


COTTON UNDER CLIMATE CHANGE: ABIOTIC STRESS MECHANISMS, MOLECULAR RESPONSES, AND STRATEGIES FOR DEVELOPING RESILIENT CULTIVARS

Fariha Razzaq¹, Ghulam Rasool¹, Muhammad Saleem Chang³, Shahid Iqbal¹, Saadia Shehzad¹, Bibi Fatima Sarwar¹, Moattar Memoon¹, Haris Javed¹, Ayesha Shafique¹, Nimra Bajwa¹, Mahnoor akram¹, Shariq Ahmed¹, Abdul Hafeez², Sabahat Afzal^{3*} and Abdul Razzaq^{4*} 

¹The Institute of Molecular Biology and Biotechnology, The University of Lahore, Lahore-Pakistan

²Department of Agronomy, Sindh Agriculture University Campus, Umerkot, Sindh, Pakistan

³Department of Plant Breeding and Genetics, University of Agriculture Faisalabad, Sub Campus Burewala, Pakistan

⁴International Center for Interdisciplinary Research in Sciences, The University of Lahore, Lahore, Pakistan

*Corresponding author: sabahatafzal489@gmail.com (SA); biolformanite@gmail.com (AR)

ABSTRACT

Cotton (*Gossypium hirsutum* L.) is a major fiber crop that strengthens the global textile industry and contributes significantly to agricultural economies. However, its productivity is increasingly affected by abiotic stresses exacerbated by climate change. Rising temperatures, irregular rainfall patterns, and increasing soil salinity disrupt cotton physiology, leading to reduced growth, inferior fiber quality, and substantial yield losses. Globally, yield reductions of 10–30% have been reported under severe drought and heat stress, while temperatures above 35–40°C during flowering significantly impair boll formation and fiber development. In addition, soil salinity affects nearly 20% of irrigated agricultural land worldwide, further limiting cotton productivity. This review aims to summarize the impacts of climate change on cotton and to elucidate the molecular and cellular mechanisms underlying plant responses to drought, heat, and salinity stress. Furthermore, recent advances in biotechnology, including multi-omics approaches, CRISPR/Cas-mediated genome editing targeting key pathways such as GhMAPK signaling and reactive oxygen species (ROS) regulation, and transgenic strategies, are discussed for developing stress-resilient cotton cultivars. In addition, adaptive agronomic practices, including efficient irrigation management and climate-smart cultivation techniques, are highlighted. Future research should focus on integrating wild *Gossypium* germplasm resources and standardized phenotyping approaches to develop climate-resilient cotton varieties.

Keywords: Climate change, abiotic stress, upland cotton, resilient cotton, fiber crop.

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1. INTRODUCTION

Climate change refers to long-term and persistent alterations in global climate patterns, primarily driven by the increasing accumulation of greenhouse gases (GHGs) and the resulting rise in global temperatures (Bibi & Rahman, 2023; Pan et al., 2026). Since the late 19th century, the global mean temperature has increased by approximately 0.9°C, largely due to anthropogenic GHG emissions. Projections indicate a further increase of around 1.5°C or higher by the mid-21st century. These climatic shifts pose significant challenges to agricultural systems by disrupting water cycles, altering crop productivity, and destabilizing overall farming systems (Eftekhari, 2022). Among these impacts, rising temperatures are a major driver of heat stress in crop plants, particularly in cotton, with anticipated global temperature increases of 2–3°C over the next few decades expected to further intensify stress conditions (Shahzad et al., 2021).

Cotton (*Gossypium hirsutum* L.) is cultivated in nearly 80 countries and represents a major source of natural fiber, contributing approximately one-third of the global textile demand (Mollae et al., 2019). As the dominant cultivated cotton species, *G. hirsutum* thrives in tropical and subtropical regions characterized by warm climates and limited water availability (Singh et al., 2021). Its economic significance is largely attributed to its critical role as a primary raw material in the textile industry (Tusief et al., 2026).

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However, cotton production is increasingly threatened by climate change-induced abiotic stresses, which adversely affect both yield and fiber quality (Saud & Wang, 2022; Kopecká et al., 2023). Abiotic stresses, including heat, drought, salinity, and cold, disrupt plant growth and development by inducing complex physiological, biochemical, and molecular alterations. These stresses influence multiple plant processes, ranging from cellular metabolism to whole-plant morphology (Zhang et al., 2021). Notably, cultivated tetraploid cotton species are particularly sensitive to environmental fluctuations (Khan et al., 2023). Consequently, climate change is projected to substantially reduce cotton productivity, with estimates suggesting potential yield losses of up to one-third by the end of the century (Liu et al., 2025).

This review aims to provide a comprehensive overview of the impacts of climate change-induced abiotic stresses on cotton. It focuses on elucidating the underlying physiological and molecular mechanisms governing stress responses, while also highlighting recent advances in breeding and biotechnological strategies. Furthermore, the review explores emerging approaches for developing climate-resilient cotton cultivars to ensure sustainable production under changing environmental conditions.

2. Abiotic Stresses in Cotton

2.1. Drought Stress

Climatic change is a primary driver shaping the soil-plant-atmosphere continuum (SPAC). Within this continuum, water scarcity emerges as a major abiotic stress factor, critically disrupting plant growth, development, and morphology (Khan et al., 2026; Murtaza et al., 2026). In cotton, exposure to drought disrupts essential physiological and biochemical processes, ultimately leading to significant reductions in both growth and yield (Chakma et al., 2021). Drought is a brief or prolonged period of exceptionally dry weather characterized by severe water-supply instability resulting from a substantial rainfall deficit. Climate change has significantly elevated Earth's average temperatures, intensifying water patterns and cycles. Although decreased and insufficient rainfall due to climate change is the leading cause of drought stress, increased rates of evaporation from water bodies and transpiration from plants are the other causative factors of this acceleration, resulting in increased precipitation in some wet areas while increasing the risks of drought for some traditional dry areas due to the depletion of moisture in the soil (Yang et al., 2019; Cohen et al., 2021). Changes in rainfall patterns pose a major threat to areas that rely solely on rainfall for irrigation, compared with areas that have access to water canals, rivers, and water supply channels. In these rainfall-dependent areas, the incidence, extent, and schedule of rainfall are very important throughout the year, and the risks of water stress are more likely to increase over a period of time (Konapala et al., 2020).

In Pakistan, rainfall patterns are highly inconsistent. The early spring and winter seasons are characterized by irregular precipitation, while the early fall and summer months are often hot and dry with minimal rainfall. During the summer, when crop water demand is at its peak, the combination of low rainfall, high evaporation, and increased transpiration leads to severe drought, exacerbating harmful impacts on plant growth and development (Nida et al., 2025).

Persistent changes in rainfall patterns lead to drought stress, which in turn triggers an internal heat stress response in plants. This results in reduced photosynthetic activity and impaired development. Cotton, characterized by its indeterminate growth habit, is particularly susceptible to such stress. When drought occurs during critical reproductive stages—such as flowering and bud-to-flower maturation—it can cause premature flower shedding and disrupt fruiting structures, ultimately leading to a significant decline in boll retention and seed yield (Zafar et al., 2023). The decrease in cotton yield due to drought stress is mainly attributable to reduced boll numbers and boll weight and is associated with increased boll abscission and large square drop (Li et al., 2019). To attain large production, it is very important to ensure the proper availability of water for the formation of squares, up to the development of bolls. With the increasing demand for cotton fiber, the quality of which is affected by drought stress, it is important to develop varieties that are more tolerant to drought. For this purpose, a better understanding and knowledge are required for the better selection and breeding of drought-resistant varieties of cotton (Patil et al., 2024). It is observed that drought stress results in a decline in the photosynthetic action of plants (Abdelraheem et al., 2020).

2.2. Temperature Stress

Heat stress, or high-temperature stress, is a major limiting factor in crop production. It occurs when temperatures rise above a threshold for a sufficient duration to cause irreversible damage to plant physiological processes and development. Cotton is moderately heat-tolerant compared to many crops. The issue is extreme heat (>38–40°C). The optimal temperature range for seed germination in cotton is 28–30°C, while root growth showed optimal ranges of 30–35°C and 22–27°C. A change in these temperature ranges can affect crop growth. The high-

temperature range influences cotton's morphology and physiology, ultimately leading to yield loss. High environmental pH and CO₂ concentrations can further exacerbate these issues by adversely affecting germination rates, fruit shedding, and nutrient availability in plants. Heat stress can negatively affect cotton plants throughout their lifespan; however, the reproductive stage is more susceptible to high temperatures than the vegetative growth phase. Heat stress primarily affects the male reproductive organ, i.e., the anther, compared with the female reproductive organ. It usually results in impaired male fertility in cotton plants (Bista et al., 2015; Khan et al., 2020).

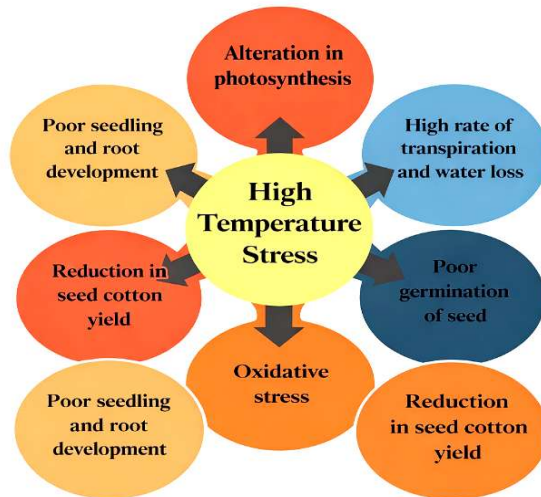


Fig. 1: Consequences of high temperature stress on the cotton plant. Legend: Effects of high temperature stress on cotton plant growth and development. High temperature stress disrupts key physiological processes, including photosynthesis and transpiration, and impairs reproductive development, leading to reduced germination, poor boll formation, and decreased seed cotton yield.

Some recent studies demonstrate that heat stress is one of the major abiotic factors that cause adverse effects on cotton yield by affecting its photosynthetic process and membrane thermostability, which ultimately affects plants' metabolism (Pilon et al., 2018; Abdelraheem et al., 2020). Elevated temperatures in cotton can affect the activity of critical enzymes such as superoxide dismutase (SOD) and catalase (CAT), which are important in maintaining oxidative stress as well as metabolic processes (Kamel et al., 2018; Shelake et al., 2024). Under temperature stress, cellular biochemistry is disrupted due to increased production of reactive oxygen species (ROS). This high ROS production impairs mitochondrial function, leading to oxidative damage due to lipid peroxidation (Fig. 1) (Zahra et al., 2023).

2.3. Salt Stress

Soil salinization has emerged as a major abiotic stress affecting agricultural productivity across both coastal and inland regions. In non-coastal areas, salinity is primarily driven by poor irrigation practices and the use of saline or brackish water (Kumar & Sharma, 2020). It results from the excessive accumulation of soluble ions in the root zone, including sodium (Na⁺), calcium (Ca²⁺), potassium (K⁺), magnesium (Mg²⁺), chloride (Cl⁻), and sulfate (SO₄²⁻). Among these, sodium salts are particularly detrimental due to their strong disruptive effects on cellular processes (Wu et al., 2023). Elevated salinity severely impairs plant metabolic, physiological, biochemical, and morphological functions, ultimately leading to reduced crop yield and quality (Salwan & Vivek, 2022).

Cotton is considered moderately tolerant to salinity, with a threshold of approximately 7.7 dS/m; however, yield losses of up to 50% have been reported when salinity levels exceed 15 dS/m (Chaudhary et al., 2024). Sensitivity to salinity varies across developmental stages, with germination, seedling establishment, flowering, and boll formation being particularly vulnerable. Notably, the seedling stage is highly susceptible, highlighting the importance of early-stage screening for the identification of salt-tolerant genotypes (Javed et al., 2022). Salinity-induced ionic imbalance disrupts enzymatic activities, inhibits photosynthesis, and damages cell membranes, thereby adversely affecting seed productivity, fiber fineness, and overall fiber quality (Zhang et al., 2023).

Climate change further exacerbates soil salinization through rising sea levels, irregular precipitation patterns, increased evapotranspiration, and recurrent flooding events (Ullah et al., 2021). Saltwater intrusion into surface and groundwater systems is becoming increasingly prevalent, particularly in coastal regions. The extent and dynamics of saltwater movement are influenced by factors such as soil texture, crop cover, geomorphology, and water flow

pathways, while tidal fluctuations further regulate the infiltration of saline water into soil profiles (Guimond & Tamborski, 2021).

At the physiological and molecular levels, plants employ complex mechanisms to cope with salinity stress, particularly by regulating ion homeostasis. Selective uptake and compartmentalization of Na^+ and Cl^- ions are critical in minimizing their toxic accumulation in plant tissues. Maintaining higher K^+/Na^+ and $\text{Ca}^{2+}/\text{Na}^+$ ratios is a key indicator of salinity tolerance in cotton. Ion transport systems, including inward-rectifying K^+ channels (AKT1), high-affinity K^+ transporters (HKT1), and Na^+/H^+ antiporters such as Salt Overly Sensitive 1 (SOS1), play pivotal roles in regulating ionic balance. These transporters enhance potassium uptake, facilitate sodium exclusion from roots, and promote sequestration of excess Na^+ into cellular compartments, thereby mitigating salinity-induced damage (Malik & Sugandh, 2022).

Genetic variability in salinity tolerance offers significant opportunities for crop improvement. For instance, *Gossypium barbadense* (Egyptian cotton) exhibits enhanced salt stress tolerance while maintaining superior fiber quality. Quantitative trait loci (QTLs) associated with growth, yield, and fiber traits have been identified, and their integration with molecular markers has facilitated marker-assisted selection (MAS) for developing salt-tolerant cultivars (Maryum et al., 2022). Furthermore, the evaluation of physiological traits such as shoot growth, water relations, and ionic homeostasis, alongside biochemical markers related to antioxidant activity and osmotic regulation, provides valuable insights for screening and selecting resilient cotton genotypes (Arif et al., 2020).

3. Impact of Climate Change on Abiotic Stress Tolerance

Cotton, a globally important crop for textile production and edible oil extraction, is increasingly threatened by the accelerating impacts of climate change. The intensification of abiotic stresses, including heat, drought, and salinity is contributing to a global decline in cotton productivity, with far-reaching economic and agricultural implications (Zhang, 2023). These stresses disrupt complex molecular networks, physiological processes, and metabolic pathways. In response, cotton plants have evolved sophisticated adaptive mechanisms that enhance stress tolerance through coordinated physiological and biochemical adjustments (Bhat et al., 2022).

At the molecular level, stress perception is initiated by specific receptors that recognize external stimuli and activate downstream signaling cascades. These cascades involve post-translational modifications and the activation of transcription factors (TFs), which regulate the expression of stress-responsive genes. Understanding these regulatory networks and gene modifications is critical for improving stress tolerance and enhancing cotton yield under adverse environmental conditions (Nagamalla et al., 2021).

Advances in omics technologies have significantly improved our understanding of plant stress responses. Transcriptomic analyses have identified numerous stress-responsive genes in cotton; however, mRNA expression alone does not fully capture the complexity of functional regulation (Zhu et al., 2021). Proteomic studies complement these findings by providing insights into protein-level changes, revealing how abiotic stresses modulate protein abundance, structure, and function. These studies highlight the upregulation of stress-associated proteins involved in defense, signaling, and metabolic adjustment (Chen et al., 2020).

Environmental interactions further complicate plant responses to climate stressors. For instance, Li et al. (2020) reported that elevated temperatures can enhance leaf-level carbon assimilation; however, this increase does not necessarily translate into higher biomass production under prolonged warm conditions. Additionally, water-deficit stress reduces both carbon gain and biomass accumulation, irrespective of temperature variations, indicating the complex, often non-linear effects of combined stress factors on cotton growth.

4. Disruption of Hormonal Signaling Pathways

4.1. Phytohormones

Phytohormones, including ethylene, salicylic acid (SA), abscisic acid (ABA), and jasmonic acid (JA), play a central role in regulating cotton responses to climate change-induced heat stress. These signaling molecules coordinate plant growth, development, and stress adaptation by modulating physiological and biochemical processes. Under elevated temperature conditions, phytohormones maintain cellular homeostasis and ensure sustained growth, productivity, and reproductive success in cotton (Ahmad et al., 2023).

4.2. Jasmonate

Jasmonates are key phytohormones that regulate plant growth, reproductive development, and defense responses against a wide range of biotic and abiotic stresses (Li et al., 2022). Jasmonic acid (JA) plays a dual role in stress responses: while it enhances tolerance to stresses such as heat, cold, and salinity, it may also inhibit photosynthesis and growth under certain conditions. Studies in *Arabidopsis* have demonstrated that methyl jasmonate (MeJA) can protect cell membranes against heat-induced damage at lower concentrations (e.g., 5 mM),

whereas higher concentrations exacerbate membrane injury. This concentration-dependent effect highlights the need for precise hormonal regulation during stress responses (Wang et al., 2021; Kamali & Singh, 2022).

4.3. Salicylic acid

Salicylic acid (SA) is a crucial phytohormone involved in regulating plant growth and development, including seed germination, photosynthesis, transpiration, senescence, and cellular redox balance. It also plays a significant role in mediating plant responses to both biotic and abiotic stresses, particularly heat stress (Ding & Ding, 2020). Exogenous application of SA has been shown to enhance heat tolerance by improving key physiological processes. Specifically, it increases the activity of photosynthetic enzymes, enhances Rubisco efficiency and PSII performance, and promotes higher chlorophyll content. Additionally, SA elevates levels of soluble proteins, proline, sugars, and heat shock proteins (HSPs), while reducing membrane damage. Importantly, it activates antioxidant defense systems, thereby mitigating oxidative stress under high-temperature conditions. These effects have been widely reported in crops such as wheat, maize, cotton, and potato (Jahan et al., 2019; Janda et al., 2020).

4.4. Ethylene

Ethylene, a gaseous phytohormone, plays a pivotal role in regulating plant growth, development, and stress adaptation. It is particularly important in mediating plant responses to high-temperature stress (Ding & Ding, 2020). Although the precise regulatory mechanisms of ethylene-mediated thermotolerance remain to be elucidated, studies in *Arabidopsis* using mutants, wild-type, and transgenic lines have demonstrated its contribution to basal heat tolerance. Comparative analyses, including seedling survival assays, have confirmed the involvement of ethylene in stress adaptation. Furthermore, interactions between ethylene and other signaling molecules—such as calcium ions (Ca^{2+}), salicylic acid, and abscisic acid—play a synergistic role in protecting plants against oxidative damage induced by heat stress (Murtaza et al., 2022).

5. Adaptive Mechanisms in Cotton

Plants have evolved a wide array of adaptive strategies to tolerate and survive under adverse environmental conditions and abiotic stresses. This adaptive capacity arises from highly coordinated and complex regulatory networks rather than a single mechanism. Recent advances in molecular biology have significantly enhanced our understanding of plant stress responses, particularly at the genetic and cellular levels. These responses involve alterations in gene expression, modulation of signaling pathways, and activation of stress-responsive genes. In cotton, such mechanisms play a critical role in determining growth, development, morphology, yield, and fiber quality under stress conditions. Identification and functional characterization of key genes associated with tolerance to salinity, heat, and drought provide valuable opportunities for developing stress-resilient cotton cultivars with improved productivity and fiber traits (Abro et al., 2022).

The response of cotton to abiotic stress is a multistage process that can be broadly categorized into four phases: stress perception, signal transduction, physiological and biochemical response, and gene expression. During stress perception, external stimuli are recognized by cellular receptors, triggering downstream signaling cascades. These signals are then transmitted through secondary messengers, leading to the activation of transcription factors and stress-responsive genes that collectively enhance plant tolerance (Li et al., 2020).

Among various abiotic stresses, drought is considered the most severe constraint limiting crop productivity worldwide. In cotton, drought stress significantly affects plant growth by reducing plant height, inhibiting leaf expansion, and impairing overall development. The severity of these effects is highly stage-dependent, with the flowering and boll formation stages being the most sensitive, followed by the bud and seedling stages. Consequently, drought stress during these critical growth phases leads to substantial reductions in yield and fiber quality (Ayele et al., 2020; Zhao et al., 2020) (Fig. 2).

5.1. Genes involved in stress response

Mitogen-activated protein kinase (MAPK) cascades represent highly conserved and essential signaling pathways that transduce external stress signals into appropriate cellular responses through phosphorylation events. The canonical MAPK cascade comprises three core components: MAPK kinase kinase (MAPKKK), MAPK kinase (MAPKK), and MAPK. These cascades play dual regulatory roles in plant stress responses, functioning as both positive and negative modulators depending on the environmental context. In upland cotton (*Gossypium hirsutum*), 166 MAPKKKs, 23 MAPKKs, and 52 MAPKs have been identified, whereas 28 MAPK cascade genes have been reported in *Gossypium raimondii*. However, only a subset of these genes has been functionally associated with drought and salinity stress responses (Yin et al., 2021).

Recent large-scale analyses have highlighted the functional significance of specific MAPK components in stress tolerance. For instance, GhMAPKK5 has been identified as one of the most responsive MAPKKs under drought and salt stress conditions in *G. hirsutum* (Ding et al., 2024). Functional validation through overexpression studies in *Arabidopsis thaliana* demonstrated enhanced seed germination and root growth under stress conditions, whereas silencing via virus-induced gene silencing (VIGS) resulted in increased wilting under drought and salinity. Further molecular investigations, including yeast two-hybrid assays and transcriptomic analyses, have revealed a GhMEKK3/8/31–GhMAPKK5–GhMAPK11/23 signaling module. This cascade interacts with WRKY transcription factors, which regulate downstream pathways associated with proline accumulation, abscisic acid (ABA) signaling, and rapid alkalization factor (RALF) peptides, thereby contributing to improved stress resilience. These interconnected adaptive responses and underlying mechanisms are collectively summarized in Table 1.

Table 1: Summary of Climate Change-Induced Abiotic Stresses, Hormonal Disruptions, Adaptive Mechanisms, and Emerging Biotechnological Strategies for Stress-Resilient Cotton Cultivars

| Impacts | Key Impacts | Molecular & Hormonal Responses | Breeding & Adaptive Mechanisms | Biotechnology Strategies | Citations |
|---------------------|--|--|---|--|---|
| Abiotic Stresses | Drought: 10–30% yield loss, reduced photosynthesis, boll abscission. Heat (>35–40°C): anther sterility, membrane damage, ROS. Salt (>7.7 dS/m): 50% yield loss >15 dS/m, poor fiber quality. | ROS overproduction; ABA, JA, SA, ethylene signaling. | QTL mapping, MAS; wild <i>Gossypium</i> germ plasm. | CRISPR/Cas, transgenic TFs. | Abdelraheem et al., 2020; Khan et al., 2020; Zafar et al., 2023; Chaudhary et al., 2024 |
| Climate Change | Projected 1/3 yield decline by 2100; altered physiology, metabolism, molecular networks. | TFs, post-translational modifications, proteomic shifts. | Receptor signaling → gene expression changes. | Multi-omics integration (genotype–phenotype). | Abdelraheem et al., 2020; Sharif et al., 2024 |
| Hormonal Disruption | Heat/drought disrupt hormone balance; JA dose-dependent; reduced growth, photosynthesis. | JA (defense, inhibits photosynthesis); SA (boosts Rubisco, proline, HSPs); ethylene (thermotolerance). | Hormonal crosstalk with MAPK cascades. | CRISPR editing of hormone-related genes. | Khan et al., 2020; Ahmad et al., 2023 |
| Adaptive Mechanisms | Stage-specific (flowering/boll most vulnerable); reduced height, leaf expansion, boll retention. | MAPK cascade (*GhMAPKK5-GhMAPK11/23*) → WRKY, proline, ABA; enzymatic (SOD, CAT, APX, GR) and non-enzymatic (proline, flavonoids, GSH) antioxidants. | 165+ QTLs; GWAS/MAS; hybridization with <i>G. barbadense</i> , <i>G. tomentosum</i> . | VIGS, transient CRISPR for gene validation. | Abdelraheem et al., 2020; Kamburova et al., 2022; Ding et al., 2024 |
| Emerging Biotech | Polyploidy challenges (redundancy, off-targets) require precise heritable edits. | Transient sgRNA editing <i>GhMAPK</i> , ROS-related genes. | Rapid functional testing of candidates. | CRISPR/Cas (<i>GhARG</i> , <i>GhCL</i> , <i>Al</i> , <i>MYB25</i>); transgenics (<i>GhABF2</i> , <i>AtDR</i> , <i>EB2A-CA</i>); multi-omics. | Shelake et al., 2022; Sharif et al., 2024; Ding et al., 2024 |

Transcription factors (TFs) constitute another critical layer of stress regulation by orchestrating gene expression in response to environmental stimuli. Upon stress perception, TFs transmit signals and activate a wide array of stress-responsive genes, enabling plants to initiate adaptive defense mechanisms. In *G. hirsutum*, approximately 30 TFs associated with stress tolerance have been identified, many of which are linked to energy metabolism and regulatory networks involved in abiotic stress adaptation (Khan et al., 2025).

In addition to signaling and transcriptional regulation, cotton plants employ multiple biochemical and physiological strategies to cope with heat stress. These include the accumulation of osmoprotectants such as

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proline, sugars, flavonoids, and phenolic compounds, along with the induction of heat shock proteins (HSPs) that stabilize proteins and maintain membrane integrity under elevated temperatures (Dev et al., 2024). Furthermore, quantitative trait loci (QTLs) associated with heat tolerance have been identified across the cotton genome, governing traits such as stomatal conductance, transpiration rate, and canopy temperature. Together, these genetic and physiological components contribute to the complex regulation of heat stress tolerance in cotton.

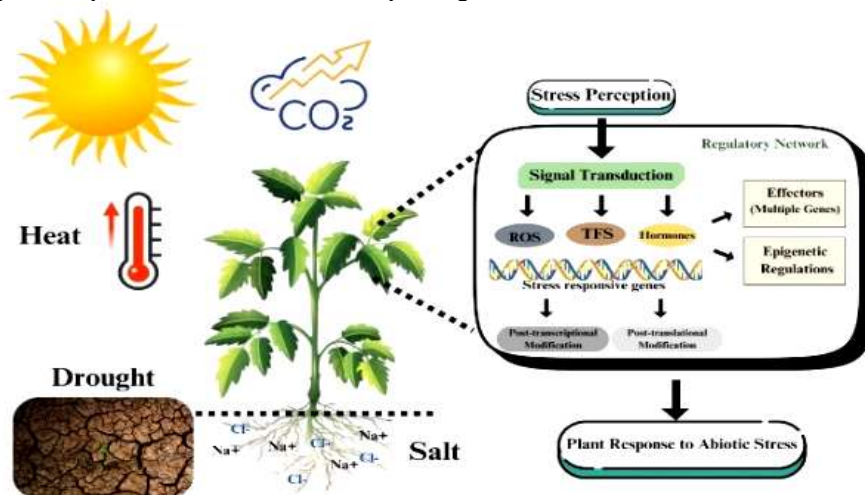


Fig. 2: Stress signaling and gene regulation in cotton against abiotic stressors. Legend: Stress signalling and gene regulation mechanisms in cotton under abiotic stress conditions. Stress perception triggers downstream signaling pathways involving reactive oxygen species (ROS), phytohormones, and transcription factors, leading to post-transcriptional and post-translational modifications. These regulatory processes activate stress-responsive genes and epigenetic mechanisms, ultimately enhancing cotton tolerance to abiotic stresses such as drought, salinity, and high temperature.

5.2. Secondary metabolites and antioxidant systems in stress mitigation

Abiotic stress stimulates overproduction of reactive oxygen species (ROS), which include hydrogen peroxide (H_2O_2), hydroxyl radicals (OH), and superoxide anion (O_2^-), which have deleterious effects on cotton yield, productivity, development, and growth. To mitigate the harmful effects of these ROS, cotton has developed a defensive mechanism of an enzymatic and non-enzymatic antioxidant system and secondary metabolites. To help neutralize the superoxide anions, which cause cellular damage, important enzymatic antioxidants like glutathione reductase (GR), superoxide dismutase (SOD), glutathione peroxidase (GPX), glutathione S-transferase (GST) and ascorbate peroxidase (APX), catalase (CAT), mono-dehydroascorbate reductase (MDAR), dehydroascorbate reductase (DHAR), peroxidase (POD) and peroxide reduction (PRX) play their part to neutralize the effects (Kamburova et al., 2022). As shown in Fig. 3, the non-enzymatic antioxidants such as glutathione, flavonoids, carotenoids, and tocopherols contribute to detoxifying the harmful ROS. Increased concentrations of these antioxidants in cotton are directly linked with greater resistance against abiotic stresses in cotton (Mahmood et al., 2020).

5.3. Breeding for stress tolerance

In recent years, breeding approaches have been widely employed to develop cotton cultivars capable of adapting to changing environmental conditions and exhibiting enhanced resistance and tolerance to abiotic stresses. To decipher inheritable patterns of drought stress tolerance from one generation to the next, Egyptian cotton (*Gossypium barbadense* L.) was studied. Moreover, the genetic underpinnings of drought and salt resilience were also thoroughly examined, and their integration was found to be essential for developing more resilient and tolerant cotton cultivars. Marker-assisted selection (MAS) has been proven advantageous to overcome the limitations of conventional breeding. The use of marker-assisted selection (MAS) has been instrumental in identifying QTLs and mapping of crucial genes that are linked to increased resistance against environmental stressors; meanwhile, genome-wide association studies (GWAS) have further aided in locating the important genes and QTLs in cotton, responsible for resistance against salt, drought, and temperature stress (Han et al., 2022). Exploring QTL mapping has shed light on key genetic foundations for stress tolerance while paving the way for innovative approaches in marker-assisted breeding. The hybridization of *G. tomentosum* and *G. hirsutum* has uncovered essential salt-tolerant

and drought-resistant QTLs, emphasizing the role of wild cotton species in breeding programs (Roychowdhury et al., 2023). With the progress made in molecular breeding, 165 QTLs were identified in *G. hirsutum* under abiotic stress, with 15 of these QTLs located on 12 chromosomes, offering promising avenues for a stress-tolerant breeding program of cotton (Abdelraheem et al., 2019).

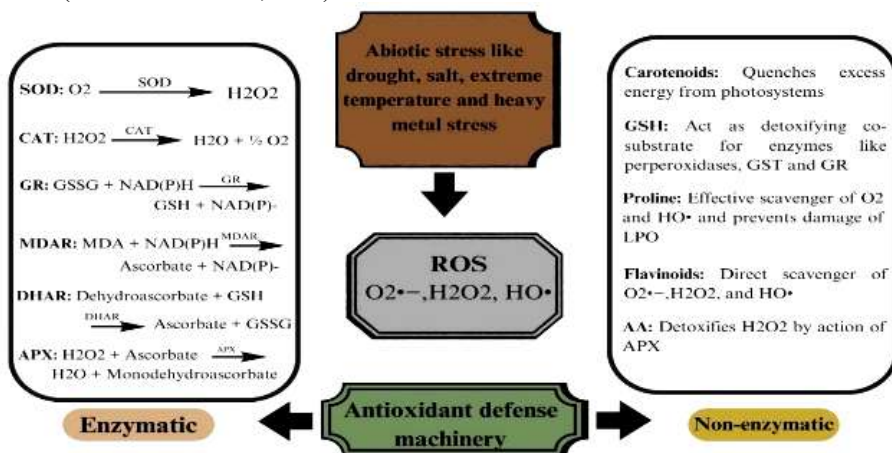


Fig. 3: Representation of the enzymatic and non-enzymatic antioxidant defense system in cotton against ROS caused by abiotic stress. Legend: Antioxidant defense mechanisms in cotton under abiotic stress conditions. Abiotic stress induces the production of reactive oxygen species (ROS), including hydrogen peroxide (H_2O_2), superoxide anions ($O_2^{\cdot-}$), and hydroxyl radicals (HO^{\cdot}), which cause oxidative damage. Cotton plants counteract this stress through enzymatic antioxidants such as superoxide dismutase (SOD), catalase (CAT), glutathione reductase (GR), ascorbate peroxidase (APX), and peroxidases, along with non-enzymatic antioxidants including glutathione, proline, flavonoids, carotenoids, and ascorbic acid. These systems work synergistically to maintain cellular redox balance and enhance stress tolerance.

6. Emerging Technologies and Innovations

The identification and utilization of functional genes for improved plant varieties is still a complex task in genetic engineering. Nevertheless, cutting-edge advancements and progress in whole-genome sequencing and omics approaches, such as proteomics, genomics, and metabolomics, provide avenues for the identification and uncovering of critical genes involved in stress resistance. Furthermore, it is also important to recognize and understand stress-related metabolites to strengthen stress tolerance in cotton (He et al., 2023).

6.1. Use of biotechnology for enhancing stress tolerance

6.1.1. CRISPR/Cas in Cotton: The precision and accuracy of CRISPR/Cas genome-editing technology enable targeted genetic manipulations, offering new opportunities for enhancing stress tolerance in cotton. This is particularly valuable in cultivars with fully sequenced genomes, where specific modifications can be efficiently designed and implemented (Shelake et al., 2022). Besides generating heritable and stable mutations, CRISPR/Cas-based editing tools provide a wide range of applications, hence overcoming the shortcomings of traditional gene silencing methods like RNA interference (Shelake et al., 2023). Although the applications of CRISPR/Cas have proven to be a successful approach, challenges like polyploidy and complex transformation processes in cotton restrict its implications. Nonetheless, the studies involving GhARG, GhCLA1, MYB25, and GhVP underscore its promising potential for genome editing in cotton (Wang et al., 2024) (Fig. 4).

Transient gene expression plays a key role in understanding and mitigating the effects of abiotic stress. To address the time-consuming nature of stable transformation in cotton, a CRISPR/Cas-based approach was developed for the rapid validation of single-guide RNAs (sgRNAs). This method enables efficient and accurate transient expression in cotyledons, facilitating faster functional analysis (Tian et al., 2021). This method has also been proven appropriate for verifying sgRNAs for various genes, such as GhEF1, GhPDS, and GhCLA1, facilitating the simultaneous and concurrent alterations of gene copies in polyploid cotton, also executing specific genomic fragments (Medina-de la Cruz et al. 2024). In cotton, CRISPR/Cas also aids in providing resistance against abiotic stresses, the incorporation of multiple advantageous traits with reduced risks of segregation, and maintaining genetic stability and regulation of expression of genes (Fiaz et al., 2021).

6.1.2. Transgenic Strategies for Abiotic Stress Resilience: Extensive research has been conducted to understand stress tolerance mechanisms in cotton at both molecular and physiological levels. These efforts have focused on identifying resistance-related genes and employing genetic engineering approaches to recombine and introduce such genes into cotton cultivars, thereby enhancing their adaptability and tolerance to abiotic stresses. Transgenic approaches offer potential to improve and enhance the yield, productivity, and growth of cotton. Overexpression of some stress-resistant genes and transcription factors in cotton has led to the development of drought-tolerant varieties in cotton through GE techniques. In *G. raimondii*, important genes for stress response in cotton have been identified by the genome-wide analysis of calcium-dependent protein kinase (CDPK) genes. A bZIP transcription factor named GhABF2 is found to be critical for drought and salt stress resistance in cotton. In cotton, calcium sensors like GhCaM7 and GhCDPK1, genetic factors play a pivotal role in resistance against water scarcity and also help in the elongation of cotton fiber (Mi et al., 2024).

Furthermore, drought and salt stress resistance are also conferred by overexpression of genes like GhABF2 and AtDRE2A-CA. The molecular and genetic research on stress-resistant varieties of cotton provides an understanding of the ROS balance, root characteristics, and important transcription factors like MYB and NAC. All these findings pinpoint the importance of transgenic approaches in combating abiotic stresses and developing resistant varieties (Kumar et al., 2024).

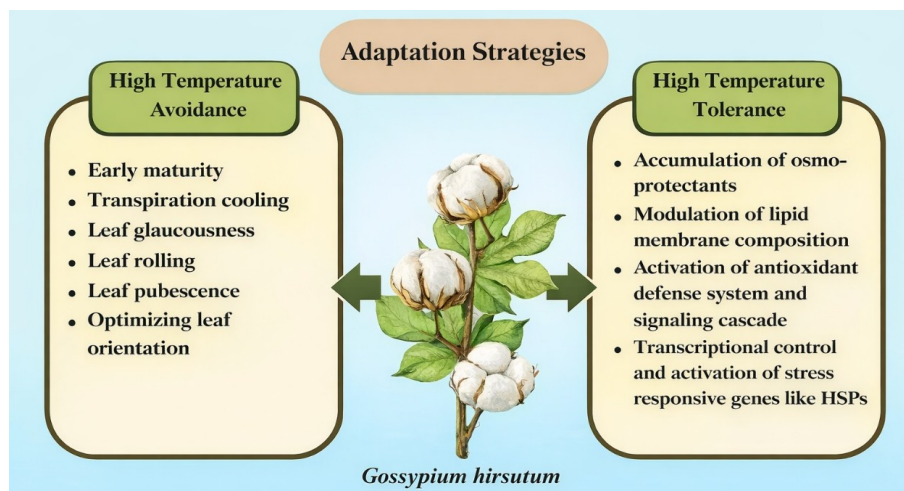


Fig. 4: Adaptation strategies of cotton (*Gossypium hirsutum*) to heat stress involving stress avoidance and stress tolerance. Legend: Adaptation strategies of cotton (*Gossypium hirsutum*) to heat stress through stress avoidance and stress tolerance mechanisms. Stress avoidance strategies include morphological and physiological adjustments such as altered leaf orientation, stomatal regulation, and transpiration control to minimize heat exposure. In contrast, stress tolerance mechanisms involve biochemical and molecular responses, including heat shock protein production, antioxidant defense activation, osmolyte accumulation, and regulation of stress-responsive genes, enabling plants to withstand elevated temperatures.

6.1.3. Omics technologies for understanding stress response: The application of multi-omics approaches—including genomics, transcriptomics, proteomics, and metabolomics—provides comprehensive insights into the molecular and physiological mechanisms by which plants adapt to changing environmental conditions and withstand abiotic stress. Leveraging the multi-layered datasets allows researchers to employ efficient cropping methods and to achieve superior outcomes beyond the conventional breeding methods. Different omics techniques have been harnessed to develop stress-resistant cotton varieties in the past few years. By integrating multi-omics, functional genomics, along with bioinformatics, advanced stress-tolerance outcomes can be achieved by deciphering the influence of genetics on phenotypic expression when exposed to stress conditions (Khan et al., 2023).

The advancements in omics have facilitated the discovery of gene networks, regulatory pathways, and QTLs that contribute to drought stress resistance. Leveraging these tools can significantly enhance the identification and incorporation of drought-resistant traits in other genotypes of cotton. The DNA variations are being examined by genomics, transcriptomics explore the gene expression, protein quantity, and interactions are being analyzed by proteomics, metabolomics decipher the measure of cotton metabolites, while morpho-physiological features are

being evaluated by phenomics. Analysis of data generated through these techniques contributes to uncovering the genes related to stress resistance in cotton (Sharif et al., 2024).

7. Prospects and Persistent Challenges

Despite considerable progress in developing stress-tolerant cotton cultivars, advancements in abiotic stress resilience have not kept pace with improvements in yield potential, fiber quality, and disease resistance. Several critical gaps remain that limit the large-scale commercialization of climate-resilient cotton varieties. One major constraint is the limited availability of robust and tightly linked molecular markers for key stress-responsive traits. Insufficient marker–trait associations and gaps in genomic tagging continue to hinder the efficiency of marker-assisted selection (MAS) in cotton breeding programs.

Although molecular markers have significantly facilitated breeding efforts, most studies on abiotic stress tolerance—particularly for drought and salinity remain at the level of preliminary QTL mapping. Only a limited number of validated markers are currently available for practical application, and many lack strong linkage with target traits, reducing their effectiveness in selection programs (Darmanov et al. 2022). Furthermore, many identified traits are associated with general stress responses rather than direct yield improvement, creating a gap between stress tolerance and agronomic performance.

The underlying genetic and molecular mechanisms governing abiotic stress tolerance in cotton are still not fully elucidated. While key components associated with tolerance to drought, heat, cold, salinity, and nutrient-use efficiency have been identified, their integration into breeding pipelines remains limited. Bridging this gap requires deeper functional characterization of candidate genes, regulatory networks, and their interactions under field conditions.

In recent years, significant progress has been made in seed breeding technologies, particularly through the application of genetic transformation and molecular breeding approaches, leading to the development of improved cotton varieties. However, future research should focus on integrating conventional breeding strategies with advanced approaches such as genomics-assisted breeding, gene editing, and high-throughput phenotyping. Additionally, interdisciplinary approaches combining seed-based innovations with biomass utilization and sustainable production systems are essential to enhance cotton productivity and resilience under changing climatic conditions (Saud & Wang, 2022).

8. CONCLUSION

Climate change represents one of the most significant threats to sustainable cotton production worldwide. Rising temperature extremes, prolonged droughts, and increasing soil salinization collectively disrupt key physiological, biochemical, and metabolic processes in cotton, ultimately reducing yield and compromising fiber quality. In response, cotton plants activate complex regulatory networks that involve hormonal signaling, transcriptional regulation, antioxidant defense systems, and stress-responsive gene cascades, such as MAPK pathways.

Recent advances in molecular breeding, genome editing, and multi-omics approaches have substantially enhanced our understanding of stress tolerance mechanisms in cotton. Innovative tools, including CRISPR/Cas-based genome editing, genome-wide association studies (GWAS), and marker-assisted selection (MAS), provide promising avenues for accelerating the development of climate-resilient cotton cultivars. Nevertheless, several challenges persist, including limited field-level validation of candidate genes, the inherent complexity of polyploid cotton genomes, and the lack of robust, high-throughput phenotyping systems under realistic environmental conditions.

Moving forward, integrating advanced genomic technologies with conventional breeding approaches will be essential to bridge the gap between laboratory discoveries and field applications. Greater emphasis should also be placed on exploiting the genetic diversity of wild *Gossypium* species and adopting climate-smart agronomic practices. Collectively, these integrated strategies will be crucial for ensuring stable cotton productivity, improved fiber quality, and long-term sustainability under increasingly variable and unpredictable climatic conditions.

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