wang et al., 2025).

1.3 Objective and Scope of the Chapter

This chapter systematically reviews the mechanisms by which plants detect abiotic stress and relay those signals to appropriate response pathways. After outlining the major abiotic stress types and their physiological impacts, we examine stress perception mechanisms: membrane-bound sensors, early second messengers (calcium, ROS), and stress-triggered phytohormone signaling(Naz et al., 2024). We then detail key signaling modules in abiotic stress: MAP kinase cascades, ABA-dependent and ABA-independent (DREB/COR) pathways, calcium-dependent protein kinases (CDPKs), and SnRK2 kinases, including cross-regulation among hormonal and stress networks(Alves et al., 2021). Subsequent sections address how stress signals reprogram gene expression: including major transcription factor families (DREB, NAC, WRKY, MYB, bZIP/AREB etc.), chromatin remodeling and epigenetic changes, and network-level expression patterns(Karmakar et al., 2021). Post-transcriptional and post-translational regulation (alternative splicing, RNA regulation, protein phosphorylation/ubiquitination, small RNAs) are also discussed. We then consider integration of multiple stress signals and systems biology approaches to understand the complex network dynamics(Sharma et al., 2023). Finally, we review biotechnological strategies (transgenic approaches, CRISPR/Cas gene editing) for enhancing stress tolerance in crops, and discuss future directions, multi-omics integration, and societal considerations. And this whole process is shown in the figure 1 (Razzaq et al., 2021).

2. Types of Abiotic Stress and Their Physiological Impact

2.1 Drought Stress

Drought stress is caused by insufficient water availability, leading to water deficit at the cellular and organismal level(Pamungkas and Farid, 2022). It is one of the most severe abiotic stresses for plants. Physiologically, drought induces osmotic stress and dehydration of tissues, resulting in loss of turgor pressure and impaired cell expansion(Ahmad et al., 2022). At the cellular level, membranes become destabilized and metabolic processes are inhibited. Indeed, drought severely disrupts plant metabolism and growth: it inhibits photosynthesis and carbon fixation, causes accumulation of ROS, and impedes biosynthesis of proteins and Osmo protectants(Qiao et al., 2024). Under drought, stomata close to limit transpiration, but this reduces CO_2 intake and further lowers photosynthesis(Qiao et al., 2024). Key consequences of drought stress include osmotic imbalance, dehydration-induced loss of cell turgor, plasma membrane dysfunction, reduced energy production, and oxidative damage to lipids, proteins and DNA(Feng et al., 2023). These cellular stresses translate into stunted growth, leaf wilting or senescence, and reduced yield. Drought during critical stages (e.g. flowering) can drastically reduce crop productivity and is a principal threat to global food security(Oguz et al., 2022).

2.2 Salinity Stress

Salinity stress arises from high concentrations of soluble salts (primarily NaCl) in soil or water. Salt stress imposes both osmotic and ionic challenges.

Initially, the high external salt creates osmotic stress, reducing water uptake and mimicking drought conditions(Oguz et al., 2022). Subsequently, toxic Na$^+$ and Cl$^-$ ions accumulate in tissues, interfering with nutrient uptake (K$^+$/Ca^{2+}) and enzymatic functions(Yadav et al., 2024). The ionic toxicity and osmotic imbalance cause physiological symptoms: reduced cell elongation, chlorosis, and necrosis(Alharbi et al., 2022). Plants under salinity stress often exhibit leaf tip burning, reduced leaf expansion, and inhibited root growth(Liu et al., 2023). Metabolically, salt stress leads to overproduction of ROS and perturbs photosynthesis and respiration. For example, salt-induced ionic stress disrupts chloroplast function and accelerates photooxidation(Hussain et al., 2021b). Stomatal conductance may decrease (through hormone signals) as a consequence of osmotic shock, reducing photosynthetic rates(Qi et al., 2021). Overall, salinity severely limits plant water relations, nutrient balance, and energy metabolism. As a result, salt stress causes significant growth inhibition and yield loss, similar in magnitude to drought stress(Angon et al., 2022). Notably, salt- and drought-induced osmotic stress share common responses, including accumulation of compatible solutes and antioxidants to mitigate damage(Khalid et al., 2023).

2.3 Temperature Extremes (Heat and Cold)

Temperature extremes pose significant stress by perturbing biochemical reactions and membrane integrity(Aslam et al., 2022). **Heat stress** occurs when temperatures exceed optimal levels for plant species. High temperatures can denature proteins, inactivate enzymes, and increase membrane fluidity to the point of leakage(Ul Hassan et al., 2021). Photosynthetic machinery (especially photosystem II) is highly heat-sensitive, leading to impaired carbon fixation and energy imbalance(Allakhverdiev et al., 2012). Heat also elevates respiration rates and transpiration, potentially causing dehydration(Cheuvront et al., 2010). Collectively, heat stress reduces photosynthesis, respiration, and transpiration efficiency, and disrupts cellular homeostasis Plants respond by producing heat shock proteins (chaperones) and adjusting lipid composition, but severe heat can be lethal(Argosubekti, 2020).

Cold stress (chilling or freezing) also affects membranes and enzymatic reactions. Low temperatures rigidify membranes and slow metabolic enzyme kinetics(Kratsch and Wise, 2000). In freezing conditions, ice crystals can physically damage cells, and cellular water potential drops dramatically, causing dehydration(Pearce, 2001). Cold inhibits photosynthesis and nutrient transport, leading to an energy deficit. Moreover, cold stress often results in ROS accumulation due to impaired electron transport in chloroplasts(Gan et al., 2019). Physiological consequences include reduced growth rate, chlorosis, wilting, and in severe cases, frost damage and plant death(Kumar and Kumar, 2016). Overall, both heat and cold stress disrupt normal metabolism and trigger protective responses (heat shock proteins, antifreeze proteins, osmolyte accumulation), but beyond thresholds, cause cellular injury(Kennelly et al., 2012).

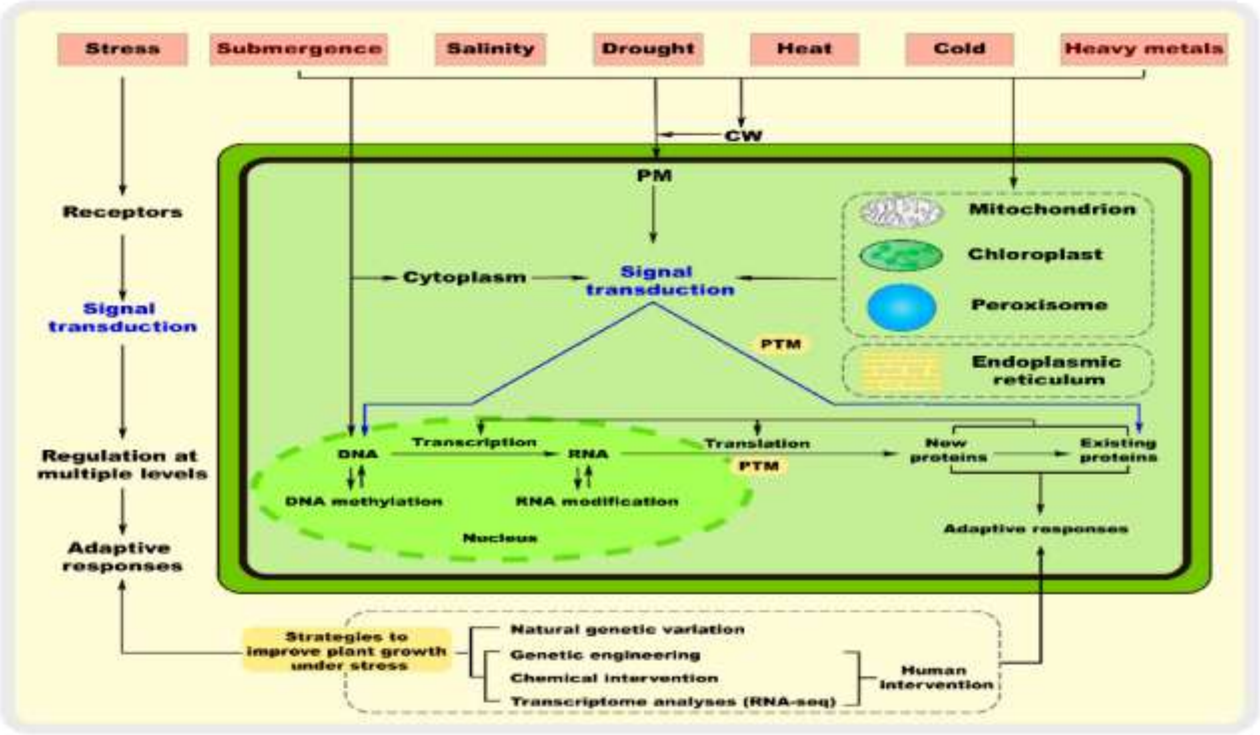

Figure 1: A schematic showing different abiotic stressors, perception (membrane receptors, Ca^{2+}, ROS), signaling pathways, transcription regulation, and stress adaptation

2.4 Heavy Metal Stress

Heavy metal stress refers to toxicity arising from excessive concentrations of metals such as cadmium (Cd), lead (Pb), mercury (Hg), or excessive micronutrient metals (e.g. Zn, Cu). While some metals (e.g. Cu, Zn) are essential at low levels, high levels of any heavy metal disrupt cellular functions(Balali-Mood et al., 2021). Heavy metals bind sulfhydryl groups in proteins, displacing essential ions and inactivating enzymes. They can also catalyze free radical formation, producing ROS such as superoxide and hydroxyl radicals(Mansoor et al., 2023). Physiologically, heavy metal accumulation often causes chlorosis (due to disrupted chlorophyll synthesis), inhibited photosynthesis, stunted growth, and early senescence(Mansoor et al., 2023). Roots exposed to heavy metals show impaired water uptake, and foliage exhibits necrotic lesions. For example, cadmium can replace calcium in cell walls and membranes, increasing permeability and leading to electrolyte leakage(Perfus-Barbeoch et al., 2002). In short, heavy metals provoke a cascade of oxidative damage and nutrient imbalance. They inhibit respiration and photosynthesis, reduce biomass, and ultimately can lead to plant death(Li et al., 2023).

2.5 Oxidative Stress

Oxidative stress is not a primary environmental factor, but rather a pervasive consequence of abiotic stresses. Abiotic conditions (drought, high light, salinity, cold, heavy metals, UV) commonly lead to overproduction of reactive oxygen species (ROS) like superoxide ($O_2\bullet^-$), hydrogen peroxide (H_2O_2), and hydroxyl radicals(Sharma et al., 2019). When ROS generation exceeds the capacity of antioxidant defenses, cells experience oxidative stress. Under oxidative stress, lipids, proteins and DNA are damaged by peroxidation and oxidation, disrupting membrane integrity and metabolic enzymes(Banerjee and Roychoudhury, 2017). However, ROS also function as signaling molecules at lower levels. Plants deliberately produce ROS in response to stress as a signal, but must carefully regulate them. In summary, oxidative stress damages cellular components and accelerates cell death, but controlled ROS bursts also participate in signal transduction(Bhattacharjee, 2012).

2.6 UV and Radiation Stress

Ultraviolet (UV) radiation stress primarily refers to UV-B (280–315 nm) and UV-A (315–400 nm) light from the sun. UV radiation can directly damage DNA (e.g. thymine dimers) and proteins, and generate ROS via photochemical reactions(Rastogi et al., 2010). High-energy UV-B is particularly deleterious: it increases membrane permeability, polymerizes proteins, and inactivates enzymes. UV stress also induces production of secondary metabolites (e.g. flavonoids) as sunscreens. UV-C (<280 nm) is largely filtered by the atmosphere, but artificial UV-C exposure causes severe DNA damage and cell death(Mosadegh, 2018).

Aside from UV, other forms of radiation (such as ionizing radiation) are generally outside the normal environmental range for plants. However, high levels of ionizing radiation (gamma rays, cosmic rays) can also induce DNA breaks, ROS bursts, and lethal mutagenesis(Sharma et al., 2017). Plants have some capacity to repair DNA damage, but intense radiation can overwhelm these systems. In summary, UV stress damages genetic and cellular structures, leading to inhibited growth, while plants respond by activating DNA repair, antioxidant production, and protective pigments(Mahdavian, 2024).

3. Stress Perception and Signal Initiation in Plants

3.1 Membrane-bound Receptors and Sensors

Plants detect abiotic stress through various membrane-associated sensors and receptor proteins. Unlike animals, plants do not have specialized sensory organs, but they use membrane-bound proteins that perceive changes in the environment. Several types of sensors have been identified:

- **Receptor-like kinases (RLKs)**: Some RLKs sense extracellular changes. For example, the Arabidopsis hybrid histidine kinase AHK1 (also known as ATHK1) acts as an Osmo sensor. AHK1 gene expression is upregulated by hyperosmotic stress, and it can functionally replace yeast Osmo sensors, suggesting it detects osmotic imbalance and activates downstream MAPK signaling(Morillo and Tax, 2006).
- **Mechanosensitive channels**: Changes in turgor or membrane tension can open mechanosensitive channels. The OSCA1 protein in Arabidopsis is a plasma-membrane Ca^{2+} channel gated by osmotic stress(Yuan et al., 2014). Under hyperosmotic shock, OSCA1 opens to allow Ca^{2+} influx, serving as an Osmo sensor that translates osmotic pressure changes into Ca^{2+} signals. Similarly, stretch-activated Ca^{2+} channels such as the MCA1/MCA2 proteins mediate Ca^{2+} influx in response to mechanical stress (including cold-induced rigidity). MCA1 and MCA2 exhibit currents when cells are stretched and enhance Ca^{2+} entry under cold shock, identifying them as mechanosensitive Ca^{2+} channels(Gorgues et al., 2022).
- **Others**: Additional sensors include membrane-bound transporters and channel proteins (e.g. vacuolar two-pore K^+ channels, G-proteins) and wall-associated kinases (WAKs) that may detect cell-wall perturbations(Joyce, 2023). In many cases, the precise stress sensors remain unknown, but membrane perturbation itself (lipid phase changes) may be perceived via associated proteins.

These membrane sensors convert physical or chemical stress cues into intracellular signals, often by altering ion fluxes or initiating phosphorylation cascades. The Ca^{2+} channels and kinases like AHK1 link perception at the membrane to downstream messengers and kinase cascades(Kacperska, 2004).

3.2 Role of Calcium Signaling

Cytosolic calcium (Ca^{2+}) acts as a ubiquitous second messenger in abiotic stress signaling. Many stress stimuli trigger rapid, transient increases in cytosolic Ca^{2+} concentration ($[Ca^{2+}]$_cyst). These "Ca^{2+} signatures" vary in amplitude, frequency, and duration depending on the stress type and cell context(Kacperska, 2004). For example, hyperosmotic shock, cold stress, or mechanical stimuli open Ca^{2+}-permeable channels (like OSCA1 or MCA1) to flood Ca^{2+} into the cytosol. This transient Ca^{2+} elevation is decoded by Ca^{2+}-binding sensor proteins (calmodulins, calcineurin B-like proteins (CBLs), Ca^{2+}-dependent protein kinases (CDPKs)) which then activate downstream pathways(Naz et al., 2024).

Alteration of intracellular Ca^{2+} is one of the very early signaling events in stress perception. Indeed, stress-induced Ca^{2+} increases often precede other signals. For instance, when plants experience osmotic stress, cytosolic Ca^{2+} spikes are among the first responses(Mudrilov et al., 2021). These Ca^{2+} transients convey specificity: different stress signals produce distinct Ca^{2+} waveforms. Sensor proteins then bind Ca^{2+} and undergo conformational changes, relaying the information. In this manner, calcium signaling links the membrane sensors to effectors(Pivato, 2023). For example, the SOS3-CIPK (CBL-CIPK) system decodes Ca^{2+} to activate salt tolerance pathways, and CDPKs (see below) become active upon Ca^{2+} binding. Thus, Ca^{2+} is a central integrator that carries stress signals into the cell's signaling networks(Tanveer and Shabala, 2020).

3.3 Reactive Oxygen Species (ROS) as Signaling Molecules

Reactive oxygen species (ROS) are generated as by-products of aerobic metabolism, and abiotic stresses usually enhance their production. While uncontrolled ROS levels cause oxidative damage, ROS also serve as critical signaling molecules(Banerjee and Roychoudhury, 2017). In response to stress, membrane-localized NADPH oxidases (respiratory burst oxidase homologs, RBOHs) produce ROS like superoxide ($O_2•^-$), which dismutase to H_2O_2. This ROS burst can propagate between cells, forming an "ROS wave" that primes distant tissues(Giulietti et al., 2024). For example, a rapid H_2O_2 signal can activate MAPKs and transcription factors in neighboring cells. In guard cells, ABA-induced ROS are required for stomatal closure. In general, moderate ROS act as secondary messengers to modulate gene expression and defense responses(Wang and Song, 2008). However, if ROS accumulate excessively (oxidative stress), they damage lipids, proteins and DNA.

Thus, ROS have a dual role: at signaling levels, they integrate stress cues and trigger defense programs; at high levels, they execute cytotoxic effects. Fine regulation of ROS production and scavenging is a key part of stress signaling(Schieber and Chandel, 2014). Enzymes like superoxide dismutase and catalase moderate ROS levels. In summary, ROS are both stress-induced damage agents and vital messengers linking perception to response(Scandalios, 2005).

3.4 Phytohormones and Early Signaling

Phytohormones play pivotal roles in early stress signaling by modulating gene expression and physiological responses. Among them, abscisic acid (ABA) is the major hormone mediating responses to osmotic and drought stress(Muhammad Aslam et al., 2022). Stresses such as drought, high salinity, cold, or heat rapidly elevate ABA levels in plants. ABA then triggers immediate responses: it promotes stomatal closure to reduce water loss and activates stress-responsive genes(Hussain et al., 2021a). For example, under osmotic stress ABA accumulation induces stomatal closure to maintain water balance, and it signaling cascade (PYR/PYL receptors → SnRK2 kinases → ABF/AREB transcription factors) leads to induction of ABA-responsive genes(Zha et al., 2025). Other hormones also contribute to stress signaling. Ethylene and jasmonates often accumulate under stress and can modulate growth or senescence. For instance, ethylene increases under flood or drought conditions to alter root growth, and jasmonic acid levels rise under ozone or UV stress to induce defense compounds(Iqbal et al., 2017). Salicylic acid primarily signals biotic stress, but can intersect with abiotic pathways. In combined stress conditions, the balance among ABA, ethylene, jasmonate, gibberellin and other hormones determines the response profile. Indeed, early stress responses usually involve crosstalk between Ca^{2+}/ROS signals and hormone pathways. For instance, early signaling events include Ca^{2+} spikes, inositol phosphates and ROS bursts, followed by activation of kinase cascades and rapid hormone production(Santisree et al., 2020). In summary, stress perception quickly leads to phytohormone-mediated signaling waves, with ABA being central for drought/salt, and other hormones (ethylene, JA, SA, brassinosteroids) modulating or fine-tuning the response. This phytohormones and early signaling shown in figure 2.

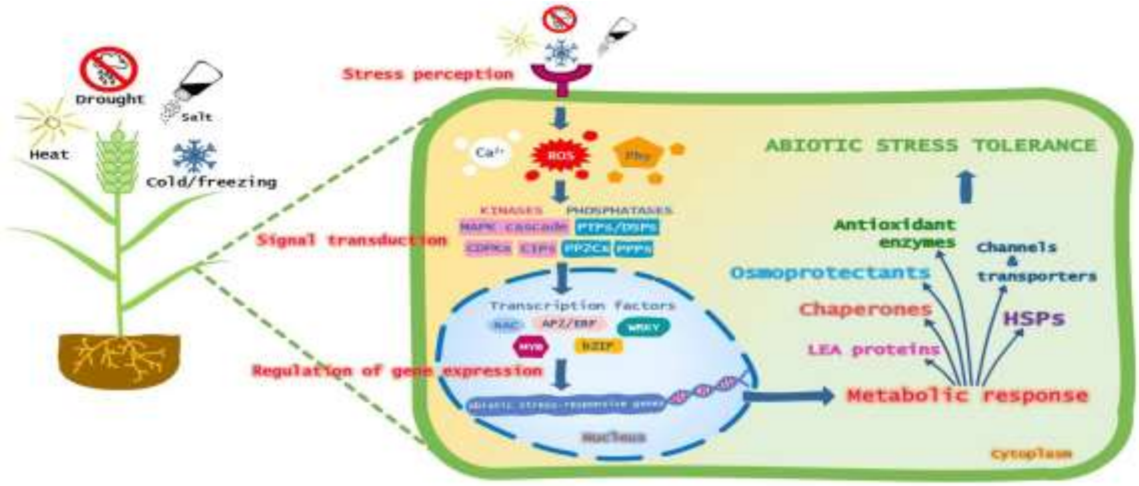

Figure 2: Signaling Pathway Leading to Plant Response to Abiotic Stresses. Illustrates how abiotic stress is detected and transduced via Ca^{2+}, ROS, kinases, TFs, and stress-tolerance proteins.

4. Key Signaling Pathways in Abiotic Stress Response

4.1 MAPK (Mitogen-Activated Protein Kinase) Cascade

Mitogen-activated protein kinase (MAPK) cascades are universal signaling modules that transduce stress signals into cellular responses. A typical MAPK cascade consists of three tiers: a MAP kinase (MAPKKK or MEKK) activates a MAP kinase (MAPKK or MKK), which in turn activates a MAP kinase (MAPK) through dual phosphorylation(Kyriakis and Avruch, 2001). Upon stress perception, specific MAPKKKs are triggered (often by other kinases or sensors), initiating this phosphorylation relay.

In plants, stress-activated MAPKs phosphorylate target transcription factors, metabolic enzymes, or other kinases, thereby modulating gene expression and biochemical responses(Moustafa et al., 2014). For example, an Arabidopsis cascade involving AtMEKK1–AtMKK2–AtMPK4/6 is activated by osmotic (salt/drought) stress(Novikova et al., 2007). Activated MAPKs can induce genes encoding Osmo protectants and detoxification enzymes. Notably, MAPK signaling is closely linked to ROS and antioxidant defenses: overexpression of certain MAPKKKs increases activities of antioxidant enzymes and improves tolerance(Yue and López, 2020). Similarly, MAPKs often function in ABA signaling; some MAPKs are phosphorylated by ABA-responsive SnRK2 kinases, integrating ABA-dependent stress signals. MAPKs also regulate developmental processes under stress (e.g. leaf expansion). In sum, MAPK cascades amplify stress signals and orchestrate appropriate transcriptional and post-translational changes(De Zélicourt et al., 2016). A specific example is that overexpressing MAPKK genes enhances expression of ROS-scavenging enzymes, demonstrating the MAPK role in controlling oxidative stress. Under drought, MAPKs activated downstream of ABA regulate many stress-response genes(Ma et al., 2024).

4.2 ABA-Dependent and Independent Pathways

Abiotic stress-responsive gene expression in plants is often described in two branches: ABA-dependent and ABA-independent pathways. In the **ABA-dependent pathway**, stress-induced ABA binds to PYR/PYL receptor proteins, which inhibit PP2C phosphatases(Liu et al., 2018). This releases SnRK2 kinases from inhibition; active SnRK2s then phosphorylate AREB/ABF bZIP transcription factors(Liu et al., 2018). The AREB/ABF factors bind to ABA-responsive elements (ABREs) in promoters of genes encoding late embryogenesis abundant (LEA) proteins, osmolyte biosynthesis enzymes, etc(Ayub et al., 2025). These genes (e.g. *RD29B*) are upregulated in response to ABA and function in drought and salinity tolerance. This pathway is predominant under osmotic stresses (drought, salt) and even some temperature stresses, as *Arabidopsis* ABF3 and ABF4 TFs are induced by dehydration(Msanne et al., 2011).

In contrast, the ABA-independent pathway involves transcription factors that respond to stress without requiring ABA accumulation. Notable among these are the DREB/CBF (dehydration-responsive element-binding/C-repeat binding) proteins, which recognize DRE/CRT cis-elements. For example, DREB1/CBF factors are induced by cold and regulate cold-responsive genes (*COR15*, *RD29A*)(Costa Alves, 2015). DREB2A is induced by dehydration and heat. Although termed "ABA-independent", these factors can intersect with ABA signaling. In fact, AREB/ABFs (from the ABA pathway) can bind to the *DREB2A* promoter and activate it in an ABA-dependent manner(Costa Alves, 2015). This illustrates crosstalk: ABA signaling components can influence ABA-independent TFs. Nevertheless, many stress genes (e.g. *RD29A*, *ERD1*) contain DRE elements and are activated by DREB proteins irrespective of ABA. Thus, the two branches converge on overlapping gene networks(Roychoudhury et al., 2013). In summary, ABA-dependent pathways (via SnRK2s and ABFs) dominate under drought/salt, while ABA-independent (via DREBs, NACs, etc.) also contribute especially to rapid early responses and cross-protection(Rehman and Mahmood, 2015).

4.3 Calcium-Dependent Protein Kinases (CDPKs)

Calcium-dependent protein kinases (CDPKs or CPKs) are a plant-specific family of Ser/Thr kinases that directly link Ca^{2+} signaling to phosphorylation events as shown in Fig 03. CDPKs contain an N-terminal kinase domain and a C-terminal calmodulin-like regulatory domain(Parvathy, 2018). When stress-induced Ca^{2+} spikes occur, Ca^{2+} binds the EF-hand motifs of CDPKs, causing a conformational change that activates the kinase. The activated CDPK can then phosphorylate downstream targets such as transcription factors, ion channels, and metabolic enzymes(Kundu et al., 2022).

CDPKs have been implicated in many abiotic stress responses. For instance, certain Arabidopsis CPKs regulate stomatal closure and ABA responses during drought. Loss-of-function *cpk10* mutants have impaired stomatal closure and are hypersensitive to water deficit, indicating that CPK10 mediates ABA-induced guard cell responses(Asano et al., 2012). In rice, OsCPK9 has been shown to enhance drought tolerance: plants overexpressing OsCPK9 exhibit better osmotic adjustment and fertility under stress. In general, CDPKs modulate stress tolerance by activating antioxidant defenses and regulating ion transport. CDPKs also phosphorylate NADPH oxidases (RBOHs) to control ROS production under stress(Yadav et al., 2025). In summary, CDPKs are essential Ca^{2+} sensors that translate cytosolic Ca^{2+} transients into phosphorylation of effectors, thereby modulating gene expression and physiological processes (e.g. stomatal closure, ion homeostasis) under abiotic stress(Singh et al., 2017).

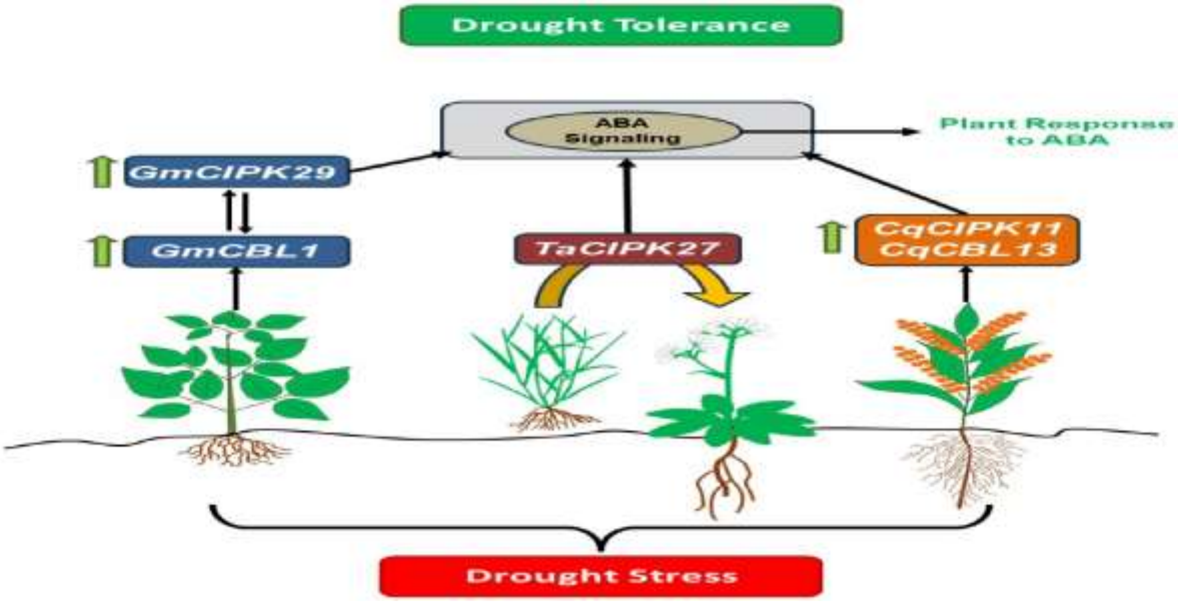

Figure 3: CBL–CIPK Calcium-Dependent Signaling Curve. This figure shows how calcium sensors interact with kinases and hormones (ABA, JA) under stress

4.4 SnRK2 (Sucrose Non-Fermenting1-Related Kinase 2) Pathway

The SnRK2 kinase family is central to ABA signaling and osmotic stress responses. Group 2 SnRK2s (such as Arabidopsis SnRK2.2/2.3/2.6 (OST1)) are activated by ABA: when ABA levels rise, PYR/PYL receptors inhibit PP2C phosphatases, allowing SnRK2s to auto phosphorylate and activate(Kulik et al., 2011). These active SnRK2s then phosphorylate key targets: they phosphorylate AREB/ABF transcription factors (see ABA section) to induce stress genes, and they phosphorylate ion channels like SLAC1 in guard cells to trigger rapid stomatal closure. In this way, SnRK2s connect ABA perception to transcriptional and physiological outputs(Fujita et al., 2013). Some SnRK2s (subclass I) are activated directly by osmotic stress even in the absence of ABA, contributing to the “ABA-independent” branch. Overall, the SnRK2 kinases are a convergent point for ABA signals and direct osmotic stress signals, relaying them into stress-specific phosphorylation cascades(Fàbregas et al., 2020).

4.5 Crosstalk Between Hormonal and Stress Signaling

Abiotic stress signaling is highly interconnected with various hormonal pathways. The interplay among hormones allows plants to balance growth, defense, and stress tolerance. For example, under drought the rise in ABA often antagonizes growth-promoting gibberellin (GA) signaling, causing DELLA protein accumulation which helps induce stress genes. Ethylene signaling can interact with ABA: in some contexts, ethylene opposes ABA effects, but it can also synergize with ABA in salt stress to regulate gene expression(Jiang and Fu, 2007). Jasmonic acid (JA) and salicylic acid (SA), typically associated with biotic stress responses, also influence abiotic tolerance: elevated JA can promote antioxidant defenses, while SA may enhance or suppress certain abiotic stress genes. Recent studies highlight that ABA and JA/SA can antagonize each other when allocating resources between abiotic stress and pathogen defense(Wang et al., 2021). In combined stresses (e.g. heat plus drought), hormone interactions can be complex: one stress-induced hormone may prime responses to another stress. In general, hormone-hormone crosstalk involves both synergistic and antagonistic interactions that finely tune the plant's strategy (growth vs defense)(Korek et al., 2025). For instance, ABF transcription factors (ABA-pathway) can directly upregulate DREB2A (a drought TF) in an ABA-dependent manner, illustrating how "ABA-independent" factors are wired into ABA networks. Overall, stress signaling is modulated by a dynamic network of hormones, with ABA at the center for drought/salt and other hormones modifying the response context as shown in the figure 04 (Nakashima and Yamaguchi-Shinozaki, 2013).

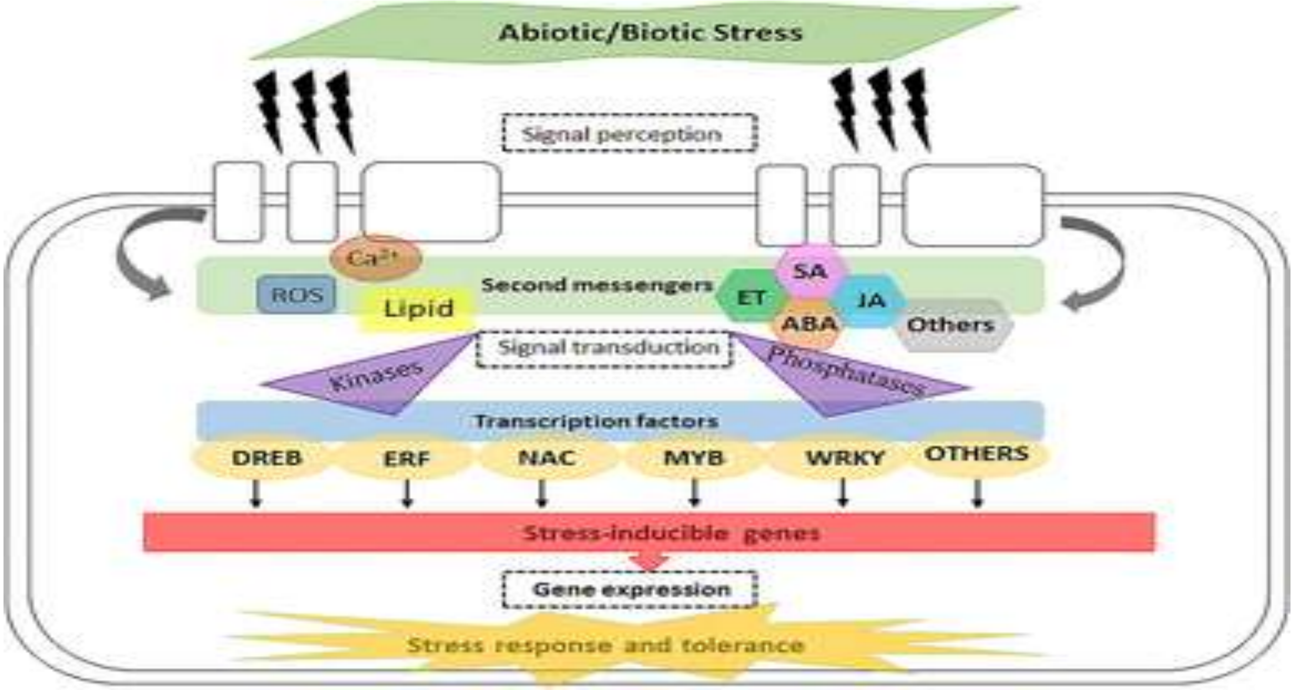

Figure 4: Schematic of Stress Signal Transduction in Plant Cells. Highlights how TF families (DREB, NAC, WRKY, MYB) integrate stress signals within the nucleus, bridging signaling to gene regulation

5. Transcriptional Regulation of Stress-Responsive Genes

5.1 Role of Transcription Factors (DREB, NAC, WRKY, MYB, etc.)

A diverse array of transcription factor (TF) families governs the reprogramming of gene expression during abiotic stress. Major TF families include AP2/ERF (notably the DREB/CBF subfamily), bZIP (ABF/AREB), NAC, WRKY, MYB, and others(PARRAY, 2019). DREB (Dehydration-Responsive Element-Binding) proteins are AP2/ERF TFs that bind drought/cold-responsive elements (DRE/CRT, consensus CCGAC) in target promoters. For example, DREB1/CBF TFs regulate cold-responsive genes, whereas DREB2 factors activate dehydration-inducible genes. NAC family members (NAM, ATAF, CUC domains) include many stress-inducible TFs (e.g., ANAC019, RD26) that control osmotic and oxidative stress genes(Wang and Dane, 2013). WRKY TFs (characterized by the WRKYGQK motif) regulate defense and stress genes; many WRKYs are upregulated by drought or salinity and target promoters with W-box elements. R2R3-MYB TFs influence stress responses such as cuticle formation, stomatal development and flavonoid metabolism. bZIP TFs (AREB/ABF subgroup) bind ABREs in ABA-responsive genes(Wang and Dane, 2013). Together, these TFs form a regulatory network: some TFs (e.g. AREBs) target other TF genes (e.g. DREB2A, MYBs), creating hierarchical cascades. For example, AREB/ABFs directly activate DREB2A in an ABA-dependent way, linking ABA and DREB pathways. The result is a coordinated activation of suites of stress-protective genes (Osmo protectant biosynthetic enzymes, Late Embryogenesis Abundant proteins, ion transporters, heat-shock proteins, etc.)(Singh and Laxmi, 2015). Overexpression of individual TFs often enhances stress tolerance in transgenic plants, underscoring their key regulatory roles. In summary, stress-responsive gene expression is orchestrated by multiple TF families acting on specific promoter elements, integrating various signals to mount an appropriate response(Hussain et al., 2011).

5.2 Chromatin Remodeling and Epigenetic Modifications

Stress-responsive gene expression is also modulated at the chromatin level. Abiotic stress can induce locus-specific changes in chromatin structure that affect gene accessibility. These include post-translational modifications of histone proteins (such as acetylation, methylation, phosphorylation) that alter nucleosome packing(Geiman and Robertson, 2002). For instance, histone acetylation generally opens chromatin and is often elevated at stress gene promoters, facilitating transcription. Conversely, repressive marks (like H3K27 methylation) may be removed from stress genes during activation. Plants also incorporate histone variants (e.g. H2A.Z, H3.3) into nucleosomes to modify chromatin dynamics under stress. DNA methylation patterns can change with stress, leading to silencing or activation of specific genes(Shvedunova and Akhtar, 2022).

Moreover, ATP-dependent chromatin remodelers (e.g. the SWI/SNF complexes) mobilize nucleosomes at stress genes. For example, the Arabidopsis SWI/SNF component BRM binds and regulates cold-responsive genes, and other SWI/SNF subunits are implicated in drought responses(Bieluszewski et al., 2023). A recent study in soybean showed that SWI/SNF subunits have stress-responsive promoters and that mutation of one subunit (GmLFR1) affected drought tolerance(Chen et al., 2023).

These epigenetic and chromatin-based mechanisms can also contribute to stress memory: past exposure to stress can leave “marks” (like sustained histone acetylation) that prime a faster response to subsequent stress. In summary, dynamic chromatin remodeling and epigenetic modifications provide an extra layer of control over stress-gene networks(Avramova, 2015).

5.3 Stress-Induced Gene Expression Networks

Abiotic stress elicits large-scale reprogramming of the transcriptome, involving hundreds or thousands of genes. These stress-responsive genes often form co-regulated modules or networks. High-throughput expression profiling (microarrays or RNA-seq) in stressed plants reveals clusters of co-expressed genes that share regulatory motifs and functions(Haak et al., 2017). Network analyses identify key “hub” genes (often transcription factors or kinases) that coordinate entire modules. For example, a systems study in pepper constructed a global gene co-expression network under various stresses and pinpointed hub regulators of defense-related gene clusters. Generally, stress gene networks include signaling components (kinases, ROS regulators), hormone genes, TFs, and protective enzymes(Zhu et al., 2021).

These networks integrate multiple inputs: signals from Ca^{2+}, ROS, hormones and kinases converge on transcription factors, which then drive interconnected expression programs. There are many feedforward and feedback loops. For instance, a TF may activate a kinase gene that in turn further modifies the TF, creating amplification(Vakulabaranam Sridharan, 2015). Large transcriptome surveys indicate that a stress signal activates a “cascade” of TFs and target genes such that the plant undergoes broad metabolic and developmental adjustments. In conclusion, stress-induced gene expression is organized into dynamic regulatory networks, whose architecture can be revealed by co-expression and network analyses(Meraj et al., 2020).

6. Post-Transcriptional and Post-Translational Modifications

6.1 RNA Processing and Alternative Splicing

Abiotic stress alters RNA metabolism at multiple levels. Notably, alternative splicing (AS) of pre-mRNAs is greatly enhanced under stress. Many stress-related genes produce multiple splice isoforms under stress, which can lead to proteins with modified function or localization. For example, stress can induce retention of introns or use of alternative splice sites in key signaling genes(Matsui et al., 2019). Splicing factors and the spliceosome itself are regulated by stress; mutants in splicing components often show impaired stress tolerance. Thus, AS provides a rapid means of diversifying the proteome and fine-tuning gene function during stress(Ganie and Reddy, 2021).

Stress also affects RNA stability and processing: specific mRNAs may be selectively stabilized or degraded (via RNA-binding proteins or miRNAs, discussed below). RNA editing (C-to-U changes) in organelles can be stress-responsive(Pandita and Pandita, 2023). Overall, post-transcriptional regulation (splicing, capping, polyadenylation, RNA turnover) allows plants to adjust their proteome more flexibly than through transcription alone as shown in Figure 5.

6.2 Protein Phosphorylation and Ubiquitination

Post-translational modifications rapidly modulate protein activity in stress pathways. Phosphorylation is a primary switch: kinases (MAPKs, SnRK2s, CDPKs) phosphorylate target proteins (TFs, enzymes, transporters) to activate or inhibit them(Damaris and Yang, 2021). For example, CDPKs phosphorylate transcription factors and NADPH oxidases to influence drought responses. Similarly, SnRK2 kinases phosphorylate ABF transcription factors in the ABA pathway. Such phosphorylation events are reversible and enable dynamic control(Yoshida et al., 2015).

Ubiquitination is equally important: many stress regulators are controlled by targeted degradation via the ubiquitin–proteasome system. E3 ubiquitin ligases attach ubiquitin to specific proteins, marking them for destruction. A clear example is the regulation of the drought TF DREB2A. Arabidopsis DRIP1 and DRIP2 are RING-type E3 ligases that interact with and ubiquitinate DREB2A. Under non-stress conditions these DRIPs promote DREB2A degradation. When drought occurs, DREB2A is stabilized (for instance, via stress-induced DRIP degradation) and can then activate downstream genes(Callis, 2014). In DRIP1/DRIP2 double mutants, DREB2A accumulates and drought-responsive genes are overexpressed. This shows how protein turnover is a critical control point: stress signaling often involves stabilizing positive regulators (by inhibiting their E3 ligases) or degrading negative regulators. Other types of PTMs are involved too: SUMOylation of TFs or kinases can modulate their activity under stress. In sum, phosphorylation and ubiquitination constitute fast “on/off” switches in stress pathways, shaping signal amplitude and duration(Qin et al., 2008).

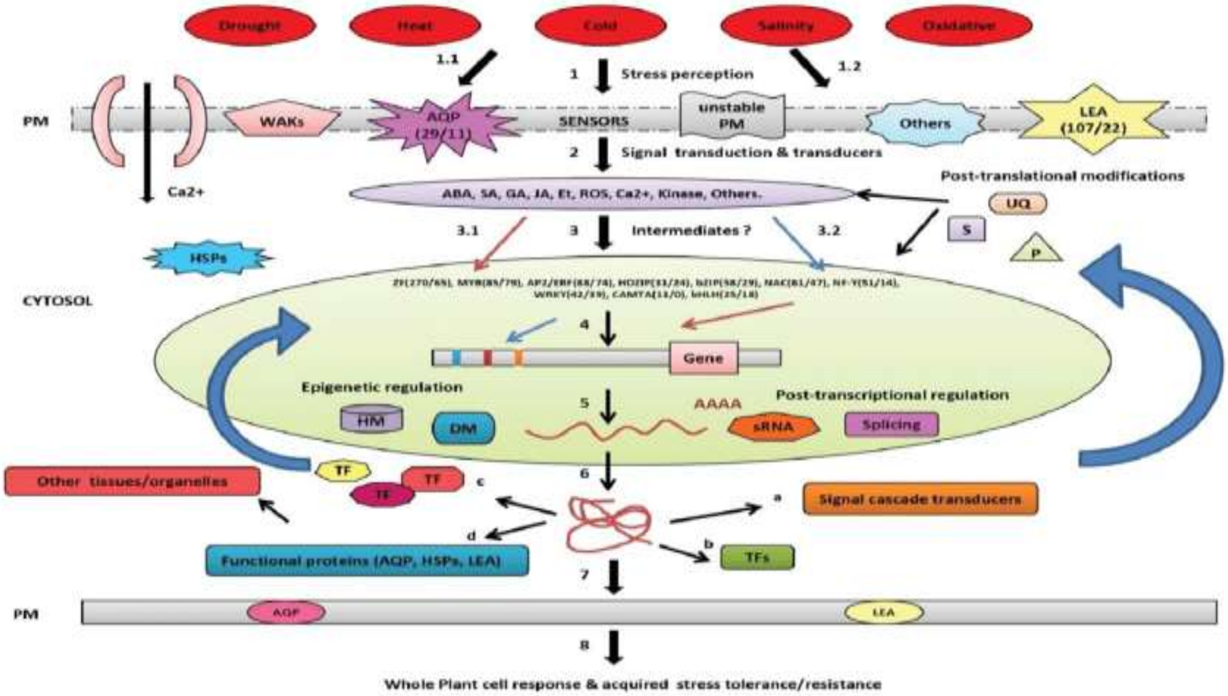

Figure 5: Abiotic Stress–Induced Changes in Plant Cell. Depicts both functional proteins and regulatory layers (splicing, epigenetics, PTMs), showcasing downstream stress responses

6.3 Role of Small RNAs in Stress Regulation

Small non-coding RNAs, especially microRNAs (miRNAs), are key regulators of gene expression under stress. Plant miRNAs (~21 nt) bind complementary mRNAs to trigger degradation or translational inhibition. Many miRNAs are stress-responsive. For example, under drought or salinity, certain miRNAs that target growth-promoting TFs are up- or down-regulated to adjust growth and development(Ma et al., 2022). The growing body of research shows that manipulating miRNAs can enhance stress tolerance. miRNAs thus form regulatory circuits: a stress signal alters miRNA expression, which in turn fine-tunes the levels of stress-related genes (often TFs or hormone receptors). In addition to miRNAs, small interfering RNAs (siRNAs) can be involved in epigenetic silencing of stress-responsive genes or transposons. Overall, small RNAs add a crucial post-transcriptional layer, ensuring that stress-response transcripts are expressed at the right levels and times(Basso et al., 2019).

7. Integration of Multiple Stress Signals

7.1 Signal Crosstalk and Network Dynamics

Plants often encounter multiple abiotic stresses simultaneously (e.g. drought plus heat), and their signaling pathways are highly interwoven. Crosstalk occurs when components of one pathway influence another. For instance, an ROS burst triggered by salt stress can activate stress-responsive MAPKs that also respond to drought(Ramegowda and Senthil-Kumar, 2015). Calcium and ROS signals from one stress can prime responses to another by pre-activating shared signaling proteins. Hormonal crosstalk is another key integration point (as noted earlier). These interactions create complex network dynamics, where stress pathways converge on common nodes and feedback loops. Network models show that hub regulators (such as certain kinases or TFs) can mediate cross-communication between stress responses, allowing the plant to mount a coordinated response to compound stresses(Ali and Chen, 2024). Systems biology studies illustrate that stress signaling networks are modular yet overlapping: modules for different stresses share connections and can be reconfigured depending on the stress combination(Singh et al., 2008).

7.2 Synergistic and Antagonistic Interactions

Within the integrated network, stress signals can interact synergistically or antagonistically. Synergistic interactions amplify stress responses; for example, drought and high light together generate greater ROS and elicit stronger antioxidant defenses than either stress alone. Conversely, antagonistic interactions can occur when one pathway inhibits another. A well-known example is the trade-off between growth and defense: stress-induced ABA can antagonize gibberellin signaling, reducing growth (via DELLA proteins) to conserve resources(Nadeem et al., 2023). Similarly, as mentioned, ABA signaling often downregulates SA/JA-mediated pathogen defense during drought. Hormones also engage in mutual antagonism: ethylene and ABA can have opposing effects on certain genes, or JA may counteract ABA in leaf senescence. Overall, plants finely balance these interactions: hormonal and second-messenger crosstalk involves both positive and negative interactions that optimize survival under complex stress scenarios(Rai et al., 2021).

7.3 Systems Biology Approaches to Pathway Analysis

Given the complexity of stress networks, systems biology tools have become invaluable. High-throughput "omics" (transcriptomics, proteomics, metabolomics) allow global snapshots of plant responses. Integrative analyses construct gene co-expression networks and identify key regulators. For example, researchers have built global co-expression networks from RNA-Seq data on stressed plants to find hub genes governing stress modules(Satrio et al., 2024). The figure below illustrates a typical pipeline for such network construction: raw RNA-Seq data from control and stress samples are processed and used to compute expression correlations, yielding a network whose topology highlights central signaling genes (hubs). These computational models, combined with experimental validation, enable discovery of novel regulators and elucidation of pathway architecture(Srivastava et al., 2022). Multi-omics integration (combining genomics, transcriptomics, proteomics and metabolomics) further reveals how different layers (mRNA, protein, metabolites) respond and interact under stress. Such systems-level approaches are essential for deciphering the full signaling network and for predicting how pathway perturbations (e.g. gene knockouts) will impact stress tolerance(Sanches et al., 2024).

Figure: Schematic of a gene co-expression network (GCN) analysis pipeline for stress transcriptome data. RNA-seq reads are quality-controlled and aligned, differential expression is assessed, and co-expression relationships are calculated to build a network. Analysis of this network identifies hub genes and stress-response modules (modified from Shimizu et al. 2023.

8. Biotechnological Applications and Genetic Engineering

8.1 Development of Stress-Resilient Crops

Translating knowledge of stress signaling into crop improvement is a major goal. Traditional breeding has produced some stress-tolerant varieties, but often with trade-offs. Genetic engineering has enabled overexpression or suppression of specific stress regulators. For example, transgenic plants overexpressing DREB or NAC transcription factors often show improved drought or salt tolerance (though sometimes with growth penalties)(Meena et al., 2025). However, due to the polygenic nature of stress tolerance and pathway crosstalk, single-gene modifications have had limited success in the field. Efforts now focus on stacking multiple genes (e.g. combinations of Osmo protectant enzymes, chaperones and signaling proteins) and using stress-inducible promoters to minimize negative effects. Genome-wide association studies (GWAS) and QTL mapping also identify alleles associated with stress tolerance for marker-assisted breeding. In all cases, understanding the underlying signaling mechanisms guides the choice of candidate genes(Villalobos-López et al., 2022).

8.2 CRISPR/Cas and Other Genome Editing Tools

Genome editing has revolutionized crop engineering. The CRISPR/Cas9 system allows precise modification of stress-related genes. For instance, knocking out negative regulators (e.g. ABA receptor repressors or ion transporter inhibitors) or editing promoters to tweak expression levels can enhance tolerance without introducing foreign DNA. A notable example: mutations in rice genes encoding Na^+ transporters have been introduced via CRISPR to improve salinity tolerance. Given that abiotic stresses can halve yield, CRISPR offers great potential to rapidly create stress-resilient cultivars(Shelake et al., 2022). The simplicity and versatility of CRISPR (and newer tools like base editing and prime editing) make it possible to target multiple genes simultaneously or create precise alleles inspired by natural variation. Recent reviews highlight the successes of CRISPR in manipulating genes for drought, heat, and salt tolerance. As regulatory frameworks adapt, CRISPR-edited crops (which may be transgene-free) are becoming feasible for agricultural deployment. Thus, genome editing stands as a powerful application of stress signaling research for crop improvement(Saber Sichani et al., 2023).

8.3 Use of Transgenic Plants for Functional Validation

Transgenic plants remain an indispensable tool for functional validation of stress-related genes. Genes of interest (signaling kinases, TFs, transporters, etc.) are often overexpressed or silenced in model plants (Arabidopsis, rice, tobacco) to assess their role in stress responses. Reporter gene fusions (e.g. promoter-GUS) and mutant analysis (T-DNA knockouts, RNAi) help decipher spatiotemporal patterns of gene activation under stress(Hussain et al., 2011). Such experiments have confirmed the functions of many components (e.g. confirming that a candidate sensor or kinase activates stress markers). In crops, transgenic lines validate whether candidate genes from other species can confer tolerance. These functional assays are critical for establishing causality and for refining which genetic modifications are likely to be effective in breeding or gene editing(Xiao et al., 2009).

9. Future Perspectives and Challenges

9.1 Integrating Multi-Omics Approaches

Future progress will rely on even deeper integration of multi-omics data. Transcriptomic, proteomic, metabolomic, epigenomic and phenomics datasets can be combined to map out the complete regulatory network of stress response. For example, quantitative phosphoproteomic has identified hundreds of new SnRK2 substrates, including factors controlling chromatin and miRNA processing. Combining such phosphoproteomic maps with transcriptomic changes under stress helps reveal causal links(Jan et al., 2025). Similarly, metabolomics can trace how stress alters key pathways (e.g. osmolyte synthesis, antioxidant pools) under different signaling regimes. Integrative computational models (machine learning, network inference) will help predict emergent behaviors of the stress network. However, challenges remain in capturing spatial and temporal dynamics of signaling in whole plants, and in modeling the complexity of multiple stresses and natural variation. Nevertheless, multi-omics and systems biology promise to fill critical knowledge gaps(Satrio et al., 2024).

9.2 Climate Change and Stress Adaptation

In a changing climate, new stresses and stress combinations will emerge. Extreme weather events, heatwaves, and erratic precipitation will test plant resilience. Understanding signaling plasticity – how plants adapt to stress changes over time or development – is therefore crucial. Breeding for climate resilience will require not only single-stress tolerance, but also hardiness under compound stresses (e.g. heat and drought)(Tripathy et al., 2023). This makes the understanding of stress crosstalk and regulatory flexibility even more important. Ultimately, insights into stress signaling must be translated into strategies for sustainable agriculture: selecting alleles that optimize stress signaling pathways, designing cropping systems that exploit natural stress-response rhythms, and developing crop varieties that balance growth with preparedness for stress(Aramburu et al., 2014).

9.3 Ethical and Ecological Considerations

While the mechanistic understanding of stress signaling offers many tools, applications must be considered in an ethical and ecological context. Genetically engineered or edited crops raise questions of biosafety, gene flow to wild relatives, and socioeconomic impact. We must weigh the benefits of stress-tolerant crops (reduced inputs, stable yields) against potential unintended effects on ecosystems(KhokharVoytas et al., 2023). Moreover, equitable access to advanced technologies (CRISPR, genomics) is a concern for global food security. Responsible deployment, transparency, and regulation will be necessary as we move from the lab to the field. Ecologically, enhancing stress tolerance could alter water and nutrient cycles, so breeding must also consider ecosystem-level feedbacks. In summary, expanding our toolkit for stress adaptation must go hand-in-hand with ethical stewardship and ecological sustainability(Rasheed et al., 2021).

10. Conclusion

This chapter has reviewed the complex network of plant responses to abiotic stress. We have seen that abiotic stress perception involves specific membrane and intracellular sensors that activate early second messengers (Ca^{2+}, ROS) and phytohormones. These signals feed into key signaling cascades: MAPKs, ABA-dependent and independent pathways, CDPKs, and SnRK2 kinases, among others, which collectively regulate stress-responsive gene expression. Transcription factors (DREBs, NACs, WRKYs, MYBs, etc.)(Duque et al., 2013) read the signaling codes and reprogram the transcriptome, while chromatin modifications and small RNAs fine-tune the response. Post-translational modifications (phosphorylation, ubiquitination) provide rapid on/off control of protein activities. These layers form an integrated network, capable of prioritizing growth or defense as needed. The resulting stress-response networks can be represented and analyzed by systems biology approaches, revealing central hub regulators and interactions. In crop plants, deciphering these mechanisms creates opportunities to improve resilience: through genetic engineering and gene editing we can modify key nodes in the network. However, stress tolerance is a highly polygenic trait, so multi-gene strategies are often needed(Mishra et al., 2021).

10.1 Summary of Key Mechanisms

In summary, abiotic stress triggers a cascade of events: sensors detect physical changes, Ca^{2+} and ROS convey urgency, ABA and other hormones modulate physiology, and specialized kinases (MAPK, CDPK, SnRK2) propagate the message by phosphorylation. Transcription factors execute a reprogramming of the genome, while post-transcriptional and epigenetic mechanisms provide additional control. The concerted action of these mechanisms allows plants to adjust metabolism, maintain homeostasis, and survive under stress. Studying stress signaling and regulation is critical to understanding how plants cope with environmental challenges(Bucholc et al., 2013).

10.2 Opportunities for Crop Improvement

The detailed understanding of stress-response pathways opens avenues for crop improvement. By targeting specific regulators (e.g. enhancing positive TFs, disabling negative regulators), we can engineer crops that better withstand drought, salinity, or temperature extremes. Marker-assisted selection and genomic prediction can incorporate favorable stress-response alleles into breeding programs. Genome editing offers precise manipulation of key genes in elite cultivars. Importantly, insights into crosstalk will help design multi-trait improvements that preserve yield while enhancing stress tolerance. As climate change intensifies, these opportunities for translating molecular knowledge into stress-resilient agriculture become ever more crucial(Kathuria, 2024).

10.3 Final Thoughts

Abiotic stress signaling in plants is a rich, multilayered field where many discoveries still await. Future work integrating diverse data types and bridging lab studies with field realities will refine our models. Continued research will likely uncover new sensors, signaling components, and regulatory feedbacks. Ultimately, the goal is to harness this knowledge to support sustainable food production under increasingly challenging environmental conditions. As one review notes, *"Studying stress signaling and regulation is critical to understand abiotic stress responses in plants to generate stress-resistant, high-yield crops.* In this spirit, the insights summarized here serve as a foundation for both scientific progress and practical applications in crop science(Singh et al., 2021).

References

Agarwal, P., Jiwani, G., Khurana, A., Gupta, P., and Kumar, R. (2017). Ethylene and stress mediated signaling in plants: a molecular perspective. *Mechanism of Plant Hormone Signaling under Stress* **1**, 295-326. https://doi.org/10.1002/9781118889022.ch12

Ahmad, H. M., Fiaz, S., Hafeez, S., Zahra, S., Shah, A. N., Gul, B., Aziz, O., Fakhar, A., Rafique, M., and Chen, Y. (2022). Plant growth-promoting rhizobacteria eliminate the effect of drought stress in plants: a review. *Frontiers in Plant Science* **13**, 875774. https://doi.org/10.1002/9781118889022.ch12

Alharbi, K., Al-Osaimi, A. A., and Alghamdi, B. A. (2022). Sodium chloride (NaCl)-induced physiological alteration and oxidative stress generation in Pisum sativum (L.): A toxicity assessment. *ACS omega* **7**, 20819-20832. https://doi.org/10.1021/acsomega.2c01427

Ali, J., and Chen, R. Z. (2024). "Chemical Ecology: Insect-Plant Interactions," CRC Press.

Allakhverdiev, S. I., Kreslavski, V. D., Fomina, I. R., Los, D. A., Klimov, V. V., Mimuro, M., Mohanty, P., and Carpentier, R. (2012). Inactivation and repair of photosynthetic machinery under heat stress. *Photosynthesis: overviews on recent progress and future perspective. IK International Publishing House Pvt. Ltd., New Delhi*, 189.

Alves, H. L., Matiolli, C. C., Soares, R. C., Almadanim, M. C., Oliveira, M. M., and Abreu, I. A. (2021). Carbon/nitrogen metabolism and stress response networks–calcium-dependent protein kinases as the missing link? *Journal of Experimental Botany* **72**, 4190-4201. https://doi.org/10.1093/jxb/erab136

Angon, P. B., Tahjib-Ul-Arif, M., Samin, S. I., Habiba, U., Hossain, M. A., and Brestic, M. (2022). How do plants respond to combined drought and salinity stress?—A systematic review. *Plants* **11**, 2884. https://doi.org/10.3390/plants11192884

Aramburu, J., Ortells, M. C., Tejedor, S., Buxadé, M., and López-Rodríguez, C. (2014). Transcriptional regulation of the stress response by mTOR. *Science signaling* **7**, re2-re2. https://doi.org/10.1126/scisignal.2005910

Argosubekti, N. (2020). A review of heat stress signaling in plants. *In* "IOP Conference Series: Earth and Environmental Science", Vol. 484, pp. 012041. IOP Publishing. https://doi.org/10.1088/1755-1315/484/1/012041

Asano, T., Hayashi, N., Kikuchi, S., and Ohsugi, R. (2012). CDPK-mediated abiotic stress signaling. *Plant Signaling & Behavior* **7**, 817-821. https://doi.org/10.4161/psb.20486

Aslam, M. A., Ahmed, M., Hassan, F.-U., Afzal, O., Mehmood, M. Z., Qadir, G., Asif, M., Komal, S., and Hussain, T. (2022). Impact of temperature fluctuations on plant morphological and physiological traits. *Building climate resilience in agriculture: theory, practice and future perspective*, 25-52. https://doi.org/10.1007/978-981-19-2730-8_2

Avramova, Z. (2015). Transcriptional 'memory'of a stress: transient chromatin and memory (epigenetic) marks at stress-response genes. *The Plant Journal* **83**, 149-159. https://doi.org/10.1111/tpj.12716

Ayub, A., Javed, T., Nayab, A., Nan, Y., Xie, Y., Hussain, S., Shafiq, Y., Tian, H., Hui, J., and Gao, Y. (2025). AREB/ABF/ABI5 transcription factors in plant defense: regulatory cascades and functional diversity. *Critical Reviews in Biotechnology*, 1-21. https://doi.org/10.1080/07388551.2024.2301234

Balali-Mood, M., Naseri, K., Tahergorabi, Z., Khazdair, M. R., and Sadeghi, M. (2021). Toxic mechanisms of five heavy metals: mercury, lead, chromium, cadmium, and arsenic. *Frontiers in pharmacology* **12**, 643972. https://doi.org/10.3389/fphar.2021.643972

Banerjee, A., and Roychoudhury, A. (2017). Abiotic stress, generation of reactive oxygen species, and their consequences: an overview. *Reactive Oxygen Species in Plants: Boon or Bane-Revisiting the Role of ROS*, 23-50. https://doi.org/10.1002/9781119368762.ch2

Basso, M. F., Ferreira, P. C. G., Kobayashi, A. K., Harmon, F. G., Nepomuceno, A. L., Molinari, H. B. C., and Grossi-de-Sa, M. F. (2019). Micro RNA s and new biotechnological tools for its modulation and improving stress tolerance in plants. *Plant biotechnology journal* **17**, 1482-1500. https://doi.org/10.1111/pbi.13088

Bhattacharjee, S. (2012). The language of reactive oxygen species signaling in plants. *Journal of Botany* **2012**, 985298. https://doi.org/10.1155/2012/985298

Bieluszewski, T., Prakash, S., Roulé, T., and Wagner, D. (2023). The role and activity of SWI/SNF chromatin remodelers. *Annual Review of Plant Biology* **74**, 139-163. https://doi.org/10.1146/annurev-arplant-102820-012728

Bucholc, M., Goch, G., Ciesielski, A., Anielska-Mazur, A., and Dobrowolska, G. (2013). Functional and biochemical characterization of Arabidopsis calcium sensor SCS a potential regulator of SnRK2 protein kinases. *BioTechnologia. Journal of Biotechnology Computational Biology and Bionanotechnology* **94**.

Callis, J. (2014). The ubiquitination machinery of the ubiquitin system. *The Arabidopsis Book/American Society of Plant Biologists* **12**, e0174. https://doi.org/10.1199/tab.0174

Chen, Q., Shi, X., Ai, L., Tian, X., Zhang, H., Tian, J., Wang, Q., Zhang, M., Cui, S., and Yang, C. (2023). Genome-wide identification of genes encoding SWI/SNF components in soybean and the functional characterization of GmLFR1 in drought-stressed plants. *Frontiers in Plant Science* **14**, 1176376. https://doi.org/10.3389/fpls.2023.1176376

Cheuvront, S. N., Kenefick, R. W., Montain, S. J., and Sawka, M. N. (2010). Mechanisms of aerobic performance impairment with heat stress and dehydration. *Journal of applied physiology* **109**, 1989-1995. https://doi.org/10.1152/japplphysiol.00367.2010

Costa Alves, G. (2015). Characterization of a candidate gene for drought tolerance in Coffea: the CcDREB1D gene, in contrasting genotypes of Coffea canephora and related species, Montpellier SupAgro.

Damaris, R. N., and Yang, P. (2021). Protein phosphorylation response to abiotic stress in plants. *Plant phosphoproteomics: methods and protocols*, 17-43. https://doi.org/10.1007/978-1-0716-1016-9_2

De Zélicourt, A., Colcombet, J., and Hirt, H. (2016). The role of MAPK modules and ABA during abiotic stress signaling. *Trends in plant science* **21**, 677-685. https://doi.org/10.1016/j.tplants.2016.04.007

Duque, A. S., de Almeida, A. M., da Silva, A. B., da Silva, J. M., Farinha, A. P., Santos, D., Fevereiro, P., and de Sousa Araújo, S. (2013). Abiotic stress responses in plants: unraveling the complexity of genes and networks to survive. *In* "Abiotic stress-plant responses and applications in agriculture". IntechOpen. https://doi.org/10.5772/45844

Fàbregas, N., Yoshida, T., and Fernie, A. R. (2020). Role of Raf-like kinases in SnRK2 activation and osmotic stress response in plants. *Nature communications* **11**, 6184. https://doi.org/10.1038/s41467-020-19972-8

Farooq, M., Wahid, A., Kobayashi, N., Fujita, D., and Basra, S. M. (2009). Plant drought stress: effects, mechanisms and management. *In* "Sustainable agriculture", pp. 153-188. Springer. https://doi.org/10.1007/978-90-481-2666-8_12

Feng, X., Liu, R., Li, C., Zhang, H., and Slot, M. (2023). Contrasting responses of two C4 desert shrubs to drought but consistent decoupling of photosynthesis and stomatal conductance at high temperature. *Environmental and Experimental Botany* **209**, 105295. https://doi.org/10.1016/j.envexpbot.2023.105295

Fita, A., Rodríguez-Burruezo, A., Boscaiu, M., Prohens, J., and Vicente, O. (2015). Breeding and domesticating crops adapted to drought and salinity: a new paradigm for increasing food production. *Frontiers in Plant Science* **6**, 978. https://doi.org/10.3389/fpls.2015.00978

Fujita, Y., Yoshida, T., and Yamaguchi-Shinozaki, K. (2013). Pivotal role of the AREB/ABF-SnRK2 pathway in ABRE-mediated transcription in response to osmotic stress in plants. *Physiologia plantarum* **147**, 15-27. https://doi.org/10.1111/j.1399-3054.2012.01635.x

Gan, P., Liu, F., Li, R., Wang, S., and Luo, J. (2019). Chloroplasts—beyond energy capture and carbon fixation: tuning of photosynthesis in response to chilling stress. *International Journal of Molecular Sciences* **20**, 5046. https://doi.org/10.3390/ijms20205046

Ganie, S. A., and Reddy, A. S. (2021). Stress-induced changes in alternative splicing landscape in rice: functional significance of splice isoforms in stress tolerance. *Biology* **10**, 309. https://doi.org/10.3390/biology10040309

Geiman, T. M., and Robertson, K. D. (2002). Chromatin remodeling, histone modifications, and DNA methylation—how does it all fit together? *Journal of cellular biochemistry* **87**, 117-125.

Giulietti, S., Bigini, V., and Savatin, D. V. (2024). ROS and RNS production, subcellular localization, and signaling triggered by immunogenic danger signals. *Journal of Experimental Botany* **75**, 4512-4534. https://doi.org/10.1093/jxb/erae235

Gorgues, L., Li, X., Maurel, C., Martinière, A., and Nacry, P. (2022). Root osmotic sensing from local perception to systemic responses. *Stress Biology* **2**, 36. https://doi.org/10.1007/s44154-022-00049-4

Gull, A., Lone, A. A., and Wani, N. U. I. (2019). Biotic and abiotic stresses in plants. *In* "Abiotic and biotic stress in plants". IntechOpen. https://doi.org/10.5772/intechopen.88886

Haak, D. C., Fukao, T., Grene, R., Hua, Z., Ivanov, R., Perrella, G., and Li, S. (2017). Multilevel regulation of abiotic stress responses in plants. *Frontiers in plant science* **8**, 1564. https://doi.org/10.3389/fpls.2017.01564

Ho, S. N. (2006). Intracellular water homeostasis and the mammalian cellular osmotic stress response. *Journal of cellular physiology* **206**, 9-15. https://doi.org/10.1002/jcp.20492

Hussain, Q., Asim, M., Zhang, R., Khan, R., Farooq, S., and Wu, J. (2021a). Transcription factors interact with ABA through gene expression and signaling pathways to mitigate drought and salinity stress. *Biomolecules* **11**, 1159. https://doi.org/10.3390/biom11081159

Hussain, S. S., Kayani, M. A., and Amjad, M. (2011). Transcription factors as tools to engineer enhanced drought stress tolerance in plants. *Biotechnology progress* **27**, 297-306. https://doi.org/10.1002/btpr.514

Hussain, T., Li, J., Feng, X., Asrar, H., Gul, B., and Liu, X. (2021b). Salinity induced alterations in photosynthetic and oxidative regulation are ameliorated as a function of salt secretion. *Journal of plant research* **134**, 779-796. https://doi.org/10.1007/s10265-021-01276-0

Iqbal, N., Khan, N. A., Ferrante, A., Trivellini, A., Francini, A., and Khan, M. (2017). Ethylene role in plant growth, development and senescence: interaction with other phytohormones. *Frontiers in plant science* **8**, 475. https://doi.org/10.3389/fpls.2017.00475

Jan, R., Hussain, A., Assad, A., Khurshid, S., and Macha, M. A. (2025). Challenges with multi-omics data integration. *In* "Multi-Omics Technology in Human Health and Diseases", pp. 223-242. Elsevier. https://doi.org/10.1016/B978-0-443-18606-3.00010-5

Jiang, C., and Fu, X. (2007). GA action: turning on de-DELLA repressing signaling. *Current opinion in plant biology* **10**, 461-465. https://doi.org/10.1016/j.pbi.2007.07.005

Joyce, J. (2023). Exploring the Molecular Mechanisms of Aphid and Thrips Perception in Arabidopsis thaliana, University of East Anglia.

Juan, C. A., Pérez de la Lastra, J. M., Plou, F. J., and Pérez-Lebeña, E. (2021). The chemistry of reactive oxygen species (ROS) revisited: outlining their role in biological macromolecules (DNA, lipids and proteins) and induced pathologies. *International journal of molecular sciences* **22**, 4642. https://doi.org/10.3390/ijms22094642

Kacperska, A. (2004). Sensor types in signal transduction pathways in plant cells responding to abiotic stressors: do they depend on stress intensity? *Physiologia Plantarum* **122**, 159-168. https://doi.org/10.1111/j.1399-3054.2004.00393.x

Kamali, S., and Singh, A. (2023). Genomic and transcriptomic approaches to developing abiotic stress-resilient crops. *Agronomy* **13**, 2903. https://doi.org/10.3390/agronomy13122903

Karmakar, S., Dutta, D., Kumari, A., and Kant, L. (2021). Comprehensive strategy to achieve drought tolerance in plants. *Climate Change and Environmental Sustainability* **9**, 233-242. https://doi.org/10.5958/2231-5131.2021.00034.3

Kathuria, P. (2024). TOLERANCE OR RESISTANCE BREEDING: PATH FORWARD FOR TO TACKLE ABIOTIC STRESS. *Amalgamation of Recent Efforts in Plant Breeding and Biotechnology*, 75.

Kennelly, M., O'Mara, J., Rivard, C., Miller, G. L., and Smith, D. (2012). Introduction to abiotic disorders in plants. *The Plant Health Instructor* **10**, 10-20. https://doi.org/10.1094/PHI-I-2012-10-29-01

Khalid, M. F., Huda, S., Yong, M., Li, L., Li, L., Chen, Z.-H., and Ahmed, T. (2023). Alleviation of drought and salt stress in vegetables: crop responses and mitigation strategies. *Plant Growth Regulation* **99**, 177-194. https://doi.org/10.1007/s10725-022-00888-7

Khan, A. A., Iqbal, B., Jalal, A., Khan, K. A., Al-Andal, A., Khan, I., Suboktagin, S., Qayum, A., and Elboughdiri, N. (2024). Advanced Molecular approaches for improving crop yield and quality: a review. *Journal of Plant Growth Regulation* **43**, 2091-2103. https://doi.org/10.1007/s00344-023-10995-3

KhokharVoytas, A., Shahbaz, M., Maqsood, M. F., Zulfiqar, U., Naz, N., Iqbal, U. Z., Sara, M., Aqeel, M., Khalid, N., and Noman, A. (2023). Genetic modification strategies for enhancing plant resilience to abiotic stresses in the context of climate change. *Functional & integrative genomics* **23**, 283. https://doi.org/10.1007/s10142-023-01056-2

Kopecká, R., Kameniarová, M., Černý, M., Brzobohatý, B., and Novák, J. (2023). Abiotic stress in crop production. *International Journal of Molecular Sciences* **24**, 6603. https://doi.org/10.3390/ijms24136603

Korek, M., Mehta, D., Uhrig, G. R., Daszkowska-Golec, A., Novak, O., Buchcik, W., and Marzec, M. (2025). Strigolactone insensitivity affects the hormonal homeostasis in barley. *Scientific Reports* **15**, 9375. https://doi.org/10.1038/s41598-025-63999-9

Kratsch, H., and Wise, R. R. (2000). The ultrastructure of chilling stress. *Plant, Cell & Environment* **23**, 337-350. https://doi.org/10.1046/j.1365-3040.2000.00551.x

Kulik, A., Wawer, I., Krzywińska, E., Bucholc, M., and Dobrowolska, G. (2011). SnRK2 protein kinases—key regulators of plant response to abiotic stresses. *Omics: a journal of integrative biology* **15**, 859-872. https://doi.org/10.1089/omi.2011.0037

Kumar, R., and Kumar, V. (2016). Physiological disorders in perennial woody tropical and subtropical fruit crops: A review. *The Indian Journal of Agricultural Sciences* **86**, 703-17.

Kumar, S., Sravani, B., Korra, T., Behera, L., Datta, D., Dhakad, P. K., and Yadav, M. (2022). Psychrophilic microbes: biodiversity, beneficial role and improvement of cold stress in crop plants. *In* "New and future developments in microbial biotechnology and bioengineering", pp. 177-198. Elsevier. https://doi.org/10.1016/B978-0-323-90573-0.00008-5

Kundu, P., Nehra, A., Gill, R., Tuteja, N., and Gill, S. S. (2022). Unraveling the importance of EF-hand-mediated calcium signaling in plants. *South African Journal of Botany* **148**, 615-633. https://doi.org/10.1016/j.sajb.2021.10.004

Kyriakis, J. M., and Avruch, J. (2001). Mammalian mitogen-activated protein kinase signal transduction pathways activated by stress and inflammation. *Physiological reviews*. https://doi.org/10.1152/physrev.2001.81.2.807

Li, Y., Rahman, S. U., Qiu, Z., Shahzad, S. M., Nawaz, M. F., Huang, J., Naveed, S., Li, L., Wang, X., and Cheng, H. (2023). Toxic effects of cadmium on the physiological and biochemical attributes of plants, and phytoremediation strategies: A review. *Environmental Pollution* **325**, 121433. https://doi.org/10.1016/j.envpol.2023.121433

Liu, H., Todd, J. L., and Luo, H. (2023). Turfgrass salinity stress and tolerance—A review. *Plants* **12**, 925. https://doi.org/10.3390/plants12040925

Liu, S., Lv, Z., Liu, Y., Li, L., and Zhang, L. (2018). Network analysis of ABA-dependent and ABA-independent drought responsive genes in Arabidopsis thaliana. *Genetics and Molecular Biology* **41**, 624-637. https://doi.org/10.1590/1678-4685-GMB-2018-0044

Ma, X., Zhao, F., and Zhou, B. (2022). The characters of non-coding RNAs and their biological roles in plant development and abiotic stress response. *International Journal of Molecular Sciences* **23**, 4124. https://doi.org/10.3390/ijms23174124

Ma, Y., Tang, M., Wang, M., Yu, Y., and Ruan, B. (2024). Advances in Understanding Drought Stress Responses in Rice: Molecular Mechanisms of ABA Signaling and Breeding Prospects. *Genes* **15**, 1529. https://doi.org/10.3390/genes15091529

Mahdavian, K. (2024). Effects of ultraviolet radiation on plants and their protective mechanisms. *Russian Journal of Plant Physiology* **71**, 184. https://doi.org/10.1007/s10709-024-00165-3

Mansoor, S., Ali, A., Kour, N., Bornhorst, J., AlHarbi, K., Rinklebe, J., Abd El Moneim, D., Ahmad, P., and Chung, Y. S. (2023). Heavy metal induced oxidative stress mitigation and ROS scavenging in plants. *Plants* **12**, 3003. https://doi.org/10.3390/plants12163003

Matsui, A., Nakaminami, K., and Seki, M. (2019). Biological function of changes in RNA metabolism in plant adaptation to abiotic stress. *Plant and Cell Physiology* **60**, 1897-1905. Meena, H., Kiran, B. U., and Bindu, H. (2025). Genetic Enhancement of Abiotic Stress Tolerance in Oilseeds Through Contemporary Breeding Approaches. *In* "Breeding Climate Resilient and Future Ready Oilseed Crops", pp. 43-99. Springer. https://doi.org/10.1093/pcp/pcz104

Mehrotra, R., Bhalothia, P., Bansal, P., Basantani, M. K., Bharti, V., and Mehrotra, S. (2014). Abscisic acid and abiotic stress tolerance–Different tiers of regulation. *Journal of plant physiology* **171**, 486-496. https://doi.org/10.1016/j.jplph.2014.02.009

Meraj, T. A., Fu, J., Raza, M. A., Zhu, C., Shen, Q., Xu, D., and Wang, Q. (2020). Transcriptional factors regulate plant stress responses through mediating secondary metabolism. *Genes* **11**, 346. https://doi.org/10.3390/genes11030346

Mishra, B., Kumar, N., and Mukhtar, M. S. (2021). Network biology to uncover functional and structural properties of the plant immune system. *Current Opinion in Plant Biology* **62**, 102057. https://doi.org/10.1016/j.pbi.2020.102057

Mondal, N. S., and Ghosh, A. R. (2024). Global Climate Change and Ecosystem Services: An Indian Perspective. *Ecosystem Management: Climate Change and Sustainability*, 171-203.

Morillo, S. A., and Tax, F. E. (2006). Functional analysis of receptor-like kinases in monocots and dicots. *Current opinion in plant biology* **9**, 460-469. https://doi.org/10.1016/j.pbi.2006.06.011

Mosadegh, H. (2018). Secondary metabolite regulation and UV-B tolerance mechanisms in Ocimum basilicum Var. Genovese.

Moustafa, K., AbuQamar, S., Jarrar, M., Al-Rajab, A. J., and Trémouillaux-Guiller, J. (2014). MAPK cascades and major abiotic stresses. *Plant cell reports* **33**, 1217-1225. https://doi.org/10.1007/s00299-014-1620-3

Msanne, J., Lin, J., Stone, J. M., and Awada, T. (2011). Characterization of abiotic stress-responsive Arabidopsis thaliana RD29A and RD29B genes and evaluation of transgenes. *Planta* **234**, 97-107. https://doi.org/10.1007/s00425-011-1415-5

Mudrilov, M., Ladeynova, M., Grinberg, M., Balalaeva, I., and Vodeneev, V. (2021). Electrical signaling of plants under abiotic stressors: transmission of stimulus-specific information. *International Journal of Molecular Sciences* **22**, 10715. https://doi.org/10.3390/ijms222010715

Muhammad Aslam, M., Waseem, M., Jakada, B. H., Okal, E. J., Lei, Z., Saqib, H. S. A., Yuan, W., Xu, W., and Zhang, Q. (2022). Mechanisms of abscisic acid-mediated drought stress responses in plants. *International journal of molecular sciences* **23**, 1084. https://doi.org/10.3390/ijms23031084

Nadeem, H., Amir, K., Gupta, R., Hashem, M., Alamri, S., Siddiqui, M. A., and Ahmad, F. (2023). Stress combination: When two negatives may become antagonistic, synergistic or additive for plants? *Pedosphere* **33**, 287-300 https://doi.org/10.1016/S1002-0160(23)60151-8

Nakashima, K., and Yamaguchi-Shinozaki, K. (2013). ABA signaling in stress-response and seed development. *Plant cell reports* **32**, 959-970. https://doi.org/10.1007/s00299-013-1474-3

Naz, M., Afzal, M. R., Raza, M. A., Pandey, S., Qi, S., Dai, Z., and Du, D. (2024). Calcium (Ca2+) signaling in plants: A plant stress perspective. *South African Journal of Botany* **169**, 464-485. https://doi.org/10.1016/j.sajb.2024.01.092

Nazareth, T. d. M., Soriano Pérez, E., Luz, C., Meca, G., and Quiles, J. M. (2024). Comprehensive review of aflatoxin and ochratoxin a dynamics: Emergence, toxicological impact, and advanced control strategies. *Foods* **13**, 1920. https://doi.org/10.3390/foods13121920

Novikova, G., Moshkov, I., and Los, D. (2007). Protein sensors and transducers of cold and osmotic stress in cyanobacteria and plants. *Molecular Biology* **41**, 427-437. https://doi.org/10.1134/S0026893307050080

Nowicka, B. (2022). Heavy metal–induced stress in eukaryotic algae—mechanisms of heavy metal toxicity and tolerance with particular emphasis on oxidative stress in exposed cells and the role of antioxidant response. *Environmental Science and Pollution Research* **29**, 16860-16911. https://doi.org/10.1007/s11356-021-16524-5

Oguz, M. C., Aycan, M., Oguz, E., Poyraz, I., and Yildiz, M. (2022). Drought stress tolerance in plants: Interplay of molecular, biochemical and physiological responses in important development stages. *Physiologia* **2**, 180-197. https://doi.org/10.3390/physiologia2030014

Pamungkas, S. S. T., and Farid, N. (2022). Drought stress: responses and mechanism in plants. *Reviews in Agricultural Science* **10**, 168-185. https://doi.org/10.1016/j.ras.2022.07.002

Pandita, D., and Pandita, A. (2023). "Plant MicroRNAs and stress response," CRC Press.

Parray, R. A. (2019). Genetic studies for improving yield under drought stress environments in rice of Assam, Assam Agricultural University Jorhat.

Parvathy, S. T. (2018). Versatile roles of ubiquitous calcium-dependent protein kinases (CDPKs) in plants. *Indian Soc. Oilseeds Res* **35**, 1-11.

Pearce, R. S. (2001). Plant freezing and damage. *Annals of botany* **87**, 417-424. https://doi.org/10.1006/anbo.2000.1298

Perfus-Barbeoch, L., Leonhardt, N., Vavasseur, A., and Forestier, C. (2002). Heavy metal toxicity: cadmium permeates through calcium channels and disturbs the plant water status. *The Plant Journal* **32**, 539-548. https://doi.org/10.1046/j.1365-313X.2002.01498.x

Pivato, M. (2023). The molecular basis of Chlamydomonas reinhardtii responses to the environment: the role of intracellular Ca2+ signalling and minor antenna proteins.

Praveena, K., and Malaisamy, A. (2024). Climatic shifts and agricultural strategies: A thorough review on impact of climate change on food security and crop productivity. *Int. J. Environ. Clim. Change* **14**, 817-831.

Qi, X., Wang, X., Wang, Q., Li, M., Ma, L., Li, Y., Li, X., and Wang, L. (2021). Photosynthesis, stomatal conductance, endogenous hormones and organic acid synergistic regulation in leaves of rice (*Oryza sativa* L.) under elevated CO 2. *Applied Ecology & Environmental Research* **19**. https://doi.org/10.15666/aeer/1904_433341

Qiao, M., Hong, C., Jiao, Y., Hou, S., and Gao, H. (2024). Impacts of drought on photosynthesis in major food crops and the related mechanisms of plant responses to drought. *Plants* **13**, 1808. https://doi.org/10.3390/plants13191808

Qin, F., Sakuma, Y., Tran, L.-S. P., Maruyama, K., Kidokoro, S., Fujita, Y., Fujita, M., Umezawa, T., Sawano, Y., and Miyazono, K.-i. (2008). Arabidopsis DREB2A-interacting proteins function as RING E3 ligases and negatively regulate plant drought stress–responsive gene expression. *The Plant Cell* **20**, 1693-1707. https://doi.org/10.1105/tpc.108.058519

Rai, K. K., Pandey, N., Rai, N., Rai, S. K., and Pandey-Rai, S. (2021). Salicylic acid and nitric oxide: insight into the transcriptional regulation of their metabolism and regulatory functions in plants. *Frontiers in Agronomy* **3**, 781027. https://doi.org/10.3389/fagro.2021.781027

Ramegowda, V., and Senthil-Kumar, M. (2015). The interactive effects of simultaneous biotic and abiotic stresses on plants: mechanistic understanding from drought and pathogen combination. *Journal of plant physiology* **176**, 47-54. https://doi.org/10.1016/j.jplph.2015.05.009

Rasheed, A., Gill, R. A., Hassan, M. U., Mahmood, A., Qari, S., Zaman, Q. U., Ilyas, M., Aamer, M., Batool, M., and Li, H. (2021). A critical review: recent advancements in the use of CRISPR/Cas9 technology to enhance crops and alleviate global food crises. *Current Issues in Molecular Biology* **43**, 1950-1976. https://doi.org/10.3390/cimb43030103

Rastogi, R. P., Richa, n., Kumar, A., Tyagi, M. B., and Sinha, R. P. (2010). Molecular mechanisms of ultraviolet radiation-induced DNA damage and repair. *Journal of nucleic acids* **2010**, 592980. https://doi.org/10.1155/2010/592980

Raza, A., Razzaq, A., Mehmood, S. S., Zou, X., Zhang, X., Lv, Y., and Xu, J. (2019). Impact of climate change on crops adaptation and strategies to tackle its outcome: A review. *Plants* **8**, 34. https://doi.org/10.3390/plants8050034

Razzaq, M. K., Aleem, M., Mansoor, S., Khan, M. A., Rauf, S., Iqbal, S., and Siddique, K. H. (2021). Omics and CRISPR-Cas9 approaches for molecular insight, functional gene analysis, and stress tolerance development in crops. *International journal of molecular sciences* **22**, 1292. https://doi.org/10.3390/ijms22031292

Rehman, S., and Mahmood, T. (2015). Functional role of DREB and ERF transcription factors: regulating stress-responsive network in plants. *Acta Physiologiae Plantarum* **37**, 1-14. https://doi.org/10.1007/s11738-015-1918-7

Roychoudhury, A., Paul, S., and Basu, S. (2013). Cross-talk between abscisic acid-dependent and abscisic acid-independent pathways during abiotic stress. *Plant cell reports* **32**, 985-1006. https://doi.org/10.1007/s00299-013-1428-1

Saber Sichani, A., Ranjbar, M., Baneshi, M., Torabi Zadeh, F., and Fallahi, J. (2023). A review on advanced CRISPR-based genome-editing tools: base editing and prime editing. *Molecular Biotechnology* **65**, 849-860. https://doi.org/10.1007/s12033-023-00739-9

Saleem, M. H., Noreen, S., Ishaq, I., Saleem, A., Khan, K. A., Ercisli, S., Anas, M., Khalid, A., Ahmed, T., and Hassan, A. (2025). Omics technologies: unraveling abiotic stress tolerance mechanisms for sustainable crop improvement. *Journal of Plant Growth Regulation*, 1-23. https://doi.org/10.1007/s00344-024-11021-1

Sanches, P. H. G., de Melo, N. C., Porcari, A. M., and de Carvalho, L. M. (2024). Integrating molecular perspectives: strategies for comprehensive multi-omics integrative data analysis and machine learning applications in transcriptomics, proteomics, and metabolomics. *Biology* **13**, 848. https://doi.org/10.3390/biology13100848

Santisree, P., Jalli, L. C. L., Bhatnagar-Mathur, P., and Sharma, K. K. (2020). Emerging roles of salicylic acid and jasmonates in plant abiotic stress responses. *Protective chemical agents in the amelioration of plant abiotic stress: biochemical and molecular perspectives*, 342-373.

Satrio, R. D., Fendiyanto, M. H., and Miftahudin, M. (2024). Tools and techniques used at global scale through genomics, transcriptomics, proteomics, and metabolomics to investigate plant stress responses at the molecular level. *In* "Molecular Dynamics of Plant Stress and its Management", pp. 555-607. Springer.

Scandalios, J. (2005). Oxidative stress: molecular perception and transduction of signals triggering antioxidant gene defenses. *Brazilian journal of medical and biological research* **38**, 995-1014. https://doi.org/10.1590/S0100-879X2005000700002

Schieber, M., and Chandel, N. S. (2014). ROS function in redox signaling and oxidative stress. *Current biology* **24**, R453-R462. https://doi.org/10.1016/j.cub.2014.03.034

Seleiman, M. F., Al-Suhaibani, N., Ali, N., Akmal, M., Alotaibi, M., Refay, Y., Dindaroglu, T., Abdul-Wajid, H. H., and Battaglia, M. L. (2021). Drought stress impacts on plants and different approaches to alleviate its adverse effects. *Plants* **10**, 259. https://doi.org/10.3390/plants10020259

Sharma, M., Sidhu, A. K., Samota, M. K., Gupta, M., Koli, P., and Choudhary, M. (2023). Post-translational modifications in histones and their role in abiotic stress tolerance in plants. *Proteomes* **11**, 38. https://doi.org/10.3390/proteomes11020038

Sharma, P., Jha, A. B., and Dubey, R. S. (2019). Oxidative stress and antioxidative defense system in plants growing under abiotic stresses. *In* "Handbook of Plant and Crop Stress, Fourth Edition", pp. 93-136. CRC press.

Sharma, S., Chatterjee, S., Kataria, S., Joshi, J., Datta, S., Vairale, M. G., and Veer, V. (2017). A review on responses of plants to UV-B radiation related stress. *UV-B Radiation: From Environmental Stressor to Regulator of Plant Growth*, 75-97. https://doi.org/10.1038/s41580-022-00457-5

Shelake, R. M., Kadam, U. S., Kumar, R., Pramanik, D., Singh, A. K., and Kim, J.-Y. (2022). Engineering drought and salinity tolerance traits in crops through CRISPR-mediated genome editing: Targets, tools, challenges, and perspectives. *Plant Communications* **3**. https://doi.org/10.1016/j.xplc.2022.100363

Shvedunova, M., and Akhtar, A. (2022). Modulation of cellular processes by histone and non-histone protein acetylation. *Nature reviews Molecular cell biology* **23**, 329-349. https://doi.org/10.1038/s41580-022-00457-5

Singh, A., Sagar, S., and Biswas, D. K. (2017). Calcium dependent protein kinase, a versatile player in plant stress management and development. *Critical Reviews in Plant Sciences* **36**, 336-352. https://doi.org/10.1080/07352689.2017.1408996

Singh, A. H., Wolf, D. M., Wang, P., and Arkin, A. P. (2008). Modularity of stress response evolution. *Proceedings of the National Academy of Sciences* **105**, 7500-7505. https://doi.org/10.1073/pnas.0802578105

Singh, D., and Laxmi, A. (2015). Transcriptional regulation of drought response: a tortuous network of transcriptional factors. *Frontiers in plant science* **6**, 895. https://doi.org/10.3389/fpls.2015.00895

Singh, R. K., Sood, P., Prasad, A., and Prasad, M. (2021). Advances in omics technology for improving crop yield and stress resilience. *Plant Breeding* **140**, 719-731. https://doi.org/10.1111/pbr.12946

Srivastava, H., Ferrell, D., and Popescu, G. V. (2022). NetSeekR: a network analysis pipeline for RNA-Seq time series data. *BMC bioinformatics* **23**, 54. https://doi.org/10.1186/s12859-021-04578-9

Tanveer, M., and Shabala, S. (2020). Neurotransmitters in signalling and adaptation to salinity stress in plants. *Neurotransmitters in plant signaling and communication*, 49-73.

Tripathy, K. P., Mukherjee, S., Mishra, A. K., Mann, M. E., and Williams, A. P. (2023). Climate change will accelerate the high-end risk of compound drought and heatwave events. *Proceedings of the National Academy of Sciences* **120**, e2219825120. https://doi.org/10.1073/pnas.2219825120

Ul Hassan, M., Rasool, T., Iqbal, C., Arshad, A., Abrar, M., Abrar, M. M., Habib-ur-Rahman, M., Noor, M. A., Sher, A., and Fahad, S. (2021). Linking plants functioning to adaptive responses under heat stress conditions: a mechanistic review. *Journal of Plant Growth Regulation*, 1-18. https://doi.org/10.1007/s00344-020-10224-z

Vakulabaranam Sridharan, S. (2015). Biological Pathways Based Approaches to Model and Control Gene Regulatory Networks.

Villalobos-López, M. A., Arroyo-Becerra, A., Quintero-Jiménez, A., and Iturriaga, G. (2022). Biotechnological advances to improve abiotic stress tolerance in crops. *International Journal of Molecular Sciences* **23**, 12053. https://doi.org/10.3390/ijms232012053

Wang, P., and Song, C.-P. (2008). Guard-cell signalling for hydrogen peroxide and abscisic acid. *New Phytologist* **178**.

Wang, S., Yao, Y., Wang, J., Ruan, B., and Yu, Y. (2025). Advancing Stress-Resilient Rice: Mechanisms, Genes, and Breeding Strategies. *Agriculture* **15**, 721. https://doi.org/10.3390/agriculture15040721

Wang, Y., Mostafa, S., Zeng, W., and Jin, B. (2021). Function and mechanism of jasmonic acid in plant responses to abiotic and biotic stresses. *International Journal of Molecular Sciences* **22**, 8568.

Wang, Z., and Dane, F. (2013). NAC (NAM/ATAF/CUC) transcription factors in different stresses and their signaling pathway. *Acta physiologiae plantarum* **35**, 1397-1408. https://doi.org/10.1007/s11738-013-1323-4

Xiao, B.-Z., Chen, X., Xiang, C.-B., Tang, N., Zhang, Q.-F., and Xiong, L.-Z. (2009). Evaluation of seven function-known candidate genes for their effects on improving drought resistance of transgenic rice under field conditions. *Molecular Plant* **2**, 73-83. https://doi.org/10.1093/mp/ssn062

Xie, X., He, Z., Chen, N., Tang, Z., Wang, Q., and Cai, Y. (2019). The roles of environmental factors in regulation of oxidative stress in plant. *BioMed research international* **2019**, 9732325. https://doi.org/10.1155/2019/9732325

Yadav, C., Rawat, N., Singla-Pareek, S. L., and Pareek, A. (2025). Knockdown of OsPHP1 leads to improved yield under salinity and drought in rice via regulating the complex Set of TCS members and cytokinin signalling. *Plant, Cell & Environment* **48**, 2769-2782. https://doi.org/10.1111/pce.14819

Yadav, S., Irfan, M., Ahmad, A., and Hayat, S. (2011). Causes of salinity and plant manifestations to salt stress: a review. *Journal of environmental biology* **32**, 667.

Yadav, S., Yadav, J., Kumar, S., and Singh, P. (2024). Metabolism of Macro-elements (Calcium, Magnesium, Sodium, Potassium, Chloride and Phosphorus) and Associated Disorders. *In* "Clinical Applications of Biomolecules in Disease Diagnosis: A Comprehensive Guide to Biochemistry and Metabolism", pp. 177-203. Springer.

Yoshida, T., Fujita, Y., Maruyama, K., Mogami, J., Todaka, D., Shinozaki, K., and Yamaguchi-Shinozaki, K. (2015). Four A rabidopsis AREB/ABF transcription factors function predominantly in gene expression downstream of SnRK2 kinases in abscisic acid signalling in response to osmotic stress. *Plant, cell & environment* **38**, 35-49. https://doi.org/10.1111/pce.12468

Yuan, F., Yang, H., Xue, Y., Kong, D., Ye, R., Li, C., Zhang, J., Theprungsirikul, L., Shrift, T., and Krichilsky, B. (2014). OSCA1 mediates osmotic-stress-evoked Ca2+ increases vital for osmosensing in Arabidopsis. *Nature* **514**, 367-371. https://doi.org/10.1038/nature13793

Yue, J., and López, J. M. (2020). Understanding MAPK signaling pathways in apoptosis. *International journal of molecular sciences* **21**, 2346. https://doi.org/10.3390/ijms21072346

Zha, D., He, Y., and Song, J. (2025). Regulatory role of ABA-responsive element binding factors in plant abiotic stress response. *Physiologia Plantarum* **177**, e70233. https://doi.org/10.1111/ppl.13823

Zhu, J.-K. (2016). Abiotic stress signaling and responses in plants. *Cell* **167**, 313-324. https://doi.org/10.1016/j.cell.2016.01.004

Zhu, Q., Gao, S., and Zhang, W. (2021). Identification of key transcription factors related to bacterial spot resistance in pepper through regulatory network analyses. *Genes* **12**, 1351.

Statements and Declarations

Data Availability Statement

All data are fully available and can be found within the manuscript file.

Acknowledgement

Not Applicable

Conflicts of Interest

The authors declare no conflict of interest.

Ethics Approval Statement

Not applicable.

Ethics Approval Statement

Not applicable.

Consent to Participate

Not applicable.

Consent to Publish

Not applicable.

Author Contributions

Conceptualization by Muhammad Hammad; Shafiq M, and Batool A writing—original draft preparation was prepared by Hammad M writing—review and editing by Sherazi SHUH, and Batool A; All authors have read and agreed to the published version of the manuscript.”

Funding

Not applicable.