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An outlook on mechanisms inciting drought tolerance in cotton (*Gossypium hirsutum*)

S MANJU[1], S RAJESWARI[1]*, N MANIKANDA BOOPATHI[1], N PREMALATHA[1], N SRITHARAN[1] and D UMA[1]

Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu 641 003, India

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ABSTRACT

Drought is a multifaceted abiotic stress that affects plants at morphological, physiological, biochemical, and molecular levels. In the face of increasing climate variability, plants exhibit diverse growth and reproductive responses to water scarcity. Cotton, a globally significant fibre crop with substantial economic value, is particularly vulnerable to drought during key developmental stages. Tolerance to drought in cotton involves a suite of physiological responses, including maintenance of relative water content, leaf water potential, stomatal conductance, and osmotic adjustment. Biochemically, the scavenging of reactive oxygen species (ROS) through antioxidant enzymes and the activation of stress-responsive phytohormones such as abscisic acid play vital roles in plant survival. At the molecular level, drought tolerance is enhanced by the upregulation of genes such as *GhSP1, GhFTL1, GhEXLB2,* and *GhGLK1*, alongside the downregulation of *MAPKKK* genes. Conversely, overexpression of *GhWRKY6* may induce ROS-mediated oxidative damage. Emerging studies highlight the importance of transcription factors like *GhirNAC2* and the regulatory influence of miR394a/b on *GhD01G0229* under drought stress. Mapping and functional characterization of these genes, transcription factors, and miRNAs provide valuable insights into the genetic architecture of drought tolerance and offer potential targets for crop improvement. This review explores the integrated physiological, biochemical, and molecular mechanisms that confer drought resilience in cotton.

Keywords: Cotton, Drought tolerance, Genes, Mechanisms

Cotton (*Gossypium hirsutum* L.) is the universally known as 'White Gold' and it is the king of fibre as 60% of industries rely on cotton, making it a crucial raw material for various sectors, particularly in textiles and related industries (Nandhini *et al*. 2019). Amidst the different cultivated species, *Gossypium hirsutum* is estimated to contribute around 90% of global cotton trade, largely due to its elite varieties (Selvaraj *et al*. 2023). But it is highly susceptible to biotic and abiotic stresses (Sukrutha *et al*. 2023). Approximately 9% of India's total agricultural land is dedicated to cotton cultivation (Sukrutha *et al*. 2023a). Globally, India stands first in area of 125.55 lakh ha and second in production of 5.84 million metric tonnes while China is the leading producer with production of 5.98 million metric tonnes and productivity of 1993 kg/ha (Anonymous 2024a). In India, Maharashtra, Gujarat and Rajasthan stands first in area, production and productivity in cotton, respectively (Anonymous 2024b). Fig. 1 shows the area, production and productivity of top cotton growing states in India.

Cotton is a versatile crop with multiple uses, including seed cotton, seed oil, lint, seed meal, hull and linters (Subhashini *et al*. 2023). Among the distinct abiotic stresses, drought and salinity significantly influences the production of cotton at global level (Boopathi *et al*. 2022). Drought stress leads to yield losses of upto 67%, showcasing more adverse effects compared to other environmental stresses (Tokel *et al*. 2022). Drought lasting even a single season can lead to significant decline in cotton seed production and stock levels. Prolonged drought may alter cropping patterns and shift the geographic distribution of cotton cultivation (Boopathi and Hoffman 2016). Moreover, cultivation of high yielding varieties made cotton cultivation susceptible to biotic and abiotic stress including drought and heat stress (Kandeepan and Boopathi 2019). Majority of cotton cultivated area is under rainfed condition and yield under drought stress depends on various factors such as boll size and number, seed no./boll and fibre/seed (Boopathi *et al*. 2014).

Drought is a polygenic trait regulated by a combination of various morphological, physiological, biochemical and molecular characteristics. Those factors help plant to withstand drought by osmotic adjustment, modifications in gaseous exchange, production of antioxidant enzymes, up

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[1]Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu. *Corresponding author email: rajeswari.s@tnau.ac.in

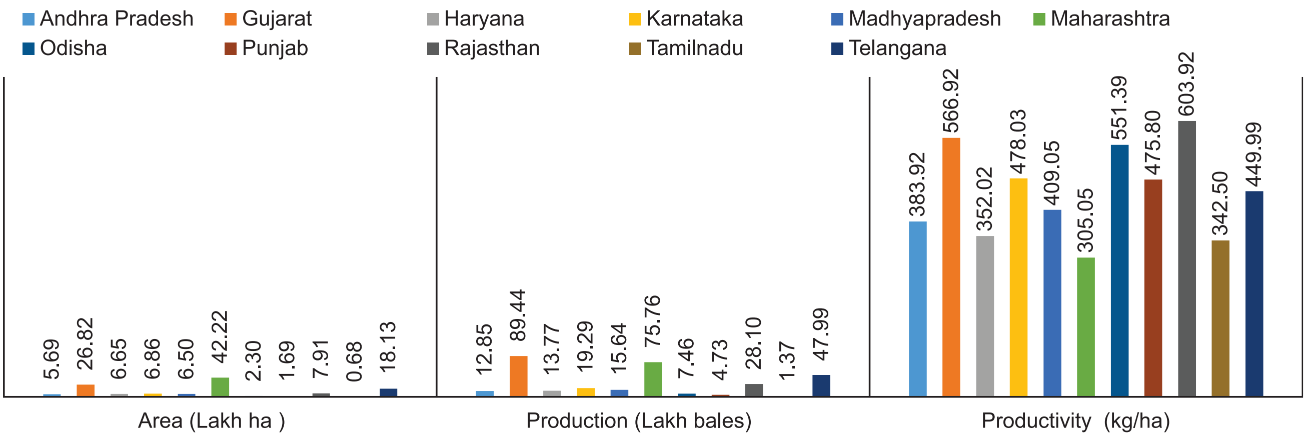

Fig. 1 Area, production and productivity of top cotton growing states in India.

regulation and down regulation of certain genes. Reaction of plants to drought is contingent upon factors such as the duration and intensity of the stress, growth stage and water use efficiency (Lawlor 2011). Flowering and square formation stages are more sensitive to water stress which lead to formation of immature flower and impairment of fruiting bodies, ultimately reducing boll number and seed yield (Zonta *et al.* 2017, Khan *et al.* 2018). Finding genes associated with drought tolerance during the flowering and boll formation stages could be beneficial for improving fibre productivity and quality in water-limited environments (Boopathi and Ravikesavan 2009). Fig. 2 shows the flowchart of different mechanisms involved in drought tolerance.

Morpho-physiological mechanisms of drought tolerance in cotton

Leaf characteristics: Plants undergo various alterations like reducing size and shedding of leaves to combat water scarcity. Rolling and wilting of leaves cause lower radiation leading to decreased water loss in cotton (Fang and Xiong 2015). Deposition of wax on leaves, thickening of cuticle, increase in the number of stomata and trichomes, vascular tissue formation and dense palisade tissue occurs to reduce transpiration (Fang *et al.* 2015, Ilyas *et al.* 2021). Okra-leaf types of upland cotton have the ability to compete with normal-leaf types in yield and fibre quality, in addition to its potential resistance to pests and drought (Kumar *et al.* 2020).

Root and shoot characteristics: Root is the pivotal part which plays key role such as sensing stimuli, receiving it and act according to the water availability. During water deficit condition nutrients are highly accumulated in the root cells (Mahmood *et al.* 2022). Plants need long and dense roots to penetrate deeply and for holding more volume of water to produce optimum yield to withstand drought (Iqbal *et al.* 2010, Comas *et al.* 2013, Luo *et al.* 2020). In cotton, elongation of root was high at the time of moderate water deficit while it decreased at the terminal level. The genotypes which are tolerant to water deficit condition had maximum root and shoot length compared to the other genotypes (Ahmad *et al.* 2020, Arif *et al.* 2023). Drought reduces yield by decreasing the root and shoot biomass. Drought tolerant cotton varieties expressed high root-shoot ratio and root length (Abdelmoghny *et al.* 2020, Zahid *et al.* 2021).

Relative water content: The measure denotes the water status of plant which affects the tissue metabolism. Drought tolerant plants improve water retention and cell volume maintenance by increasing their relative water content (RWC) which helps to maintain the appropriate level of transpiration which is crucial for the plant's survival. A decrease in RWC indicates a reduction in turgor, which in turn restricts cell expansion and ultimately hinders crop growth (Lu *et al.* 2010). RWC was lower in *G. herbaceum* compared to *G. hirsutum* (Patil *et al.* 2011). An increase in the RWC is ascribed to reduced cell wall flexibility or increased osmotic control (Erice *et al.* 2010). RWC is positively associated with boll retention percentage under both irrigated and water deficit conditions (Anwar *et al.* 2022). A set of 220 recombinant inbred lines (RILs), along with their parent, lines and a check, were assessed for drought tolerance at two different locations. Among them, RIL 74 and RIL 73 showed the lowest percentage of injury maintaining high RWC, indicating superior drought tolerance (Nandhini *et al.* 2022).

Cell membrane thermostability: The survival of a plant under stressful conditions relies on the integrity and stability of its cell membrane. Processes like respiration and photosynthesis depends on optimal condition of cell membrane. Any alteration in these structures damages every metabolic function in the plant. The disruption of cell membrane can occur through either denaturation of protein or elevated concentration of unsaturated fatty acids (Wahid and Shabbir 2005). The susceptible cotton cultivars on exposure to drought stress showed significantly lower cell membrane thermostability (CMS) and excised leaf water loss (Hafeez *et al.* 2015, Saleem *et al.* 2015, Mehari *et al.* 2021). During drought stress, increased CMS could be due to the protective role of proline on cell membrane (Chen and Murata 2011). Drought tolerant cultivars showed high RWC and CMS during water deficit conditions (Imtiaz *et al.* 2023).

Osmotic adjustment: Osmotic adjustment helps plants

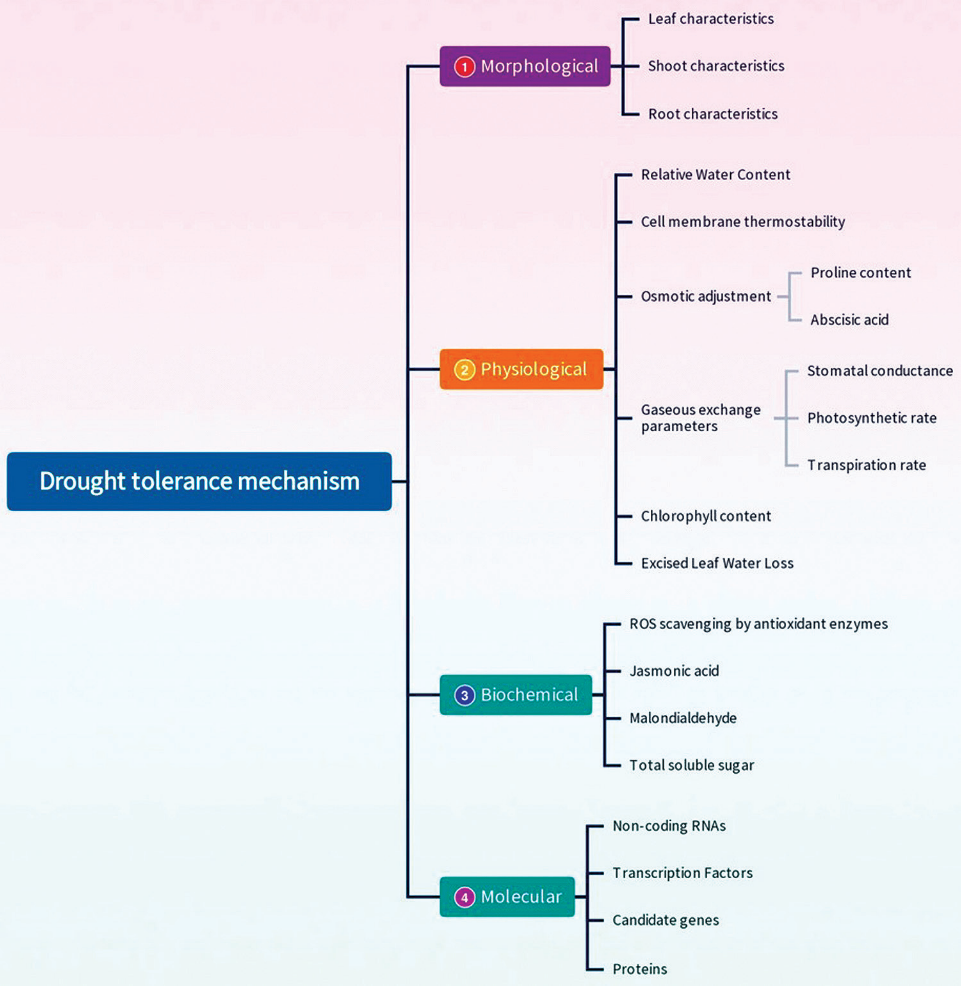

Fig. 2 Flowchart depicting different mechanisms involved in drought tolerance.

tolerate drought by accumulating compatible solutes like proline and abscisic acid in the cytosol, lowering osmotic potential and enhancing water uptake to maintain cell turgor (Mafakheri *et al.* 2010, Pilon *et al.* 2019). Since cell enlargement depends on turgor, a drop in turgor hampers growth (Serraj and Sinclair 2002). Tolerant cultivars maintain lower osmotic potential than sensitive ones, aiding water retention under stress (Fang and Xiong 2015). Polyphenol levels increase during drought, suggesting their role in osmotic regulation and ROS scavenging (Boopathi *et al*. 2015). Substances such as proline and abscisic acid which substantially involved in osmotic adjustment are explained further.

Proline: Proline acts as an osmo-protectant, accumulating under stress to help plants maintain low water potential, enhance water uptake, and stabilize osmotic balance. It also mitigates ROS damage by supporting antioxidant systems and preserving cell membrane stability (Hayat *et al.* 2012, Reddy *et al.* 2015). Proline boosts the expression of stress-related genes, highlighting its multifaceted role. Phytohormones influence proline metabolism, though their exact regulatory roles remain unclear. Increased proline levels under drought have been observed in cotton (Zhang *et al.* 2014a, Aslam *et al.* 2023).

Abscisic acid: Abscisic acid (ABA) stands out as one of the most vital stress hormones, playing a key role in numerous physiological processes in the plant. Osmotic adjustment substances like ABA accumulate in response to drought stress leading to an increase in osmotic pressure within guard cells, which gradually induces narrowing or complete closure of stomatal pore apertures. During dehydration, stimulation of ABA biosynthesis initiates the activation of multiple genes, resulting in the closure of stomata, enhancement of root architecture and augmentation of the synthesis of substances contributing to drought tolerance (Lim *et al.* 2014). Light initiates stomatal opening, whereas ABA and elevated level of CO_2 triggers partial or complete closure of stomata (Cutler *et al.* 2010, Munemasa *et al.* 2015). ABA also causes changes in seed dormancy and germination as an outcome of diverse abiotic and biotic stresses (Lee and Luan 2012, Wang *et al.* 2018).

Gaseous exchange parameters: Stomatal conductance is a plausible index of drought stress tolerance in cotton. It represents either the rate of carbon dioxide intake or the rate of water vapour release through stomata. Plants acquire energy through the process of photosynthesis that happens in the leaves. During drought stress the stomata will be closed most of the time to avoid transpiration and causes a decline in internal CO_2 concentration. Gaseous exchange in the cell is decreased due to decline in transpiration as well as photosynthetic rate (Mittler and Blumwald 2015). Physiological changes associated with transpiration regulate the stomatal development by modification of size, closure, aperture and stomatal density (Sirichandra *et al.* 2009). Opening of stomatal aperture is the reason for 90% of H_2O loss (Wang *et al.* 2016). Under elevated temperatures, there was no discernable reduction in the photosynthetic rate of young leaves, but it is decreased by 66% in mature leaves (Chastain *et al.* 2014). As the water deficit progressively intensified in cotton fields, photosynthesis and growth were significantly impaired (Ullah *et al.* 2017).

Leaf water potential: The quantity of water present in leaf is termed as leaf water potential (LWP). The rate of decrease in photosynthesis is directly proportional to the decrease in LWP and RWC (Lawlor and Cornic 2002). Cotton plants maintain LWP by different ways of osmotic adjustments in the cell. The LWP is linked with cell membrane integrity, as indicated by significantly less leakage of electrolytes observed in tolerant genotypes (Argyrokastritis *et al.* 2015). The drought tolerant cultivars expressed lower LWP than the other cultivars (Jie *et al.* 2020).

Chlorophyll content and chlorophyll fluorescence: Chlorophyll content (CC) serves as an indicator of the plant's capacity for photosynthetic processes. *Gossypium barbadense* exhibited highest levels of photosynthetic rate, chlorophyll content and total soluble sugar followed by *G. arboretum, G. herbaceum* and *G.hirsutum* (Patil *et al.* 2011). CC is decreased by reduction in soil water potential. Potassium is involved in conserving CC and soluble proteins by regulation of osmotic adjustment and nitrogen metabolism which in turn lead to drought tolerance (Zahoor *et al.* 2017). Drought stress resulted in decreased gas exchange, chlorophyll fluorescence and photosynthetic rate. It lead to a reduction of the maximum to minimum ratio of chlorophyll fluorescence and also hindered electron flow from PS II (photosystem II). This affects modulated fluorescence, fluorescence induction kinetics and chlorophyll fluorescence. Furthermore, osmotic stress lowered the efficiency of excitation energy captured by PS II and notably reduced photochemical quenching (Mathobo *et al.* 2017).

Excised leaf water loss: Excised leaf water loss (ELWL) demonstrates how reduced water loss from leaves contributes to the durability of cell membranes by preserving RWC. ELWL had strong association with transpiration rate. When five high yielding upland cotton were subjected to drought stress at consecutive intervals, a decline in ELWL was recorded (Riaz *et al.* 2013, Anwar *et al.* 2022). Many genotypes recorded variable response to ELWL under drought based on the thickness of leaf cuticle in cotton (Zahid *et al.* 2021, Arif *et al.* 2023). The morpho-physiological traits responsible for drought tolerance in cotton are given in the Table 1.

Biochemical mechanisms targeting drought tolerance in cotton

Reactive oxygen species scavenging by antioxidant enzymes: A partial drop in atmospheric O_2 leads to the production of reactive oxygen species (ROS), including singlet oxygen ($^1O_2$), hydrogen peroxide (H_2O_2), superoxide (O_2^-), and hydroxyl radicals (HO•), which can damage lipids, proteins, and DNA, potentially causing apoptosis (Fang *et al.* 2015).

Under drought, reduced CO_2 fixation limits $NADP^+$ regeneration, increasing electron leakage via the Mehler reaction and ROS production (Cruz de Carvalho 2008). Superoxide is converted to H_2O_2 by SOD and further degraded by catalase and peroxidase, maintaining redox balance (Heber 2005, Wang *et al.* 2018).

Hydrogen peroxide (H_2O_2), a prevalent reactive oxygen molecule damages the cell membrane and expedites the aging and breakdown of cells. The degradation of H_2O_2 can be catalyzed by enzymes such as catalase and peroxidase. The antioxidant enzyme catalase plays a pivotal role in degrading reactive ROS, thereby minimizing oxidative damage induced by drought (Ullah *et al.* 2017).

Jasmonic acid: Jasmonic acid (JA) is a phytohormone emanated from alpha-inolenic acid. Jasmonates, (fuctional derivative of JA) together with JA acts crucially in numerous biotic and abiotic stress responses, regulating the response to stress in plants. The Jasmonate ZIM domain (JAZ), a repressor protein holds a key role in JA signalling pathways during stress state. The JAZ protein activates transcription factors like MYC2 and various stress-responsive genes, thereby contributing to the enhancement of drought stress tolerance (Zhang *et al.* 2015). JA has been also involved in activities like plant growth, pollen production and fruit ripening in cotton (Zahid *et al.* 2023).

Total soluble sugar: In plants, non-green tissues such as roots, flowers, and stems act as carbon sinks, relying on leaves to supply them with soluble sugars produced through photosynthesis. A decline in photosynthetic activity, especially under stress, reduces sugar availability to these sink organs. To maintain vital metabolic processes, plants undergo various physiological and biochemical adjustments.

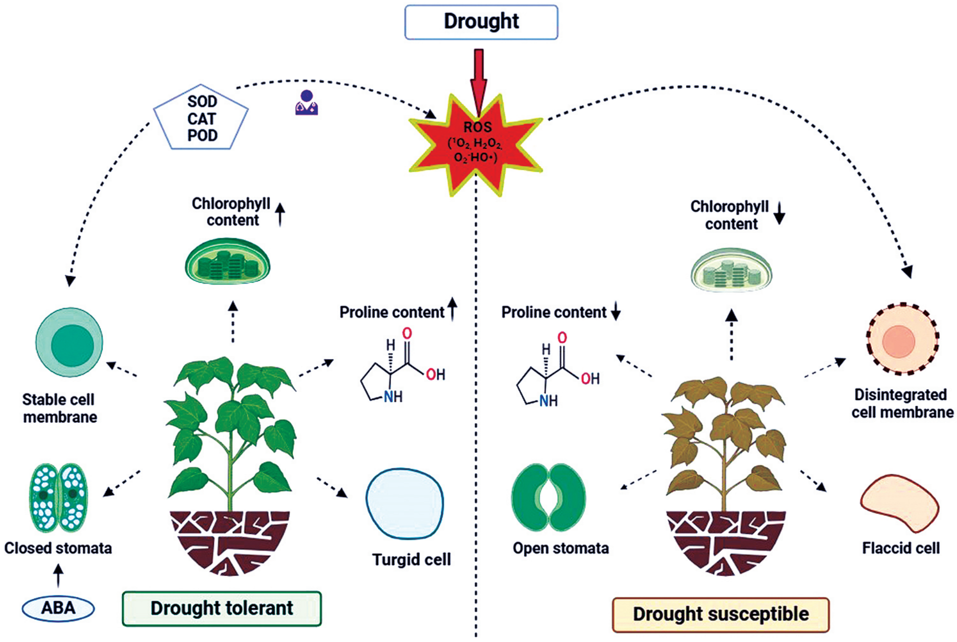

Fig. 3 Physiological and biochemical changes in plants under drought stress. Created with BioRender.com

Table 1 Key morpho-physiological traits responsible for drought tolerance in cotton

Mechanism	Key features	Effect under drought
Leaf characteristics	Leaf rolling, wax deposition, cuticle thickening, increased stomata/trichomes	Reduced transpiration, lower radiation loss
Root and shoot traits	Deep, long, dense roots, higher root:shoot ratio	Better water absorption, improved yield
Relative water content	Measure of tissue water status	High RWC maintains turgor and growth
Cell membrane thermostability	Integrity of membranes under heat/drought	High CMS linked to tolerance
Osmotic adjustment	Accumulation of solutes in cytosol	Maintains turgor pressure and water intake
Proline	Osmoprotectant and ROS scavenger	Enhances osmoregulation, CMS and gene expression
Abscisic acid	Stress-induced hormone, regulates stomata	Promotes stomatal closure, root growth, gene expression
Gaseous exchange parameters	Stomatal conductance, CO_2 uptake	Decline in transpiration, photosynthesis under drought
Leaf water potential	Indicates water status in leaf tissue	Lower LWP in tolerant cultivars, linked with less electrolyte leakage
Chlorophyll content and fluorescence	Photosynthetic pigments and PS II activity	Reduced under stress; potassium helps conserve it
Excised leaf water loss	Water loss in detached leaves	Lower ELWL in tolerant lines; correlates with RWC
ROS scavenging	SOD, CAT, POD enzymes neutralize ROS	Protect cellular structures from oxidative damage
Jasmonic acid	Phytohormone regulating stress response	Activates TFs (e.g. MYC2) and stress responsive genes
Total soluble sugar	Carbohydrate reserves for osmotic balance	Role in osmoregulation, source-sink transitions
Malondialdehyde	Lipid peroxidation marker	Lower MDA indicates less membrane damage

Studies have shown that sugar levels often increase under abiotic stresses like drought, salinity, cold, and flooding. However, this sugar accumulation varies depending on plant genotype and the specific type of stress (Morsy *et al.* 2007). In Arabidopsis, drought and heat stress were found to disrupt source-sink transitions and CO_2 assimilation, altering carbon distribution and protein expression (Gupta and Kaur 2005).

In cotton, fibre elongation depends largely on turgor pressure, driven by osmotically active solutes. Soluble sugars, potassium ions, and malate play key roles in maintaining this pressure, with sucrose being the most critical sugar involved. Research by Shu *et al.* (2009) and Hou *et al.* (2018) highlighted the importance of sucrose in fibre development. Drought stress alters carbohydrate metabolism and reduces sucrose availability in fibre cells, thereby impacting osmotic adjustment and fibre elongation.

Malondialdehyde: Malondialdehyde (MDA) is a key marker of lipid peroxidation, indicating oxidative damage to cell membranes. It forms from oxygen free radicals acting on unsaturated fatty acids. Drought-tolerant genotypes show lower MDA levels, suggesting better membrane integrity and oxidative stress resilience (Zhang *et al.* 2014, Rehman *et al.* 2022). In contrast, that proline and MDA level are elevated in Chinese cotton varieties under water stress (Jie *et al.* 2020). Fig. 3 illustrates the different physiological and biochemical changes in plants during water deficit condition.

Molecular mechanisms of drought tolerance: Gene expression enables targeted selection for drought tolerance by identifying and manipulating specific genes associated with favourable traits. In allotetraploid cotton, the development of whole-genome single nucleotide polymorphisms (SNPs) has been achieved through advancements in *in silico* methods and next-generation sequencing techniques. Notably, in cotton, the creation of SNP63K array, comprising 17,954 interspecific and 45,104 intraspecific SNP marker assays, has proven to be valuable in drought tolerance studies (Ashrafi *et al.* 2015).

GhMKK3 has been recognized as a constituent of the mitogen-activated protein kinase (MAPK) cascade was activated by drought stress. It caused root growth and ABA-induced stomatal closure which aids in plant survival under drought (Wang *et al.* 2016). A novel cotton gene *GhMAP3K449* was induced by ABA and ROS production. Constitutive expression of *GhMAPKKK49* was found in root, stem and leaves under abiotic stresses. Application of signalling molecules comprising ABA, H_2O_2, gibberellins, ethylene, methyl jasmonate, 6-benzylaminopurine, salicylic acid and a-naphthylacetic acid gives rise to response in upregulation of *GhMAP3K449* (Dongdong *et al.* 2016)

Over expression of *GhCBF3* in transgenic lines found to improve salinity and drought tolerance along with increase in RWC, proline and CC. Notably, the expression level of *AREB 1* and *AREB 2* was greater and stomatal aperture was smaller in transgenic lines (Ma *et al.* 2016). The *GhFTL1* and *GhSP1* differed according to level of stress tolerance indicating that these genes are crucial for conferring drought tolerance in cotton (Hamoud *et al.* 2016).

Magwanga *et al.* (2020) identified five key genes, viz. *Gh D01G0205*, *Gh D01G0186*, *Gh D01G0234*, *Gh D01G0182* and *Gh D01G0229* which could be allowed for targeted genetic manipulation for improving drought stress tolerance. miR394a/b targeted the gene *Gh D01G0229*, which could play significant role in regulating gene expression in response to drought stress. Boopathi and Pathbanaban (2012) identified 11 candidate miRNAs related to different abiotic stress in cotton. Among them miR159, miR319, miR529, miR170 and miR1030 were found to be associated with drought stress in cotton. Comparative transcriptome analysis between drought tolerant *G. hirsutum* cultivar KC3 and susceptible *G. barbadense* cultivar suvin showed that miRNA, viz. miR750, miR2, miR14, miR276, miR279, miR-bantam and miR5176 were downregulated in KC3 during water limited condition (Boopathi *et al.* 2016).

Overexpression of *GhEXLB2*, an expansin-like gene exhibited enhanced drought tolerance at germination, seedling and flowering stages in cotton. Specifically, after polyethylene glycol (PEG) treatment at germination stage, the main root and hypocotyl lengths of overexpressing lines were notably longer compared to wild-type and RNAi lines. This suggests that *GhEXLB2* as candidate gene in enhancing drought tolerance in cotton (Zhang *et al.* 2021). MAPKKKs (Mitogen-Activated Protein Kinase Kinases) have been reported to participate in plant resistance to drought stress (Shou *et al.* 2004). Transcription levels of *GhRAF18, GhRAF50, GhRAF69* and *GhMEKK39* were decreased in leaves under drought stress (Zhang *et al.* 2020). Co-suppression of *GhirNAC2*, a NAC transcription factor, resulted in larger stomatal apertures, increased water loss, and reduced tolerance of drought stress in transgenic plants. Furthermore, the endogenous ABA content was significantly lower in leaves of *GhirNAC2*-suppressed transgenic plants than in those of the wild type (Shang *et al.* 2020). Relative expression levels of the transcription factors like *GhHsfA, GhNAC* and *GhbZIP* were significantly associated with various physiological and biochemical factors under different stress conditions (Fan *et al.* 2021). Two novel QTL hotspots CIDT-QTL2 and CIDT-QTL4 novel were associated with drought stress. It includes six differentially expressed genes, in which *Gh A06G1325*, *Gh A06G1327*, *Gh A12G0874*, *Gh A12G0882* and *Gh A12G0888* were significantly upregulated while the gene *Gh A12G0888* was down regulated during drought stress (Li *et al.* 2020).

Several key genes contribute to drought tolerance in cotton. Suppression of *GhGLK1* led to increased ROS and stress sensitivity (Liu *et al.* 2021), while overexpression of *GhAnn1* enhanced drought and salt tolerance by increasing proline, sugar, and SOD activity (Zhang *et al.* 2015). Overexpression of *GhWRKY6* intensified ROS damage. The *GhA11G1858* gene (SnRK2.6/OST1) was upregulated under moderate drought but downregulated under severe stress (Li *et al.* 2019). The ABA signalling pathway involving genes such as *GhNCED, GhbHLH1, GhNAC9, GhV-ATPase, GrHisH1* and *GhSUT1*, plays vital role on drought tolerance. Based on coexpression and RT-qPCR analysis. *Gh D01G0514* was identified as a hub gene with consistent drought-responsive expression (Abdelmoghny *et al.* 2020). The genes that show prominent function in drought tolerance are given in the Table 2.

Strategies for enhancing drought tolerance in cotton

Conventional breeding approaches for drought tolerance in cotton: The conventional breeding method for drought tolerance in cotton involves selecting and crossing plants using traditional breeding approaches such as mass selection, pure-line selection, and pedigree breeding. This approach relies on the genetic diversity found in wild relatives, landraces, and existing cultivated cotton varieties. Breeders evaluate cotton germplasm under drought stress conditions, identify tolerant individuals, and use them as parents in breeding programmes. The process includes screening for morphological, physiological and biochemical traits associated with drought tolerance**.**

Genetic architecture: Most studies indicate that drought tolerance in cotton is controlled by multiple genes with predominantly additive gene action, though dominance and epistatic effects are also significant (Ullah *et al*. 2019, Mahmood *et al*. 2021, Imtiaz *et al*. 2022).

Breeding strategies: Certain researches suggested that pedigree selection and population improvement methods are effective, with the choice depending on the genetic architecture of the specific drought tolerance traits. BH-167 is a drought- and heat-tolerant cotton variety developed by crossing VH-53 × BH-142 through pedigree methods exhibited superior yield, early maturity, and enhanced fibre quality (Minhas *et al*. 2018). RH-668 is another high-yielding, heat and drought-tolerant variety developed through crossing VH-259 × RH-620 and gene pyramiding via the bulk pedigree method (Yasin *et. al*. 2020).

Selection criteria: Breeders make use of key traits for indirect selection include root characteristics, osmotic adjustment, leaf water potential, and physiological parameters like photosynthetic rate under stress (Ilyas *et al*. 2021, Anwar *et al*. 2022, Imtiaz *et al*. 2023, Arif *et al*. 2023).

Combining ability: Studies consistently shows that both GCA and SCA are important, indicating the value of both additive and non-additive genetic effects in drought tolerance (Khamdullaev *et al*. 2021)

Molecular breeding approaches for drought tolerance in cotton: Molecular breeding has emerged as a tool for targeting particular genes governing desired traits. Quantitative trait loci (QTL) mapping, transcription factor analysis, transcriptome analysis and transgenic approach have been utilized efficiently in identification of candidate genes controlling drought tolerance in cotton.

QTL mapping is an eloquent technique used in genetics to find regions of the genome associated with particular phenotypic traits. The identification of QTLs is often constrained by various factors, including the genetic characteristics of QTLs, environmental influences,

Table 2 Key genes responsible for drought tolerance in cotton

Genes	Particulars	Expression
GhMKK3	Mitogen-activated protein kinase (MAPK) kinase 3	Upregulation
GhCBF3	ABA induced gene	Upregulation
GhMAP3K449	MAPM3K family	Upregulation
GhSP1	Heat shock protein 1	Upregulation
GhFTL1	Flowering locus T-like protein 1 gene	Upregulation
GhEXLB2	Expansin-like gene	Upregulation
GhirNAC2	NAC transcription factor	Upregulation
Gh A06G1325	Pyridoxal phosphate (PLP)-dependent enzyme Core-2/IBranching enzyme	Upregulation
Gh A06G1327	Palmitoyl protein thioesterase	Upregulation
Gh A12G0874	RWD domain -	Upregulation
Gh A12G0882	Cyclin-dependent protein serine/threonine Kinase (CDK) activity	Upregulation
Gh A12G0886		Upregulation
Gh A12G0888		Downregulation
GhGLK1	Golden2-like (GLK) gene, GARP family	Upregulation
GhWRKY6	WRKY family	Downregulation
GhAnn1	Annexin gene	Upregulation
GhRAF18, GhRAF50, GhRAF69b, GhMEKK39	MAPKKK gene family	Upregulation
Gh A11G1858	Homology to SnRK2.6/OST1 (sucrose non-fermenting 1-related protein kinase 2.6/OPEN STOMATA 1)	Upregulation at moderate drought stress Downregulation at severe drought stress
Gh D01G0229	Targeted by miR394a/b	Upregulation
GhNCED	NCED gene family	Downregulation
GhbHLH,	bHLH/HLH genes	Downregulation
GhDREB1	Dehydration responsive element binding protein NAC transcription factor	Upregulation
GhNAC9	Vacuolar-type ATPase	Upregulation
GhV-ATPase	H1 variant of histone	Upregulation
GrHisH1	sucrose transporter 1	Upregulation
GhSUT1		Upregulation
GhHsfA, GhbZIP and GhNAC	Transcription factors	Upregulation

population size, and experimental error (Boopathi *et al.* 2011). QTL mapping coupled with decoding of cotton genome has revolutionized cotton breeding by facilitating the identification, validation, and utilization of QTLs associated with drought stress tolerance and other important traits through high-throughput DNA markers like SNPs and marker-assisted selection techniques (Boopathi and Ravikesavan 2009, Rasheed *et al.* 2023). Shukla *et al.* 2021 discovered 19 QTLs in nine chromosomes for notable traits in cotton crucial for drought tolerance. A study identified 20 QTLs associated with drought tolerance and 23 QTLs linked to salt tolerance out of a pool of 473,516 polymorphic SNPs. Notably, nine QTLs were identical for drought and salt tolerance, indicating a shared genetic foundation for both traits (Abdelraheem *et al.* 2021). Nine stable, major QTLs that were co-localized with multiple traits were identified under irrigated, water stress and rainfed condition (Boopathi *et al.* 2022). Several QTL/genes and single nucleotide polymorphisms (SNPs) linked with drought tolerance have been discovered by Genome Wide Association Studies (GWAS) in cotton. Such QTLs can be exploited in molecular breeding for development of drought tolerant varieties in cotton (Baytar *et al.* 2018, Hou *et al.* 2018, Guo *et al.* 2020 and Sun *et al.* 2023).

Transcription factor analysis helps to discover the essential proteins that regulate gene expression under drought stress. Transcription factor identification has paved the way to speed up molecular breeding programmes in cotton (El-Esawi and Alayafi 2019, Basso *et al.* 2021, Mehari *et al.* 2021). Profiling expression of genes in cotton genotypes assists in finding the promising genetic factors governing drought stress tolerance. Studies on heat shock protein genes, various ATP-binding cassette genes, VIGS (Virus Induced Gene Silencing) and ATP-binding cassette transporter genes demonstrated their importance in drought tolerance of cotton (Sajjad *et al.* 2021, Han *et al.* 2022, Zheng *et al.* 2022, Yuan *et al.* 2023).

Agrobacterium-mediated transformation is a powerful technique for enhancing drought tolerance in cotton. Transgenic cotton expressing *GUSP1* showed improved leaf water content, chlorophyll, and photosynthesis with reduced membrane permeability (Hassan *et al.* 2021). Overexpression of *TaMnSOD* and *K2-NhaD* increased proline, sugars, and antioxidant activity (Zhang *et al.* 2014). Several studies by Gunapati *et al.* (2016), Guo *et al.* (2020), Hao *et al.* (2018), Luo *et al.* (2020) confirmed gene transformation as an effective strategy for drought stress improvement. Genes like AtZAT10/STZ1 enhanced root biomass and stress responses (Qin *et al.* 2024). While ALDH21 from *Syntrichia caninervis* improved ROS scavenging and drought tolerance, boosting field yield (Yang *et al*. 2022).

Gene editing tools are currently used for developing improved genotypes with different traits such as quality and abiotic and biotic stress tolerance. CRISPR/Cas 9 (Clustered Regularly Interspaced Palendromic Repeats) is the major gene editing tool used by researchers to manipulate DNA for creation of biotic and abiotic stress tolerance in various crops. CRISPR/Mb2Cas12a demonstrated high editing efficiency (over 90%) in cotton, allowing for multiplex editing of multiple genes, which is crucial for complex traits like drought tolerance. Mb2Cas12a can target a broader range of PAM sites, enhancing its utility in cotton genome editing (Hui *et al*. 2024).

Genomic selection is a currently trending method among the researchers for accelerating research owing to its early stage estimation, tremendous accuracy in prediction and selection efficiency. It is created for selection of traits governed by many genes and those with low heritability. Cotton, genomic selection have been successfully exploited for fibre quality and yield related characters (Gapare *et al.* 2018, Islam *et al.* 2020 and Billings *et al.* 2022). But, this method is under-exploited for drought tolerance studies in cotton. Hence genomic selection could be efficiently used to conquer the potential genes identified by markers to improve superior drought tolerant genotypes in cotton.

Future prospects for improving drought tolerance in cotton

Integration of conventional and molecular breeding: The integration of conventional breeding with genetic and genomic tools is paving the way for more efficient development of drought-resistant cotton varieties. This approach is crucial given the increasing frequency of drought events due to climate change, which poses a significant threat to cotton production worldwide.

Omics and gene editing: Omics approaches, including transcriptomics, genomics, metabolomics, and proteomics, have expanded the knowledge of cotton's response to drought stress. These methodologies facilitate the identification of gene regulatory networks and candidate genes for drought tolerance. Advanced biotechnologies like CRISPR/Cas9 and RNA interference (RNAi) are being used to explore molecular mechanisms and improve drought tolerance traits in elite genotypes (Sharif *et al*. 2024).

Genetic engineering and transgenics: Genetic engineering, including transgenic modification, is a primary approach in molecular breeding for drought tolerance. This involves regulating transgene effects on plant responses to drought, which has shown success in understanding and manipulating plant physiological pathways (Lubbers *et al*. 2007).

Drought stress is a critical abiotic factor limiting cotton productivity, requiring identification of key traits and mechanisms for developing tolerant varieties. Cotton adapts to drought through morphological changes such as reduced leaf area, enhanced root growth, and optimal root-shoot ratio. Physiological responses include improved relative water content, leaf water potential, and accumulation of osmolytes like proline and abscisic acid. Biochemically, drought triggers ROS scavenging via antioxidant enzymes and increases in soluble sugars and jasmonic acid. Molecularly, genes and transcription factors from MAPK, WRKY, and NAC families play key roles. Techniques like QTL mapping, GWAS, and transcriptome analysis have identified major drought-responsive genes. However, tools like CRISPR/Cas9 and genomic selection remain underexplored. CRISPR enables precise gene editing to suppress drought susceptibility genes, while genomic selection accelerates identification of resilient genotypes. Combining conventional and advanced breeding strategies can significantly enhance drought tolerance and ensure sustainable cotton production under water-limited conditions.

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