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PHYSIO-BIOCHEMICAL INSIGHTS INTO COTTON'S RESPONSE TO DROUGHT STRESS: A MINI REVIEW

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Abstract

Drought, due to inadequate irrigation or rainfall, poses a significant challenge for cotton production, affecting 45% of global cultivated land, with 19.5% of irrigated areas also facing salinity. The combination of drought and salt stress can lead to substantial yield losses, potentially accounting for up to half of agricultural losses worldwide. This article provides a comprehensive examination of the multifaceted responses of cotton to drought stress, focusing on the interplay of morphophysiological, biochemical, and molecular mechanisms that contribute to enhanced drought tolerance. It highlights the critical roles of solute accumulation, photosynthesis enhancement, and the production of key biochemicals like glycine, betaine, and proline, which mitigate the detrimental effects of drought and salinity. Additionally, the review explores advanced strategies, such as QTL mapping, genetic engineering, and exogenous solute applications, to improve drought resilience. Emphasizing the importance of transcription factors and ABA in regulating key stress responses, this work presents a novel perspective on cotton breeding for drought tolerance, particularly through transgenic approaches aimed at optimizing stress-related gene expression.

Key words: Cotton, Drought, Solutes, Chlorophyll, Photosynthetic rate, Genes.

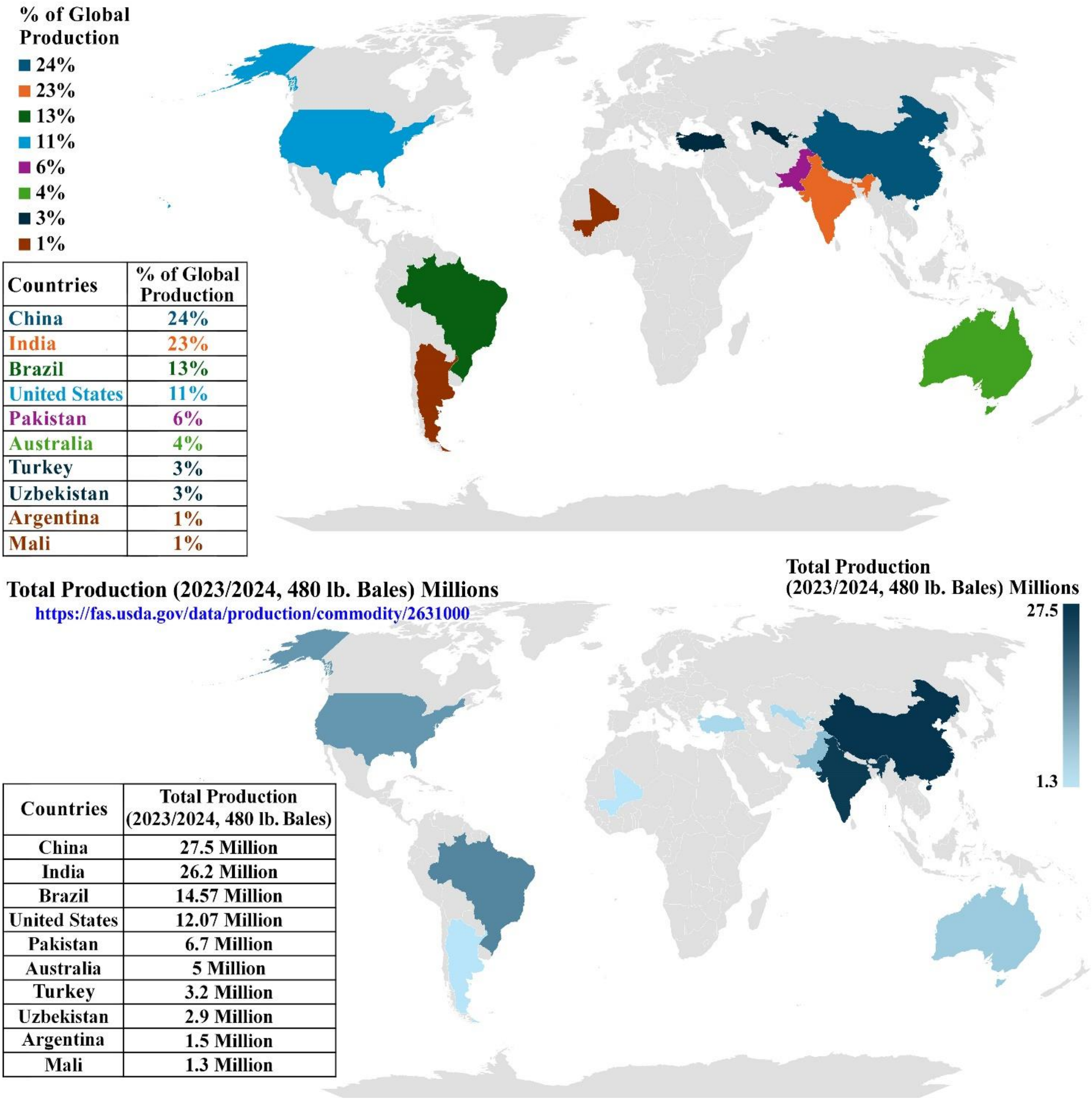
Introduction

Importance of cotton in global agriculture: Cotton (*Gossypium hirsutum* L.) is the primary crop used for producing natural fibers, and its yield holds significant economic value in cotton-growing regions due to its relevance in the textile and oil industries (Dorman *et al.*, 2022). Leading cotton producers include Brazil, China, India, and the United States (Fig. 1). However, cotton production in these countries, along with other tropical regions, faces significant challenges due to reduced water availability, altered rainfall patterns, increased drought frequency, heat waves, and escalating soil salinity. Approximately 25 million farmers worldwide depend on cotton cultivation for their livelihoods (Voora *et al.*,2023). Drought is one of the most severe abiotic stresses, adversely impacts cotton growth and yield (Zahid *et al.*, 2021; Zafer *et al.*, 2023). Globally, 40% of agricultural land is threatened by water scarcity (Duan *et al.*, 2022), and shifts in rainfall patterns over the past 30 years have placed cotton production at risk in regions such as Brazil, China, Pakistan, India, and the USA (Khan *et al.*, 2019).

A forecasted temperature rise of 3-5°C over the next century is likely to result in severe drought conditions, directly impacting agricultural productivity, especially in crops like cotton (Zhao *et al.*, 2024). As climate change accelerates, it is crucial to consistently expose cotton plants to various stress factors to better understand their responses and adapt them to these environmental shifts (Haroon *et al.*, 2023). Climate change affects ecosystems and agricultural systems in several ways, including increased salinity, reduced water availability, abrupt temperature fluctuations, flooding, heavy metal stress, and unpredictable rainfall patterns (Duchenne-Moutien & Neetoo, 2021). These shifts not only endanger wild species and landraces but also compromise genetic diversity in agricultural crops. For instance, approximately 75% of the genetic variation of agricultural crops has been lost since the early 20th century, further heightening the vulnerability of current crop cultivars (Hanjra & Qureshi, 2010). As climate variability threatens crop diversity, especially cotton, a primary fiber crop, there is an urgent need to develop resilient cultivars capable of enduring harsh environmental conditions (Zafar *et al.*, 2021).

Impact of drought stress on cotton productivity: Cotton production in the above-mentioned countries, along with other tropical regions, faces significant challenges due to reduced water availability, altered rainfall patterns, increased drought frequency, heat waves, and escalating soil salinity. Approximately 25 million farmers worldwide depend on cotton cultivation for their livelihoods (Voora *et al.*, 2023).

Globally, 40% of agricultural land is threatened by water scarcity (Dunn *et al.*, 2020) and shifts in rainfall patterns over the past 30 years have placed cotton production at risk in regions such as Brazil, China, Pakistan, India, and the USA (Khan *et al.*, 2019). While cotton is generally drought-tolerant during its vegetative stages, it is especially susceptible to drought stress during reproductive growth (Niu *et al.*, 2018). As a result, drought has caused significant yield declines in cotton, with reports of a 34% reduction in fiber yield due to water scarcity (Ullah *et al.*, 2017). Water scarcity, affecting 33% of the world's arable land, continues to hinder plant growth and agricultural productivity, negatively impacting cotton yields (Mahmood *et al.*, 2021; Deeba *et al.*, 2012).



Countries	% of Global Production
China	24%
India	23%
Brazil	13%
United States	11%
Pakistan	6%
Australia	4%
Turkey	3%
Uzbekistan	3%
Argentina	1%
Mali	1%

Countries	Total Production (2023/2024, 480 lb. Bales)
China	27.5 Million
India	26.2 Million
Brazil	14.57 Million
United States	12.07 Million
Pakistan	6.7 Million
Australia	5 Million
Turkey	3.2 Million
Uzbekistan	2.9 Million
Argentina	1.5 Million
Mali	1.3 Million

Fig. 1. Leading cotton producing countries worldwide in 2023/2024 (in million bales).

To address growing global demands for food, bioenergy, and fibers, agricultural productivity in arid and semi-arid regions must be increased by at least 50% (Shaar-Moshe *et al.*, 2017), yet the recent 58% yield loss in cotton due to climate change underscores the urgent need for improved drought resilience (Wang *et al.*, 2016b).

Screening cotton germplasm for drought resilience is vital for improving cotton's resistance to climate change. Identifying key traits, understanding the molecular pathways that underlie drought tolerance, and pinpointing stress-related genes are fundamental in developing more resilient cotton varieties. The integration of modern breeding techniques with an understanding of climate change impacts will lead to the creation of cultivars that are better suited to withstand the biotic and abiotic stresses induced by a changing climate (Table 1; Figs. 2-5).

Objectives and scope of the review: This review explores into the physiological, biochemical, and molecular mechanisms underlying drought tolerance in cotton and discuss strategies for improving crop resilience through genetic and biotechnological innovations.

Drought stress: Drought stress refers to a period of water deficiency that disrupts normal plant growth and metabolic activities, primarily due to reduced soil moisture and atmospheric water availability (Farooq *et al.*, 2009). It is one of the most critical abiotic stresses affecting crop productivity worldwide, particularly in arid and semi-arid regions. Drought stress can be classified based on its onset and duration into four main types: (i) meteorological drought, characterized by a prolonged period of low precipitation; (ii) agricultural drought, where soil moisture becomes insufficient for crop needs; (iii) hydrological drought, which involves reduced water levels in surface and groundwater sources; and (iv) physiological or plant drought, describing internal water deficit at the cellular or tissue level despite the presence of soil moisture (Anjum *et al.*, 2011). Understanding these classifications is essential for developing effective drought mitigation strategies and tailoring cotton breeding programs toward specific drought scenarios.

Physiological phases of drought response in plants: Plants exhibit a sequence of physiological responses to drought stress that can be broadly divided into three phases: alarm phase, resistance phase, and exhaustion phase.

Alarm phase: Plants perceive the initial water deficit and respond by closing stomata to reduce transpiration, leading to an immediate decline in photosynthesis and gas exchange (Chaves *et al.*, 2003).

Resistance phase: During this, adaptive mechanisms are activated, including osmotic adjustment through the accumulation of solutes like proline, changes in root-to-shoot ratio to enhance water uptake, and increased antioxidant enzyme activity to combat oxidative stress (Tardieu *et al.*, 2018).

Exhaustion phase: If drought persists, the plant enters in this phase, where prolonged stress overwhelms protective mechanisms, leading to impaired metabolic functions, reduced growth, leaf senescence, and, ultimately, cell death (Anjum *et al.*, 2011). Understanding these phases helps in pinpointing critical intervention points for improving drought tolerance in crops like cotton.

Sensitivity of cotton to water deficit conditions: Cotton (*Gossypium* spp.) is moderately drought-tolerant compared to other crops, but its growth, development, and yield are significantly affected under prolonged or severe water deficit conditions. Sensitivity to drought varies with the crop's developmental stage, with the flowering and boll development stages being the most critical, as water shortage stress during these periods leads to reduced boll number, fiber quality, and overall yield (Pettigrew, 2004). Early-stage drought may limit leaf area expansion and root development, while late-season drought can accelerate leaf senescence and boll shedding (Basal *et al.*, 2009). Water deficit also disrupts photosynthesis, stomatal conductance, and nutrient uptake, leading to impaired physiological function and lower productivity (Zhang *et al.*, 2010). Despite its deep-rooted nature, cotton's drought sensitivity is heightened under high evaporative demand and poor soil water-holding capacity. Understanding these vulnerabilities is essential for breeding and managing cotton under increasingly variable climate conditions.

Physiological responses of cotton to drought stress: Cotton exhibits a range of physiological responses to drought stress aimed at maintaining water balance and sustaining growth under limited water availability. One of the earliest responses is stomatal closure, which reduces transpiration but also limits CO_2 uptake, leading to decreased photosynthetic efficiency (Chaves *et al.*, 2009). Leaf water potential and relative water content typically decline under drought, resulting in reduced cell turgor and leaf expansion. This often causes a decrease in leaf area index and biomass accumulation (Pettigrew, 2004). Drought stress also prompts root system adjustments, with deeper or more extensive root growth enhancing water uptake from subsoil layers (Kamal *et al.*, 2021). In addition, water use efficiency may improve temporarily under moderate stress due to reduced stomatal conductance, although prolonged stress generally leads to metabolic disruptions and lower overall productivity. Understanding these physiological responses is crucial for improving cotton's drought resilience through breeding and agronomic strategies.

Table 1. Genes related to drought tolerance in cotton.

Gene	**Function**	**Reference**
StDREB2	Enhanced proline and protein accumulation Scavenge, antioxidants, and upregulate genes associated with stress	Esawi & Alayafi, 2019
MAPKs	Defense responses, regulate numerous physiological responses	Zhang *et al.*, 2021
DgCspC	Improve drought and other abiotic stress resistance in cotton promotes the synthesis of proline and betaine	Xia *et al.,* 2022
Ac1-SST	Increase the amounts of proline, relative water, soluble sugars (particularly 1-ketose), and malondialdehyde.	Liu *et al.*, 2022
GhCDPK60	Regulate proline and ROS level	Yan *et al.*, 2022
GhSS9	Regulates drought tolerance, starch synthase	Dai *et al.*, 2023
GaZnF	During drought, increase cotton's stomatal conductance, transpiration rate, photosynthesis, and chlorophyll content	Batool *et al.*, 2023
SikCOR413PM1	Drought tolerance is improved by increased antioxidants, decreased peroxide content, enhanced soluble sugar levels, and the regulation of genes linked to stress, osmotic adjustment factors, and peroxide content	Wang *et al.*, 2023
GhdadD	Increased ABA pathway resilience in plants against salt stress and drought. Reduced soluble sugar contents, Increased MDA contents depressed stoma opening under drought or salt stress	Zhang *et al.*, 2024
GhHH3	Involved in plant growth and development, ovule development. Expressed during drought stress. improve drought tolerance in cotton breeding	Qanmber *et al.*, 2019; Sarwar *et al.,* 2025
GhIDD	Role in both seed and fiber development, involved in stress resistance, improving drought tolerance in cotton breeding	Ali *et al.*, 2019; Sarwar *et al.*, 2025

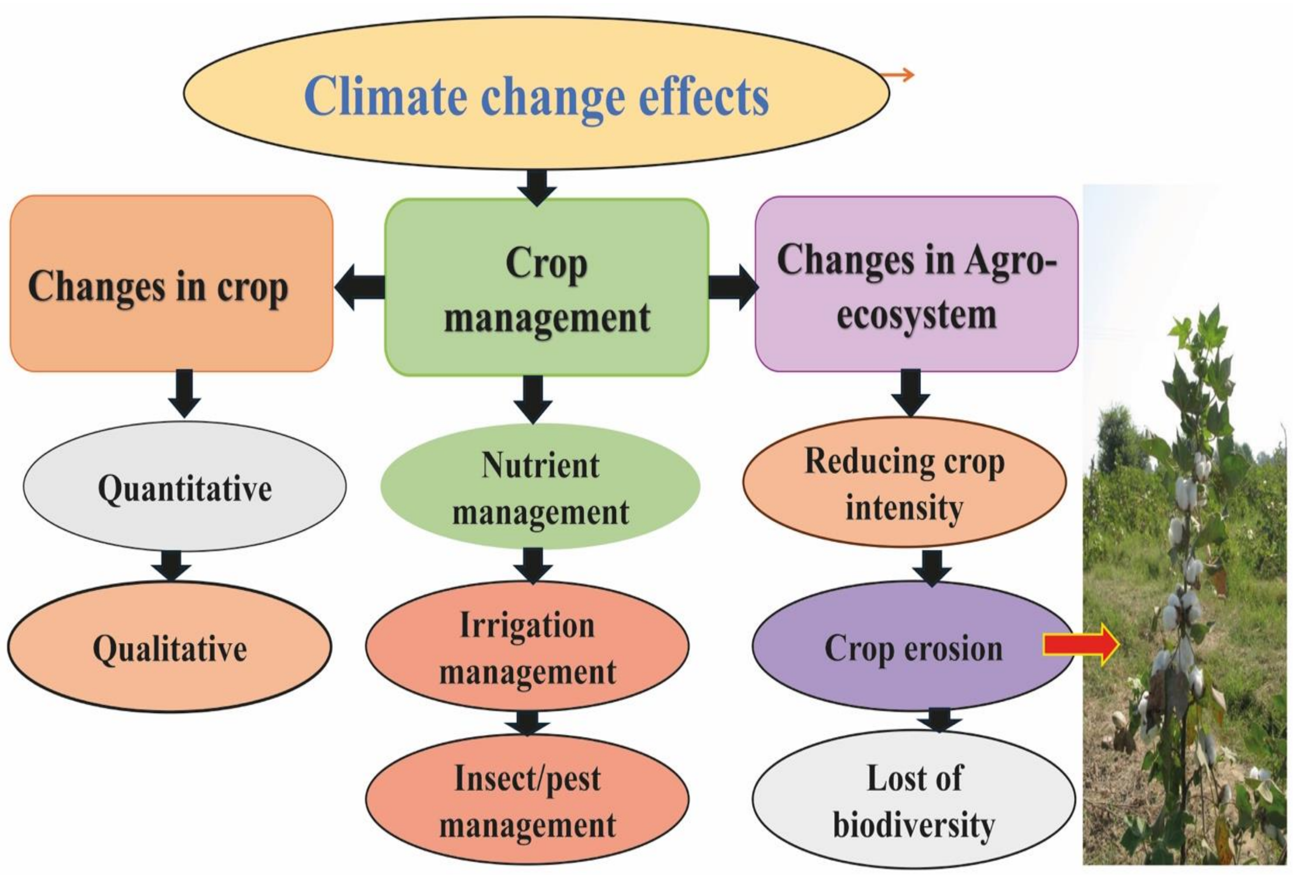


Fig. 2. Climate change effects cotton crop.

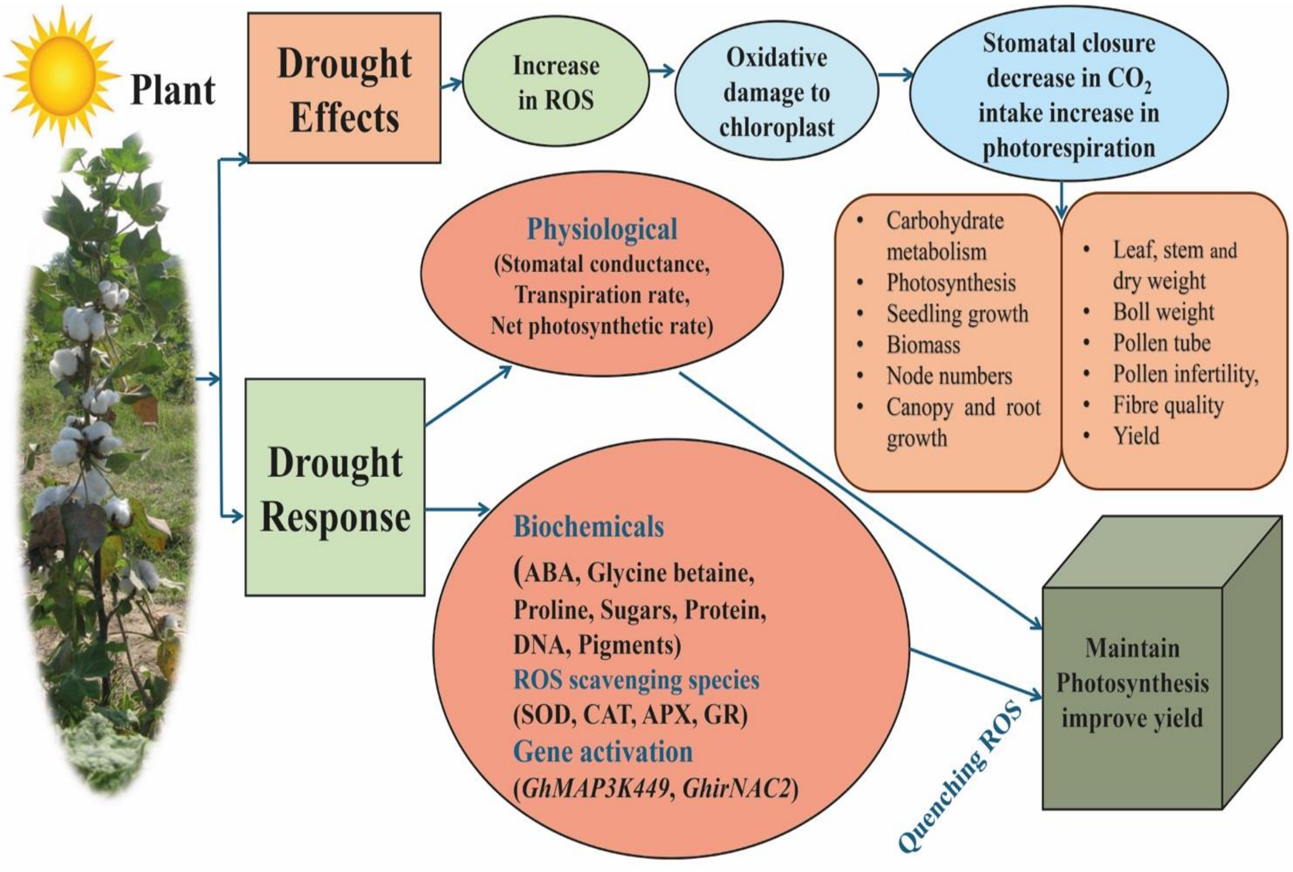


Fig. 3. Effect of drought stress on cotton plant linked to quality traits and yield.

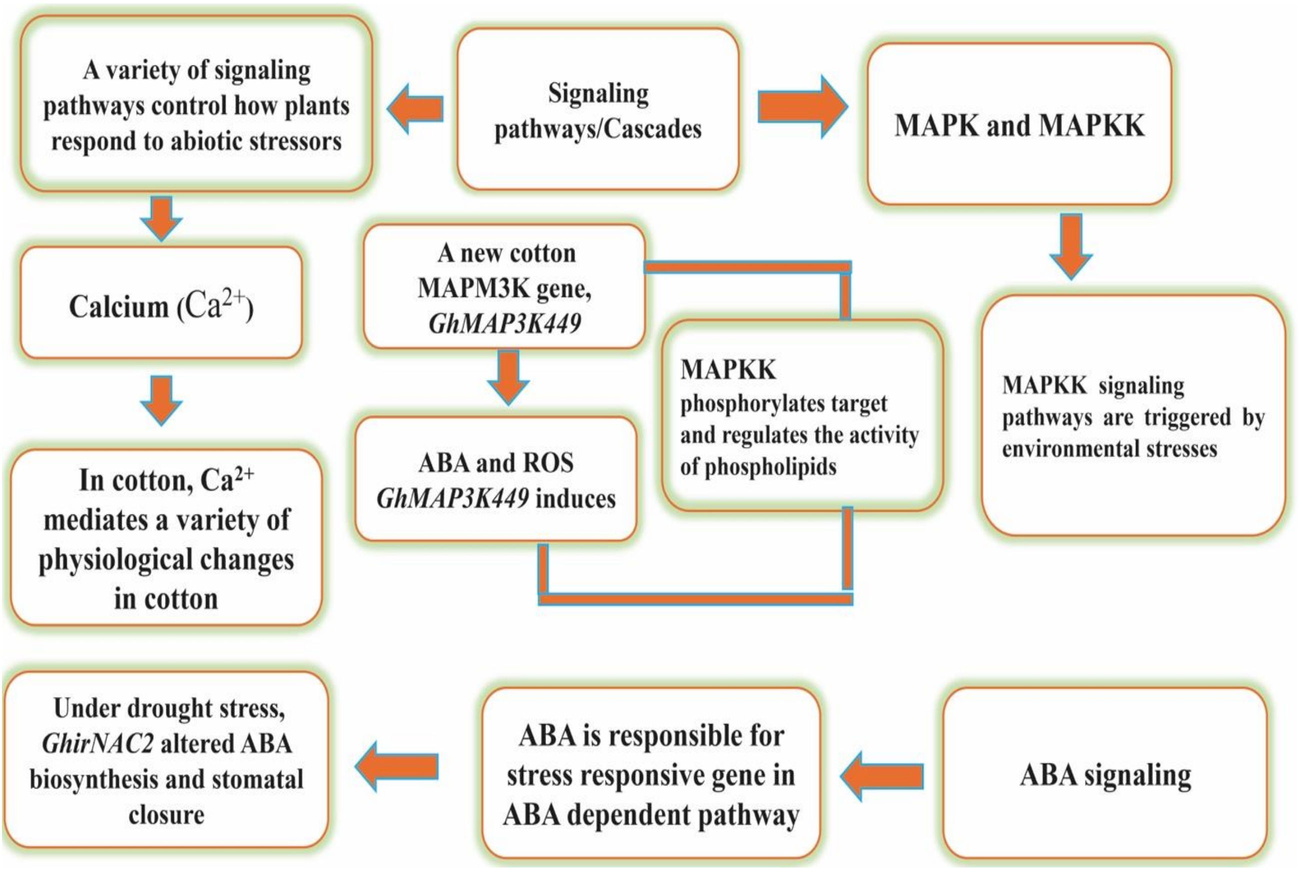


Fig. 4. Signaling Pathways for drought tolerance in cotton Multiple genes and their interconnected networks govern drought tolerance, and MAPK, Ca^{2+} and ABA signaling are crucial for cotton drought resistance.

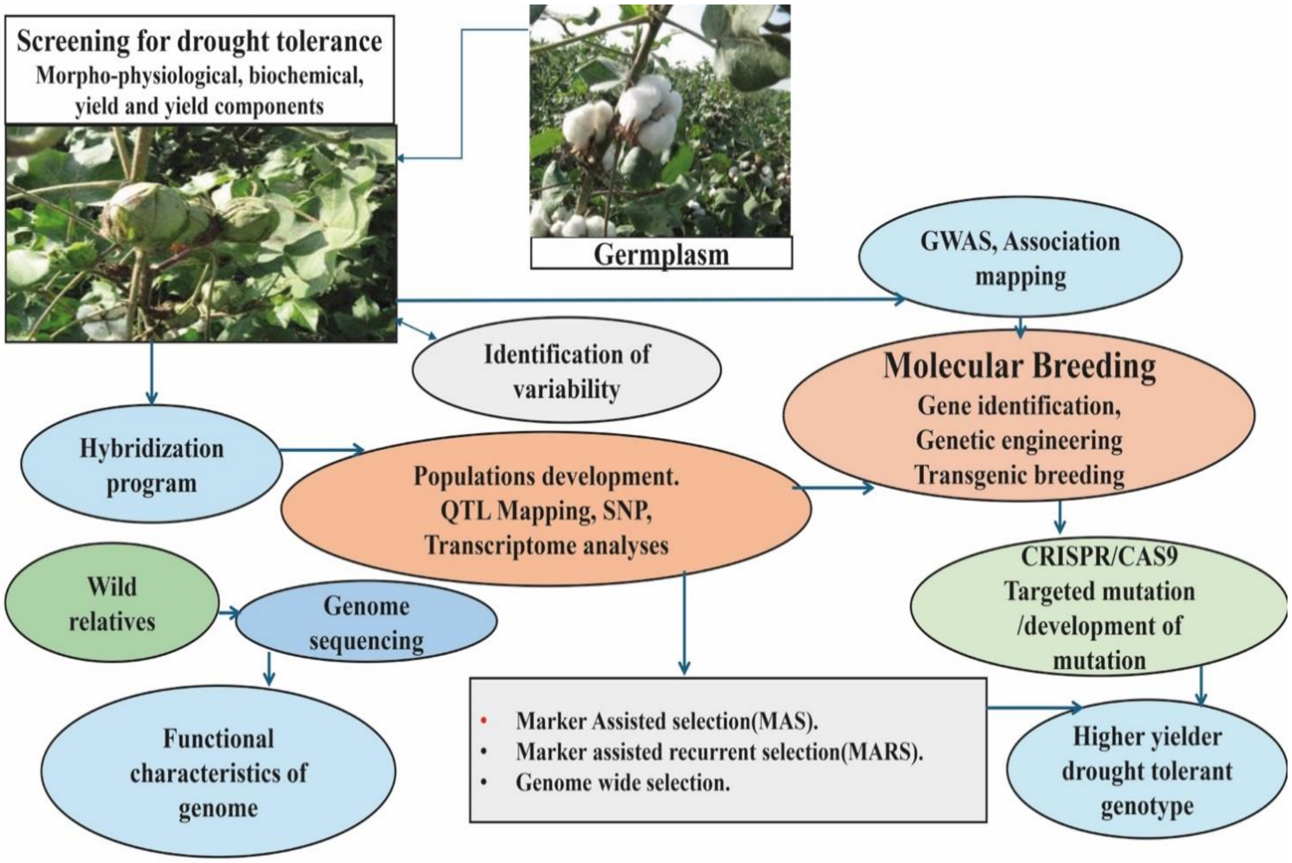


Fig. 5. Drought-tolerant cotton genotypes: A forward-thinking technique that may be used to speed the drought breeding program.

Changes in stomatal conductance and transpiration: Drought stress directly affects stomatal conductance in cotton, leading to reduced transpiration and photosynthesis. Stomata regulate gas exchange, and their closure under water deficit limits CO_2 uptake, thereby impairing photosynthetic activity and plant growth (Iqbal *et al.*, 2013; Ullah *et al.*, 2017). The degree of stomatal conductance varies depending on genotype, leaf type, and environmental factors such as temperature and leaf age (Ackerson *et al.*, 1985; Chastain *et al.*, 2014). For instance, cotton genotypes with okra-type leaves exhibit lower stomatal conductance, a trait associated with enhanced drought resistance (Pettigrew, 2004). Identifying genotypes with optimal stomatal behavior is vital for breeding drought-tolerant cotton cultivars.

Photosynthetic pigments and drought stress: Photosynthetic pigments, primarily chlorophyll a and b, play a key role in light absorption and energy production. Under drought conditions, these pigments degrade due to oxidative stress and photo-oxidation, resulting in reduced photosynthetic efficiency (Farooq *et al.*, 2009; Hamayun *et al.*, 2010). Carotenoids help mitigate oxidative damage. Reduced chlorophyll content-commonly observed in stressed cotton is an early indicator of physiological damage and correlates with lower yield attributes like boll weight and seed index (Pauli *et al.*, 2017; Rizwan *et al.*, 2022). Hence, pigment stability can serve as a marker for selecting drought-tolerant genotypes (Sahito *et al.*, 2015; Zhou *et al.*, 2022).

Modulation of photosynthesis and chlorophyll content: Photosynthesis in cotton is impaired by both stomatal and non-stomatal limitations under drought. Stomatal closure reduces CO_2 influx, while oxidative stress and enzyme inhibition particularly of Rubisco further diminish carbon assimilation (Chaves *et al.*, 2003; Li *et al.*, 2025). Damage to chloroplasts also reduces chlorophyll content and light absorption capacity, thus lowering photosynthetic performance (Anjum *et al.*, 2011; Farooq *et al.*, 2025). However, drought-tolerant genotypes often retain higher chlorophyll levels and better photosynthetic efficiency, making these traits promising targets in breeding programs.

Alterations in water use efficiency (WUE): WUE, defined as the biomass or carbon gained per unit water transpired, is a critical indicator of drought adaptation. Moderate drought may enhance WUE via partial stomatal closure, which limits water loss more than carbon uptake (Flexas *et al.*, 2004). However, prolonged stress impairs both gas exchange and metabolic activity, ultimately decreasing WUE (Shani *et al.*, 2025). Genetic variability exists in cotton for WUE, with some cultivars showing superior performance under drought due to better stomatal regulation and photosynthetic resilience (Pettigrew, 2004).

Growth and biomass allocation under drought: Drought reduces overall cotton growth by limiting leaf expansion, cell division, and photosynthetic output (Shani *et al.*, 2025). To adapt, cotton reallocates biomass from shoots to roots, increasing the root-to-shoot ratio and enhancing deep water absorption (Basal *et al.*, 2009). However, this reallocation limits shoot growth, leaf area index, and yield. Drought during flowering and boll development stages further exacerbates yield losses (Pettigrew, 2004). Therefore, selecting genotypes that balance biomass allocation and maintain reproductive output under drought is vital.

Drought and physiological adaptations: At the onset of drought stress, plants experience disruption in osmotic balance, leading to cellular dehydration, reduced vacuolar and cytosolic contents, and stomatal closure, which restricts growth (Thompson & Islam, 2021). These physiological changes significantly impair cotton growth, reducing plant height, fresh and dry weights of shoots and roots, leaf area, photosynthesis, and transpiration rates. In severe cases, drought stress can reduce both fiber quality and yield (Zahoor *et al.*, 2017; Gao *et al.*, 2020). Studies have shown that drought affects various aspects of cotton growth, such as boll weight, flowering, boll formation, and seed index (Gao *et al.*, 2020). Cotton plants synthesize osmolytes, such as proline, glycine betaine (GB), and sugars, which are critical for maintaining cellular water balance during drought conditions. These osmolytes not only help cotton plants survive under water-deficit conditions but also serve as potential indicators for identifying drought-resistant genotypes (Fig. 3).

Drought stress and cotton productivity: Drought, intensified by climate change, severely limits cotton productivity, especially during flowering and boll formation key yield-determining stages (Mooney *et al.*, 2009 ; Iqbal *et al.*, 2023). Global data show drought can reduce cotton yield by up to 67% (Riyazuddin *et al.*, 2023; Zafer *et al.*, 2023). Besides drought, abiotic factors such as heat waves, erratic rainfall, and salinity also impact productivity, with drought ranked as the most critical (Ton, 2011). These factors disproportionately affect smallholder farmers, emphasizing the need for climate-resilient cotton varieties.

Drought and cotton crop management: Climate change has heightened stress on cotton production through rising temperatures and irregular rainfall (Ullah *et al.*, 2022). Cotton is especially vulnerable to such abiotic stresses, with high temperatures (above 36°C) impairing flower and boll development (Ali *et al.*, 2009; Ekinci *et al.*, 2017). These issues are compounded by reduced irrigation and increased salinity, particularly in major cotton-growing regions (Ton, 2011). Drought-tolerant cotton varieties, supported by modern breeding tools such as functional genomics and CRISPR/Cas9, are essential for mitigating yield losses (Mahmood *et al.*, 2020).

Biochemical responses of cotton to drought stress: Cotton plants respond to drought stress by activating various biochemical, physiological, and molecular mechanisms that aim to minimize cellular damage and maintain metabolic function. One of the primary biochemical responses is the accumulation of osmolytes such as proline, glycine betaine, and soluble sugars, which help maintain cell turgor and protect cellular structures from dehydration (Hasanuzzaman *et al.*, 2018). Among these osmolytes, proline functions both as an osmoprotectant and a reactive oxygen species (ROS) scavenger, helping to stabilize proteins and membranes during drought stress (Szabados & Savouré, 2010). Glycine betaine and trehalose also play important roles in maintaining cell viability and regulating turgor pressure under water stress conditions (Liu & Lu, 2016).

Drought stress further induces antioxidant defense systems in cotton, including key enzymes such as superoxide dismutase (SOD), catalase (CAT), and peroxidases (POD). These enzymes work to detoxify ROS that are generated during oxidative stress, thereby protecting vital cellular components and supporting overall plant tolerance (Wang *et al.*, 2018). In addition to osmolyte accumulation and antioxidant activity, drought also triggers the production of stress-related hormones, such as abscisic acid (ABA) in particular. ABA plays a pivotal role in regulating stomatal closure, reducing water loss, and activating stress-responsive genes (Zhang *et al.*, 2006). Cotton plants also experience changes in secondary metabolites, such as phenolics and flavonoids, which contribute to drought tolerance by acting as antioxidants and signaling molecules (Dixon & Paiva, 1995). These coordinated biochemical responses are essential for sustaining growth and productivity under drought conditions and are critical targets for improving cotton resilience.

Drought tolerance in cotton is a complex trait involving the integration of biochemical, cellular, and physiological events (Zahoor *et al.*, 2017). These include the accumulation of solutes and osmolytes, reduced transpiration, adjustments in stomatal behavior, and the activation of antioxidant defense systems (Joshi *et al.*, 2016). Under drought stress, cotton experiences negative effects on yield components, such as fiber quality, bloom production, boll size, and seed index, with substantial yield reductions often linked to boll loss (Qian *et al.*, 2020). Moreover, hormonal imbalances under drought contribute to square and boll shedding, compounding yield loss (Snowden *et al.*, 2014).

Biochemical traits including the accumulation of glycine betaine (Sarwar *et al.*, 2006), proline (Chattha *et al.*, 2021b) and soluble sugars (Zahid *et al.*, 2021), as well as enzymatic and non-enzymatic antioxidants play a central role in helping cotton maintain metabolic activity and cope with drought (Liu & Lu, 2016). These traits not only support physiological functioning but also correlate with improved yield components, making them valuable indicators for drought tolerance in breeding programs (Langat *et al.*, 2019). These parameters provide quantifiable traits that can guide breeding efforts and help identify drought-resilient cotton genotypes.

Osmolytes and their role in drought tolerance: Drought is one of the major abiotic stresses that adversely affect plant growth, development, and productivity. In response to water stress, plants activate a series of physiological and biochemical mechanisms to enhance their survival and maintain cellular functions. Among these responses, the accumulation of osmotically active substances, known as osmolytes, plays a crucial role in enabling plants to tolerate drought conditions.

Osmolytes are small organic molecules that contribute to osmotic adjustment, which is a vital process during drought stress. These substances include organic acids, proline, sugars, and glycine betaine. Under water-deficit conditions, the concentration of these solutes increases in plant tissues, which aids in regulating water movement by promoting endosmosis the inward movement of water thereby maintaining cell turgor pressure. This osmotic regulation helps in sustaining cellular hydration and physiological functions despite the limited external water availability.

Among the various osmolytes, proline is particularly significant. It acts as a key osmoprotectant during drought stress, facilitating osmotic adjustment and protecting cellular structures. Proline not only stabilizes proteins and membranes but also scavenges reactive oxygen species (ROS), thus playing a dual role in stress tolerance.

Additionally, the maintenance of chlorophyll content, pigment levels, and stomatal conductance is essential for preserving photosynthetic activity during drought (Loka & Oosterhuis, 2013). Osmolytes such as proline and glycine betaine interact closely with chlorophyll and other photosynthetic components to enhance the efficiency of photosynthesis. This improved photosynthetic performance contributes significantly in maintaining plant biomass and yield even under limited water conditions. The combined effect of these physiological and biochemical adjustments enhancing the drought resilience of plants. For instance, in cotton, these mechanisms allow the plant to continue growing and reproducing under stress, thereby improving its overall drought tolerance (Ranganayakulu *et al.*, 2013). The osmolytes serve as crucial elements in the plant's defense against drought stress by facilitating water retention, protecting cellular structures, and supporting photosynthesis. Their role is integral to plant adaptation strategies aimed at sustaining growth and productivity in arid and semi-arid environments.

Role of glycine betaine in drought tolerance: Drought stress significantly affects cotton growth, yield, and fiber quality. Among the various adaptive mechanisms, osmolytes such as glycine betaine (GB) have emerged as crucial components in mitigating the adverse effects of drought. Glycine betaine, a quaternary ammonium compound, functions as an important osmoprotectant that helps cotton plants to maintain cellular homeostasis under abiotic stress, particularly drought (Ranganayakulu *et al.*, 2013).

Under drought conditions, GB accumulates in cotton tissues and shows a positive correlation with cotton yield (Fig. 3). It plays a multifaceted role in enhancing drought tolerance by protecting chloroplasts, stabilizing photosynthetic machinery, and maintaining cell membrane integrity (Quan *et al.*, 2004; Sarwar *et al.*, 2006). The osmoprotective action of GB contributes to improved water retention, cellular stability, and photosynthetic efficiency.

Several studies have demonstrated that cotton genotypes capable of accumulating higher levels of GB tend to exhibit enhanced drought tolerance and increased seed cotton yield (Sarwar *et al.*, 2006; Prajapat *et al.*, 2018). Specifically, GB accumulation has been linked in improving boll weight, boll number, and overall seed cotton yield under drought stress (Singh *et al.*, 2021). Moreover, cultivars with elevated GB concentrations generally perform better under both well-watered and water-limited conditions, positioning GB as a valuable biochemical marker for the selection of drought-tolerant cotton varieties (Prajapat *et al.*, 2018).

In addition to natural accumulation, external strategies such as the exogenous application of GB have also been effective. These applications help to alleviate photoinhibition and enhance antioxidant enzyme activities, thereby supporting plant resilience under drought (Kurepin *et al.*, 2015; Pan *et al.*, 2019; Ramazanoglu *et al.*, 2024). Furthermore, overexpression of genes responsible for GB biosynthesis has been shown to improve drought resistance significantly, making genetic engineering a promising avenue for enhancing GB levels in cotton plants.

Conventional breeding alone may not sufficiently address the challenges posed by increasing drought frequency and severity due to climate change. Therefore, integrating modern molecular tools and focusing on biochemical markers like GB is crucial for advancing drought-tolerant cotton breeding programs. By selecting genotypes with higher endogenous GB levels or engineering pathways to boost GB synthesis, it is possible to develop resilient cotton cultivars capable of sustaining high yield and quality in water-limited environments.

Role of proline in drought tolerance: Proline is a key amino acid that accumulates in plants under environmental stresses, particularly drought. Acting as a multifunctional molecule, proline serves primarily as an osmolyte, stabilizing proteins and cellular structures, and scavenging reactive oxygen species (ROS), thus mitigating oxidative stress during dehydration (Szabados & Savoure, 2010). Besides its osmoprotective role, proline also acts as a signaling molecule, influencing mitochondrial function, gene expression, and cell proliferation, all of which contribute to enhanced stress recovery (Szabados & Savouré, 2010).

In cotton, proline plays a critical role in facilitating osmotic adjustment under low water potential, helping the plant maintain cell turgor and metabolic activity during drought conditions (Ozturk *et al.*, 2021). Accumulation of proline has been consistently observed in cotton genotypes exposed to water deficit, highlighting its importance in drought tolerance mechanisms.

Research on diverse cotton genotypes supports the significant association between proline accumulation and enhanced drought resilience. Niu *et al.*, (2018) demonstrated that proline buildup could be used as a reliable biochemical marker for evaluating drought tolerance in cotton genotypes (Fig. 3). Similarly, Zou *et al.*, (2020) reported that elevated proline levels under drought stress stimulate seedling growth and activate key antioxidant enzymes, such as catalase and superoxide dismutase, which protect root tissues from oxidative damage.

Earlier studies have also confirmed the positive correlation between proline concentration and cotton yield under drought conditions. Stress-tolerant cotton cultivars tend to accumulate more proline than stress-sensitive ones, reinforcing its role in plant survival and recovery (Deeba *et al.*, 2012; Mwadzingeni *et al.*, 2016). Chattha *et al.*, (2021b) observed increases in proline concentration by 38.68% and 37.70% under well-watered and water-limited conditions, respectively, demonstrating its critical function in maintaining physiological performance.

Furthermore, higher proline accumulation during drought has been positively linked to improved yield outcomes. Chattha *et al.*, (2021a) found a strong association between proline levels and seed cotton yield, suggesting that proline served not only as a stress mitigator but also as a yield-protective mechanism. This relationship underlines the potential of using proline as a selection criterion in breeding programs aimed at developing drought-tolerant cotton cultivars.

Role of soluble sugars in drought tolerance: The accumulation of soluble sugars is a vital physiological response that supports drought tolerance in cotton plants. During water-deficit conditions, plants modify their metabolism to adapt to the reduced rate of photosynthesis. In such scenarios, non-photosynthetic tissues like roots and stems function as carbon sinks, ensuring the continued operation of essential metabolic processes. Soluble sugars, particularly sucrose, are translocated from photosynthetic tissues (leaves) to these sinks to sustain metabolic activity during drought (Watanabe *et al.*, 2000).

Soluble sugars act as osmolytes and play a central role in osmotic adjustment by maintaining cell turgor pressure. This function is critical during drought conditions when water availability is limited. In cotton, the accumulation of sugars helps protect cell membranes and proteins from oxidative damage caused by water stress (Chen *et al.*, 2011; Kadkhodaie *et al.*, 2014). These protective mechanisms make soluble sugars essential components of the plant's biochemical defense system. The production and accumulation of soluble sugars under drought stress are influenced by the genotype of the cotton plant and the specific nature of the drought stress applied (Morsy *et al.*, 2007). Moreover, soluble sugars have been identified as reliable physiological markers of drought tolerance, especially during critical growth phases such as flowering and boll development (Nosrati *et al.*, 2014; Kuai *et al.*, 2014).

Drought stress also impacts the source-sink relationship in cotton. For instance, the outward transport of sucrose from developing bolls is disrupted, which reduces boll biomass accumulation (Changqin *et al.*, 2014). In addition, studies by Timpa *et al.* (1986) and Liu *et al.* (2004) revealed that drought conditions resulted in increased levels of hexose sugars and decreased starch accumulation in cotton leaves. These alterations highlight the plant’s shift in carbohydrate metabolism as an adaptive response to drought. Ultimately, changes in soluble sugar content are closely linked to cotton yield. By contributing to osmotic balance, protecting cellular components, and sustaining carbon allocation under drought, soluble sugars help mitigate yield losses. Their multifunctional role emphasizes their significance in breeding and management strategies aimed at enhancing cotton’s drought resilience.

Role of protein accumulation in drought tolerance: Proteins are vital for maintaining cellular structure and functionality, especially under adverse conditions. The synthesis of stress-induced proteins contributes to osmotic balance and helps stabilize cellular membranes during dehydration stress (Eisenstein, 2023). These proteins play a critical role in enabling cotton plants to adapt to and survive water-deficit environments. Research has shown that drought stress can accelerate the accumulation of total soluble proteins in cotton. Elevated protein content is frequently linked to improved drought tolerance and increased yield potential (Vaidya *et al.*, 2015; Kaur and Kumar, 2020). This adaptive response is especially crucial during extended periods of water scarcity.

In an investigative study by Parida *et al.* (2007), protein levels were analyzed in two cotton accessions exposed to drought stress. Their findings revealed that minor fluctuations in protein content during short dry spells had a negligible impact on overall protein synthesis. However, under prolonged drought conditions, significant changes were observed. Specifically, a decrease in soluble protein content was recorded in cotton roots when soil moisture levels dropped to 45% and 60% relative water content over several days (Niu *et al.*, 2018). Overall, the accumulation of soluble proteins under drought stress is an essential adaptive mechanism in cotton. These proteins not only support structural and functional stability but also enhance the plant's resilience and productivity under water-limited conditions.

Cottonseed protein and yield under drought stress: Drought stress significantly impacts the physiological and biochemical traits of cotton plants, with notable effects on cottonseed composition and overall yield. One of the key components affected is the protein and oil content in cottonseed kernels, which are vital determinants of cottonseed quality and economic value. Research by Li *et al.* (2022) has demonstrated that cottonseed yield is markedly reduced under drought conditions. This reduction is primarily attributed to a decrease in both single-seed weight and the total number of seeds produced per plant. Such yield losses highlight the sensitivity of cotton reproductive development to water deficits. An interesting observation is the inverse relationship between protein and oil content in cottonseed under drought stress. While protein levels tend to increase and oil content often declines. This negative correlation suggests a trade-off in seed composition, where the plant prioritizes protein synthesis, potentially as a protective mechanism to maintain seed viability and functionality during stress.

Protein accumulation in cottonseed kernels during drought may serve multiple purposes. It can enhance the structural integrity of seeds, support enzymatic functions, and contribute to stress resistance, thereby improving the chances of successful germination and seedling establishment under unfavorable conditions. However, this adaptive response appears to come at the cost of reduced oil synthesis, which could affect the commercial value of the crop, especially in varieties cultivated for oil extraction. Drought-induced changes in cottonseed protein and oil content reflect the plant's physiological adjustments aimed at survival and reproductive success. While increased protein levels may support seed viability, the concurrent reduction in oil content poses a challenge for maintaining both seed quality and yield. Understanding these dynamics is crucial for developing cotton varieties with improved drought resilience and optimal seed composition.

Implications for breeding: Drought stress poses a significant challenge to cotton production, influencing key physiological traits such as photosynthetic pigment concentration, soluble sugar accumulation, stomatal conductance, and osmotic adjustment. These factors are closely linked to the plant's ability to maintain growth and productivity under water-limited conditions. Among these traits, chlorophyll content**,** soluble sugars, and osmoprotectants have been identified as critical components in sustaining photosynthetic activity and cellular stability during drought. Soluble sugars contribute to osmotic adjustment and carbon allocation, while chlorophyll levels reflect the integrity of photosynthetic machinery. Similarly, stomatal conductance regulates water loss and gas exchange, making it a crucial determinant of drought adaptation.

Understanding these physiological and biochemical responses is essential for guiding cotton breeding programs aimed at developing drought-resilient cultivars. Identifying and selecting genotypes that exhibit enhanced traits, such as superior photosynthetic efficiency, improved osmotic regulation, and optimal stomatal behavior can lead to varieties better suited for arid and semi-arid regions. With the increasing threat of climate change and shifting rainfall patterns, the integration of these physiological markers into breeding strategies is vital. By focusing on drought-responsive traits, breeders can develop cotton varieties that sustain higher yields and better fiber quality under water-deficient conditions, thereby securing agricultural productivity and farmer livelihoods in vulnerable regions.

Use of osmoprotectants in breeding for drought tolerance: Osmotic adjustment is a vital physiological mechanism that enables plants to endure water stress by maintaining cell turgor and functional stability. In response to drought, cotton plants accumulate various osmoprotectants, including proline, free amino acids, sugars and glycine betaine, which help mitigate the damaging effects of water deficit on cellular structures and metabolic processes (Chen and Murata, 2011).

These osmolytes function by stabilizing proteins and cellular membranes, protecting cells from oxidative stress, and sustaining physiological processes under conditions of limited water availability (Khan *et al.*, 2015). Their role is not only limited to drought resistance but also extends to coping with salinity stress, highlighting their broader significance in plant stress physiology. Experimental evidence supports the beneficial effects of exogenous application of osmoprotectants in improving cotton's drought resilience. Furthermore, transgenic cotton plants engineered to accumulate higher levels of glycine betaine have shown enhanced tolerance to drought. These plants demonstrate improved photosynthetic performance, better osmotic regulation, and lower lipid peroxidation, which collectively contribute to improved drought stress adaptation (Fang and Xiong, 2015). The ability to manipulate osmoprotectant levels, either through breeding strategies **or** genetic engineering, offers a promising pathway for enhancing drought tolerance in cotton. Integrating traits related to osmolyte accumulation into breeding programs can lead to the development of cotton cultivars that are more resilient to climatic stresses, particularly in arid and semi-arid regions.

Proline and protein in breeding for drought tolerance: Drought stress significantly affects cotton growth, development, and productivity. One of the key adaptive strategies in cotton under water deficit conditions is the accumulation of osmolytes and stress-responsive proteins, which play essential roles in maintaining cellular function and structural stability during dehydration.

Among these osmolytes, proline is especially important. It functions as an osmoprotectant by stabilizing proteins and membranes, scavenging reactive oxygen species (ROS), and contributing to osmotic adjustment. Due to its consistent accumulation under drought stress, proline has been widely recognized as a reliable biochemical marker for assessing drought tolerance in cotton (Niu *et al.*, 2018; Chattha *et al.*, 2021a).

In parallel, the accumulation of soluble proteins during drought stress supports metabolic activity and reinforces the structural integrity of plant cells, contributing to overall stress adaptation and recovery. These proteins enhance cotton's resilience by helping the plant in maintaining essential physiological processes under limited water availability. Understanding the functional roles of proline and stress-related proteins is critical for breeding programs targeting drought-prone environments. Selecting genotypes that exhibit higher proline content and efficient protein accumulation under drought conditions can accelerate the development of drought-tolerant cotton cultivars with improved yield stability.

Given proline's central role in enhancing drought resistance, it has been widely proposed as a biochemical marker for screening cotton genotypes. Drought-tolerant cultivars typically exhibit higher proline levels, making this trait valuable for selecting varieties that perform well under water-limited conditions. Research by Singh *et al.* (2021) and Chattha *et al.* (2021b) further supports the utility of proline as a selection tool in breeding, showing strong correlations between proline accumulation and seed cotton yield. Moreover, the combined accumulation of proline and proteins enhances cotton's physiological capacity to cope with drought by preserving cellular homeostasis and supporting growth under stress. Recent studies confirm that genotypes with elevated proline and protein levels tend to exhibit improved seed cotton yield and overall drought resilience. As such, integrating proline content as a selection criterion into breeding pipelines is essential for developing cotton cultivars capable of sustaining productivity amid climate variability and increasing water scarcity.

Adaptive strategies for enhancing drought resilience in cotton agriculture: Climate change presents escalating challenges to cotton production, including rising temperatures, increased water scarcity, and the growing frequency of extreme weather events. In response, it is vital to implement adaptive strategies that combine scientific innovation with policy support to ensure the long-term sustainability of cotton farming. A central focus of adaptation lies in the development of drought-resistant cotton cultivars. These efforts are critical for maintaining productivity under variable and often harsh environmental conditions. The research discussed in this study underscores the significance of understanding the physiological, biochemical, and molecular mechanisms underlying drought resistance. Such knowledge forms the foundation for targeted breeding programs that are aligned with both current climatic challenges and the future resilience needs of cotton crops.

Moreover, integrating these scientific advancements with climate-resilient agricultural practices and sustained investment will enable cotton farming systems to better withstand environmental stressors. This not only supports global food and fiber security but also contributes to the economic stability of regions dependent on cotton production.

Morphological adaptation for drought tolerance in cotton: Drought stress is one of the most critical abiotic factors limiting cotton growth, development, and yield. It not only affects the physiological and biochemical processes of the plant but also significantly influences various morphological traits, which are essential indicators of a plant's ability to withstand water-deficient conditions. At the onset of drought, key physiological functions such as gas exchange, photosynthesis, and transpiration efficiency begin to deteriorate, resulting in reduced stomatal permeability and disrupted metabolic activity (Deeba *et al.*, 2012). These physiological impairments translate into visible morphological changes, which are part of the plant's adaptation mechanisms to reduce water loss and maintain productivity.

Several morphological traits have been identified as crucial in conferring drought tolerance in cotton. These include: Reduced plant height and compact plant architecture, which limit the transpiration surface area and conserve water. Smaller and thicker leaves, which reduce stomatal density and transpiration rates. Deeper and more extensive root systems, which enhance the plant's ability to extract water from deeper soil layers. Leaf rolling or leaf wilting, as protective mechanisms to reduce water loss.

Under prolonged drought stress, significant reductions are observed in important agronomic characteristics, such as boll size, boll number per plant, plant height, fresh biomass, and seed cotton yield (Bakhsh *et al.*, 2019; Saleem *et al.*, 2020). These reductions directly impact the quantity and quality of cotton fiber, further emphasizing the importance of drought adaptation. Morphological traits are not only the result of immediate stress responses but also reflect the plant's genetic capacity to adapt over time. As such, these traits are often used as selection criteria in breeding programs aimed at developing drought-tolerant cotton cultivars. For instance, cotton genotypes exhibiting enhanced root growth, robust stem development, and stable reproductive traits under drought conditions are considered more resilient and are preferred in drought-prone agricultural regions. Morphological adaptations play a pivotal role in enhancing cotton's drought tolerance. Traits such as reduced canopy size, optimized leaf structure, and efficient root systems enable cotton plants to survive and produce under limited water availability. Recognizing and utilizing these traits in breeding and management strategies is essential for sustaining cotton productivity in the face of increasing climate variability.

Physiological adaptation for drought tolerance in cotton: Drought stress is a major environmental factor affecting cotton (*Gossypium* spp.) growth, development, and productivity. The plant's ability to survive and maintain yield under water-deficit conditions depends largely on its physiological adaptations, which help mitigate the adverse effects of reduced water availability.

One of the key physiological responses to drought is osmotic adjustment, wherein cotton plants accumulate compatible solutes also known as osmoprotectants such as proline, glycine betaine, and soluble sugars. These compounds help maintain cell turgor, stabilize proteins and membranes, and protect against oxidative damage (Chen and Murata, 2011; Khan *et al.*, 2015). Proline, in particular, has been identified as a critical biochemical marker for drought tolerance and is positively correlated with seed cotton yield under drought conditions (Niu *et al.*, 2018; Chattha *et al.*, 2021a; Singh *et al.*, 2021; Chattha *et al.*, 2021b).

Cotton plants exhibit stomatal regulation as an adaptive mechanism to reduce water loss through transpiration. Under drought stress, stomatal conductance decreases, thereby limiting water loss but also affecting carbon dioxide uptake and photosynthesis (Deeba *et al.*, 2012). Improved water use efficiency (WUE), defined as the ratio of carbon assimilation to water loss, is a desirable trait in drought-tolerant cotton genotypes. Selection for optimal stomatal behavior can contribute to sustained growth under water-limited conditions.

Photosynthetic efficiency is another physiological trait influenced by drought. Drought stress reduces chlorophyll content and affects the light-harvesting capacity of leaves, leading to reduced photosynthesis. However, drought-tolerant cotton cultivars tend to maintain higher chlorophyll levels, supporting better photosynthetic activity even under stress (Loka & Oosterhuis, 2013). The interaction between osmoprotectants like proline and glycine betaine with chlorophyll also contributes to the preservation of photosynthetic function and biomass production (Ranganayakulu *et al.*, 2013).

A well-developed root system is essential for physiological adaptation to drought. Deeper and more extensive roots improve water uptake from lower soil profiles, maintaining water supply to aerial parts. This supports turgor maintenance and metabolic function during drought episodes. Drought induces the generation of reactive oxygen species (ROS), which can cause oxidative damage to lipids, proteins, and DNA. Cotton plants respond by activating their antioxidant defense system, including enzymes like superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD). These enzymes help detoxify ROS and protect cellular integrity during drought stress.

The integration of physiological traits such as osmolyte accumulation, chlorophyll stability, water use efficiency, and stomatal behavior into breeding programs is essential for developing drought-resilient cotton cultivars. Marker-assisted selection and transgenic approaches are increasingly employed to enhance these physiological traits in elite cotton lines (Zulfiqar *et al.*, 2022; Fang and Xiong, 2015). Physiological adaptations play a vital role in enabling cotton plants to cope with drought stress. Mechanisms such as osmotic adjustment, efficient stomatal control, sustained photosynthesis, strong root systems, and enhanced antioxidant defenses collectively contribute to drought resilience. Understanding these physiological responses and incorporating them into modern breeding strategies is crucial for sustaining cotton production under increasingly unpredictable climate conditions.

Biochemical adaptation for drought tolerance in cotton: Biochemical adaptations involve the accumulation of compatible solutes, modulation of antioxidant enzyme systems, stabilization of proteins and membranes, and changes in metabolic processes, all of which help the plant mitigate the harmful effects of drought.

One of the primary biochemical responses to drought in cotton is the accumulation of osmoprotectants such as proline, glycine betaine, and soluble sugars. These low molecular weight compounds function to maintain cellular osmotic balance, protect cellular structures, and prevent oxidative damage. Proline serves multiple roles under stress: it stabilizes proteins and membranes, scavenges reactive oxygen species (ROS), and contributes to osmotic adjustment. Its accumulation is widely used as a biochemical marker for drought tolerance in cotton (Niu *et al.*, 2018; Chattha *et al.*, 2021a). Studies have also shown a significant correlation between proline content and seed cotton yield under drought stress (Singh *et al.*, 2021; Chattha *et al.*, 2021b).

Glycine betaine plays a protective role by maintaining the integrity of photosynthetic membranes and enzyme activities during water stress (Chen & Murata, 2011). Transgenic cotton lines engineered to accumulate glycine betaine have shown improved drought tolerance through better photosynthesis, reduced lipid peroxidation, and enhanced osmotic balance (Fang & Xiong, 2015). Soluble sugars, such as sucrose and glucose, function as osmolytes and also protect cellular structures from dehydration. Their accumulation contributes to osmotic adjustment and is often observed in drought-tolerant genotypes (Kadkhodaie *et al.*, 2014; Chen & Murata, 2011).

Drought stress leads to increased generation of reactive oxygen species (ROS), which cause oxidative damage to cellular components such as lipids, proteins, and nucleic acids. To counter this, cotton activates its antioxidant defense system, which includes both enzymatic and non-enzymatic components: Enzymatic antioxidants such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) play a critical role in scavenging ROS and protecting the plant from oxidative injury. Non-enzymatic antioxidants, including ascorbate and glutathione, further assist in maintaining cellular redox homeostasis under stress conditions. The enhanced activity of antioxidant enzymes has been correlated with improved drought tolerance in cotton, suggesting that antioxidant capacity is a key biochemical trait for drought adaptation (Khan *et al.*, 2015).

Drought stress also affects protein metabolism, leading to the accumulation of stress-related proteins, such as heat shock proteins (HSPs), late embryogenesis abundant (LEA) proteins, and other protective enzymes. These proteins help stabilize cellular structures, assist in protein folding, and maintain enzymatic activity under stressful conditions (Eisenstein, 2023). Cotton plants under drought stress have been shown to exhibit increased total soluble protein content, which supports stress adaptation and contributes to yield maintenance (Kaur & Kumar, 2020; Vaidya *et al.*, 2015). However, prolonged drought may lead to decreased protein levels in roots and other tissues, depending on the severity and duration of the stress (Niu *et al.*, 2018). Biochemical adaptations form a crucial part of cotton's defense mechanism against drought stress. The synthesis and accumulation of osmoprotectants like proline and glycine betaine, the activation of robust antioxidant defenses, and the modulation of protein metabolism help maintain cellular stability and physiological function during drought. These biochemical traits are not only indicators of stress tolerance but also serve as valuable targets in cotton breeding programs aimed at improving resilience to water-deficient environments.

Molecular adaptation for drought tolerance in cotton: Molecular adaptation plays a critical role in enhancing drought tolerance by regulating the expression of drought-responsive genes, activating signaling pathways, and modifying transcriptional and post-transcriptional responses. These mechanisms work in concert to initiate protective responses, maintain cellular homeostasis, and ensure survival under water-deficient conditions. One of the core components of molecular adaptation in cotton is the differential expression of stress-responsive genes. Under drought stress, genes involved in osmotic adjustment, antioxidant activity, hormone signaling, and stress protein production are upregulated. These include: Dehydration-responsive element-binding proteins (DREBs), Heat shock proteins (HSPs), Late embryogenesis abundant (LEA) proteins, Aquaporins, which facilitate water transport across cell membranes, The transcriptional regulation of these genes is often controlled by specific transcription factors (TFs), such as *DREB*, *NAC*, *MYB*, *WRKY*, and *bZIP* families, which bind to promoter regions of target genes to activate drought-specific responses (Zulfiqar, 2022).

Drought stress and signal pathways in cotton: Plant responses to abiotic stresses such as drought are governed by complex signaling pathways, yet these processes remain underexplored in cotton (Raza *et al.*, 2023). Molecular responses to drought are initiated through signal transduction pathways, primarily involving the plant hormone abscisic acid (ABA). ABA plays a central role in regulating stomatal closure, activating stress-responsive genes, and initiating protective physiological changes. It also controls seed dormancy, germination, and water use efficiency, all of which are critical for plant survival under water-limited conditions (Mittal *et al.*, 2014).

Key signaling molecules such as calcium ions (Ca^{2+}), mitogen-activated protein kinases (*MAPKs*), and reactive oxygen species (ROS) act as secondary messengers that amplify drought signals and coordinate cellular responses (Khan *et al.*, 2015). In cotton, calcium signaling contributes to drought tolerance through genes such as *GhCIPK6*, with changes in Ca^{2+} concentration induced by ABA and drought stress (He *et al.*, 2013). Cotton also utilizes *MAPK* and *MAPK* kinase (*MAPKK*) cascades, which require sequential phosphorylation for proper function. These pathways are activated by environmental stressors like drought, and specific genes such as *GhMAP3K449*, induced by both ABA and ROS, play crucial roles in regulating cotton's drought response (Dongdong *et al.*, 2016).

Furthermore, transcription factors such as *GhirNAC2* are key regulators in cotton's drought response, influencing ABA biosynthesis and stomatal closure—both vital for improving drought resilience (Shang *et al.*, 2020). A comprehensive understanding of the interactions between ABA and *MAPK* pathways is essential to advance molecular breeding techniques aimed at enhancing cotton's drought tolerance.

Modern genetic approaches to overcome the limitations of traditional cotton breeding: Traditional breeding methods have played a significant role in improving cotton yields over time. However, as the global population surpasses 7 billion, the rising demand for food, fiber, and shelter presents mounting challenges for conventional breeding to meet these needs efficiently. One major limitation is the inherently slow reproductive rate of plants, which makes it difficult to rapidly develop new varieties with specific adaptive traits such as drought tolerance, within practical timeframes (Moose *et al.*, 2008; Lyzenga *et al.*, 2021). To overcome these challenges, modern biotechnological tools such as genetic engineering and genome editing have emerged as transformative solutions. When combined with detailed knowledge of physiological and biochemical traits, these advanced methods offer precision and speed in developing resilient crop varieties. Genetic engineering enables the direct introduction of genes associated with enhanced tolerance to abiotic stresses such as drought, salinity, heat, and cold, especially when such traits are not readily available within the natural cotton gene pool (Tanksley *et al.*, 1997; Sharma *et al.*, 2013).

These technologies allow researchers to bypass the limitations of traditional breeding by targeting specific genes responsible for stress adaptation and integrating them into high-yielding cultivars. Moreover, genome editing tools like CRISPR-Cas enable fine-tuned modifications of endogenous genes, further improving stress tolerance without introducing foreign DNA. While traditional breeding has contributed to historical yield improvements in cotton, it falls short of addressing the urgent demands imposed by global population growth and climate change. Genetic engineering and genome editing, especially when guided by physiological and biochemical trait data, offer powerful, targeted solutions for developing drought- and stress-resilient cotton varieties. These tools hold the key to ensuring sustainable cotton production in a rapidly changing world (Tanksley *et al.*, 1997; Moose *et al.*, 2008; Sharma *et al.*, 2013; Lyzenga *et al.*, 2021).

Role of recent research in developing drought-tolerant cotton varieties: Recent studies have made significant strides in identifying key traits for drought resistance in cotton. Sun *et al.*, (2021) assessed 104 cotton genotypes under both normal and drought-stress conditions, finding that traits like plant height, sympodia, boll weight, transpiration rate, and chlorophyll content are essential indicators of drought tolerance. Further research has shown that biochemical traits such as glycine betaine, proline, total soluble sugars, and proteins play a crucial role in evaluating drought resistance in cotton (Sarwar *et al.*,2006; Prajapat *et al.*, 2018; Chattha *et al.*, 2021**b**; Singh *et al.*,2021; Zahid *et al.*, 2021). These findings highlight the importance of screening cotton germplasm for drought resistance based on these biochemical markers. Additionally, the ability of cotton to conserve water during periods of drought is an essential trait, and transpiration rates have been identified as key to sustaining growth during water-deficit conditions (Wedegaertner, 2022).

An assessment of four distinct cotton cultivars under induced water stress revealed significant variations in water-use efficiency, particularly in terms of the fraction of transpirable soil water (FTSW) threshold. These findings underscore the differences in how cotton varieties respond to water limitations and their respective water-saving potentials (Wedegaertner, 2022). Such studies provide valuable insights into selecting and breeding cotton cultivars that can better withstand drought and conserve water during critical growth phases.

Integrated genetic and biotechnological approaches for developing drought-resilient cotton: Enhancing drought resistance in cotton has become a crucial priority amid growing water scarcity and climate variability. To address these challenges, a combination of genetic, molecular, and biotechnological approaches offers promising pathways for developing cotton cultivars capable of sustaining high performance under water-limited conditions.

Transgenic strategies represent one of the most direct approaches for improving drought tolerance in cotton. These methods involve the introduction of genes often from other species-that confer beneficial traits such as enhanced water-use efficiency, deeper root systems, and increased osmoprotectant accumulation. By manipulating drought-responsive genes at the molecular level, transgenic techniques allow for targeted improvements in plant adaptation to water stress. Beyond genetic engineering, molecular breeding tools such as Quantitative Trait Loci (QTL) mapping and Genome-Wide Association Studies (GWAS) have become essential for drought tolerance research. These approaches help identify genomic regions and genetic markers associated with key drought-related traits. Once identified, these markers are used in marker-assisted selection (MAS), enabling breeders to efficiently select parent lines and accelerate the development of drought-tolerant varieties.

A major breakthrough in recent years is the advent of CRISPR-Cas genome editing technology. This powerful tool enables precise, targeted modification of native genes involved in drought response without introducing foreign DNA, making it a more publicly acceptable and potentially regulation-friendly alternative to traditional transgenics (Nguyen *et al.*, 2024). CRISPR can be employed to knock out negative regulators or enhance positive drought-resistance genes, significantly improving stress adaptation. Modern breeding programs are also increasingly focused on broadening genetic diversity and creating novel allelic combinations to strengthen drought resilience. Identifying key genes, signaling networks, and biochemical pathways related to drought stress remains fundamental to enhancing plant responses and maintaining yield under adverse conditions (Zulfiqar *et al.*, 2022). The integration of transgenic methods, molecular breeding tools, and genome editing technologies is revolutionizing drought-resistance breeding in cotton. These innovations are not only increasing breeding efficiency and precision but also reducing development timelines. Collectively, they pave the way toward a more sustainable and resilient cotton production system in the face of climate challenges.

Genomic tools and marker development for drought tolerance in cotton: Advances in molecular biology have significantly enhanced our understanding of drought tolerance in cotton. A key milestone has been the identification of Quantitative Trait Loci (QTLs) and the development of molecular markers associated with drought-resilient traits. Cutting-edge genomic tools such as Genome-Wide Association Studies (GWAS) and RNA-Seq have proven invaluable in identifying candidate genes and regulatory networks involved in cotton's adaptation to drought stress. These technologies form the foundation of marker-assisted selection (MAS), allowing breeders to efficiently screen and develop drought-tolerant cotton genotypes (Zulfiqar *et al.*, 2022).

Research on *Gossypium hirsutum* has increasingly focused on identifying genotypes that can produce osmolytes and maintain essential physiological functions under drought conditions (Anwar *et al.*, 2022). In field trials, drought resistance is evaluated by imposing varying levels of water stress at different growth stages. Agronomic traits such as crop maturity, sympodia formation, seed weight, boll number, boll size and weight, lint percentage, and seed cotton yield are measured to assess the impact of drought on plant performance (Ullah *et al.*, 2017). Additionally, screening for physiological and molecular traits such as osmolyte accumulation, activation of drought-responsive pathways, and yield-related characteristics has provided deeper insight into how cotton plants adapt to water-deficit environments (see Figs. 2, 3, 4). The continuous identification of genes associated with improved yield, growth, and stress tolerance under drought conditions has been vital in advancing our knowledge of drought adaptation mechanisms (Esawi & Alayafi, 2019; Zhang *et al.*, 2021; Xia *et al.*, 2022; Yan *et al.*, 2022; Batool *et al.*, 2023; Dai *et al.*, 2023; Wang *et al.*, 2023; Zhang *et al.*, 2024).

The integration of genomic tools and physiological assessments has revolutionized drought tolerance research in cotton. By linking molecular markers with field-based traits and stress-responsive genes, researchers and breeders can accelerate the development of high-yielding, drought-resilient cotton varieties. Continued exploration of genetic resources and refinement of selection techniques will be essential to ensure sustainable cotton production under increasingly variable climate conditions.

Transgenic and genome editing approaches to enhance drought tolerance in cotton: Transgenic technologies are significantly advanced for improving drought tolerance in cotton by enabling the introduction of drought-responsive genes from other species. These modifications have resulted in enhanced water-use efficiency, increased osmolyte production, and better oxidative stress management. For instance, transgenic cotton lines engineered to overexpress glycine betaine synthesis genes exhibit improved photosynthetic performance and membrane stability under drought conditions, contributing to overall enhanced drought resistance (Fang & Xiong, 2015). More recently, CRISPR-Cas9 genome editing has emerged as a precise and efficient tool for manipulating native genes associated with drought tolerance. Unlike traditional transgenic methods, CRISPR-Cas9 allows for targeted modifications within the cotton genome without the need for foreign gene insertion. This approach is not only scientifically effective but also offers a more publicly acceptable and regulatory-friendly alternative for crop improvement (Nguyen *et al.*, 2024).

In addition to these methods, research has identified several transcription factors that can be leveraged to improve drought resilience in cotton. A prominent example is the Arabidopsis-derived transcription factor *AtHDG11*. When expressed in cotton, *AtHDG11* enhances drought tolerance by promoting root growth, which is essential for water uptake during dry conditions (Yu *et al.*, 2016). These genetic and regulatory advancements are critical for mitigating the harmful effects of drought and maintaining vital physiological processes such as photosynthesis and plant growth in cotton. Transgenic and genome editing technologies offer powerful and complementary approaches for improving drought tolerance in cotton. By integrating stress-responsive genes, transcription factors, and precise genome editing tools like CRISPR-Cas9, researchers can develop resilient cotton varieties capable of thriving in water-limited environments. Continued innovation in these areas will be crucial for ensuring cotton productivity and sustainability under changing climate conditions.

Transcriptomic and proteomic approaches: The development of drought-tolerant cotton varieties has been significantly advanced through transcriptomic and proteomic technologies, which provide comprehensive insights into gene and protein expression changes under drought stress.

Transcriptomic approaches: such as RNA sequencing (RNA-Seq), are used to analyze the expression profiles of drought-responsive genes in cotton. These studies identify key regulatory genes, transcription factors (e.g., *NAC*, *DREB*, *MYB* families), and signaling pathways involved in stress perception, signal transduction, and physiological adaptation. RNA-Seq has enabled the identification of differentially expressed genes (DEGs) in drought-stressed tissues, including roots and leaves, contributing to our understanding of how cotton responds at the molecular level (Zhang *et al.*, 2020; Zhang *et al.*, 2021). For instance, studies have revealed the upregulation of genes involved in abscisic acid (ABA) signaling, osmolyte biosynthesis, and antioxidant defense mechanisms.

Proteomic approaches: Complement transcriptomics by revealing changes in protein abundance, modifications, and interactions during drought stress. Techniques like two-dimensional gel electrophoresis (2-DE) and mass spectrometry (MS) have been used to identify drought-responsive proteins involved in photosynthesis, reactive oxygen species (ROS) detoxification, carbohydrate metabolism, and cell wall remodeling (Ali & Komatsu, 2006; Hu *et al.*, 2013). Proteomic profiling of drought-tolerant vs. susceptible cotton genotypes helps identify candidate proteins and biomarkers for breeding applications. The integration of transcriptomic and proteomic data provides a systems-level understanding of drought response and aids in pinpointing key molecular targets for genetic engineering or marker-assisted selection (MAS). These approaches support the development of resilient cotton cultivars with improved yield stability under water-limited conditions.

Advancing cotton breeding for climate resilience: The integration of advanced genomic tools and functional genomics, alongside molecular breeding strategies, is crucial for enhancing drought tolerance in cotton. Understanding the molecular pathways involved in drought response, including key genes like *GhMAP3K449*, *GhCIPK6*, and *GhirNAC2*, will allow for the development of cotton cultivars that are better suited to withstand the challenges posed by climate change. By focusing on these molecular mechanisms and integrating transgenic approaches, the cotton industry can achieve significant strides in developing drought-resistant varieties that ensure sustained production under adverse environmental conditions. Continued research and breeding efforts in this area are essential for securing cotton yields and promoting global agricultural sustainability.

Drought stress-related genes: Drought stress is one of the major environmental challenges that limits cotton production worldwide. Recent studies have shown that certain genes can enhance plant stress tolerance by regulating osmolyte accumulation, antioxidant enzyme activities, and other critical processes. These findings open up new possibilities for improving drought resistance in cotton through genetic interventions. Recent research focuses on identifying and overexpressing key genes in cotton to improve its resilience to drought conditions. For example, the transcription factor *StDREB2* has been shown to play a crucial role in regulating stress-related gene expression, leading to enhanced drought tolerance in cotton by boosting osmolyte accumulation, scavenging reactive oxygen species (ROS), and improving gas exchange and antioxidant activities (El-Esawi & Alayafi, 2019).

Overexpression of drought-resistant genes for improved cotton growth: Genetic modification has been explored to enhance drought resistance by overexpressing or introducing genes from other species. A study by Xia *et al.*, (2022) demonstrated that heterologous expression of *DgCspC* in cotton led to enhanced drought tolerance. Transgenic cotton plants expressing this gene showed improved growth, with larger leaves and taller plants compared to wild-type controls. These plants exhibited better resistance to both salt stress and drought, as evidenced by physiological indicators such as higher osmolyte accumulation, increased proline and betaine levels, and a higher rate of photosynthetic efficiency. This genetic modification resulted in greater stress tolerance and higher productivity, showcasing *DgCspC* as a promising tool for improving cotton's resilience to environmental stressors (Xia *et al.*,2022).

The role of Ac1-SST gene in drought tolerance: In another study, the *Ac1-SST* gene from *Allium cepa* was mis expressed in cotton under drought conditions, resulting in improved stress tolerance. Cotton plants with *Ac1-SST* misexpression showed significantly higher levels of soluble sugars, particularly 1-kestose, as well as enhanced proline content and relative water content compared to wild-type plants. The transgenic cotton also demonstrated better photosynthetic efficiency, with improved PSII performance and increased chlorophyll content under drought stress (Liu *et al.*, 2022). This study provides evidence that genetic modifications to increase soluble sugar levels can effectively enhance cotton's drought tolerance, making *Ac1-SST* a strong candidate for improving cotton resilience to water scarcity.

CDPKs and their role in cotton drought resistance: Calcium-dependent protein kinases (*CDPKs*) have been identified as key regulators of stress responses in plants, including cotton. A study by Yan *et al.*, (2022) investigated the role of *GhCDPK60* in drought stress tolerance. Their findings revealed that the expression of *GhCDPK60* was upregulated under drought stress, and its overexpression in cotton led to enhanced osmotic regulation and reduced ROS levels, both of which contributed to improved drought resistance. The silence of *GhCDPK60* resulted in lower stress tolerance, reinforcing the critical role of *CDPKs* in maintaining plant stability under water-limited conditions. This highlights the importance of *GhCDPK60* in regulating osmotic adjustment and antioxidant activity during drought stress.

GhdadD and ABA signaling pathways in drought resistance: The *GhdadD* gene, which is involved in osmotic stress signaling, was shown to play a role in enhancing cotton's resistance to drought and salt stress through ABA (abscisic acid) signaling pathways. Zhang *et al.*, (2024) found that *GhdadD* overexpression in cotton resulted in improved plant height, reduced leaf damage, and increased resistance to drought and salt stress. Furthermore, *GhdadD* silencing led to decreased stress tolerance, with higher levels of malondialdehyde (*MDA*) and reduced antioxidant enzyme activity. These findings suggest that *GhdadD* plays a crucial role in modulating osmotic stress responses via ABA signaling, enhancing drought resilience in cotton.

Zinc finger transcription factors and their role in drought tolerance: Transcription factors are pivotal in regulating stress responses, and the zinc finger transcription factor *GaZnF* has been identified as a key player in cotton's drought tolerance. Batool *et al.*, (2023) demonstrated that cotton plants overexpressing *GaZnF* showed superior morphological, physiological, and biochemical parameters under drought stress. Transgenic cotton plants exhibited less severe reductions in biomass, photosynthetic rate, chlorophyll content, and stomatal conductance compared to wild-type plants, indicating that the expression of *GaZnF* helps mitigate the adverse effects of drought on cotton's growth and productivity. These results highlight the potential of *GaZnF* as a tool for developing drought-resistant cotton cultivars.

GhHH and GhIDD transcription factors and their role in drought tolerance: Advances in genome sequencing and functional genomics have enabled the identification of key genes involved in biotic and abiotic stress responses in crops (Ali *et al.*, 2019; Qanmber *et al.*, 2019; Rauf *et al.*, 2024; Zafer *et al.*, 2023). In *Gossypium hirsutum*, 65 Indeterminate Domain (IDD) genes have been identified, with *GhIDD2*, *GhIDD7*, *GhIDD9*, *GhIDD11*, *GhIDD15*, *GhIDD21*, *GhIDD39*, and *GhIDD42* associated with seed formation and fiber elongation. GhOIDD4 and GhIDD32 show predominant expression in stem tissues, while *GhIDD48* is mainly expressed in floral organs, highlighting diverse roles in plant development (Ali *et al.*, 2019). Additionally, *GhIDD4*, *GhIDD7*, *GhIDD11*, and *GhIDD21* have been linked to drought stress tolerance. Furthermore, 34 Histone H3 (HH3) genes have been reported in *G. hirsutum*, with *GhHH3-1*, *GhHH3-4*, and *GhHH3-17* showing potential for enhancing drought resistance in breeding programs (Qanmber *et al.*, 2019). Based on expression analyses, *GhHH3* and *GhIDD* genes serve as valuable molecular markers for selecting high-yielding and stress-tolerant genotypes during various developmental stages of cotton. Incorporating newly developed crosses into breeding programs is recommended to facilitate the development of drought-resistant cotton cultivars for future agricultural use (Sarwar *et al.*, 2025).

Advancements in drought tolerance through genetic engineering: The integration of drought tolerance genes into cotton has shown promising results in enhancing its resilience to water scarcity. Genes involved in osmotic regulation, antioxidant activity, photosynthesis, and stress signaling pathways have proven to be critical in improving drought resistance. Studies on genes such as *StDREB2*, *DgCspC*, *Ac1-SST*, *GhCDPK60*, *SikCOR413PM1*, *GhdadD*, GaZnF *GhHH3 and GhIDD* highlight the potential of genetic engineering in creating drought-resistant cotton varieties. These advances in functional genomics, combined with techniques like CRISPR/Cas9, provide new opportunities for improving cotton productivity and resilience in the face of climate change. Continued research into these genes and their mechanisms will be essential for developing sustainable agricultural practices to ensure global cotton production under increasingly challenging environmental conditions.

Conclusion

Cotton remains a vital crop for many regions, providing essential raw material for the textile industry and supporting local economies. Enhancing cotton yield through improved drought tolerance is critical to sustaining farming communities amid increasing climate variability. Drought stress disrupts key biological processes in cotton, activating cellular defense mechanisms such as oxidative stress responses and complex signaling pathways including ROS, MAPK, Ca^{2+}, and hormonal regulation. Recent advances have deepened our understanding of the genetic, biochemical, physiological, and molecular bases of drought tolerance. Biochemical markers like proline, glycine betaine, proteins, and sugars play crucial roles in maintaining cellular stability under water deficit, serving as valuable indicators for identifying drought-resilient cultivars. While the complex, quantitative nature of these traits presents evaluation challenges, emerging tools like QTL mapping and molecular markers are enhancing genetic analysis precision. Looking ahead, a clear roadmap is needed for translating these scientific insights into practical applications. For breeders, integrating QTL data and marker-assisted selection into breeding programs will accelerate the development of drought-tolerant cotton varieties with enhanced osmolyte accumulation and improved fiber quality. Molecular biologists are encouraged to focus on applying advanced gene editing and genomic selection technologies to validate and manipulate key drought-responsive genes effectively. Furthermore, interdisciplinary collaborations that combine genomics, phenomics, and agronomy will be essential for developing resilient cotton cultivars capable of withstanding increasingly severe environmental stresses. Emphasizing osmolyte-mediated traits in breeding strategies offers a promising avenue to bolster cotton's adaptive capacity. By following this forward-looking framework, researchers and breeders can contribute to sustainable cotton production, bolster food and fiber security, and support resource-poor farmers in developing regions vulnerable to climate change. This proactive approach will be vital to ensuring cotton's productivity and economic viability in a rapidly changing global environment.

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