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Posted Date: 13 May 2024

doi: 10.20944/preprints202405.0751.v1

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Review

# Unravelling Abiotic Stress Physiology in Cotton (*Gossypium hirsutum* L.): Biotechnological Interventions in Mitigating Abiotic Stress

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**Abstract:** Climate change has resulted in increased incidences of abiotic stresses, such as heat, drought, salinity, and waterlogging. These stressors have a negative impact on the cotton (*Gossypium hirsutum* L.) crop and cause significant yield losses. Each stressor induces specific physiological and metabolic alterations interconnected with the complex changes at molecular levels. Understanding the molecular pathways that govern the cotton plant's stress responses is crucial to develop stress-tolerant cotton cultivars that can withstand different stresses. Molecular investigations have mapped the changes in the expression of stress-responsive genes, encompassing heat shock proteins and ion transporters, which play a vital role in facilitating adaptive responses. These approaches have been shown to help identify dynamic gene expression patterns and elucidate intricate regulatory networks using advanced metagenomics and multi-omics techniques. By leveraging genetic diversity and utilizing advanced molecular methods, it would be possible to develop stress-resilient cotton varieties to ensure sustainable cotton production in the face of abiotic stresses. This review provides an overview of the effects of various abiotic stressors on cotton plants, including drought, salt, heat, and waterlogged soil. We also explore the extensive network of stress-responsive genes, proteins, and signaling pathways in cotton by summarizing the studies on gene expression regulation, proteins involved in stress response, and biochemical characteristics.

**Keywords:** Abiotic stress; cotton; CRISPR/Cas9; stress tolerance; stress physiology; heat; drought; salinity

## 1. Introduction

Cotton is an important fiber crop that has grown worldwide, and it has recently faced challenges due to climate change and the increased frequency of abiotic stress [1,2]. These stressors negatively

affect the overall yield and quality of cotton (*Gossypium* spp.) fibers and seeds [3]. Abiotic stress has resulted in a 50% decline in cotton crop production globally [4]. As cotton is a vital crop used in textile production and for edible oil extraction, any reduction in its yield due to abiotic stress can have global economic implications [5]. Cotton crops are processed for textiles, home goods, and medicinal medicines. Cotton crop meets both the need for human oil consumption and as a raw resource for the textile industry [6].

Critical abiotic stresses are thought to be the principal cause of limited cotton productivity. These stressors include various environmental conditions such as extreme temperatures (both high and low), drought, salinity, heavy metals, and radiation that disrupt cotton plants' normal physiological and metabolic processes [7,8]. The cotton crop prefers a temperature between 27 and 32°C when forming the boll [9]. In higher temperatures, like  $\geq 36^{\circ}\text{C}$ , cotton crops showed the most significant decrease in carbon fixation; under heat stress, cotton struggles with an unpredictable growth habit and is susceptible to stress like drought [10–15]. According to recent studies, high temperatures are one of the main abiotic factors that negatively affect cotton yields by impairing the photosynthetic process and membrane thermostability, which impacts plant metabolism [16]. Higher temperatures have the potential to denature proteins and increase the sensitivity of enzyme activity [17]. Ultimately, the resulting reduction in turgor pressure in the cotton crop results from the effects of drought stress on cell development. Drought stress has a direct or indirect impact on photosynthesis and the metabolism of carbohydrates [18,19]. Drought lowers the cotton plant's ability to maintain its bolls and the leaf area that responds to those changes [20]. In this review study, we have covered the effects of various abiotic stressors on cotton performance and listed potential ways to improve cotton performance through biotechnological approaches.

## 2. Different Abiotic Stressors Impact on Cotton Plants

Understanding these diverse stressors and their impacts on cotton is crucial for developing strategies to mitigate their effects. Research on enhancing stress tolerance is pivotal in sustaining cotton productivity in changing environmental conditions. These efforts involve breeding stress-tolerant cotton varieties, improving agricultural practices, and developing innovative technologies to ensure sustainable cotton production under challenging ecological stressors.

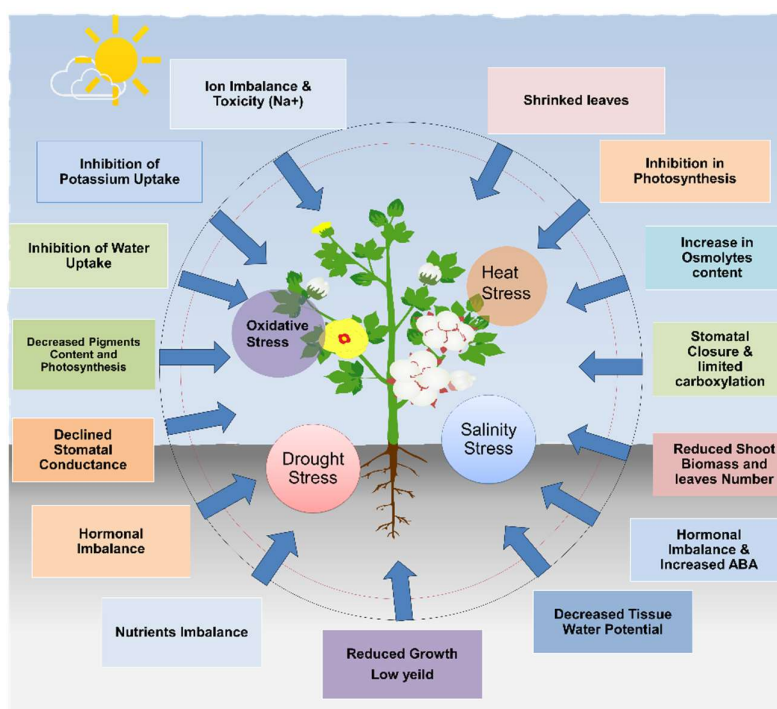
### 2.1. Impact of Salinity Stress on Cotton

Excessive salt concentration in the soil interferes with water uptake and ion balance in cotton plants, causing ion toxicity, reduced growth, leaf burn, and diminished yield. (Table 1) Salinity stress has been the primary limiting factor for agricultural productivity across the biosphere. Salinity significantly threatens cotton fibers' growth, productivity, and quality [21,22]. The kind of salt and the growth stage determine how sensitive a plant is to salt stress. A better understanding of cotton's resilience to salt, its response, and management tactics can help develop ways to enhance cotton performance in saline environments [23,24]. Around 20% of the world's cultivated area is impacted by salt stress [25,26]. Many plant species build up large amounts of proline in response to salinity and drought stress; this protein is involved in stress adaptation [27,28]. Germination is affected by salt stress, which results in a decrease in water intake by developing seeds, plant roots, photosynthesis, respiration, and protein synthesis [29]. The biochemical and physiological characteristics of cotton under salt stress, with references to stress and photosynthetic metabolism for regulating survival and productivity [30].

Additionally, it impacts the cotton crop's growth and yield. Salinity and drought are two of the most significant environmental problems that have impeded agricultural productivity globally [31,32]. Through various processes, both stresses can cause morphological, physiological, biochemical, and metabolic changes that ultimately affect plants' growth, development, and productivity. Soil salinity stress causes an excessive build-up and production of reactive oxygen species (ROS) in mitochondria and chloroplasts, such as superoxide anion ( $\text{O}_2^-$ ), hydroxyl radicals ( $\text{OH}\cdot$ ), and hydrogen peroxide ( $\text{H}_2\text{O}_2$ ). [33–35]. Understanding cotton's resilience to salt, response, and management tactics can help develop solutions to enhance cotton performance in saline

environments [36]. Salt stress causes reduced boll weight, less fruiting positions, delayed flowering, and fruit shedding, all impacting seed cotton yield [37]. ROS are highly reactive, and without any protective mechanism, they can seriously disrupt normal metabolism through oxidative damage to lipids, proteins, and nucleic acids. However, plants develop defense strategies against salt stress by activating antioxidant enzymes [38,39]. Excess salinity of soil has a detrimental effect on cotton growth and productivity. With notable variations between genotypes, the induced salt stress harmed germination and vegetative growth (Table 1.) The shoots, roots, and leaf area weights reduced as the salinity increased [40]. But among crops that tolerate salt, the best is cotton. Several antioxidant enzymes, including *superoxide dismutase* (SOD), *glutathione reductase* (GR), and *ascorbate peroxidase* (APX), are found in plants and are used to strengthen defenses against ROS, such as superoxide anion ( $O_2^-$ ) [41].

Furthermore, antioxidant enzymes create transgenic plants that can withstand salinity stress [42]. When the environment is unfavorable, cotton's osmolytes metabolize the function to form sugar alcohol. Rising salinity causes include little precipitation, excessive surface evaporation, weathering local rocks, irrigation with saline water, and unfavorable cultural practices [43]. Specifically, secondary salinization causes formerly productive agricultural lands to lose their suitability for agriculture because of substandard irrigation water. Proline and glycine betaine are effective ROS scavengers and protective agents acting as osmolytes for macromolecules under salt stress (Figure 1).



**Figure 1.** Effects of stress on cotton plant physiology.

illustrations of the physiological effects of various abiotic stress factors on cotton plants. Stress factors such as heat, drought, salinity, heavy metal toxicity, and waterlogging can induce a range of physiological responses, including Heat: Inhibition of water and potassium uptake, decreased photosynthesis and stomatal conductance, and increased production of osmolytes—drought: Decreased water uptake and stomatal conductance, reduced shoot biomass and leaf number. Salinity: Ion imbalance and toxicity, water and potassium uptake inhibition, decreased photosynthesis, and stomatal conductance. Heavy metal toxicity: Nutrient imbalance, decreased tissue water potential, and hormonal imbalance. Waterlogging: Decreased nutrient uptake and oxygen availability, hormonal imbalance, and reduced stomatal conductance.

**Table 1. Impact of abiotic stress on cotton physiological changes.** Growth impacts are indicated based on the severity of the effect observed, ranging from negative (---) to positive (+++). Citations reference contributing to a comprehensive understanding of cotton’s response to abiotic stress cotton plant physiological changes.

Abiotic stress factor	Impact on cotton plant development and traits	Growth impact	Citations
Heat stress	Leaves: wilting	+++	[257]
	Reduced photosynthesis	---	[258]
	Fiber quality	---	[259]
	Leaf number	---	[24]
	Stomatal density	---	[260]
	Trichome density	+++	[261]
	Flowering	---	[262]
	Bolls: boll size	---	[263]
	Root length	---	[258]
	Shoot length	---	[264]
	Premature boll opening		[265]
Drought	Leaf rolling,	+++	[266]
	Leaf growth,	---	[267]
	Leaf area	---	[268]
	Fiber quality	---	[269]
	Root length	---	[270]
	Shoot length	---	[271]
	Stomatal density	+++	[272,273]
	Trichome density	+++	[274]
	Flowering	----	[119]
	Leaf number	----	[275]
	Bolls size	---	[276]
	Premature bolls opening	+++	[119]
Salinity	Root length	---	[277]
	Leaf necrosis	+++	[278]
	Nutrient absorption,	---	[116]
	Fiber quality	---	[279]
	Stomatal density	+++	[280]
	Bolls size	---	[281]
	Premature bolls opening	+++	[282]
	Leaves: leaf rolling	+++	[283]
	Leaf area	---	[284]
	Root length	---	[285]
	Shoot length	---	[286]
	Trichome density	---	[287]
	Flowering delay	+++	[288]
	Leaf number	---	[289]
	Shoot length	---	[290]
	Leaf chlorosis, necrosis	+++	[291]
	Leaf rolling	+++	[292]
	Leaf area	---	[291]
	Fiber quality	---	[293]
Heavy metal toxicity	Root length	---	[290]
	Stomatal density	+++	[291]



Water logging	Flowering	---	[294]
	Leaf number	---	[295]
	Bolls size	---	[296]
	Premature bolls opening	---	[296]
	Nutrient deficiency	+++	[297]
	Leaves: chlorosis	+++	[298]
	Shoot length,	---	[299]
	Leaf area	---	[300]
	Fiber quality	---	[301]
	Root length	---	[302]
	Stomatal density	---	[303]
	Trichome density	+++	[303]
	Flowering	---	[300]
	Leaf number		[304]
	Bolls size	---	[303]
	Premature bolls opening	+++	[305]

2.2. Impact of Drought Stress on Cotton

Drought or insufficient soil moisture adversely affects cotton plants, leading to reducing growth, wilting, stunted development, and decreased yield. The predominant elite cotton species, *Gossypium hirsutum* L., is often grown in tropical and subtropical climates [44]. Roughly one-third of the world’s arable land is plagued by insufficient water supply. Droughts regularly lower the yields of rainfed crops, and global climate change may worsen the problem. Stress from water shortages or droughts can affect reproductive growth phases, which lowers agricultural productivity [45].

The impact of water stress on yield depends on the length and duration of the drought. High phosphorus in non-acclimated plants enhanced photosynthesis and leaf conductivity at high water potentials. High phosphorus in acclimated plants enhanced photosynthesis but decreased conductance, enhancing water consumption efficiency at the single-leaf level [46]. Due to dryness, other factors that lower the rate of transpiration include the temperature of the canopy, the differentiation of carbon isotopes, the water content of the leaves, the conductance of stomata, and the rate of photosynthesis. As the relative water content of the soil decreases, so do the transpiration rates and photosynthetic processes [47–51]. Previous research has demonstrated that stomatal and non-stomatal restriction reduces photosynthetic rates during drought stress. The stomatal limitation was the primary cause of the decline in photosynthetic rate during a moderate drought.

On the other hand, non-stomatal variables were primarily responsible for the reduction in photosynthetic rate during periods of severe drought [52]. A lack of water will directly reduce photosynthesis by lowering the availability of CO<sub>2</sub>, limiting the stomata’s and mesophyll’s ability to diffuse [53]. Numerous morpho-physiological traits have been suggested as essential selection criteria for breeding cotton crop cultivars, in contrast to drought tolerance [54]. It also causes an increase in taproot weight, seedling vigor, the number of lateral roots, and the rate at which the stomata and mesophyll develop in the root system [55,56]. Sustainable cotton cultivation demands a clear awareness of its impacts on cotton and the development of appropriate mitigation techniques [57]. Drought stress impairs physiological and biochemical processes in the cotton plant, particularly photosynthesis. Water shortage lowers water availability for photosynthesis, reducing carbon uptake and affecting plant development [58]. Cotton plants respond to drought by closing their stomata to conserve water, which reduces gas exchange and inhibits transpiration and nutrient uptake. Drought stress throughout the flowering and boll development stages can considerably impact fiber length and strength [59,60]. Cotton has numerous adaptive strategies for dealing with drought stress [61]. Under drought conditions, cotton plants may modify their root architecture, enhancing deep root penetration to acquire water from deeper soil layers [62]. Due to Osmotic Changes, the accumulation of suitable solutes such as proline and carbohydrates helps to maintain cell turgor and safeguard

cellular structures [63]. Cotton plants activate particular genes involved in stress response pathways to reduce drought impacts [64]. Breeding for drought tolerance: Creating drought-resistant cotton cultivars through breeding programs prioritizing features including deep root systems, enhanced water-use efficiency, and stress tolerance [65,66]. Implementing efficient irrigation methods such as drip or micro-sprinkler systems to optimize water use and minimize water loss [67]. Employing soil conservation practices like mulching and conservation tillage to enhance soil water retention and reduce evaporation [68]. Identifying the impact of drought stress on cotton and applying effective ways to mitigate its effects is critical for assuring sustainable cotton production, safeguarding yields, and sustaining fiber quality.

### *2.3. Impact of Heat Stress on Cotton*

Heat stress can cause wilting, decreased photosynthesis, and flower and boll loss, whereas cold stress can cause chilling injury, delayed growth, and poorer yield. Navigating the challenges of heat stress in cotton: implications, responses, and mitigation techniques [69]. Heat stress is a severe danger to cotton agriculture globally, affecting this key fiber crop's growth, development, and productivity [70]. Cotton crops are especially vulnerable to high temperatures during critical growth stages, causing a cascade of physiological and biochemical changes that can radically impair yield and fiber quality [59,71]. Increased temperatures may increase respiration rates in cotton plants, potentially exceeding the rate of photosynthesis, resulting in energy deficits and lower biomass formation [72]. Heat stress exacerbates water loss through transpiration, resulting in water deficit circumstances and impairing the plant's capacity to maintain enough hydration [73]. Heat stress during critical periods like blooming and boll development can result in decreased fiber quality, including reduced fiber length and strength, eventually diminishing the market value of the cotton produced [60].

Modulating stomatal conductance in cotton helps regulate transpiration rates, conserving water and maintaining plant hydration [74]. Developing heat-tolerant cotton cultivars through breeding programs focusing on features such as HSP expression, increased photosynthetic efficiency, and tolerance to high temperatures. Implementing controlled deficit irrigation strategies to optimize water use efficiency and maintain adequate soil moisture levels during heat stress [75]. Understanding the multifaceted impacts of heat stress on cotton and adopting proactive measures to mitigate its effects is crucial for sustaining cotton production, maintaining fiber and quality, and ensuring yield stability in the face of escalating temperature extremes due to climate change [76]. Osmoregulation-related genes, protein-acting genes, and transcription-regulatory factor genes shed light on cotton's mechanism to regulate its internal environment in response to stress [77]. Understanding these genes and their functions can pave the way for developing genetically engineered cotton varieties that exhibit improved tolerance to adverse environmental conditions [78]. It is a foundational reference for future research endeavors to bolster cotton resilience against biotic stress.

## **3. Effects of Abiotic Stress on Cotton Plants**

### **3.1.1. Physiological Changes in Response to Abiotic Stress in Cotton**

Physiological changes that cotton plants undergo in response to abiotic stressors. As a major global crop, cotton faces various environmental challenges, and understanding its physiological responses is crucial for sustainable agriculture [79]. Physiological changes provide a comprehensive insight into the intricate molecular mechanisms within cotton plants under abiotic stress [80]. Physiological changes in cotton plant stress physiology and responses to environmental stressors are summarized in Figure 1 and Table 1. Plant water status significantly influences stomatal activity, photosynthesis, and nitrate reductase activity in field-grown cotton. Investigating temporal and daily changes in field-grown cotton leaf water, osmotic, and turgor potentials [81]. Cotton's growth balance hinges on water availability. Adequate water promotes vegetative growth but inhibits reproduction. Excess water during flowering leads to vegetative dominance, causing flower and boll drop [82]. The investigation delves explicitly into the nuanced relationship between leaf carbohydrate status and

osmotic adjustment, offering precise insights into the plant’s adaptive responses under water stress conditions [83,84]. A noteworthy aspect is the discussion on the physiological responses to temperature extremes. It delves into ion toxicity, osmotic stress, and the pivotal role of diverse transporters in sustaining ionic homeostasis [85,86]. The amalgamation of these findings offers a comprehensive perspective on how cotton plants effectively manage physiological disruptions triggered by salinity stress. Drawing on current research, it intricately outlines the response of plants to water scarcity, elucidating the adaptive mechanism of reduced stomatal conductance as a strategic effort to conserve water [87,88]. A noteworthy contribution of the chapter lies in its exploration of altered water potential under drought conditions. The findings, seamlessly integrated into the discussion, reveal the nuanced changes in water potential as cotton plants grapple with limited water availability. This analysis enhances our understanding of the plant’s hydraulic adjustments and their implications for overall water status [89]. Leaves of preconditioned plants maintain turgor at lower water potential than well-watered counterparts, accompanied by reduced osmotic potential [90]. Soluble sugars and malate accumulate similarly in conditioned and unconditioned plants under stress, which cannot explain the turgor change [91]. Analysis of relative water content indicates conditioned cotton plants hold less water per unit of dry weight, contributing significantly to the observed osmotic potential difference [92,93]. This detailed examination of reduced stomatal conductance and altered water potential enhances the theoretical understanding of cotton physiology under drought stress and has practical implications [24,94]. Leveraging this knowledge, farmers and agronomists can implement targeted irrigation strategies and choose drought-tolerant cultivars, optimizing cotton production in water-limited environments.

**Table 2. Cotton genotype for biochemical traits under different stress conditions.** Summary of the effects of various stress conditions on biochemical traits in cotton genotypes. Explant source refers to the tissue used for analysis, and the screening method indicates the technique employed for measurement.

Biochemical raits	Effects on biochemical traits	Explant source	Screening method	References
Proline accumulation	Increased under drought stress, indicative of osmotic adjustment	Leaf tissue	High-performance liquid chromatography (HPLC)	[306,307]
Chlorophyll content	Decreased under heat stress, indicating photoinhibition	Leaf tissue	HPLC	[308,309]
Antioxidant enzyme activity	Enhanced activity under oxidative stress, protecting against damage	Leaf tissue	Enzyme Assays	[310,311]
Ion homeostasis	Alterations in nutrient uptake, essential for plant growth	Root tissue	Ion Analysis	[312]
Heat shock protein expression	Induced expression under high temperatures, aiding protein stability	Leaf tissue	Protein Analysis	[131,314]
Peroxidase (pod) activity	Changes in metabolic pathways, impacting plant growth and development	Root tissue	Enzyme Assays	[315,316]
Lipid peroxidation	Increased levels indicate membrane damage under stress conditions	Leaf tissue	Thiobarbituric Acid Assay	[317,318]
Soluble sugar content	Accumulation acts as an osmoprotectant, maintaining cellular integrity	Leaf tissue	Spectrophotometry	[317,319]



Total phenolic content	Elevated levels contribute to antioxidant defense against stress	Leaf tissue	Spectrophotometry[320,321]
Malondialdehyde (mda) content	Elevated levels indicate lipid peroxidation and cellular damage	Leaf tissue	Spectrophotometry[322,323]
Superoxide dismutase (sod) activity	Increased activity under oxidative stress, scavenging superoxide radicals	Leaf tissue	Enzyme Assays [324,325]
Catalase (cat) activity	Enhanced activity under oxidative stress, decomposing hydrogen peroxide	Leaf tissue	Enzyme Assays [326]
Carotenoid content	Decreased levels impact photosynthetic efficiency under stress	Leaf tissue	HPLC [327]
Flavonoid content	Increased synthesis contributes to stress tolerance mechanisms	Leaf tissue	Spectrophotometry[328]
Ascorbic acid content	Decreased levels affect antioxidant capacity and stress tolerance	Leaf tissue	Titration Method [329]
Glutathione content	Altered levels impact oxidative stress response and redox regulation	Leaf tissue	Enzymatic Assay [330]
Polyphenol oxidase activity	Enhanced activity in response to stress, leading to tissue browning	Leaf tissue	Enzyme Assay [4]

### 3.1.2. Morphological Changes in Response to Abiotic Stress in Cotton

Water plays a critical role at every stage of plant growth, from seed germination to maturation and overall morphology [95]. Any imbalance in water availability can have harmful effects, varying with the nature of the crop species. Given the substantial demand for food, enhancing crop tolerance to drought stress is of prime importance, necessitating a profound understanding of the morphological and physiological basis for selecting and breeding drought-tolerant plants [96]. Drought stress adversely affects cotton plants, limiting fiber yield and lint quality. As with other crops, moisture stress significantly affects cotton's growth, development, and performance [97]. Leaf anatomical alterations reduced cotton mesophyll conductance under dynamic drought conditions [98]. Plant water stress occurs when water potential and turgor pressure decrease, impairing normal plant functions. The severity and duration of stress, growth stage, and genotype influence its effects [99]. Water deficit impacts physiological processes like stomatal conductance, CO<sub>2</sub> diffusion, and photosynthesis [100–102]. Reduced relative water content and leaf water potential lead to lower photosynthetic rates. The effects are complex, involving stomatal closure and potential chlorophyll reduction. Drought stress significantly limits plant growth and establishment. Understanding these responses is vital for effective crop management [103]. Drought stress particularly impacts the initial plant growth and establishment phase, affecting elongation and expansion growth [104]. Water stress can suppress cell expansion and growth due to low turgor pressure. Osmotic regulation may help maintain cell turgor for survival or assist plant growth under severe drought conditions [105]. Factors like stem length, root dry weight, and root-to-shoot ratio are influenced by water stress. Understanding root systems' role in water acquisition and managing relative water content is crucial for improving crop drought tolerance [47,106]. Overall, morphological changes are essential for effective agricultural management to avoid the abiotic stress of cotton.

### 3.1.3. Yield Reduction in Response to Abiotic Stress in Cotton

Factors affecting cotton yield include a shortened boll development period, increased bud and boll abscission rates, and temperature extremes during flowering and boll formation. Elevated

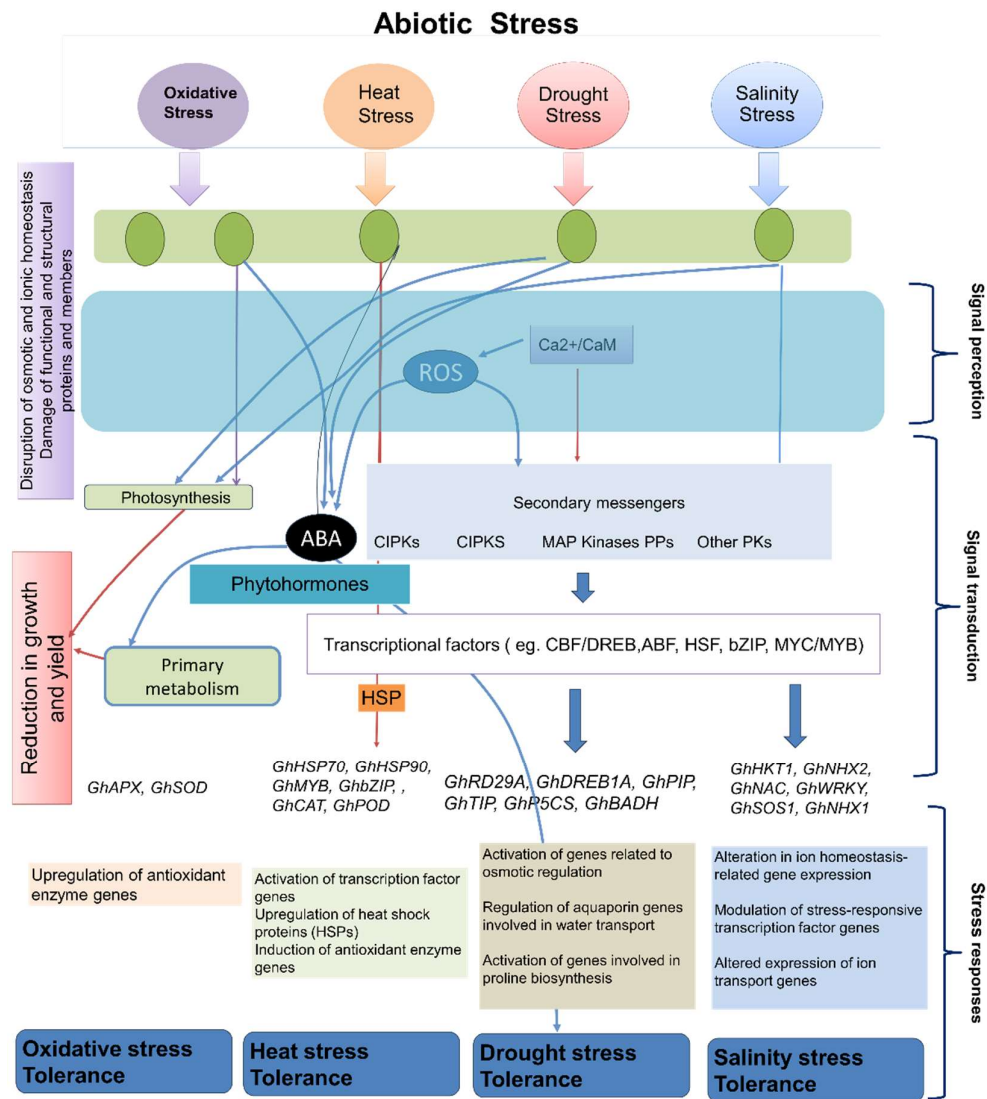
temperatures can lead to undesirable changes in fiber traits. Drought stress is another limiting factor, primarily reducing boll numbers and, to a lesser extent, boll weight [107–110]. Adequate water availability is crucial for yield formation. The effects of drought on fiber quality are inconclusive, with mild deficits considered beneficial but intensified stress negatively impacting elongation [111]. In field conditions, drought, and high temperatures rarely occur in isolation. Mechanisms resulting from water deficit or high-temperature stress differ among crops, making it challenging to determine a genotype's tolerance based on its response to the other stressor [112]. Limited studies have explored the interaction of elevated temperatures and drought under field conditions, necessitating further research [113]. Factors contributing to cotton yield reduction include a shortened boll development period, increased bud and boll abscission rates, and a subsequent decline in total boll load. Temperature extremes before and during flowering and boll formation can also impact fiber quality development. Elevated temperatures have been associated with undesirable fiber trait changes, such as increased micronaire values [114]. Fibre quality parameters can be influenced by the yield component responses to stressors, with elevated temperatures during the boll development period leading to fewer seeds per boll but increased fiber strength [115].

Drought stress is another critical factor limiting cotton growth, impacting fiber development and quality. Reduced cotton yield under drought conditions is primarily attributed to decreased boll numbers and, to a lesser extent, reduced boll weight.[116] The decrease in yield and final boll density is linked to increased square and young boll abscission under drought conditions [117]. Adequate water availability from the squaring stage to early flowering is crucial for yield formation [118]. The effects of drought stress on fiber quality are inconclusive, with mild water deficits often considered beneficial for fiber elongation but intensified drought stress negatively impacting elongation [119]. Notably, abiotic stresses like drought and high temperatures rarely occur in isolation under field conditions [120]. The mechanisms resulting from water deficit or high-temperature stress can differ among crops [121]. Thus, it is challenging to determine a genotype's tolerance to high temperature or drought based on its response to the other stressor [122]. Limited studies have evaluated the interaction of elevated temperatures and drought impact on cotton yield under field conditions, highlighting the need for comprehensive research.

### *3.2. Mechanisms of Cotton Plants in Response to Abiotic Stress*

#### *3.2.1. Stress Signaling Pathways*

Plant cell membranes act as sensors for stress signals, triggering both self-activated and hormone-dependent signaling mechanisms. These processes often involve mitogen-activated protein kinase (MAPK) networks. Calcium ions ( $\text{Ca}^{2+}$ ) frequently serve as common second messengers in stress signaling pathways, influenced by drought stress as well as various hormones like abscisic acid (ABA), jasmonic acid (JA), and ethylene. ABA interacts with *SnRK2* proteins, initiating molecular and physiological responses to drought stress [123–129]. Plants adopt drought recovery mechanisms following successful stress signal transduction. Cotton has developed various morpho-physiological approaches to drought tolerance, such as photosynthetic response, osmotic adjustment, stomatal regulation, low leaf water loss, high relative water contents (RWC), and enlarged tap roots [130]. Genetic statistics and improvements in physio-morphological characters are crucial for mitigating the effects of drought [131]. We further focus on cellular and molecular signaling networks, abiotic stress-coping adaptations, and the use of functional genomics to overcome abiotic stress. The impact of various abiotic stress and the intrinsic relationship of genes and hormones for the development of stress tolerance is depicted in Figure 2.



**Figure 2.** Stress Responses at the Gene Level in Cotton Plants.

The stress response pathways activated in cotton (*Gossypium hirsutum*) plants upon exposure to various abiotic stresses, including oxidative, heat, drought, and salinity stress. Illustration of the stress type impact on signal transduction pathways, modulation hormone balance, gene regulation, and impact on plants resilience to the stress.

3.2.2. Stress-Responsive Genes and Proteins

Abiotic stresses, such as cold, drought, and salinity, challenge crop growth. Plants have evolved stress-responsive mechanisms and pathways like SOS, ICE-CBF/DREB1, CDPK, and MAPK. ABA plays a crucial role in stress signaling, with crosstalk between ABA-dependent and independent pathways. Identifying the molecular mechanisms that drive stress responses in cotton is critical for increasing its resilience to varied environmental challenges. Table 3 shows the stress-responsive genes and proteins in cotton utilizing primary references, focusing on the vital function of WRKY transcription factors. The draft genome sequencing of diploid cotton *Gossypium raimondii* and allotetraploid cotton *Gossypium hirsutum* L. TM-1 has significantly advanced cotton genomics, providing valuable resources for investigating stress-responsive genes [132–136]. Analysis of stress-

related pathways using this genomic data offers insights into cotton’s molecular mechanisms governing stress responses. This knowledge facilitates the identification of stress-tolerance genes, informing targeted genetic improvement strategies for enhancing cotton resilience and productivity under various environmental stressors [137]. Abiotic stresses, particularly drought and salinity, present substantial challenges to global cotton cultivation. Studies underscore the critical importance of comprehending the genetic regulation of stress tolerance in cotton [138,139]. Investigating drought coping strategies, such as enhancing crop water-use efficiency, has been a focal point in cotton research. The involvement of *WRKY* transcription factors in abiotic stress responses is well-established. The review delves into the regulatory role of *WRKY* proteins during stress conditions [140]. *WRKY* transcription factors are signaling and regulatory components in plant stress responses [141,142]. The *WRKY* gene family, extensively studied in model plants and crops, plays a crucial role in stress signaling. The intricate network of transcription factors in cotton and other plants responds to abiotic and biotic stresses [143–146]. The involvement of *GhWRKY15* in disease resistance and plant development underscores the multifaceted roles of these transcription factors [147].

Additionally, the review sheds light on the regulatory mechanisms of *WRKY* transcription factors in specialized metabolism [148]. *WRKY* transcription factors govern stress responses and detoxifying processes in cotton. The relevance of *WRKY* genes in stress responses in cotton stresses their significance in plant adaptability to changing environmental conditions [149]. The complex interaction of *WRKY* transcription factors with abscisic acid and ethylene adds to the intricacies of stress signaling in cotton. [149,150]. The interaction of ABA signaling pathways and *WRKY* proteins is critical for plant response to diverse stresses [151]. Here, we discussed the generation of ROS and the activation of transcription factors that initiate the stress response.

**Table 3.** Overview of Gene Expression Regulation in Cotton Under Abiotic Stress ConditionsThe table provides information on specific genes, the corresponding abiotic stress, the plant part affected, the impact on gene expression regulation, the analysis method, and references for further reading.

Sr.no	Genes	Abiotic stress	Plant part	Impact on gene expression	Regulation	Method	References
1.	<i>GhHSP70</i> , <i>GhHSP90</i>	High Temperature	Leaves	Upregulation of heat shock proteins (HSPs)	Upregulated	qRT-PCR	[331,332]
2.	<i>GhRD29A</i> , <i>GhDREB1A</i>	Drought	Roots	Activation of genes related to osmotic regulation	Upregulated	RNA-Seq	[333,334]
3.	<i>GhSOS1</i> , <i>GhNHX1</i>	Salinity	Roots	Altered expression of ion transport genes	Upregulated	Microarray	[335,336]
4.	<i>GhMT1</i> , <i>GhPCS</i>	Heavy Metal Toxicity	Roots	Induction of metal detoxification genes	Upregulated	qPCR	[174,196,337]
5.	<i>GhUVR8</i> , <i>GhCOP1</i>	UV-B Radiation	Leaves	Activation of genes involved in UV protection	Upregulated	RNA-Seq	[338,339]
6.	<i>GhAPX</i> , <i>GhSOD</i>	Oxidative Stress	Leaves	Upregulation of antioxidant enzyme genes	Upregulated	qRT-PCR	[340,341]
7.	<i>GhLEA</i> , <i>GhRAB</i>	Waterlogging	Roots	Induction of genes related to waterlogging tolerance	Upregulated	Microarray	[342,343]
8.	<i>GhPIP</i> , <i>GhTIP</i>	Drought	Leaves	Regulation of aquaporin genes involved in water transport	Upregulated	RNA-Seq	[344–346]

9.	<i>GhMYB</i> , <i>GhbZIP</i>	Heat Stress	Leaves	Activation of transcription factor genes	Upregulated	qPCR	[347]
10.	<i>GhNAC</i> , <i>GhWRKY</i>	Salt Stress	Roots	Modulation of stress-responsive transcription factor genes	Upregulated	RNA-Seq	[348–351]
11.	<i>GhPAL</i> , <i>GhCHS</i>	UV-B Radiation	Leaves	Regulation of genes involved in phenylpropanoid biosynthesis	Upregulated	qRT-PCR	[352–355]
12.	<i>GhCAT</i> , <i>GhPOD</i>	High Temperature	Leaves	Induction of antioxidant enzyme genes	Upregulated	RNA-Seq	[356,357]
13.	<i>GhP5CS</i> , <i>GhBADH</i>	Drought	Leaves	Activation of genes involved in proline biosynthesis	Upregulated	qPCR	[358]
14.	<i>GhHKT1</i> , <i>GhNHX2</i>	Salinity	Roots	Alteration in ion homeostasis-related gene expression	Upregulated	RNA-Seq	[359,360]
15.	<i>GhDHN</i> , <i>GhERF</i>	Cold Stress	Leaves	Modulation of genes related to cold response	Upregulated	qRT-PCR	[361,362]

4. Breeding and Biotechnological Approaches to Improve Abiotic Stress Tolerance to Overcome in Cotton

4.1. Breeding for Stress Tolerance

Breeding techniques have traditionally been used to produce resilient cotton cultivars. Despite its importance in the textile industry, cotton productivity is constantly challenged by abiotic factors such as drought, salinity, and high [152]. Because of breeding operations, Cotton’s abiotic stress tolerance has significantly improved recently. This review summarizes the findings of significant studies focusing on genetic analyses, molecular markers, and physiological responses related to abiotic stress tolerance in cotton.[153]. Using amplified fragment length polymorphism to investigate the genetic diversity and connections between diploid and tetraploid cotton. This seminal work paved the way for the following studies, highlighting the relevance of genetic variety in breeding programs.[154]. A genetic investigation of drought tolerance in Egyptian cotton (*Gossypium barbadense* L.) yielded important insights into the heritability of drought tolerance features. A thorough exploration of the genetic foundations underlying tolerance to drought and salinity and resistance to Verticillium wilt and thrips has been undertaken. Integrating these diverse stress resistances is imperative in developing robust cotton varieties [155]. The investigation into PEG-induced osmotic stress has been a central focus in comprehending cotton’s reaction to abiotic stress. The genetic analysis and mapping of quantitative trait loci (QTL) related to PEG-induced osmotic stress in cotton have been conducted. This study has illuminated distinct genomic regions linked to osmotic stress tolerance, offering valuable targets for subsequent breeding endeavors [156]. The creation of molecular tools is crucial for the success of breeding programs. Shukla et al. have successfully established the inaugural linkage map for a recombinant inbred line population in cotton, employing it to investigate PEG-induced dehydration tolerance. This map is a valuable asset, facilitating the identification of genomic regions associated with dehydration tolerance [157]. Comprehensive genetic analyses were undertaken to enhance the overall performance of cotton, with a specific emphasis on yield, fiber quality, and abiotic stress tolerance in Pima cotton [79]. QTL mapping has played a pivotal role in unraveling the genetic underpinnings of stress tolerance.



Specifically, QTL mapping was employed to investigate drought and salt tolerance in an introgressed recombinant inbred line population of Upland cotton in greenhouse and field conditions. This research pinpointed genomic regions linked to tolerance, providing potential avenues for marker-assisted selection in breeding programs [158]. Genome-wide association studies (GWAS) have played a crucial role in identifying markers linked to stress tolerance. In this context, a GWAS was conducted to explore tolerance to biotic and abiotic stresses in a MAGIC (Multi-parent Advanced Generation Inter-Cross) population of upland cotton. This study aimed to identify significant genomic markers associated with stress tolerance in the cotton population under investigation [159]. Numerous studies have concentrated on pinpointing drought and salt-tolerant cotton germplasm. Identifying such germplasm within the U.S. upland cotton pool has been achieved, making notable contributions to the conservation and utilization of genetic resources endowed with stress tolerance [160]. Water stress responses in cotton, revealing changes in photosynthesis and leaf structure. Investigated the regulation of stomatal and non-stomatal water use in cotton, corn, and sorghum to enhance crop water use efficiency [161]. Compared to corn, cotton and sorghum have more efficient transport systems, conferring drought tolerance to these species [162].

Mapping studies of (QTL) offer valuable insights into the genetic foundations of stress tolerance, providing potential avenues for marker-assisted breeding strategies. Identifying QTLs for salt tolerance through the interspecific cross of *Gossypium tomentosum* with *Gossypium hirsutum* illustrates the potential of incorporating wild cotton species into breeding programs [163,164]. A genome-wide analysis of the calcium-dependent protein kinase gene family in *Gossypium raimondii*, reveals a network involved in stress signaling [165]. Similarly, *GhABF2*, a bZIP transcription factor, is pivotal in conferring drought and salinity tolerance in cotton [166]. The significance of overexpressing rice NAC gene *SNAC1* in enhancing drought and salt tolerance.[167]. Highlighting the potential of cross-species gene transfer to improve stress resilience.

Understanding the physiological responses of cotton to abiotic stress is crucial for targeted breeding. Overexpressing the *Thellungiella halophila* *H<sup>+</sup>-PPase* gene enhances salt tolerance and improves growth and photosynthetic performance [168]. The effects of water stress on photosynthesis, root activity, and cotton yield under drip irrigation, offering insights into irrigation strategies for stress mitigation [169].

Water use efficiency (WUE) in cotton breeding programs provides important selection traits in selecting varieties to cope with water scarcity [170]. Cotton's response to drought stress, studying growth reactions of an interspecific breeding line and its parents under controlled drought conditions with an automated irrigation system, provides valuable insights and a practical technique for drought tolerance studies in cotton [171]. The calcium sensor *GhCaM7* modulating reactive oxygen species (ROS) production promotes cotton fiber elongation [172]. The *GhCDPK1* gene in cotton regulates proline content and ROS levels and enhances drought tolerance [173]. The functional genomics of stress-responsive genes provides further molecular insights into drought response mechanisms, stress tolerance mechanisms, including zinc-induced antioxidative defense and osmotic adjustment, along with the role of genes like *GhNHX1* in salt stress [174,175].

#### 4.2. Transgenic Approaches

Recent advancements in genetic engineering approaches aimed at bolstering abiotic stress tolerance in cotton, utilizing key references to understand and evaluate these strategies. To overcome these challenges, researchers have employed various genetic engineering strategies. This comprehensive review provides an in-depth analysis of genetic engineering approaches for breeding abiotic stress-tolerant cotton. Overexpression of genes associated with drought tolerance improved drought resistance in transgenic cotton. Targeting critical genes involved in stress response pathways holds promise for developing cotton varieties resilient to water scarcity. Drought poses a significant threat to cotton production [161,176]. Variability for drought tolerance in cotton genotypes. Genetic engineering approaches to enhance drought tolerance include expressing drought-responsive genes and transcription factors. Overexpression of *AtHDG11* in tall fescue resulted in enhanced tolerance to drought and salt stress [177]. Salt tolerance mechanisms through somatic embryo initiation and

germination in diploid cotton [178]. Comparative microarray analysis to identify salt-responsive genes in upland cotton, providing a valuable resource for unraveling the molecular basis of salt tolerance [179]. The augmentation of glycine betaine synthesis, exemplifies a genetic engineering strategy enhancing drought tolerance in cotton [180]. Genes associated with heat and salinity tolerance offer potential targets for genetic engineering [181,182]. Salt tolerance in cotton emphasizes the need to develop resistant varieties. In cotton, the overexpression of vacuolar Na<sup>+</sup>/H<sup>+</sup> antiporters and (AVP1) Arabidopsis vacuolar H<sup>+</sup>-pyrophosphatase gene improves drought and salt tolerance while increasing fiber yield [183].

The balance between reactive oxygen species and antioxidant defenses is vital for enhancing stress tolerance in cotton [184]. Increased glycine betaine synthesis in transgenic cotton lines, improving salinity tolerance. Understanding osmotic regulation and maintaining a balance in reactive oxygen species (ROS) are pivotal aspects of stress adaptation—Osmo protectants and antioxidant defences in conferring stress tolerance [185]. The overexpression of the Arabidopsis vacuolar H<sup>+</sup>-pyrophosphatase gene (*AVP1*) in cotton further exemplifies the potential of genetic engineering in augmenting osmotic regulation [186]. As explored, understanding and manipulating root traits would be crucial for improving drought resistance in cotton [187]. Genetic engineering approaches focusing on root architecture and function may provide an optimization of root traits is essential for improving water-use efficiency in cotton [188]. Overexpression of rice NAC gene *SNAC1* in transgenic cotton enhanced drought and salt tolerance by improving root development and reducing transpiration rate for developing cotton plants with increased water-use efficiency [161].

Transcription factors such as *NAC* and *MYB* are pivotal in regulating stress-responsive gene expression. Overexpression of *OsMYB2* [189] and *GhHOX3* illustrates the potential of transcription factors in conferring stress tolerance.[190] Signal transduction pathways, including those mediated by *ABA*, are explored for their relevance in stress response [191]. The cotton's Arabidopsis vascular sodium/proton antiporter gene has improved photosynthetic performance under salt conditions [192]. Transcription factors, including *NAC*, *MYB*, *WRKY*, *bZIP*, and *ERF/DREB*, have vital roles in conferring abiotic stress tolerance [193,194]. Signal transduction pathways, such as those mediated by *ABA*, enhance photosynthetic performance under salt conditions [195].

#### 4.3. CRISPR/Cas in Cotton: Challenges and Solutions

The revolutionary CRISPR/Cas technology, which stands for clustered regularly interspaced short palindromic repeats (CRISPR)/CRISPR-associated protein (Cas), offers precise capabilities for genome editing (GE) [196–198]. Recent applications of CRISPR/Cas in cotton, specifically in whole genome-sequenced cotton species, have opened up new possibilities for targeted genetic modifications related to stress response pathways [199,200]. In the post-genomic era, developing efficient biotechnological tools for studying gene functions, such as GE, reverse genetics, or omics-based approaches, has become necessary [201,202]. Since the early 2000s, gene silencing technologies have been widely used to uncover gene function, revealing regulatory mechanisms and metabolic pathways [203]. However, the limitations of existing gene silencing technologies, like RNA interference, have led to the exploration of CRISPR/Cas-based GE tools, which have diverse applications beyond the introduction of stable and heritable mutations [204,205].

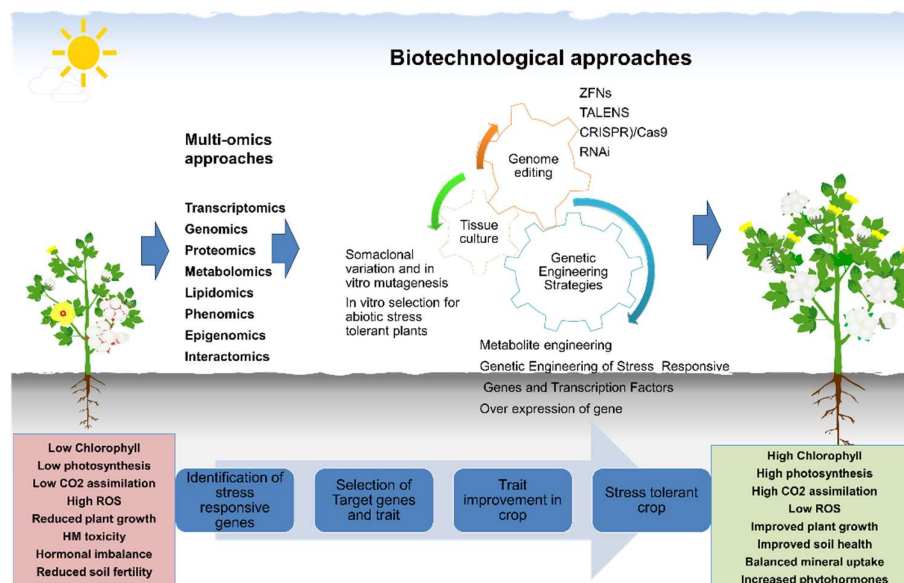
Various approaches are available for target-specific GE, such as CRISPR/Cas, zinc finger nucleases (ZFNs), and transcription activator-like effector nucleases (TALENs)[206]. The CRISPR/Cas system has transformed the field of plant GE with its simple design and high efficiency, which uses short RNA molecules called single guide RNAs (sgRNAs). This system has overshadowed the complexity and limitations associated with ZFNs and TALENs in designing and cloning desired gene constructs [207,208]. Its cost-effectiveness and ease of use have made CRISPR/Cas the preferred choice for GE in animals and plants, transforming the landscape of genetic research. Cotton, a vital fiber, biofuel, and oil crop, requires efficient GE tools for large-scale gene functional studies [209].

While CRISPR/Cas has been successful in GE for various crops and model systems, its applications in cotton have faced challenges, partly due to the time-consuming transformation process and polyploidy [210]. Several studies targeting genes, such as *MYB25*, *GhVP*, *GhCLA1*, or

*GhARG*, have demonstrated the potential of CRISPR/Cas in cotton GE [211–214]. In a recent study, the CRISPR/Cas system was efficiently used to generate knockout plants for the *GhNAC3* gene [215]. The *GhNAC3* gene encodes an NAC family transcription factor involved in drought stress tolerance through abscisic acid-related and independent pathways [216]. Mutant lines exhibited phenotypic variations, confirming the role of *GhNAC3* in average growth and development, apart from drought stress tolerance. CRISPR/Cas-based base editing allows for precise nucleotide substitutions, enabling accurate base modifications and directed evolution of intended genetic loci [217]. Different research groups have already shown the potential use of base editing tools for cotton GE [218,220]. For example, Wang and coworkers [220] utilized the recent version of ABE (*GhABE8e*) to install A-to-G base changes in *GhTFL1*, an anti-florigen encoding gene. The evolved *GhTFL1* led to the generation of new cotton germplasm with unique plant architectural features, such as compact size, shortened breeding cycle, and moderate height, which are beneficial for harvesting and potentially suitable features to evade drought stress situations. This study demonstrates the potential of base editing technology for directed evolution studies in the cotton genome. It can be applied to produce weak or strong alleles in abiotic stress-related genes, which would have been considered an unattainable task in the past.

A rapid method for validating sgRNAs for CRISPR/Cas GE was devised to tackle the challenges associated with time-consuming transformation methods in cotton [221]. This method involves transient expression in cotyledons, enabling experimental validation in cotton. Successfully applied for multiple purposes, including validation of sgRNAs for individual genes (*GhPDS*, *GhCLA1*, and *GhEF1*), simultaneous editing of homologous genes, and genomic fragment deletions, this new method showcased its versatility. CRISPR/Cas-induced mutations in stably transformed cotton plants targeting *GhCLA1* also resulted in typical albino phenotypes [222–227].

The integration of reverse genetics methodologies and targeted GE technologies has propelled significant advancements in understanding gene function [228]. CRISPR/Cas-based techniques enable the production of transgene-free cotton plants through selfing or backcrossing, aligning with current guidelines for genetically modified organisms (GMOs) [229]. Prospective application of CRISPR/Cas-based methods across the entire cotton genome provides a novel avenue to bolster cotton productivity, enhance genetic traits, confer pathogen resistance, and optimize agronomic characteristics, as reported for other crops [230–232]. CRISPR/Cas, with its simplicity and efficiency, stands out as a powerful tool for large-scale gene functional studies in cotton [233]. Creating a swift validation method for sgRNAs tackles the hurdles linked with prolonged transformation processes, thus rendering CRISPR/Cas more accessible for extensive applications in cotton GE [234]. As the GE field continues to evolve, advanced GE technologies like base editing and prime editing hold immense promise for unravelling the complexities of gene function and driving new breeding innovations in cotton crop improvement for developing abiotic stress-tolerant varieties (**Figure 3**).



**Figure 3.** Multi-omics and Biotechnological Approaches to Improve Abiotic Stress Resilience in Cotton Plants.

Illustration of abiotic stress resilient cotton (*Gossypium hirsutum*) crop by using various biotechnological approaches. Utilize a combination of omics technologies (genomics, transcriptomics, proteomics, metabolomics, etc.) to gain comprehensive insights into the molecular mechanisms underlying stress responses in cotton. Genome editing techniques like CRISPR/Cas9 allow for targeted manipulation of the cotton genome to introduce stress-resistant traits. RNA Interference (RNAi): Silences specific genes that may hinder the plant's stress tolerance. Genetic Engineering: Introduces genes from other organisms or modifies existing genes within cotton to enhance stress resistance.

## 5. Future Prospects and Challenges

### 5.1. Advanced Biotechnological Interventions in Mitigating Abiotic Stress

Conventional breeding has indeed led to substantial improvements in crop yield, but it has fallen short in boosting crops' resilience to abiotic stresses. This shortfall can be attributed, in part, to breeders' inclination to assess genetic materials solely under optimal conditions. However, this approach overlooks the intricate nature of abiotic stresses and the fact that plants exhibit varying sensitivities to different stressors at different life cycle stages. As a result, conventional breeding faces challenges in effectively selecting for increased stress tolerance. Therefore, there is a pressing need for an alternative approach to enhance abiotic stress tolerance and improve both crop yield and quality. Creating drought-resistant cotton cultivars through breeding programs prioritizing features including deep root systems, enhanced water-use efficiency, and stress tolerance [65,66]. Implementing efficient irrigation methods such as drip or micro-sprinkler systems to optimize water use and minimize water loss [67]. Employing soil conservation practices like mulching and conservation tillage to enhance soil water retention and reduce evaporation [68].

Genetic engineering of the chloroplast holds promise for developing transgenic crops suited to changing environments. In recent decades, scientists have successfully created transgenic plants by modifying the expression of specific genes using various transformation methods and tissue culture methods [235]. Manipulating individual genes in plants through transgenic approaches involves understanding a network of pathways related to stress response [236]. Modern genome-wide profiling and engineering technologies present unprecedented opportunities for understanding the dynamics of epigenetic modifications in response to stress [237]. Epigenetics regulates plant stress

responses, including methodologies for detecting genome-wide epigenetic changes and distinguishing their effects on plant phenotypes from other sources of variation epigenetic mechanisms in stress memory and advocates for integrating plant responses with patterns of epigenetic variation to guide breeding strategies aimed at improving crop performance under stress conditions. Including signal perception, transduction cascades, activation of transcription factors, gene expression or modulation, and synthesis of functional proteins. Also, enzymes, osmolyte production, antioxidant defense against reactive oxygen species (ROS), and adjustments to biochemical, physiological, and cellular processes [238–244]. This section explores how altering the expression of single genes via transgenic methods can enhance plant performance under primary abiotic stress conditions. Marker-assisted selection (MAS) has facilitated the construction of gene maps and the identification of (QTL) associated with improved stress tolerance from wild plants by de-novo domestication [245]. Genome-wide association studies covering the entire genome have been instrumental in detecting major QTLs that enhance abiotic stress tolerance in crops [246]. Emerging technologies like CRISPR/Cas-based GE tools hold promise for the future of crop biotechnology [247]. CRISPR/Cas offers the advantage of editing a few nucleotides in the organism's original DNA without introducing large foreign DNA fragments, potentially easing the acceptance of GMOs worldwide due to minimal changes in crop genomes.

### *5.2. Genes Pyramiding Approach to Improve Multi-Stress Tolerance in Crops*

“Gene acquisition” remains a significant barrier in plant genetic engineering. Advances in whole-genome sequencing and omics technologies, including genomics, proteomics, and metabolomics, hold promise for discovering novel genes expressed under stressful circumstances [248,249]. Newly discovered genes hold potential as options for improving plant stress tolerance. Identifying stress-related metabolites in crops is also critical to developing stress resilience. Since overexpressing single genes in crops provides limited stress tolerance, the gene pyramiding method, which involves simultaneously overexpressing numerous functionally related genes, appears to be a more sensible strategy [250–252]. Recent progress in enhancing plant tolerance to coupled abiotic stresses via multi-gene assembly raises hopes for mitigating the negative effects of these pressures on agricultural production. Sustainable agriculture requires using learned knowledge to cultivate crops that flourish and reproduce effectively in complex conditions.

### *5.3. Challenges in Mitigating Abiotic Stress in Cotton*

The need for increased cotton output, driven by changing climates and a growing human population, has historically relied on conventional breeding methods to introduce genes into superior cultivars. Modern GE technologies have emerged as promising solutions to tackle these challenges more effectively. They encompass techniques such as zinc-finger nucleases, transcription-activator-like effector nucleases, and clustered regularly interspaced palindromic repeats (CRISPR). The CRISPR/Cas system is notable for its simplicity, efficiency, and adaptability [253]. Leveraging CRISPR/Cas, researchers aim to enhance cotton's tolerance to both biotic and abiotic stresses, modify gene expression, and stack genes for desired traits, all while addressing regulatory concerns associated with GMOs through the transgene clean strategy (Table 3) [254]. This approach underscores a range of research opportunities, including improving fiber quality, plant architecture, and flowering and addressing challenges related to epigenetic changes and gene stacking for economically significant traits in cotton cultivation.

Along with genetic techniques, biotic and abiotic factors provide considerable obstacles to cotton farming, jeopardizing growth, output, and fiber quality. Cotton's antioxidant systems are affected by abiotic stresses such as high temperatures, drought, heavy metal toxicity, and salinity. It investigates the functions of significant antioxidants such as glutathione, proline, and phenolics, as well as essential antioxidant enzymes such as ascorbate peroxidase, superoxide dismutase, peroxidase, catalase, and glutathione reductase, in cotton's defense mechanisms against these stressors. Potential mechanisms and linkages of signaling pathways activated by various stress factors [255,256] (Table 2); this review also addresses the implications of stress-induced alterations in antioxidant levels and



enzyme activities for cotton productivity, proposing breeding strategies to mitigate these stressors. Interdisciplinary methodologies integrating physiological, biochemical, and molecular investigations are essential for comprehending how cotton adapts to stress and fostering resilience in sustainable agriculture.

## 6. Conclusions

Climate change frequently causes abiotic stress factors like heat, drought, salinity, heavy metal toxicity, and waterlogging, which reveals their profound impact on cotton physiology and yield. Each stressor induces specific physiological and biochemical changes, from leaf wilting under heat to root length reduction in saline conditions. Here we discuss how molecular insights have shown the upregulation of stress-responsive genes, including heat shock proteins and ion transporters, aiding in adaptive responses. Advanced metagenomics and multi-omics techniques are essential to unveil dynamic gene expression patterns, elucidating intricate regulatory networks. Further, genetic engineering, particularly CRISPR/Cas9, offers promise in developing stress-tolerant cotton varieties. Interdisciplinary approaches merging physiological, biochemical, and molecular studies are vital for understanding cotton's stress adaptation and cultivating resilience for sustainable agriculture.

**Author Contributions:** AMP and BDP initiated the study idea. AMP and SGW wrote a manuscript draft with critical feedback from BDP, NM, HS, NB, JC, RMS, and RSW. SGW, AMP, and RSW prepared figure illustrations.

**Funding:** Funded by the Government of Maharashtra for Cotton Improvement Project Mahatma Phule Krishi Vidyapeeth (MPKV), Rahuri., under (GR) No. MPV 1422/L.No.253/7. Also, the support provided by the National Research Foundation of Korea (grants NRF 2021R1I1A3057067, 2021R1A5A8029490, and 2022R1A2C3010331) is acknowledged.

**Conflicts of Interest:** The authors declare no conflict of interest.

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