Journal of Agricultural Sciences (JAS) 32(3):564-578
DOI: 10.15832/ankutbd.1824410

J Agr Sci-Tarim Bili
e-ISSN: 2148-9297
jas.ankara.edu.tr

Genetic and Molecular Mechanisms of Plant Stress Tolerance and Strategies for Improvement: A Comprehensive Review

Areej S. Jalal[a*]

[a]*Department of Biology, College of Science, Princess Nourah bint Abdulrahman University, Riyadh 11671, SAUDI ARABIA*

ARTICLE INFO
Review Article
Corresponding Author: Areej S. Jalal, E-mail: asjalal@pnu.edu.sa
Received: 15 November 2025 / Revised: 26 January 2026 / Accepted: 06 February 2026 / Online: 28 July 2026

Cite this article
Jalal A S (2026). Genetic and Molecular Mechanisms of Plant Stress Tolerance and Strategies for Improvement: A Comprehensive Review. *Journal of Agricultural Sciences (Tarim Bilimleri Dergisi),* 32(3):564-578. DOI: 10.15832/ankutbd.1824410

ABSTRACT
Environmental stresses impose a significant threat on plant growth and agricultural productivity. Abiotic stresses, such as drought, salinity, and extreme temperatures, impair plant physiology and development, while biotic stresses, like those caused by pathogens and herbivores, trigger a range of defense responses. Plants have evolved intricate genetic and molecular mechanisms to cope with these challenges. The plant response to stress is governed by transcription factors (TFs), including the AP2/ERF, bZIP, WRKY, and NAC families, which regulate stress-responsive gene expression. Phytohormones like ABA, ethylene, and jasmonic acid (JA) serve as crucial signaling molecules that initiate adaptive physiological changes. These signals are transmitted via signal transduction components, such as receptor-like kinases and MAP kinases, which translate external events into cellular responses. Additionally, epigenetic regulation and gene-by-environment (G × E) interactions allow plants to acquire a stress memory and exhibit adaptive plasticity, enhancing their resilience to future challenges. Improving these natural mechanisms is vital for developing stress-tolerant crops. Traditional breeding and modern techniques like Marker-Assisted Selection, Genetic Engineering, Genome Editing and Genomic Selection are used to identify and integrate desirable traits into new crop varieties. These methods enable breeders to develop more robust and stable crops, ultimately helping to ensure global food security in the face of climate change.

Keywords: Abiotic and biotic stresses, Genomic selection, Hormonal signalling, Signal transduction, Stress responses

1. Introduction

Environmental stresses are major limiting factors that affect plant growth, development, and crop productivity worldwide (Vennapusa et al. 2023). Plants cannot escape these harsh conditions and have therefore evolved intricate mechanisms at the molecular, physiological, morphological, and biochemical levels to respond and adapt (Mareri et al. 2022). The environmental stresses can be broadly categorized as abiotic and biotic stresses. The survival and natural distribution of plants are heavily impacted by various abiotic stresses. Metal and nutrient stresses also play a role in this regard (Zhang et al. 2020). It is often common for these environmental challenges to occur together, as seen with high temperatures and drought (Swain et al. 2023). A key focus in biological researches is to understand the intricate processes by which plants sense, transmit, and react to these stress signals. The response of plants to stress is deeply encoded within their genome. A complex network of genes, transcription factors, hormones, and signaling pathways coordinate a plant's response (Zhang et al. 2023). When a plant perceives a stress signal, such as drought or an attack by a pathogen, it triggers a response reaction that begins with signal transduction (Zhang et al. 2023). This process involves sensors like receptor-like kinases that relay the signal, often through messengers like calcium ions and reactive oxygen species (ROS), to a cascade of mitogen-activated protein kinases (MAPKs) (Ravi et al. 2023). Ultimately, this leads to the activation of transcription factors which act as master regulators by turning on or off the specific stress-responsive genes. These genes produce the necessary protective molecules such as osmoprotectants for drought, heat shock proteins for high temperatures, or defensive compounds for pathogen attacks (Manna et al. 2021). Beyond the direct genetic code, epigenetic regulation which involves modifications to the DNA that don't alter the sequence itself, plays a crucial role in enabling plants to dynamically adjust gene expression and even pass on a stress memory to their offspring (Abdolmaleky et al. 2025).

Leveraging this deep understanding of plant stress genetics is vital for developing more robust crops resilient to a variable climate. Conventional breeding, a cornerstone of agriculture for centuries, involves the selection and cross-pollination of naturally stress-tolerant plants to develop new genotypes. While effective, this approach can be time-consuming and is constrained by the limited genetic diversity within a species (Hafeez et al. 2023). To overcome these limitations, scientists are employing modern biotechnological approaches. Marker-Assisted Selection (MAS) uses DNA markers, which facilitate the identification and subsequent selection of advantageous genes responsible for stress tolerance at the seedling stage, leading to a

substantial reduction in the overall breeding cycle (Kumari et al. 2024). A more advanced method, genomic selection (GS), uses a much larger set of genetic markers to predict a plant overall breeding value for complex traits, allowing for more accurate and rapid selection (Krishnappa et al. 2021). Finally, genetic engineering which includes transformation and genome editing tools like CRISPR-Cas9, offers the most precise and rapid way to introduce or enhance specific stress-tolerance mechanisms directly into a crop's genome (Rai et al. 2023). This article provides a comprehensive overview of the genetic basis of plant responses to various environmental stresses and explores modern strategies for developing crops tolerant to climate changes to ensure global food security.

2. The nature of environmental stresses

Environmental stressors affecting plants are categorized into two main types: Abiotic and Biotic. Abiotic stresses consist of non-living physical and chemical factors such as water availability (drought), soil composition (salinity, nutrient deficiency, and heavy metals), and energy-related elements (temperature, light, and UV radiation). In contrast, Biotic stress stems specifically from the impact of living organisms on their environment (Table 1).

Table 1- The nature of environmental stresses

Category	*Stress Type*	*Primary Effects on Plants*	*Adaptations/Responses*
Abiotic	Drought	Cellular dehydration, reduced turgor, stomatal closure, ROS overproduction (oxidative damage).	Deeper roots, osmotic regulation (proline), antioxidant systems, ABA signaling.
	Salinity	Osmotic stress, ionic toxicity, stunted growth, leaf yellowing/wilting.	Thicker cuticles, succulent leaves (in tolerant species), salt exclusion from roots.
	Temperature	Heat: Wilting, scorching, reduced pollen viability. Cold: Hindered growth, impaired photosynthesis.	Heat: Increased respiration, enzyme damage (RuBisCO). Cold: Activation of cold-response genes via JA.
	Nutrient Deficiency	Stunted growth; N (yellowing), P (purplish leaves), K (chlorosis/necrosis on leaf margins).	Changes in root development and metabolic prioritization.
	Heavy Metals	Stunted growth, root damage, ROS generation, enzyme inactivation (Pb).	Vacuole sequestration, conversion to less toxic forms (phytochelatins).
	UV Radiation	DNA damage, ROS generation, Photosystem II damage, smaller/thickened leaves.	UV-shielding molecules, DNA repair mechanisms, antioxidant activation.
	Light	High light: Leaf damage. Low light: Elongation (taller/thinner leaves) to capture light.	Adjusting light-harvesting pigments (chlorophyll) and chloroplast reorganization.
Biotic	Living Threats	Damage from pathogens (microbes) and herbivores (insects to mammals).	Physical (thorns, waxy cuticles) and chemical (alkaloids, tannins) defenses.

2.1. Abiotic stresses

Abiotic stress occurs when non-biological environmental conditions exceed a plant's normal range of variation, leading to significant adverse effects on its physiological performance and overall health. These stressors are increasingly exacerbated by climate change; notably, drought represents a primary global constraint on food security and crop productivity, as water deficits induce severe cellular dehydration. This may result in a decline in turgor pressure, stomatal closure for water conservation, and reduced photosynthetic efficiency (Shumayla et al. 2025). Furthermore, water deficit triggers a cascade of detrimental responses including the overproduction of ROS. ROS accumulation results in oxidative damage to critical cellular components such as DNA, proteins, and lipids (Rao et al. 2025). To avoid these effects, plants have evolved tolerance mechanisms. These include morphological adaptations like developing deeper root systems, physiological adjustments, osmotic regulation through the accumulation of proline and the activation of antioxidant defense systems (Haghpanah et al. 2024). At the molecular level, these responses are orchestrated by complex signaling pathways, often mediated by phytohormones like ABA, which regulate the expression of key stress-responsive genes (Das et al. 2025).

Salinity stress significantly impacts plants health, causing a cascade of negative effects on their morphology, physiology, and cellular machinery. These effects vary across different plant species, with some being tolerant and others being sensitive. The primary effects of damage are osmotic stress and ionic toxicity (Praveen and Singh 2024). Salinity typically leads to overall growth reduction, causing stunted height, smaller leaf area, and decreased biomass (Alghamdi 2024). Sensitive plants often show

symptoms like leaf yellowing and wilting, while tolerant species may adapt with thicker cuticles and succulent leaves to conserve water.

Heat and cold stress, significantly hinder plant growth and productivity by impacting their morphology, physiology, and cellular functions. Plants have developed intricate strategies to manage these stresses, but the specific effects and tolerance levels vary widely among species.

Plants have distinct mechanisms for coping with heat and cold stress, affecting their morphology, physiology, and cellular functions. Under heat stress, plants often exhibit stunted growth, wilting, and scorching, with sensitive stages like reproduction being particularly vulnerable, leading to reduced pollen viability and poor fruit set (Mehmood et al. 2025). High temperatures impair photosynthesis by damaging chloroplasts and enzymes like RuBisCO, while also increasing respiration rates. Ullah et al. (2024) found that at a physiological level, high temperatures disrupt key processes such as water balance, respiration, and photosynthesis, leading to reduced leaf size, fewer crowns, and lower fruit yield due to poor flower bud differentiation and pollen viability.

Nutrient deficiency stress, the lack of essential mineral elements required for plant growth, significantly impairs plant health. This stress manifests with distinct symptoms depending on the specific nutrient lacking and the plant species (Lu et al. 2025). Nutrient deficiency stress profoundly impacts plant health, with specific symptoms linked to the missing element. A lack of nitrogen (N), for instance, leads to stunted growth and yellowing of older leaves because it is a key component of chlorophyll and proteins (Sakuraba 2022). A deficiency in phosphorus (P) often results in dark green or purplish leaves and poor root development. Since phosphorus is essential for ATP, the cell energy currency, its absence severely limits all energy-requiring processes and compromises the synthesis of nucleic acids and cell membranes (Liu 2021). Crucially, a lack of potassium (K) typically causes chlorosis and necrosis on the margins of older leaves (Ladikou et al. 2025).

Another significant environmental stress factor is heavy metal toxicity that negatively affects plant health and productivity. The effects vary depending on the specific metal, its concentration, and the plant species' tolerance level (Asiminicesei et al. 2024). For example, cadmium (Cd) toxicity primarily leads to stunted growth, leaf yellowing, and severe root damage. It disrupts water uptake and photosynthesis by damaging chloroplasts, while on a cellular level, it generates ROS that cause oxidative stress and destroy the cell membranes (Ran et al. 2024). Similarly, lead (Pb) mainly accumulates in the roots, inhibiting their growth and leading to a cascade of nutrient deficiency symptoms. It inactivates crucial enzymes by binding to protein sulfhydryl groups and can alter the structure of organelles like mitochondria (Rani et al. 2024). Like other heavy metals, arsenic also induces oxidative stress, and plants attempt to detoxify it by sequestering it in vacuoles or converting it to less toxic forms often involving phytochelatins (Teschke 2024).

Increased UV radiation, a consequence of ozone depletion, induces DNA damage and the generation of ROS in plants. To mitigate these effects, plants employ various protective strategies including the production of UV-shielding molecules, the activation of specific DNA repair mechanisms, and the use of robust antioxidant systems (Mahdavian 2024). High exposure to UV radiation often causes plants to have stunted growth, smaller leaves, and discolored or thickened foliage as a defense mechanism. This radiation also directly hinders photosynthesis, particularly by damaging Photosystem II, which ultimately reduces its efficiency (Shafiei-Masouleh 2025).

Light stress, whether from excessive or insufficient light, significantly impacts plant health, leading to a variety of morphological, physiological, and cellular changes. The effects are directly tied to the disruption of photosynthesis and vary among species (Zafar et al. 2024). Both high and low light have distinct effects on plants; high light stress often causes stunted growth and leaf damage, resulting in smaller and thicker leaves (Vilyanen and Kozuleva 2025). Conversely, low light stress causes the plants to grow taller with larger and thinner leaves to maximize light capture. Insufficient light limits the production of energy molecules like ATP, directly restricting growth (You et al. 2024). To cope with this stress, plants acclimate their cellular machinery by increasing the synthesis of light-harvesting pigments like chlorophyll and reorganizing chloroplasts to improve light absorption (Zhang et al. 2024).

2.2. Biotic stresses

Plants are in a constant state of defense against a wide range of living threats. These challenges, collectively known as biotic stresses, are caused by other organisms including microscopic pathogens and macroscopic herbivores (A. Lal et al. 2018). Unlike abiotic stresses, biotic stresses represent a dynamic, co-evolutionary struggle. This persistent battle significantly affects plant development and productivity. Understanding of biotic stress and plant defense mechanisms is crucial for developing sustainable strategies to protect crops from living organisms (Dixit et al. 2024). Beyond microbial threats, plants also face biotic stress from herbivores, which range from tiny insects to large grazing mammals. The plant defenses against these threats include physical barriers like thorns, spines, and waxy cuticles, as well as alkaloids, tannins, and terpenoids that make the plant unpalatable or toxic (Balakrishnan et al. 2024).

3. Genetic basis of plant stress responses

3.1. Transcription factors (TFs)

TFs are essential regulators for plant response to abiotic and biotic stresses by controlling gene expression. Several key TF families mediate these responses, often by binding to specific DNA sequences to activate or repress target genes (Table 2).

Table 2- Regulatory roles of key transcription factors in stress signalling

Transcription Factor	*Primary Functions & Stress Responses*	*Signaling Mediators / Mechanisms*	*References*
AP2/ERF	Regulates responses to drought, light, and cold.	Mediated by ABA and ethylene.	(Owji et al. 2017; Wani et al. 2025)
bZIP	Critical for drought and salinity signaling.	Binds to ABA-responsive elements.	(Guo et al. 2024)
WRKY	Handles pathogen defense, wound responses, and antioxidant signaling.	Primarily defense-oriented.	(Chen et al. 2019)
NAC	Drought/salt tolerance; promotes root development and ROS scavenging.	Integrates multiple stress signals.	(Xiong et al. 2025)

The AP2/ERF family play an important role in regulating responses to various stresses. They are remarkably involved in abscisic acid (ABA) and ethylene signaling. AP2/ERF TFs help plants manage a wide range of abiotic stresses as well as defense against pathogens (Wani et al. 2025). The expression levels of most AP2/ERF genes are at low levels under normal conditions. However, their expression can be upregulated or downregulated during specific growth phases or in response to hormones and stress (Owji et al. 2017). In *A. thaliana*, as a model plant, several AP2/ERF transcription factors play an important role in regulating plant development and stress responses through interacting with DRE/CRT and GCC motifs. For example, TINY positively regulates a variety of abiotic stress responses (Sun et al. 2008). Similarly, RAP2.4 and RAP2.4b are positive regulators of drought and light tolerance (Akhtar et al. 2012). The HARDY and ERF1 genes positively control responses to multiple abiotic stresses (Akhtar et al. 2012). Other factors like CBF1 and DREB2A are known to enhance tolerance to cold while RAP2.3 is specifically involved in low oxygen, oxidative, and osmotic stress responses (Yang et al. 2009). Additionally, ERF4 and ERF53 mediate responses related to ethylene, ABA, and heat, and HRE2 positively regulates both development and hypoxia. Collectively, these transcription factors demonstrate a broad and interconnected role in helping *Arabidopsis* adapt to diverse environmental challenges (Yang et al. 2009).

As another major family of transcription factors, bZIPs play a critical role in regulating how plants respond to a variety of abiotic stresses. Many bZIP TFs are activated by ABA and are critical for a plant response to drought and high salinity. They can bind to specific DNA sequences known as ABA-responsive elements, which are found in the promoter regions of many stress-related genes (Guo et al. 2024). Numerous examples have been found across different species of bZIP transcription factors as critical regulators for plant responses to abiotic stress. In *Populus trichocarpa* and *Zea mays*, genes like *PtrbZIP3* and *ZmbZIP7*6 are involved in drought, salinity, and heat tolerance, often by regulating ABA-dependent signaling and other downstream genes (Zhou et al. 2023). Rice utilizes several bZIPs including *OsbZIP62*, *OsbZIP63*, and *OsbZIP20*, to enhance tolerance to drought, oxidative stress, and salinity by controlling various target genes (Baoxiang et al. 2022). In soybean, bZIPs such as *GmbZIP152* and *GmbZIP2* help the plant cope with multiple stresses (Yang et al. 2020). Similarly, *AtbZIP62* and *AtbZIP4* in *Arabidopsis thaliana* regulate various signaling pathways of drought and salt response (Noh et al. 2021). The role of these transcription factors is also seen in other crops, with *TabZIP15* in wheat and *CabZIP25* in pepper contributing to salt tolerance (Gai et al. 2020).

WRKY is one of the largest families of transcription factors in vascular plants. These proteins are key regulators of a plant response to both biotic and abiotic stresses. They regulate gene expression by binding to a specific DNA sequence, known as the W-box, located in the promoter region of target genes (Chen et al. 2019). They are important for pathogens defense and are also involved in managing various stresses. WRKY genes that promote disease resistance can do so by activating resistance genes expression. For example, some WRKY proteins bind specifically to a DNA sequence called the W-box located in the promoter of the *NPR1* gene in *Arabidopsis*. This binding then turns on defense genes, ultimately helping the plant resist disease (Yu et al. 2001). In Arabidopsis, the AtWRKY29 and AtWRKY22 proteins are key components of the plant defense against pathogens, and increasing the expression of AtWRKY29 specifically boosts resistance to *P. syringe (*Asai et al. 2002*)*. Similarly, the NaWRKY3 and NaWRKY6 genes in *Nicotiana attenuata* are involved in a wound response, with NaWRKY6 activity being significantly risen by compounds in insect oral secretions (Skibbe et al. 2008). In rice, the OsWRKY45 protein is essential for disease resistance mediated by salicylic acid (SA); when its expression is reduced, the plant becomes more susceptible to pathogens, while increased expression provides strong resistance (Nakayama et al. 2013).

NAC TFs are a plant-specific family that integrate various stress signals to activate downstream genes which enhance tolerance (Xiong et al. 2025). The WRKY TFs, while known for their role in pathogen defense and in abiotic stress responses, often regulate genes within the antioxidant and hormonal signaling systems (Li et al. 2024). There are transcription factors responsible for drought tolerance belonging to the NAC TFs. These transcription factors, such as ONAC022 and ONAC066 in rice are involved in ABA-dependent pathways, where they can act as either positive or negative regulators of drought resistance (Yuan et al. 2019). Other NACs, like IPA1 and SNAC1, enhance drought resistance through ABA-independent pathways, primarily by regulating downstream genes that control antioxidant stress or cell death (Chen et al. 2023). Additionally, several NAC genes including OsNAC6, OsNAC5, and TaSNAC8-6A contribute to drought tolerance by promoting root development which improves water absorption (Mao et al. 2020). Also, NAC TFs play an important role in enhancing salinity tolerance in plants through a variety of mechanisms. They help maintain cellular water balance by regulating genes involved in the synthesis of osmoregulators like proline, as seen with ONAC022 in rice and SlNAC10 in a halophyte (Du et al. 2022). NACs also mitigate oxidative damage by regulating ROS scavenging and signaling, as exemplified by GmSIN1 in soybean (Li et al. 2019) and CmoNAC1 in pumpkin (Peng et al. 2023). Furthermore, they influence plant hormone signaling pathways such as those for ABA, JA, and auxin, to coordinate stress responses. Finally, NACs can activate the expression of general stress-responsive genes like DREB1A and RD29A and can even affect root growth so that avoid spreading into high-salinity areas (Yang et al. 2019).

3.2. Hormonal signaling

Phytohormones are essential chemical signals that regulate plant growth, development, and their reactions to environmental stresses (Ali et al. 2024) (Table 3). Under stress conditions, the levels of certain hormones change, initiating signaling cascades that lead to physiological and genetic adaptations (Angon et al. 2024).

Table 3- Physiological functions of phytohormones in stress adaptation

Phytohormone	*Common Name / Role*	*Key Physiological Actions*	*References*
Abscisic Acid (ABA)	Stress Hormone	Triggers stomatal closure and root hydrotropism.	(Khan 2025)
Ethylene	Gaseous Hormone	Manages flooding/hypoxia and heavy metal stress; triggers leaf senescence.	(Yang et al. 2009; Nazir et al. 2024)
Jasmonic Acid (JA)	Defense Hormone	Essential for herbivore defense and cold/heat tolerance.	(Wu et al. 2024)
Gibberellins (GA)	Growth Hormone	Usually decreased during stress to prioritize defense over growth.	(Wu et al. 2024)

ABA is a central regulator for drought, salinity, cold, and heat stress, promoting stomatal closure and the expression of stress-responsive genes (Khan 2025). In response to drought and osmotic stress in roots, ABA is synthesized in shoots. This process is triggered by hydraulic signals and a specific peptide (CLE25) which increases the expression of the *NCED3* gene (Takahashi et al. 2018). Additionally, exposure to osmotic and salt stress activates SnRK2-type protein kinases, a process that is mediated by subgroup B Raf-like kinases (Lin et al. 2021). When the soil has a non-uniform distribution of water, ABA signaling in the root elongation zone causes root hydrotropism. Salt stress specifically leads to the inhibition of lateral root development which relies on ABA synthesis and signaling in the endodermis. Here, ABA also interferes with the auxin signaling pathway (Korver et al. 2020). Both salt stress and deficiencies in potassium and sulfate can lead to endodermal suberization. For cold stress, ABA helps by phosphorylating the transcription factor ICE1, a process mediated by the kinase SnRK2.6 (Ding et al. 2015). Finally, ABA also helps promote the survival of seedlings during heat stress (Larkindale et al. 2005).

Ethylene, a gaseous hormone, mediates responses to drought, flooding, and heavy metals triggering leaf senescence or the formation of new roots under hypoxia (Nazir et al. 2024). In response to salt stress, plants induce both the production of ethylene and its associated signaling pathways. When plants experience flooding or submergence they produce ethylene, which in turn activates specific genes. For instance, in *Arabidopsis*, group VII ERF genes are activated, while in rice, related genes like SUBMERGENCE TOLERANCE 1, SNORKEL1, and SNORKEL2 are involved (Gasch et al. 2015). These genes likely induce the biosynthesis of gibberellins, another plant hormone. To conclude, ethylene plays a role in metal deficiency by causing a reduction in endodermal suberization which can affect the plant's ability to regulate ion uptake (Barberon et al. 2016).

JA is crucial for defending against herbivores and insects, as well as stresses from ozone and heavy metals (Wu et al. 2024). In conditions of cold stress, plants increase their production of jasmonic acid. This leads to the degradation of JAZ proteins, which in turn frees the transcription factors ICE1 and ICE2 from repression, allowing them to activate cold-response genes (Hu et al. 2013). During heat stress, plant accumulates the JA receptor protein COI1, which helps to amplify the downstream signaling pathways and responses controlled by jasmonic acid (Havko et al. 2020).

Lastly, gibberellins (GA), which are typically growth-promoting, often decrease under stress, leading to inhibited growth in favor of defense (Wu et al. 2024). For drought stress, gibberellin signaling is impacted by DELLA proteins, which interfere with the transcription factor ABF2 that is regulated by ABA (Wang et al. 2020). In response to salt stress, plants likely reduce their levels of bioactive gibberellin through ABA signaling, as demonstrated by *della* quadruple mutants being hypersensitive to salt stress

(Achard et al. 2006). During heat stress, gibberellin promotes hypocotyl elongation by inducing its own biosynthesis and degrading DELLA proteins through a COPI-dependent pathway (Blanco-Touriñán et al. 2020).

3.3. Signal transduction components

Signal transduction components are a diverse group of proteins that translate external stress signals into a coordinated cellular response. RLKs and RLPs act as initial sensors, perceiving stress signals and initiating signaling cascades (Cai et al. 2024). These cascades often involve MAPKs, which form a three-level module that amplifies the signal through sequential phosphorylation ultimately regulating gene expression in response to stresses like drought, cold, and heat (Khan et al. 2024). Another key group of kinases, calcium-dependent protein kinases (CDPKs), directly sense and respond to changes in cytosolic calcium ions (Ca^{2+}), a crucial second messenger whose concentration and pattern of increase serve as a unique "calcium signature" for almost all types of stress (Goher et al. 2025). Also, ROS which are typically known to be harmful, also function as signaling molecules at low concentrations, creating a redox signal that activates defense pathways against a variety of stresses, including drought and pathogens (Haghpanah et al. 2025).

3.4. Genetic Diversity and Gene-by-Environment (G × E) ınteractions

Genetic diversity and gene-by-environment (G × E) interactions are critical for plant to adapt to environmental stresses. Genetic diversity provides natural plant populations with a range of different stress responses, which is a fundamental requirement for adaptation to varied environments (Safhi 2024). When a plant experiences stress, its reaction is not solely determined by its genetic makeup or the environmental conditions, but by the interaction between the two. This is where G × E interactions come into play, as different plant genotypes exhibit varying degrees of resilience when exposed to the same environmental stress factors, such as drought or extreme temperatures. Samineni et al. (2025) assessed 24 proso millet genotypes in the United Arab Emirates to find out which ones could handle a combination of water, heat, and salt stress. They tested the plants under different conditions, including 100% and 50% freshwater, and a high-salinity environment (10 dS/m) across both normal and hot summer seasons. The goal was to pinpoint the most resilient genotypes and to understand how their traits and genetics influenced their performance in these stressful environments. Elkelish et al. (2025) used a genome-wide association study (GWAS) to explore how barley plants respond to stress. They discovered that exposure to an initial stressful event helps plants better cope with future stress. A deep understanding of these interactions is therefore crucial for plant breeding programs, as it helps in identifying genotypes that display stable and high-performing traits across diverse conditions, a phenomenon known as adaptive plasticity. By using this knowledge, breeders can develop crops that are more robust and can maintain yields even when faced with unpredictable environmental challenges.

3.5. Epigenetic regulation

Epigenetic regulation has an important role in enabling plants to respond dynamically and adapt to stresses without changing their DNA sequence (Akhter et al. 2021). Mechanisms such as DNA methylation, histone modification, and small RNAs act as a flexible layer of control, fine-tuning gene expression in response to abiotic stresses. These modifications can repress or activate specific genes, allowing the plant to quickly adjust its physiological functions to cope with current threats (Shilpa et al. 2024). Importantly, this epigenetic response can persist even after the stress is removed, preparing the plant for a faster and more robust response if the same stress occurs again. In some cases, this memory can be even passed down to the next generation, giving offspring with an enhanced ability to survive similar challenges and contributing to long-term adaptation (Kumar & Mohapatra 2024). This dynamic regulatory system is a vital component of plant resilience and is a major focus of research for developing more stress-tolerant crops. Under drought stress, plants can change their DNA methylation patterns. These epigenetic modifications are crucial for how plants respond to environmental stress. Research on abiotic stress has shown that stress can cause changes in DNA methylation, either across the entire genome or at specific genes (Fan et al. 2024). Drought-induced DNA methylation has been documented as a mechanism contributing to drought stress adaptation in rice and numerous other crops (Yin et al. 2024). According to a study by Song et al. (2012), salt stress induced contrasting changes in DNA methylation levels in two *Brassica napus* cultivars. The salt-tolerant cultivar Exagone exhibited a decrease in overall DNA methylation, whereas the salt-sensitive cultivar Toccata showed an increase. In a study on *B. napus*, Ghahramani et al. (2019) found that heat stress caused different changes in cytosine methylation patterns and overall methylation levels in rapeseed plants.

4. Strategies for plant tolerance improvement

4.1. Conventional breeding

Conventional breeding is a basic and widely utilized strategy for developing crops with enhanced environmental stress tolerance (Sabar et al. 2024). This method, which involves the intentional cross-pollination of plants with desirable traits leverages existing genetic diversity to create new, improved varieties. The process begins with identifying parent plants that exhibit natural resilience to specific stress factors like drought, salinity, or high temperatures (Arif et al. 2025). These parents are then hybridized and their offspring are rigorously screened over multiple generations to select for individuals that combine the desired stress tolerance with high yield and other favorable agricultural characteristics. While this strategy can be time-consuming and labor-

intensive, it has been a tool for creating hardier, more stable crop varieties that can maintain productivity in a wide range of climatic conditions, forming the backbone of modern agricultural resilience (Şimşek 2025). Conventional breeding has successfully produced numerous stress-tolerant crop varieties through techniques like selection and hybridization. These methods leverage existing genetic variation within a species or its wild relatives to develop new cultivars with improved resilience. The International Rice Research Institute (IRRI) has used conventional breeding to develop several high-yielding, drought-tolerant rice varieties. These varieties were created by crossing traditional drought-tolerant landraces with high-yielding cultivars. The resulting progeny are then selected over multiple generations for both their yield potential and ability to withstand water scarcity (Kumar et al. 2014). James et al. (2012) studied two genes, *Nax1* and *Nax2*, from an ancient wheat variety (*Triticum monococcum*). These genes help exclude salt from the roots and leaves. By crossing this ancient variety with modern durum wheat, they were able to use conventional breeding to develop new salt-tolerant cultivars. While modern techniques like genetic engineering and molecular breeding can accelerate the process, conventional breeding remains a basic and crucial method for developing new resilient crop varieties.

4.2. Marker-Assisted selection (MAS)

MAS is an indirect selection process that uses DNA markers as indicator of specific genes (Figure 1). Instead of waiting for a plant to mature to see if it has a certain trait, a breeder can take a small leaf sample from a seedling and test its DNA for a specific marker. This marker is a short DNA sequence that is located very close to the gene (or genes) that controls the desired trait (Kumar et al. 2024). Because of this close proximity, the marker and the gene are almost always inherited together. By identifying the presence of the marker, breeders can confidently infer the presence of the beneficial gene. This allows for a more efficient and reliable selection process than relying on visual observation alone (Chavhan et al. 2024).

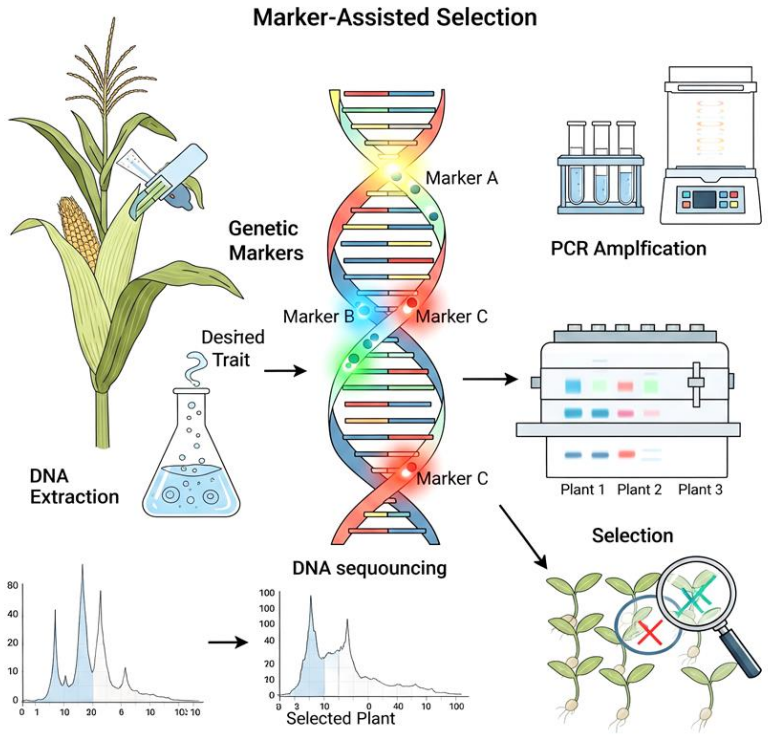


Figure 1- Illustration of MAS breeding technique used to enhance plant traits

MAS offers several critical advantages that accelerate the breeding process and increase its precision. Conventional breeding can take many years, as breeders must grow plants to maturity in the field to observe traits. With MAS, selection can be performed in a laboratory at the seedling stage, which significantly shortens breeding cycles and reduces the land, time, and resources needed for field trials (Ćeran et al. 2024). Plant physical traits can be heavily influenced by its environment. A drought-tolerant plant might not indicate its best if a season is particularly wet, which could confuse a breeder using conventional methods. DNA markers, however, are not affected by the environment, ensuring consistent and reliable selection (Bidyananda et al. 2024). Many stress tolerance traits are controlled by multiple genes, each contributing a small effect. Combining these genes into a single plant (gene pyramiding) is extremely difficult with conventional methods. MAS allows breeders to track and combine multiple desirable markers at once, making it possible to stack multiple genes for more robust and durable stress tolerance (Kumari et al. 2024).

MAS has been successfully applied to develop resilient crops around the world. A prime example is the breeding of drought-tolerant pearl millet. Researchers have identified Quantitative Trait Loci (QTLs) sections of DNA that contain genes controlling a specific trait linked to drought tolerance (Bollam et al. 2024). By using markers associated with these QTLs, they have been able to select and introduce these traits into new, high-yielding varieties, improving grain production in dry regions. Similarly, in rice, MAS has been used to combat salinity stress, a major issue in coastal and arid regions (Saleem et al. 2025). Breeders have identified genes that confer salt tolerance at both the seedling and reproductive stages. By using MAS to combine these genes, they have produced new rice varieties that can maintain a stable yield even when grown in salty soils (Mheni et al. 2024). While MAS is a powerful tool, it is not free of limitations. It is most effective on traits that are controlled by a single gene or a few genes with large effects. For highly complex traits, which are often controlled by many genes with small effects, MAS can be less reliable (Jadhav et al. 2024). The future of crop breeding lies on integrating MAS with even more advanced technologies.

4.3. Genomic selection (GS)

Genomic Selection (GS) represents a paradigm shift in plant breeding, moving beyond the limitations of traditional and even MAS to address complex traits with greater efficiency (Figure 2). Unlike MAS, which targets a few specific genes with major effects, GS is a breeding strategy that uses a large number of DNA markers scattered across the entire genome to predict a plant genetic potential (Adunola et al. 2024). This approach is particularly effective on traits like drought or salinity tolerance, which are influenced by a multitude of genes, each with a small effect. By capturing the cumulative impact of all these minor genes, GS provides a more holistic and accurate picture of a plant performance potential (Wang et al. 2021).

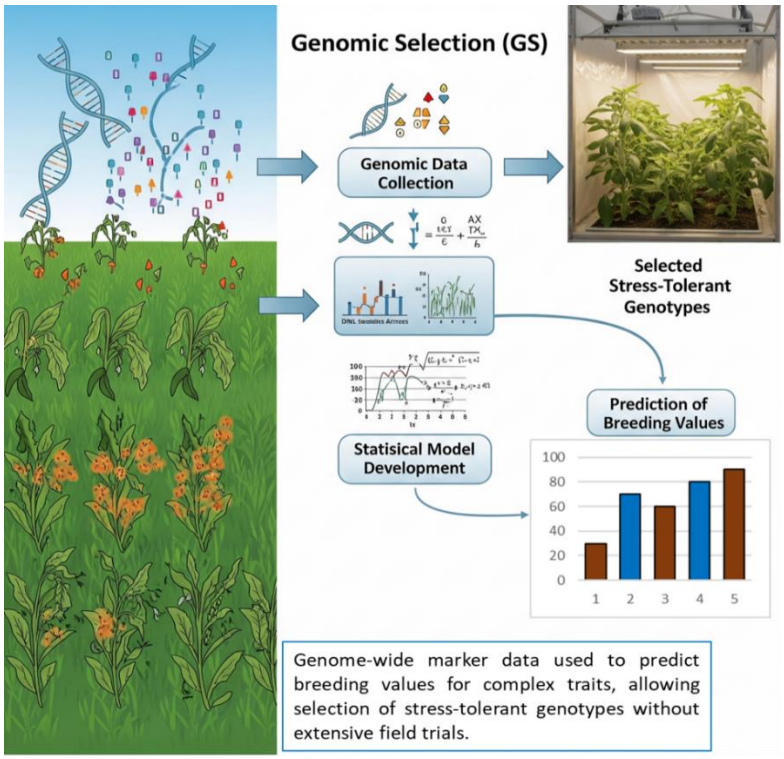


Figure 2- The GS breeding method that uses genome-wide DNA marker data to predict the breeding values of plants for complex traits like stress tolerance

The process of Genomic Selection hinges on the concept of training population. Breeders first produce a population of plants for which they have two key pieces of information, including phenotypic data (how the plants physically perform under specific environmental stress, such as measuring yield under drought conditions) and genotypic data (a comprehensive map of their DNA using thousands of genetic markers). This combined data is then used to build a sophisticated statistical model. This model learns the relationship between the genetic markers and the observed performance. Once the model is trained, breeders can generate new plants in their breeding program often at the seedling stage and use the model to predict their Genomic Estimated Breeding Value (GEBV) for stress tolerance, without growing them in the field (Alemu et al. 2024).

The key advantage of GS is its ability to dramatically accelerate the breeding cycle and improve accuracy for complex traits (Sharma et al. 2023). Conventional breeding can take over a decade, and even MAS requires significant time for field trials to confirm a marker effect. With GS, a breeder can predict the performance of thousands of new candidate plants in a lab within a matter of weeks. This predictive power means they can select the most promising individuals early on, allowing them to shorten the breeding cycle by several years (Raza et al. 2025). This is especially crucial for developing resilience to environmental stresses like drought and heat, which are difficult to consistently measure in the field due to year-to-year weather variation. GS

models are more robust and less susceptible to environmental noise because they are built on data from multiple years and environments (Crossa et al. 2022).

The application of GS has already shown great promise in developing climate-resilient crops. In maize and wheat, GS models are being used to select for traits that contribute to drought tolerance, such as improved water-use efficiency and deeper root systems (Siddiqui et al. 2020). For crops like rice, GS is helping to identify and select genes that confer salinity tolerance, critical for maintaining yield in coastal regions affected by rising sea levels (Haque et al. 2021). While the initial investment in genotyping the training population can be high, the long-term gains in time, labor, and precision make GS a highly effective strategy. As genotyping technology becomes cheaper and more accessible, GS is expected to play an even more central role in securing global food supplies against the backdrop of climate change.

4.4. Genetic engineering

Genetic engineering is powerful field of biotechnology offers a precise and accelerated strategy to develop crops with enhanced tolerance to environmental stress, by surpassing the speed and limitations of traditional breeding methods. By directly manipulating a plant genetic material, scientists can equip crops with the biological tools needed to thrive in adverse conditions (Figure 3).

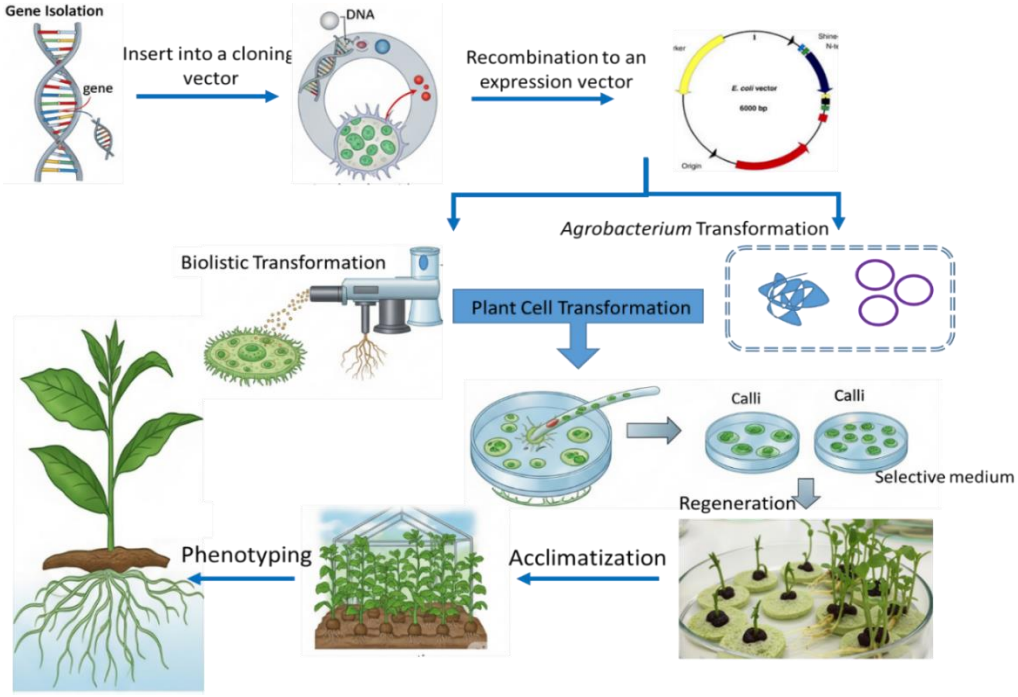


Figure 3- A generalized workflow for plant genetic transformation: illustrating the key steps involved in creating a genetically modified plant

Genetic engineering as a strategy for developing stress-tolerant crops relies on two primary techniques, including transformation and genome editing, with the latter often being more precise. Transformation involves the insertion of a foreign gene, often from a different species into a crop genome. This transgene provides the plant with a novel ability to cope with a specific stress (Rahman et al. 2024). A well-known example is the development of a drought-tolerant maize variety, which was engineered with a gene from a soil bacterium that helps maintain cellular functions under drought stress (Ibarra et al. 2020). The enhanced resilience in these engineered crops is built through specific molecular and cellular mechanisms. For instance, a common strategy to combat drought and salinity is to increase production of osmolytes like proline or glycine betaine (Singh et al. 2015). These molecules accumulate in the plant cells and help maintain the crucial balance of water, preventing dehydration and cell damage. Similarly, genetic engineering can boost the production of antioxidant enzymes such as superoxide dismutase (SOD). These enzymes act as a defense system, neutralizing harmful free radicals that are produced in abundance when a plant is under stress. By improving these intrinsic protective mechanisms, genetic engineering allows crops to endure harsh conditions with minimal yield loss (Rao et al. 2025).

Numerous examples highlight the success of this approach. For drought, a commercially available maize variety, DroughtGard maize, was developed to express a bacterial cold shock protein which helps the plant maintain normal growth and yield in a water-deficient environment (Wang et al. 2015). For salinity, research has shown that genetically modified tomato plants can be

engineered to overexpress a gene for a protein that actively pumps excess sodium ions into their cellular vacuoles, effectively sequestering the salt away from sensitive parts of the cell. This allows the plant to tolerate high salt concentrations in the soil that would otherwise be toxic (Wang et al. 2015). These breakthroughs demonstrate that genetic engineering is not merely a theoretical concept but a practical, effective strategy for producing more resilient and productive crops.

4.5. Genome editing

Climate change and expanding global population have made the development of tolerant crops a critical priority for ensuring future food security. In response, modern biotechnology has introduced genome editing, a revolutionary strategy that allows for precise and rapid genetic modifications (Khalil 2020). To combat these limitations, modern biotechnology, particularly the CRISPR-Cas9 system, is being utilized to develop crops with improved tolerance to environmental stresses like drought, salinity, and temperature. This powerful tool represents a new frontier for sustainable agriculture (Safhi 2025).

The primary tool for this genetic engineering is the CRISPR-Cas9 system. The CRISPR-Cas9 system operates through two key components, including a guide RNA (gRNA) and a Cas9 protein. The gRNA is a RNA molecule engineered to match a specific DNA sequence, which directs the Cas9 protein to the precise location for gene editing. Upon delivery to the nucleus, the Cas9 protein creates a precise double-strand break in the DNA. The cell innate repair machinery then attempts to fix this cut, a process that can be exploited to disable a gene (knockout), modify its function (editing), or insert new genetic material (Aljabali et al. 2024). This level of precision and efficiency makes CRISPR-Cas9 superior to earlier methods of genetic modification, which were often less specific and could introduce foreign DNA in an unpredictable manner.

An important application of this technology is the development of drought-tolerant crops. Water scarcity is a major threat to agricultural productivity, and genome editing provides a way to enhance a plant natural ability to conserve water. For example, in maize, a gene called *ARGOS8* was targeted with CRISPR-Cas9. By editing a regulatory element, scientists were able to increase the gene expression, which in turn improved grain yield in maize plants grown under drought stress conditions (Singh et al. 2024). Similarly, research on rice has shown that editing genes involved in root development can lead to deeper and more robust root systems, allowing the plant to access water from lower soil levels. These targeted changes help crops survive and thrive with less water, improving yields in arid and semi-arid regions (Rengasamy et al. 2024).

Beyond drought, genome editing is also being used to create crops that can withstand salinity and heat. Salt accumulation in soil can be toxic to most plants, inhibiting water uptake and nutrient absorption (Sugumar et al. 2024). Through genome editing, researchers have successfully modified genes in crops like rice and tomato that are responsible for regulating ion transport and maintaining cellular salt balance. For instance, by knocking out the *OsRR22* gene in rice, scientists were able to improve salt tolerance (Keerthana et al. 2025). In response to heat stress, plants often produce heat shock proteins and other protective compounds. Genome editing allows scientists to enhance the function of these genes or even turn off genes that negatively regulate a heat stress response. A study on tomatoes, for example, successfully edited a gene to improve both salt and heat stress tolerance simultaneously, highlighting the potential for creating crops with multiple stress-tolerant traits (Shawky et al. 2024).

5. Conclusions

Plants adapt to abiotic and biotic stresses through a complex interplay of physiological, molecular, and genetic mechanisms. These responses are orchestrated by a sophisticated network of transcription factors, phytohormones, and signal transduction components, which collectively activate genes to produce protective molecules like osmolytes and antioxidant enzymes. A plant capacity to withstand stress is shaped by G x E interactions and epigenetic regulation. These interactions highlight how genetic diversity provides the raw material for adaptation, ensuring that some individuals are naturally more resilient than others. Simultaneously, epigenetic memory such as DNA methylation, allows plants to adjust gene expression without changing the DNA sequence, a trait that can even be inherited by future generations to confer an advantage against recurring stress factors. Advancements in crop development reflect this understanding, moving from traditional conventional breeding to more precise biotechnologies. Methods like MAS and GS use DNA markers to accelerate the breeding process, while genetic engineering and CRISPR-Cas9 enable direct, targeted modifications to a plant's DNA. Ultimately, securing future food production requires a synergistic approach that merges the basic principles of conventional breeding with the speed and accuracy of modern biotechnology.

Author Declarations

Authors' contributions: Concept: A.S.J., Design: A.S.J., Data collection: A.S.J., Analysis: A.S.J., Writing: A.S.J.

Conflict of interest/Competing interests: The author(s) declare no conflict of interest.

Ethics approval/declarations: No need/ Not applicable.

Funding: This research received no external funding.

Consent to participate: No need/ Not applicable.

Consent for publication: No need/ Not applicable.

Data availability: Data are available on request due to privacy or other restrictions.

References

A Lal M, Kathpalia R, Sisodia R & Shakya R (2018). Biotic Stress, in: Bhatla, S.C., A. Lal, M. (Eds.), Plant Physiology, Development and Metabolism. Springer Nature Singapore, Singapore, pp. 1029-1095. 10.1007/978-981-13-2023-1_32

Abdolmaleky H M, Nohesara S, Zhou J-R & Thiagalingam S (2025). Epigenetics in evolution and adaptation to environmental challenges: pathways for disease prevention and treatment. *Epigenomics* 17: 317-333. 10.1080/17501911.2025.2464529

Achard P, Cheng H, De Grauwe L, Decat J, Schoutteten H, Moritz T, Van Der Straeten D, Peng J & Harberd N P (2006). Integration of Plant Responses to Environmentally Activated Phytohormonal Signals. *Science* 311: 91-94. 10.1126/science.1118642

Adunola P, Ferrão L F V, Benevenuto J, Azevedo C F & Munoz P R (2024). Genomic selection optimization in blueberry: Data-driven methods for marker and training population design. *The Plant Genome* 17: e20488. 10.1002/tpg2.20488

Akhtar M, Jaiswal A, Taj G, Jaiswal J P, Qureshi M I & Singh N K (2012). DREB1/CBF transcription factors: their structure, function and role in abiotic stress tolerance in plants. *Journal of Genetics* 91: 385-395. 10.1007/s12041-012-0201-3

Akhter Z, Bi Z, Ali K, Sun C, Fiaz S, Haider F U & Bai J (2021). In Response to Abiotic Stress, DNA Methylation Confers EpiGenetic Changes in Plants. *Plants* 10: 1096. 10.3390/plants10061096

Alemu A, Åstrand J, Montesinos-Lopez O A, y Sanchez J I, Fernandez-Gonzalez J, Tadesse W, Vetukuri R R, Carlsson A S, Ceplitis A & Crossa J (2024). Genomic selection in plant breeding: Key factors shaping two decades of progress. *Molecular Plant* 17: 552-578. 10.1016/j.molp.2024.03.007

Alghamdi S (2024). Drought and salinity effects on plant growth: A comprehensive review. *SABRAO Journal of Breeding and Genetics* 56: 2331-2340. 10.54910/sabrao2024.56.6.14.

Ali J, Mukarram M, Ojo J, Dawam N, Riyazuddin R, Ghramh H A, Khan K A, Chen R, Kurjak D & Bayram A (2024). Harnessing Phytohormones: Advancing Plant Growth and Defence Strategies for Sustainable Agriculture. *Physiologia Plantarum* 176: e14307. 10.1111/ppl.14307

Aljabali A A A, El-Tanani M & Tambuwala M M (2024). Principles of CRISPR-Cas9 technology: Advancements in genome editing and emerging trends in drug delivery. *Journal of Drug Delivery Science and Technology* 92: 105338. 10.1016/j.jddst.2024.105338

Angon P B, Das A, Roy A R, Khan J J, Ahmad I, Biswas A, Pallob A T, Mondol M & Yeasmin S T (2024). Plant development and heat stress: role of exogenous nutrients and phytohormones in thermotolerance. *Discover Plants* 1: 17. 10.1007/s44372-024-00020-3

Arif M, Haroon M, Nawaz A F, Abbas H, Xu R & Li L (2025). Enhancing wheat resilience: biotechnological advances in combating heat stress and environmental challenges. *Plant Molecular Biology* 115: 41. 10.1007/s11103-025-01569-7

Asai T, Tena G, Plotnikova J, Willmann M R, Chiu W-L, Gomez-Gomez L, Boller T, Ausubel F M & Sheen J (2002). MAP kinase signalling cascade in Arabidopsis innate immunity. *Nature* 415: 977-983. 10.1038/415977a

Asiminicesei D-M, Fertu D I & Gavrilescu M (2024). Impact of Heavy Metal Pollution in the Environment on the Metabolic Profile of Medicinal Plants and Their Therapeutic Potential. *Plants* 13: 913. 10.3390/plants13060913

Balakrishnan D, Bateman N & Kariyat R R (2024). Rice physical defenses and their role against insect herbivores. *Planta* 259: 110. 10.1007/s00425-024-04381-7

Baoxiang W, Bo X, Yan L, Jingfang L, Zhiguang S, Ming C, Yungao X, Bo Y, Jian L, Jinbo L, Tingmu C, Zhaowei F, Baiguan L, Dayong X & Bello B K (2022). A Novel mechanisms of the signaling cascade associated with the SAPK10-bZIP20-NHX1 synergistic interaction to enhance tolerance of plant to abiotic stress in rice (Oryza sativa L.). *Plant Science* 323: 111393. 10.1016/j.plantsci.2022.111393

Barberon M, Vermeer Joop Engelbertus M, De Bellis D, Wang P, Naseer S, Andersen Tonni G, Humbel Bruno M, Nawrath C, Takano J, Salt David E & Geldner N (2016). Adaptation of Root Function by Nutrient-Induced Plasticity of Endodermal Differentiation. *Cell* 164: 447-459. 10.1016/j.cell.2015.12.021

Bidyananda N, Jamir I, Nowakowska K, Varte V, Vendrame W A, Devi R S & Nongdam P (2024). Plant Genetic Diversity Studies: Insights from DNA Marker Analyses. *International Journal of Plant Biology* 15: 607-640. 10.3390/ijpb15030046

Blanco-Touriñán N, Legris M, Minguet E G, Costigliolo-Rojas C, Nohales M A, Iniesto E, García-León M, Pacín M, Heucken N, Blomeier T, Locascio A, Černý M, Esteve-Bruna D, Díez-Díaz M, Brzobohatý B, Frerigmann H, Zurbriggen M D, Kay S A, Rubio V, Blázquez M A, Casal J J & Alabadí D (2020). COP1 destabilizes DELLA proteins in Arabidopsis. *Proceedings of the National Academy of Sciences* 117: 13792-13799. 10.1073/pnas.1907969117

Bollam S, Mahendrakar M, Marla S, Kanuganahalli V, Addanki K R & Srivastava R K (2024). Genetic and Genomic Approaches for Accelerated Pearl Millet Breeding, Pearl Millet, pp. 81-120. 10.1002/9780891184034.ch4

Cai M, Yu H, Sun E & Zuo C (2024). Receptor-like proteins: decision-makers of plant immunity. *Phytopathology Research* 6: 58. 10.1186/s42483-024-00279-0

Ćeran M, Miladinović D, Đorđević V, Trkulja D, Radanović A, Glogovac S & Kondić-Špika A (2024). Genomics-assisted speed breeding for crop improvement: present and future. *Frontiers in Sustainable Food Systems* Volume 8 - 2024. 10.3389/fsufs.2024.1383302

Chavhan R L, Hinge V R, Wankhade D J, Deshmukh A S, Mahajan N & Kadam U S (2024). Bioinformatics for Molecular Breeding and Enhanced Crop Performance, Bioinformatics for Plant Research and Crop Breeding, pp. 21-74. 10.1002/9781394209965.ch2

Chen F, Zhang H, Li H, Lian L, Wei Y, Lin Y, Wang L, He W, Cai Q, Xie H, Zhang H & Zhang J (2023). IPA1 improves drought tolerance by activating SNAC1 in rice. *BMC Plant Biology* 23: 55. 10.1186/s12870-023-04062-9

Chen X, Li C, Wang H & Guo Z (2019). WRKY transcription factors: evolution, binding, and action. *Phytopathology Research* 1: 13. 10.1186/s42483-019-0022-x

Crossa J, Montesinos-López O A, Pérez-Rodríguez P, Costa-Neto G, Fritsche-Neto R, Ortiz R, Martini J W R, Lillemo M, Montesinos-López A, Jarquin D, Breseghello F, Cuevas J & Rincent R (2022). Genome and Environment Based Prediction ModelsPrediction models and Methods of Complex TraitsComplex traits Incorporating Genotype × Environment Interaction, in: Ahmadi, N., Bartholomé, J. (Eds.), Genomic Prediction of Complex Traits: Methods and Protocols. Springer US, New York, NY, pp. 245-283. 10.1007/978-1-0716-2205-6_9

Das S, Shil S, Rime J, Alice A K, Yumkhaibam T, Mounika V, Singh A P, Kundu M, Lalhmangaihzuali H P, Hazarika T K, Singh A K & Singh S (2025). Phytohormonal signaling in plant resilience: advances and strategies for enhancing abiotic stress tolerance. *Plant Growth Regulation* 105: 329-360. 10.1007/s10725-025-01279-6

Ding Y, Li H, Zhang X, Xie Q, Gong Z & Yang S (2015). OST1 Kinase Modulates Freezing Tolerance by Enhancing ICE1 Stability in Arabidopsis. *Developmental Cell* 32: 278-289. 10.1016/j.devcel.2014.12.023

Dixit S, Sivalingam P N, Baskaran R K M, Senthil-Kumar M & Ghosh P K (2024). Plant responses to concurrent abiotic and biotic stress: unravelling physiological and morphological mechanisms. *Plant Physiology Reports* 29: 6-17. 10.1007/s40502-023-00766-0

Du X, Su M, Jiao Y, Xu S, Song J, Wang H & Li Q (2022). A Transcription Factor SlNAC10 Gene of Suaeda liaotungensis Regulates Proline Synthesis and Enhances Salt and Drought Tolerance. *International Journal of Molecular Sciences* 23: 9625. 10.3390/ijms23179625

Elkelish A, Alqudah A M, Alhudhaibi A M, Alqahtani H, Saied E M, Börner A & Thabet S G (2025). Mapping stress memory: genetic and epigenetic insights into combined drought and heat tolerance in barley. *Plant Cell Reports* 44: 120. 10.1007/s00299-025-03501-1

Fan Y, Sun C, Yan K, Li P, Hein I, Gilroy E M, Kear P, Bi Z, Yao P, Liu Z, Liu Y & Bai J (2024). Recent Advances in Studies of Genomic DNA Methylation and Its Involvement in Regulating Drought Stress Response in Crops. *Plants* 13: 1400. 10.3390/plants13101400

Gai W-X, Ma X, Qiao Y-M, Shi B-H, ul Haq S, Li Q-H, Wei A-M, Liu K-K & Gong Z-H (2020). Characterization of the bZIP Transcription Factor Family in Pepper (Capsicum annuum L.): CabZIP25 Positively Modulates the Salt Tolerance. *Frontiers in Plant Science* Volume 11 - 2020. 10.3389/fpls.2020.00139

Gasch P, Fundinger M, Müller J T, Lee T, Bailey-Serres J & Mustroph A (2015). Redundant ERF-VII Transcription Factors Bind to an Evolutionarily Conserved cis-Motif to Regulate Hypoxia-Responsive Gene Expression in Arabidopsis. *The Plant Cell* 28: 160-180. 10.1105/tpc.15.00866

Ghahramani A, Howden S M, del Prado A, Thomas D T, Moore A D, Ji B & Ates S (2019). Climate Change Impact, Adaptation, and Mitigation in Temperate Grazing Systems: A Review. *Sustainability* 11: 7224. 10.3390/su11247224

Goher F, Shafique Khan F, Sun S & Wang Q (2025). Calcium-dependent protein kinase (CDPK/CPK)-mediated salicylic acid cascade: the key arsenal of plants under pathogens attack. *Critical Reviews in Biotechnology*: 1-17. 10.1080/07388551.2025.2498463

Guo Z, Dzinyela R, Yang L & Hwarari D (2024). bZIP Transcription Factors: Structure, Modification, Abiotic Stress Responses and Application in Plant Improvement. *Plants* 13: 2058. 10.3390/plants13152058

Hafeez A, Ali B, Javed M A, Saleem A, Fatima M, Fathi A, Afridi M S, Aydin V, Oral M A & Soudy F A (2023). Plant breeding for harmony between sustainable agriculture, the environment, and global food security: an era of genomics-assisted breeding. *Planta* 258: 97. 10.1007/s00425-023-04252-7

Haghpanah M, Hashemipetroudi S, Arzani A & Araniti F (2024). Drought Tolerance in Plants: Physiological and Molecular Responses. *Plants* 13: 2962. 10.3390/plants13212962

Haghpanah M, Namdari A, Kaleji M K, Nikbakht-dehkordi A, Arzani A & Araniti F (2025). Interplay Between ROS and Hormones in Plant Defense Against Pathogens. *Plants* 14: 1297. 10.3390/plants14091297

Haque M A, Rafii M Y, Yusoff M M, Ali N S, Yusuff O, Datta D R, Anisuzzaman M & Ikbal M F (2021). Advanced Breeding Strategies and Future Perspectives of Salinity Tolerance in Rice. *Agronomy* 11: 1631. 10.3390/agronomy11081631

Havko N E, Das M R, McClain A M, Kapali G, Sharkey T D & Howe G A (2020). Insect herbivory antagonizes leaf cooling responses to elevated temperature in tomato. *Proceedings of the National Academy of Sciences* 117: 2211-2217. 10.1073/pnas.1913885117

Hu Y, Jiang L, Wang F & Yu D (2013). Jasmonate Regulates the INDUCER OF CBF EXPRESSION–C-REPEAT BINDING FACTOR/DRE BINDING FACTOR1 Cascade and Freezing Tolerance in Arabidopsis *The Plant Cell* 25: 2907-2924. 10.1105/tpc.113.112631

Ibarra J G, Colombo R P, Godeas A M & López N I (2020). Analysis of soil bacterial communities associated with genetically modified drought-tolerant corn. *Applied Soil Ecology* 146: 103375. 10.1016/j.apsoil.2019.103375

Jadhav Y, Thakur N R, Ingle K P & Ceasar S A (2024). The role of phenomics and genomics in delineating the genetic basis of complex traits in millets. *Physiologia Plantarum* 176: e14349. 10.1111/ppl.14349

James R A, Blake C, Zwart A B, Hare R A, Rathjen A J & Munns R (2012). Impact of ancestral wheat sodium exclusion genes Nax1 and Nax2 on grain yield of durum wheat on saline soils. *Functional Plant Biology* 39: 609-618. 10.1071/FP12121

Keerthana R, Rakshana P, Salunkhe S R, Sakthi A R, Kokiladevi E, Saraswathi T, Pushpam R, Raveendran M & Sudha M (2025). CRISPR-Cas9 mediated enhancement of abiotic stress resilience in tomato: a comprehensive review of target genes. *Molecular Biology Reports* 52: 538. 10.1007/s11033-025-10634-9

Khalil A M (2020). The genome editing revolution: review. *Journal of Genetic Engineering and Biotechnology* 18: 68. 10.1186/s43141-020-00078-y

Khan A, Shah S T, Basit A, Mohamed H I & Li Y (2024). Mitogen-Activated Protein Kinase: A Potent Signaling Protein that Combats Biotic and Abiotic Stress in Plants. *Journal of Plant Growth Regulation* 43: 1762-1786. 10.1007/s00344-024-11239-5

Khan N (2025). Molecular Insights into ABA-Mediated Regulation of Stress Tolerance and Development in Plants. *International Journal of Molecular Sciences* 26: 7872. 10.3390/ijms26167872

Korver R A, van den Berg T, Meyer A J, Galvan-Ampudia C S, ten Tusscher K H W J & Testerink C (2020). Halotropism requires phospholipase Dζ1-mediated modulation of cellular polarity of auxin transport carriers. *Plant, Cell & Environment* 43: 143-158. 10.1111/pce.13646

Krishnappa G, Savadi S, Tyagi B S, Singh S K, Mamrutha H M, Kumar S, Mishra C N, Khan H, Gangadhara K, Uday G, Singh G & Singh G P (2021). Integrated genomic selection for rapid improvement of crops. *Genomics* 113: 1070-1086. 10.1016/j.ygeno.2021.02.007

Kumar A, Dixit S, Ram T, Yadaw R B, Mishra K K & Mandal N P (2014). Breeding high-yielding drought-tolerant rice: genetic variations and conventional and molecular approaches. *Journal of Experimental Botany* 65: 6265-6278. 10.1093/jxb/eru363

Kumar R, Das S P, Choudhury B U, Kumar A, Prakash N R, Verma R, Chakraborti M, Devi A G, Bhattacharjee B, Das R, Das B, Devi H L, Das B, Rawat S & Mishra V K (2024). Advances in genomic tools for plant breeding: harnessing DNA molecular markers, genomic selection, and genome editing. *Biological Research* 57: 80. 10.1186/s40659-024-00562-6

Kumar S & Mohapatra T (2024). Epigenetic Modifications in Genome Help Remembering the Stress Tolerance Strategy Adopted by the Plant. *Frontiers in Bioscience-Landmark* 29. 10.31083/j.fbl2903126

Kumari M, Dubey A K, Kumar R & Kumar A (2024). Chapter 18 - Marker-assisted selection in plant breeding for stress tolerance, in: Ahanger, M.A., Bhat, J.A., Ahmad, P., John, R. (Eds.), Improving Stress Resilience in Plants. Academic Press, pp. 371-387. 10.1016/B978-0-443-18927-2.00005-4

Ladikou E-V, Daras G, Landi M, Chatzistathis T, Sotiropoulos T, Rigas S & Papadakis I E (2025). Physiological and Biochemical Effects of Potassium Deficiency on Apple Tree Growth. *Horticulturae* 11: 42. 10.3390/horticulturae11010042

Larkindale J, Hall J D, Knight M R & Vierling E (2005). Heat Stress Phenotypes of Arabidopsis Mutants Implicate Multiple Signaling Pathways in the Acquisition of Thermotolerance *Plant Physiology* 138: 882-897. 10.1104/pp.105.062257

Li S, Khoso M A, Xu H, Zhang C, Liu Z, Wagan S, Dinislam K & Liu L (2024). WRKY Transcription Factors (TFs) as Key Regulators of Plant Resilience to Environmental Stresses: Current Perspective. *Agronomy* 14: 2421. 10.3390/agronomy14102421

Li S, Wang N, Ji D, Zhang W, Wang Y, Yu Y, Zhao S, Lyu M, You J, Zhang Y, Wang L, Wang X, Liu Z, Tong J, Xiao L, Bai M-y & Xiang F (2019). A GmSIN1/GmNCED3s/GmRbohBs Feed-Forward Loop Acts as a Signal Amplifier That Regulates Root Growth in Soybean Exposed to Salt Stress. *The Plant Cell* 31: 2107-2130. 10.1105/tpc.18.00662

Lin Z, Li Y, Wang Y, Liu X, Ma L, Zhang Z, Mu C, Zhang Y, Peng L, Xie S, Song C-P, Shi H, Zhu J-K & Wang P (2021). Initiation and amplification of SnRK2 activation in abscisic acid signaling. *Nature Communications* 12: 2456. 10.1038/s41467-021-22812-x

Liu D (2021). Root developmental responses to phosphorus nutrition. *Journal of Integrative Plant Biology* 63: 1065-1090. 10.1111/jipb.13090

Lu Z, Ren T, Li Y, Cakmak I & Lu J (2025). Nutrient limitations on photosynthesis: from individual to combinational stresses. *Trends in Plant Science* 30: 872-885. 10.1016/j.tplants.2025.03.006

Mahdavian K (2024). Effects of Ultraviolet Radiation on Plants and Their Protective Mechanisms. *Russian Journal of Plant Physiology* 71: 184. 10.1134/S1021443724607481

Manna M, Thakur T, Chirom O, Mandlik R, Deshmukh R & Salvi P (2021). Transcription factors as key molecular target to strengthen the drought stress tolerance in plants. *Physiologia Plantarum* 172: 847-868. 10.1111/ppl.13268

Mao C, He J, Liu L, Deng Q, Yao X, Liu C, Qiao Y, Li P & Ming F (2020). OsNAC2 integrates auxin and cytokinin pathways to modulate rice root development. *Plant Biotechnology Journal* 18: 429-442. 10.1111/pbi.13209

Mareri L, Parrotta L & Cai G (2022). Environmental Stress and Plants. *International Journal of Molecular Sciences* 23: 5416. 10.3390/ijms23105416

Mehmood M, Tanveer N A, Joyia F A, Ullah I & Mohamed H I (2025). Effect of high temperature on pollen grains and yield in economically important crops: a review. *Planta* 261: 141. 10.1007/s00425-025-04714-0

Mheni N T, Kilasi N, Quiloy F A, Heredia M C, Bilaro A, Meliyo J, Dixit S & Nchimbi Msolla S (2024). Breeding rice for salinity tolerance and salt-affected soils in Africa: a review. *Cogent Food & Agriculture* 10: 2327666. 10.1080/23311932.2024.2327666

Nakayama A, Fukushima S, Goto S, Matsushita A, Shimono M, Sugano S, Jiang C-J, Akagi A, Yamazaki M, Inoue H & Takatsuji H (2013). Genome-wide identification of WRKY45-regulated genes that mediate benzothiadiazole-induced defense responses in rice. *BMC Plant Biology* 13: 150. 10.1186/1471-2229-13-150

Nazir F, Peter P, Gupta R, Kumari S, Nawaz K & Khan M I R (2024). Plant hormone ethylene: A leading edge in conferring drought stress tolerance. *Physiologia Plantarum* 176: e14151. 10.1111/ppl.14151

Noh M, Huque A K M M, Jung K W, Kim Y Y & Shin J S (2021). A Stress-Responsive CaM-Binding Transcription Factor, bZIP4, Confers Abiotic Stress Resistance in Arabidopsis. *Journal of Plant Biology* 64: 359-370. 10.1007/s12374-021-09315-4

Owji H, Hajiebrahimi A, Seradj H & Hemmati S (2017). Identification and functional prediction of stress responsive AP2/ERF transcription factors in Brassica napus by genome-wide analysis. *Computational Biology and Chemistry* 71: 32-56. 10.1016/j.compbiolchem.2017.09.004

Peng Y, Cao H, Cui L, Wang Y, Wei L, Geng S, Yang L, Huang Y & Bie Z (2023). CmoNAC1 in pumpkin rootstocks improves salt tolerance of grafted cucumbers by binding to the promoters of CmoRBOHD1, CmoNCED6, CmoAKT1;2 and CmoHKT1;1 to regulate H2O2, ABA signaling and K+/Na+ homeostasis. *Horticulture Research* 10. 10.1093/hr/uhad157

Praveen A & Singh S (2024). The role of potassium under salinity stress in crop plants. *Cereal Research Communications* 52: 315-322. 10.1007/s42976-023-00393-3

Rahman S U, Khan M O, Ullah R, Ahmad F & Raza G (2024). Agrobacterium-Mediated Transformation for the Development of Transgenic Crops; Present and Future Prospects. *Molecular Biotechnology* 66: 1836-1852. 10.1007/s12033-023-00826-8

Rai G K, Khanday D M, Kumar P, Magotra I, Choudhary S M, Kosser R, Kalunke R, Giordano M, Corrado G, Rouphael Y & Pandey S (2023). Enhancing Crop Resilience to Drought Stress through CRISPR-Cas9 Genome Editing. *Plants* 12: 2306. 10.3390/plants12122306

Ran T, Cao G, Xiao L, Li Y, Xia R, Zhao X, Qin Y, Wu P & Tian S (2024). Effects of cadmium stress on the growth and physiological characteristics of sweet potato. *BMC Plant Biology* 24: 850. 10.1186/s12870-024-05551-1

Rani M, Vikas, Kumar R, Lathwal M & Kamboj A (2024). Effect and Responses of Lead Toxicity in Plants, in: Kumar, N., Jha, A.K. (Eds.), Lead Toxicity Mitigation: Sustainable Nexus Approaches. Springer Nature Switzerland, Cham, pp. 211-241. 10.1007/978-3-031-46146-0_10

Rao M J, Duan M, Zhou C, Jiao J, Cheng P, Yang L, Wei W, Shen Q, Ji P, Yang Y, Conteh O, Yan D, Yuan H, Rauf A, Ai J & Zheng B (2025). Antioxidant Defense System in Plants: Reactive Oxygen Species Production, Signaling, and Scavenging During Abiotic Stress-Induced Oxidative Damage. *Horticulturae* 11: 477. 10.3390/horticulturae11050477

Ravi B, Foyer C H & Pandey G K (2023). The integration of reactive oxygen species (ROS) and calcium signalling in abiotic stress responses. *Plant, Cell & Environment* 46: 1985-2006. 10.1111/pce.14596

Raza A, Zaman Q U, Shabala S, Tester M, Munns R, Hu Z & Varshney R K (2025). Genomics-assisted breeding for designing salinity-smart future crops. *Plant Biotechnology Journal* 23: 3119-3151. 10.1111/pbi.70104

Rengasamy B, Manna M, Thajuddin N B, Sathiyabama M & Sinha A K (2024). Breeding rice for yield improvement through CRISPR/Cas9 genome editing method: current technologies and examples. *Physiology and Molecular Biology of Plants* 30: 185-198. 10.1007/s12298-024-01423-y

Sabar M, Mustafa S E, Ijaz M, Khan R A R, Shahzadi F, Saher H, Javed H M, Zafar S A, Saleem M U, Siddique S & Sabir A M (2024). Rice Breeding for Yield Improvement through Traditional and Modern Genetic Tools. *European Journal of Ecology, Biology and Agriculture* 1: 14-19. 10.59324/ejeba.2024.1(1).02

Safhi F A (2024). Genomic insights into the diversity of mango cultivars in Saudi Arabia: Fluorescent SSR marker analysis. *Journal of King Saud University - Science* 36: 103528. 10.1016/j.jksus.2024.103528

Safhi F A (2025). Enhancing barley resilience: advanced genetic techniques to improve drought tolerance for sustainable cultivation under current climatic fluctuations. *Cereal Research Communications* 53: 17-33. 10.1007/s42976-024-00519-1

Sakuraba Y (2022). Molecular basis of nitrogen starvation-induced leaf senescence. *Frontiers in Plant Science* Volume 13 - 2022. 10.3389/fpls.2022.1013304

Saleem M A, Khan A, Tu J, Huang W, Liu Y, Feng N, Zheng D & Xue Y (2025). Salinity Stress in Rice: Multilayered Approaches for Sustainable Tolerance. *International Journal of Molecular Sciences* 26: 6025. 10.3390/ijms26136025

Samineni S, Gummadi S, Thushar S, Khan D N, Gkanogiannis A, Becerra Lopez-Lavalle L A & Singh R K (2025). Exploring Proso Millet Resilience to Abiotic Stresses: High-Yield Potential in Desert Environments of the Middle East. *Agronomy* 15: 165. 10.3390/agronomy15010165

Shafiei-Masouleh S-S (2025). Biostimulants for Sustainable UV Stress Tolerance in Oilseed Crops, in: Abdel Latef, A.A.H. (Ed.), Oilseed Crops Under Abiotic Stress: Mitigation Strategies and Future Perspectives. Springer Nature Singapore, Singapore, pp. 199-222. 10.1007/978-981-96-8346-8_7

Sharma U, Sankhyan H P, Kumari A, Thakur S, Thakur L, Mehta D, Sharma S, Sharma S & Sankhyan N (2023). Genomic selection: a revolutionary approach for forest tree improvement in the wake of climate change. *Euphytica* 220: 9. 10.1007/s10681-023-03263-5

Shawky A, Hatawsh A, Al-Saadi N, Farzan R, Eltawy N, Francis M, Abousamra S, Ismail Y Y, Attia K, Fakhouri A S & Abdelrahman M (2024). Revolutionizing Tomato Cultivation: CRISPR/Cas9 Mediated Biotic Stress Resistance. *Plants* 13: 2269. 10.3390/plants13162269

Shilpa, Thakur R & Prasad P (2024). Epigenetic regulation of abiotic stress responses in plants. *Biochimica et Biophysica Acta (BBA) - General Subjects* 1868: 130661. 10.1016/j.bbagen.2024.130661

Shumayla, Alejo-Jacuinde G, Silva-Villatoro P, Nwoko C L, Oliver M J & Herrera-Estrella L (2025). The promise of resurrection plants in enhancing crop tolerance to water scarcity. *Philosophical Transactions B* 380: 20240231. 10.1098/rstb.2024.0231

Siddiqui M N, Léon J, Naz A A & Ballvora A (2020). Genetics and genomics of root system variation in adaptation to drought stress in cereal crops. *Journal of Experimental Botany* 72: 1007-1019. 10.1093/jxb/eraa487

Şimşek Ö (2025). Harvesting sustainability: Innovations and practices in modern agriculture. *Green Technologies and Sustainability* 3: 100192. 10.1016/j.grets.2025.100192

Singh M, Kumar J, Singh S, Singh V P & Prasad S M (2015). Roles of osmoprotectants in improving salinity and drought tolerance in plants: a review. *Reviews in Environmental Science and Bio/Technology* 14: 407-426. 10.1007/s11157-015-9372-8

Singh S B, Kumar B, Singh A & Kumar S (2024). Conventional and Advance Breeding Approaches for Developing Abiotic Stress Tolerant Maize, in: Sheraz Mahdi, S., Singh, R., Dhekale, B. (Eds.), Adapting to Climate Change in Agriculture-Theories and Practices: Approaches for Adapting to Climate Change in Agriculture in India. Springer Nature Switzerland, Cham, pp. 281-302. 10.1007/978-3-031-28142-6_13

Skibbe M, Qu N, Galis I & Baldwin I T (2008). Induced Plant Defenses in the Natural Environment: Nicotiana attenuata WRKY3 and WRKY6 Coordinate Responses to Herbivory. *The Plant Cell* 20: 1984-2000. 10.1105/tpc.108.058594

Song J, Angel A, Howard M & Dean C (2012). Vernalization – a cold-induced epigenetic switch. *Journal of Cell Science* 125: 3723-3731. 10.1242/jcs.084764

Sugumar T, Shen G, Smith J & Zhang H (2024). Creating Climate-Resilient Crops by Increasing Drought, Heat, and Salt Tolerance. *Plants* 13: 1238. 10.3390/plants13091238

Sun S, Yu J-P, Chen F, Zhao T-J, Fang X-H, Li Y-Q & Sui S-F (2008). TINY, a Dehydration-responsive Element (DRE)-binding Protein-like Transcription Factor Connecting the DRE- and Ethylene-responsive Element-mediated Signaling Pathways in Arabidopsis. *Journal of Biological Chemistry* 283: 6261-6271. 10.1074/jbc.M706800200

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

Takahashi F, Suzuki T, Osakabe Y, Betsuyaku S, Kondo Y, Dohmae N, Fukuda H, Yamaguchi-Shinozaki K & Shinozaki K (2018). A small peptide modulates stomatal control via abscisic acid in long-distance signalling. *Nature* 556: 235-238. 10.1038/s41586-018-0009-2

Teschke R (2024). Copper, Iron, Cadmium, and Arsenic, All Generated in the Universe: Elucidating Their Environmental Impact Risk on Human Health Including Clinical Liver Injury. *International Journal of Molecular Sciences* 25. 10.3390/ijms25126662

Ullah I, Toor M D, Yerlikaya B A, Mohamed H I, Yerlikaya S, Basit A & Rehman A u (2024). High-temperature stress in strawberry: understanding physiological, biochemical and molecular responses. *Planta* 260: 118. 10.1007/s00425-024-04544-6

Vennapusa A R, Nimmakayala P, Zaman-Allah M A & Ratnakumar P (2023). Editorial: Physiological, molecular and genetic perspectives of environmental stress response in plants. *Frontiers in Plant Science* Volume 14 - 2023. 10.3389/fpls.2023.1213762

Vilyanen D V & Kozuleva M A (2025). Photosynthetic Control and Its Role in Protection of Photosystem I against Photoinhibition. *Biochemistry (Moscow)* 90: 840-859. 10.1134/S0006297925601121

Wang C, Burzio L A, Koch M S, Silvanovich A & Bell E (2015). Purification, characterization and safety assessment of the introduced cold shock protein B in DroughtGard™ maize. *Regulatory Toxicology and Pharmacology* 71: 164-173. 10.1016/j.yrtph.2014.12.014

Wang J, Li C, Li L, Reynolds M, Mao X & Jing R (2021). Exploitation of Drought Tolerance-Related Genes for Crop Improvement. *International Journal of Molecular Sciences* 22. 10.3390/ijms221910265

Wang Z, Liu L, Cheng C, Ren Z, Xu S & Li X (2020). GAI Functions in the Plant Response to Dehydration Stress in Arabidopsis thaliana. *International Journal of Molecular Sciences* 21: 819. 10.3390/ijms21030819

Wani A B, Noor W, Pandit A & Husaini A M (2025). Upregulated expression of MYB4, DREB1 and AP37 transcription factors modulates cold stress response in high-altitude Himalayan rice via time-dependent ROS regulation. *Molecular Biology Reports* 52: 417. 10.1007/s11033-025-10507-1

Wu J, Chen Y, Xu Y, An Y, Hu Z, Xiong A & Wang G (2024). Effects of Jasmonic Acid on Stress Response and Quality Formation in Vegetable Crops and Their Underlying Molecular Mechanisms. *Plants* 13: 1557. 10.3390/plants13111557

Xiong H, He H, Chang Y, Miao B, Liu Z, Wang Q, Dong F & Xiong L (2025). Multiple roles of NAC transcription factors in plant development and stress responses. *Journal of Integrative Plant Biology* 67: 510-538. 10.1111/jipb.13854

Yang S, Wang S, Liu X, Yu Y, Yue L, Wang X & Hao D (2009). Four divergent Arabidopsis ethylene-responsive element-binding factor domains bind to a target DNA motif with a universal CG step core recognition and different flanking bases preference. *The FEBS Journal* 276: 7177-7186. 10.1111/j.1742-4658.2009.07428.x

Yang X, Kim M Y, Ha J & Lee S-H (2019). Overexpression of the Soybean NAC Gene GmNAC109 Increases Lateral Root Formation and Abiotic Stress Tolerance in Transgenic Arabidopsis Plants. *Frontiers in Plant Science* Volume 10 - 2019. 10.3389/fpls.2019.01036

Yang Y, Yu T-F, Ma J, Chen J, Zhou Y-B, Chen M, Ma Y-Z, Wei W-L & Xu Z-S (2020). The Soybean bZIP Transcription Factor Gene GmbZIP2 Confers Drought and Salt Resistances in Transgenic Plants. *International Journal of Molecular Sciences* 21: 670. 10.3390/ijms21020670

Yin M, Wang S, Wang Y, Wei R, Liang Y, Zuo L, Huo M, Huang Z, Lang J, Zhao X, Zhang F, Xu J, Fu B, Li Z & Wang W (2024). Impact of Abiotic Stress on Rice and the Role of DNA Methylation in Stress Response Mechanisms. *Plants* 13: 2700. 10.3390/plants13192700

You D, Rasul F, Wang T & Daroch M (2024). Insufficient Acetyl-CoA Pool Restricts the Phototrophic Production of Organic Acids in Model Cyanobacteria. *International Journal of Molecular Sciences* 25. 10.3390/ijms252111769

Yu D, Chen C & Chen Z (2001). Evidence for an Important Role of WRKY DNA Binding Proteins in the Regulation of NPR1 Gene Expression. *The Plant Cell* 13: 1527-1540. 10.1105/tpc.010115

Yuan X, Wang H, Cai J, Bi Y, Li D & Song F (2019). Rice NAC transcription factor ONAC066 functions as a positive regulator of drought and oxidative stress response. *BMC Plant Biology* 19: 278. 10.1186/s12870-019-1883-y

Zafar S, Khan M K, Aslam N & Hasnain Z (2024). Impact of Different Stresses on Morphology, Physiology, and Biochemistry of Plants, in: Shahid, M., Gaur, R. (Eds.), Molecular Dynamics of Plant Stress and its Management. Springer Nature Singapore, Singapore, pp. 67-91. 10.1007/978-981-97-1699-9_4

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

Zhang M, Ming Y, Wang H-B & Jin H-L (2024). Strategies for adaptation to high light in plants. *aBIOTECH* 5: 381-393. 10.1007/s42994-024-00164-6

Zhang Y, Xu J, Li R, Ge Y, Li Y & Li R (2023). Plants' Response to Abiotic Stress: Mechanisms and Strategies. *International Journal of Molecular Sciences* 24. 10.3390/ijms241310915

Zhou M, Cheng H, Chiang V L, Li W, Yang C & Wang C (2023). PtrbZIP3 transcription factor regulates drought tolerance of Populus trichocarpa. *Environmental and Experimental Botany* 208: 105231. 10.1016/j.envexpbot.2023.105231

Copyright © 2026 The Author(s). This is an open-access article published by Faculty of Agriculture, Ankara University under the terms of the Creative Commons Attribution License which permits unrestricted use, distribution, and reproduction in any medium or format, provided the original work is properly cited.