Khan *et al. Journal of Cotton Research (2025) 8:17*
https://doi.org/10.1186/s42397-025-00223-3

Journal of Cotton Research

REVIEW **Open Access**

Impacts of climate change on cotton production and advancements in genomic approaches for stress resilience enhancement

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Abstract

Cotton is an essential agricultural commodity, but its global yield is greatly affected by climate change, which poses a serious threat to the agriculture sector. This review aims to provide an overview of the impact of climate change on cotton production and the use of genomic approaches to increase stress tolerance in cotton. This paper discusses the effects of rising temperatures, changing precipitation patterns, and extreme weather events on cotton yield. It then explores various genomic strategies, such as genomic selection and marker-assisted selection, which can be used to develop stress-tolerant cotton varieties. The review emphasizes the need for interdisciplinary research efforts and policy interventions to mitigate the adverse effects of climate change on cotton production. Furthermore, this paper presents advanced prospects, including genomic selection, gene editing, multi-omics integration, high-throughput phenotyping, genomic data sharing, climate-informed breeding, and phenomics-assisted genomic selection, for enhancing stress resilience in cotton. Those innovative approaches can assist cotton researchers and breeders in developing highly resilient cotton varieties capable of withstanding the challenges posed by climate change, ensuring the sustainable and prosperous future of cotton production.

Keywords Cotton, Climate Change, Stress tolerance, Genomic selection, Gene editing, QTLs, Fiber

Background

Global warming and climate change pose significant threats to both humanity and biodiversity (Abbas 2020). Among the sectors vulnerable to climate change, agriculture stands out, as global climate shifts lead to reduced crop productivity and altered development patterns (Rahman et al. 2018). Cotton (*Gossypium* spp.), a prominent cash and fiber crop cultivated in over 50 countries, is particularly affected. This perennial shrub thrives in warm day and night conditions and needs optimal conditions for growth and development (Imran et al. 2018). Cotton belongs to the genus *Gossypium* and family Malvaceae. The genus *Gossypium* consists of more than 50 species, in which most of them are diploids (2n =26) and five are allotetraploids (2n =52). Based on the chromosome similarity, these species are grouped into eight

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genome groups designated as A to G and K (Si et al. 2022). The five allotetraploid species are designated as $(AD)_1$ to $(AD)_5$ based on their genomic composition. The phylogenetic analyses of *Gossypium* grouped the five AD-genome species into one lineage and grouped two major lineages of the diploid species, which includes 13 species of D-genome and more than 30 species of A-, B-, E-, F-, C-, G-, and K-genome (Yang et al. 2023a).

Cotton fiber is primarily composed of cellulose and relies on abundant sunlight, frost-free conditions, and sufficient rainfall to grow. Cotton is vital in the livelihoods of millions in developing countries and contributes significantly to the 2030 Sustainable Development Goals (SDGs). It was reported that cotton production and trade were valued at nearly $46 billion and $15 billion globally in 2019 respectively (FAO 2021). However, the cotton industry is highly sensitive to climate change (Jans et al. 2021). Abiotic stresses, including drought, salinity, and temperature fluctuations, are affecting the quality and yield of cotton (Bawa et al. 2022).

Climate change has an intense effect on cotton at the reproductive stage, which is for flowering and boll formation, therefore greatly decreasing the overall yield (Li et al. 2020). Temperature stress has one of the most significant effects in cotton production. In the scenario of global rising temperature above the optimal growth condition (20 °C to 30 °C), climate change will result in heat stress during flowering (Majeed et al. 2024; Wu et al. 2015). When cotton plants are exposed to intense heat stress, they may experience rapid flowering, frequently accompanied by incomplete flower development, declined pollen viability, and increased flower abortion; these result in fewer bolls as well as negatively affecting the yield and quality (Min et al. 2014; Zafar et al. 2018). Chen et al. (2019) emphasizes that cotton is particularly sensitive to water availability and temperature fluctuations during flowering and boll formation. Meanwhile, the unexpected cold spells may also interrupt the flowering, decrease boll formation, and limit the cotton reproductive growth (Zhang et al. 2024).

Drought stress is another serious factor induced by climate change, especially influencing the cotton reproductive stage (Wang et al. 2022). The drought stress condition results in early flower shedding and affects the boll development (Sun et al. 2021). The deficiency of water during the flowering stage reduces the ability of plants to sustain healthy flowers and decreases the overall productivity (Wu et al. 2018). On the other hand, extreme rainfalls or floods may also destroy the root system, reduce the nutrient uptake and oxygen supply, and result in decreased flower production and boll formation (Zhang et al. 2021; Qian et al. 2020). In addition, drought also affects boll size and number, especially on upper flowering branches (Wang et al. 2016). Although cotton at the reproductive stage is very sensitive to drought stress, which may lead to flower and boll shedding, smaller boll size, reduced fiber quality and yield loss (Gao et al. 2020b), the drought stress has no significant effect on early stage of cotton, which is more tolerant to drought stress and can withstand the period of inadequate water accessibility (Meshram et al. 2022).

Furthermore, intense weather events like strong winds, hurricanes, and tornadoes caused by climate change can damage cotton flowers as well as the plant structure and decrease boll formation (Broughton et al. 2019). Climate change caused rising sea levels and soil degradation and increased soil salinity; these are estimated to affect over 20% of agricultural soils worldwide. Cotton is negatively affected by higher salinity levels in soil, leading to retarded plant growth and development (Roy et al. 2014).

We provide in this review a comprehensive overview of the impacts of climate change on cotton production and summarize the genomic approaches to enhance stress resilience in cotton. We also emphasize the critical importance of interdisciplinary collaboration and propose practical strategies to assist cotton farming communities in addressing climate-related challenges. Ultimately, we offer concise insights into the potential of genomic research to fortify resilience (Fig. 1).

Effect of abiotic stress on cotton

The Intergovernmental Panel on Climate Change (IPCC) reported a 0.78 °C increase in global land surface temperature from 2003–2012 compared with 1850–1900, with projections indicating an additional 4.8 °C rise by 2100 (IPCC 2014). Elevated temperatures, particularly exceeding 32 °C, pose significant threats to cotton crops, especially during the reproductive phase (Qian et al. 2018). This impact is evident in various regions such as China, which has experienced an average temperature increase of 0.5–0.8 °C over the past century (Ding et al. 2007).

Altered temperature patterns substantially influence cotton growth cycles and overall production (Khan et al. 2020). Cotton germination is optimal within a range of 20–30 °C but declines below 20 °C or above 38 °C (Gao et al. 2020a). High temperatures also damage the roots of cotton plant, impairing their ability to absorb water and nutrients (Zahid et al. 2016; Rosolem et al. 2013; Wu et al. 2014). Furthermore, temperatures above 33 °C during bud formation lead to the shedding of floral buds, flowers, and bolls (Brown 2008), resulting in smaller boll sizes and reduced weight (Tariq et al. 2017; Karademir et al. 2012). The quality and quantity of cotton fiber are also influenced by higher temperatures, leading to lower

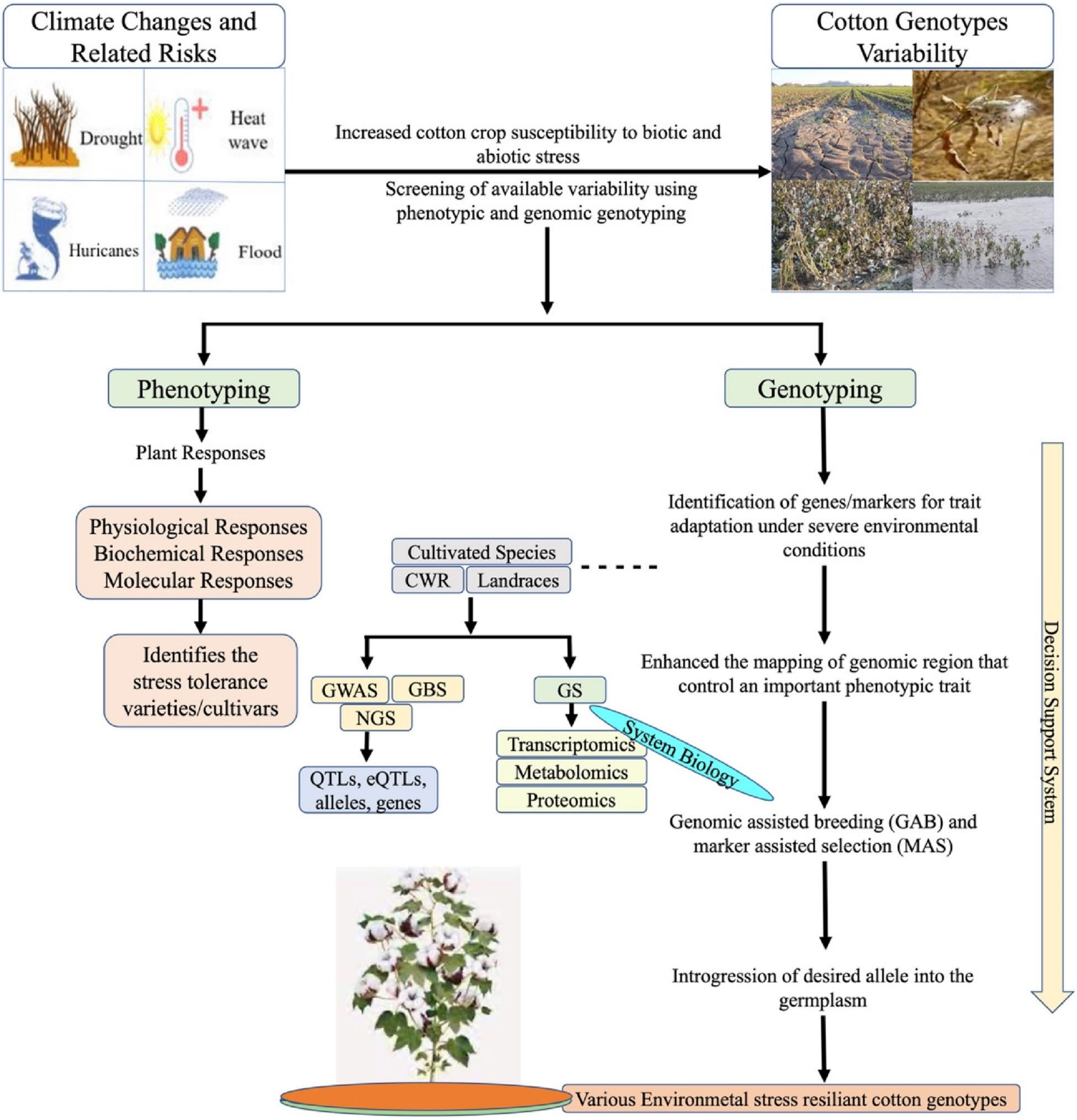

Fig. 1 The illustration of improving cotton resilience to various environmental stresses through breeding

yield and poorer fiber quality (Liu et al. 2015; Abro et al. 2015; Yaqoob et al. 2016; EL-Sabagh et al. 2020; Zafar et al. 2018). Maintaining a minimum temperature of 22 °C is essential for cotton yield (Majeed et al. 2021). Prolonged exposure to elevated temperatures can irreversibly damage cellulose, thereby reducing cotton yield and fiber quality (Xu et al. 2017). Heat stress negatively affects key physiological processes in plants, including photosynthesis, stomatal conductance, and membrane permeability (Gago et al. 2016). Cotton plants exposed to high temperatures reduce the chlorophyll content, decrease photosynthesis rates, and disrupt cell membrane integrity (Karademir et al. 2018). Additionally, rising temperatures increase stomatal conductance, which affects water potential in leaves (Bita et al. 2013). The adverse effects of elevated temperature on various stages of cotton development are illustrated in Fig. 2.

Changes in precipitation patterns are one of the prominent outcomes of climate change (Giorgi et al. 2019). Global land precipitation has increased by 2%,

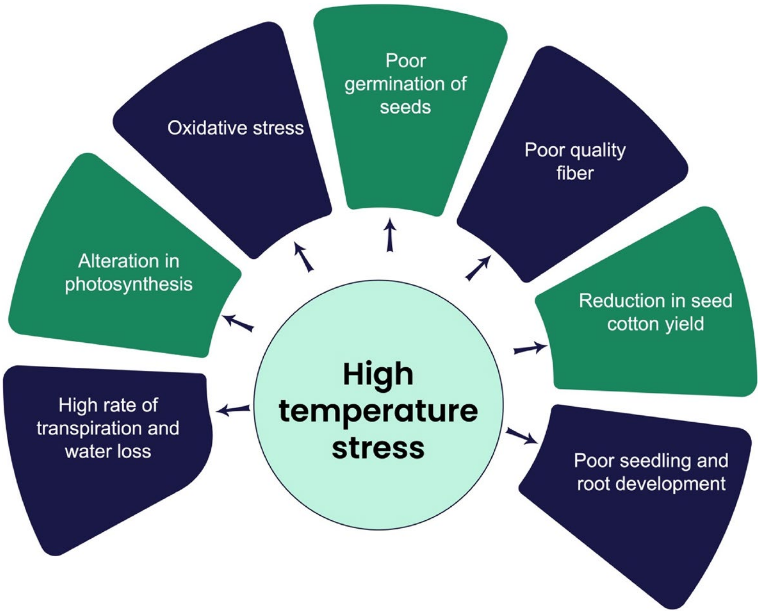

Fig. 2 Negative impacts of high temperature on various stages of cotton growth

yet regional variations show significant increases or decreases due to extreme weather events (IPCC 2014; Lehmann et al. 2015). This unpredictability in rainfall patterns is particularly notable in major cotton-growing regions such as India, China, the USA, Brazil, and Pakistan. In China, historical data indicate a shift from declining rainfall from the 1960s to the 1990s, followed by a recovery trend in the late 1990s (Dai et al. 2014). Heavy rainfall during the reproductive stages of cotton leads to pollination issues and cause abscission of buds, flowers, and bolls (Xu et al. 2024). Additionally, prolonged and intense rainfall during the rainy season can result in boll rotting disease, plant lodging, reduced cotton yield, and poorer fiber quality (Wang et al. 2014). Cotton, being a water-sensitive cash crop, is particularly susceptible to changes in precipitation patterns (Hussain et al. 2020; Sengupta et al. 2023).

Drought stress and waterlogging have significant impacts on cotton growth, affecting germination, nutrient uptake, fiber quality, yield, and pest and disease resistance (Arshad et al. 2021). While moderate drought stress encourages deeper root growth and enhances lateral root density, allowing the plant to access water from deeper soil layers (Zafar et al. 2023a), excessive drought stress can reduce overall root biomass and inhibit root elongation, thereby impairing nutrients and water absorption (Guo et al. 2024). Drought-induced water scarcity raises cotton leaf temperatures, leading to morphological changes and physiological disorders that hinder nutrient uptake and photosynthesis (Siddique et al. 2016; Zahoor et al. 2017). This stress also affects chlorophyll content, osmotic potentials, and relative water content, ultimately reducing cell growth and elongation (Shareef et al. 2018).

Waterlogging, characterized by excessive soil saturation, reduces oxygen levels in soil, causing hypoxia or anoxia. These conditions disrupt nutrient uptake and energy metabolism in cotton plants, promote the accumulation of toxic chemicals like lactic acid and ethanol, and negatively impact growth (Zhang et al. 2016; Kuai et al. 2015; Khalid et al. 2018; Somaddar et al. 2023). Waterlogging also impairs photosynthesis by decreases Rubisco activity, chlorophyll content, and net photosynthetic rate, leading to premature senescence and yield loss (Wang et al. 2017; Najeeb et al. 2015). Furtherover, waterlogging disrupts carbon and nitrogen metabolism, affecting protein and soluble sugar levels, while also causing deficiencies in nitrogen, potassium, magnesium, calcium, and phosphorus in cotton plants (Ren et al. 2017; Khan et al. 2017).

Physiological and biochemical mechanisms under abiotic stress

Elevated temperatures can denature proteins and disrupt enzyme activities, compromising essential cellular processes (Majeed et al. 2019a; Acosta-Martinez et al. 2014; Khan et al. 2017). While cotton plants thrive optimally at around 32 °C, temperatures higher than this threshold impair protein and enzyme functioning, whereas temperatures below 20 °C hinder their activity without

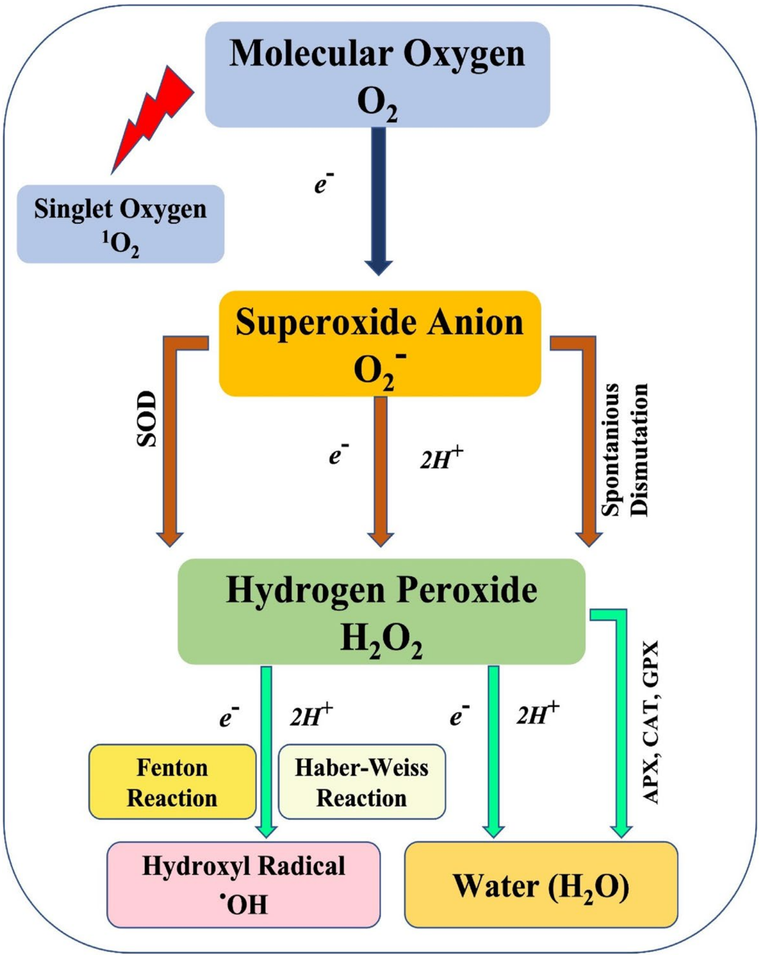

Fig. 3 The schematic diagram of oxidative stress and ROS production in cotton

risking denaturation (Wang et al. 2015). Enzymes, critical for biochemical reactions and metabolic activities, are particularly sensitive to temperature changes, which negatively affect their structure and efficiency (Abro et al. 2023). In addition, temperature fluctuations alter metabolic processes in cotton plants, leading to the accumulation of reactive oxygen species (ROS) (Considine et al. 2015; Singh et al. 2016). Excessive ROS production damages various cellular components, resulting in cellular dysfunction (Sekmen et al. 2014; Sarwar et al. 2018). The production of ROS in cotton plants is shown in Fig. 3.

Under high temperatures, heat shock proteins (HSPs) play a crucial role in maintaining cellular homeostasis (Haslbeck et al. 2015). Various classes of HSPs based on molecular weight have been shown in Table 1, including HSP100, HSP90, HSP80, HSP60, and small HSPs, which assist in protein folding and cellular protection (Li et al. 2014). Among HSPs, HSP60 aids in photosynthesis under high-temperature stress (Winkler et al. 2012; Mishra et al. 2016).

Additionally, HSP70 contributes to temperature tolerance and fiber development, while HSP90 is involved in signal transduction and is abundant in cotton, particularly under elevated temperatures (Song et al. 2015; Ma et al. 2019). HSP100, a member of the AAA ATPase family, aids in protein disaggregation and folding, impacting chloroplast development and temperature stress tolerance in cotton plants (Erdayani et al. 2020).

During drought, cotton plants experience a range of physiological and biochemical mechanisms to sustain water balance as well as ensure survival (Babar et al. 2023). For example, cotton plants aggregate osmoprotectants such as glycine betaine and proline that assist in maintaining cell turgor and defend cell membranes and proteins under drought (Aslam et al. 2023). Although water deficit encourages the formation of antioxidant enzymes like catalase, peroxidase (POD), catalase (CAT), and superoxide dismutase (SOD) to reduce

Table 1 Characteristics of various HSP groups in plants

Sub-families		Representative members	Intracellular localization	Major role	References
HSP100	Class 1	ClpB, ClpA/C, ClpD	Cytosol, mitochondria, chloroplast	Unfolding and disaggregation of proteins	Zietkiewicz et al. 2004
	Class 2	ClpM, ClpN, ClpX, ClpY			Winkler et al. 2012
HSP90		Hsp90 - 1	Cytosol	Facilitates in buffering genetic variation and maturation of signaling molecule	Krishna et al. 2001
		Hsp90 - 5	Chloroplast		
		HSP90 - 6	Mitochondria		Kadota et al. 2012
		HSP90 - 7	Endoplasmic reticulum		Sable et al. 2018
HSP70	Dnak	Hsp/Hsc70	Cytosol	Protein import, signal transduction, transcriptional activation, assist refolding and prevent aggregation of protein	Sung et al. 2001
		Hsp70	Chloroplast, mitochondria		Scarpeci et al. 2008
		Bip1	Endoplasmic reticulum		Li et al. 2014
HSP110/SSE		Hsp91	Cytosol		Rehman et al. 2020
HSP60	Group 1	Cnp602	Chloroplast, mitochondria	Folding of proteins	Boston et al. 1996
	Group 2	CCT3	Cytosol		Hartl et al. 2011
sHSP	I	Hsp17.6	Cytosol	Stabilization of non-native protein and prevent aggregation	Lee et al. 2000
	II	Hsp17.9	Cytosol		
	III	Hsp21, Hsp26.25	Chloroplast		
	IV	Hsp22	Endoplasmic reticulum		Haslbeck et al. 2015
	V	Hsp235	Mitochondria		
	VI	Hsp22.3	Membrane		

the oxidative damage induced by the aggregation of reactive oxygen species (ROS), in addition to increasing the drought resilience through sustaining cell homeostasis and defending the plant from heat stress damage (Zafar et al. 2023b).

Under waterlogging situations, cotton plants altered physiologically and biochemically to withstand the oxygen deficit in the root zone (Zhang et al. 2023a). Cotton plants improve the activity of antioxidant enzymes such as POD, CAT, and SOD to withstand the oxidative stress induced by waterlogging. In addition, plants may also stimulate the formation of root aerenchyma to assist oxygen transport and enhance the survival rate in flooded situations (Owusu et al. 2023).

Similarly to salinity stress, the cotton plants also show several physiological and biochemical responses to cope the osmotic stress and ion toxicity (Chaudhary et al. 2024). Physiologically, salt stress results in water uptake decline, causes stomatal closure, reduces photosynthesis and hinders growth. In addition, the excess sodium and chloride ions interrupt ionic balance and nutrient absorption, mainly potassium, which is vital for cellular function in cotton (Zhang et al. 2023c). Biochemically, cotton plants initiate the antioxidant defense mechanism by producing enzymes like CAT, POD, and SOD to alleviate the oxidative stress, as well as aggregating osmo-protectants such as proline, which aids in sustaining cellular homeostasis and osmotic adjustment (Keya et al. 2023).

Omics approaches for enhancing stress resilience

Cotton remains a popular fiber crop due to its simplicity and comfort, even with advancements in synthetic fibers (Tausif et al. 2018). However, traditional breeding efforts to improve cotton productivity are challenging due to genetic complexity and limited trait knowledge (Ashraf et al. 2022). Molecular breeding, which utilizes tools such as genetic markers and gene expression analysis, has revolutionized cotton breeding by enhancing traits of productivity and stress tolerance, as well as other economically significant traits (Katageri et al. 2020; Wen et al. 2021).

Genomic tools like next-generation sequencing (NGS) have played a pivotal role in the development of molecular breeding. Advanced techniques such as Illumina MiSeq, HiSeq2500, Ion Torrent PGM, and Roche 454 FLX Titanium have enabled cost-effective marker discovery, which can be used to improve stress resilience (Ahmed et al. 2024; Siddique et al. 2019). Genetic mapping has successfully identified candidate genes associated with stress resistance, as shown in Tables 2, and 3 (Hayat et al. 2020; Majeed et al. 2019b). Genotyping by sequencing (GBS) aids genetic diversity analysis, linkage studies, genome-wide association studies (GWAS), and marker discovery, particularly for stress resistance (Zhang et al. 2019a; Song et al. 2019; Abdelraheem et al. 2020; Liu et al. 2020). Table 4 is a list of candidate genes associated with drought stress response as an example.

Genomic selection (GS) utilizes genetic markers to accurately predict the breeding values of complex traits,

Table 2 List of candidate genes associated with salt-tolerance related traits in cotton (Sun et al. 2018)

Gene ID	Anotation
Gh_A01G0224	ACLB- 2 | ATP citrate lyase subunit B 2
Gh_A01G0225	DNA-binding enhancer protein-related
Gh_A01G0226	Pectin lyase-like superfamily protein
Gh_A01G0227	ECHIA, E-COAH- 2 | enoyl-CoA hydratase/isomerase A
Gh_A01G0228	PFD3 | prefoldin 3
Gh_A01G0229	GAL1, GALK | Mevalonate/galactokinase family protein
Gh_A01G0230	unknown protein
Gh_A01G0231	Plant invertase/pectin methylesterase inhibitor superfamily protein
Gh_A01G0232	Plant invertase/pectin methylesterase inhibitor superfamily protein
Gh_A01G0233	Plant invertase/pectin methylesterase inhibitor superfamily protein
Gh_A01G0234	Pentatricopeptide repeat (PPR) superfamily protein
Gh_A01G0235	F-box family protein
Gh_A01G0236	agenet domain-containing protein
Gh_A01G0237	ATGA2OX4, ATGA2OX6, DTA1, GA2OX6 | gibberellin 2-oxidase 6
Gh_A01G0238	ECT7 | evolutionarily conserved C-terminal region 7
Gh_A01G0239	Protein kinase superfamily protein
Gh_A01G0240	Nucleotide-sugar transporter family protein
Gh_A01G0241	PDK, ATPDHK | pyruvate dehydrogenase kinase
Gh_A01G0242	unknown protein
Gh_A01G0243	ATNHX6, NHX6 | Na +/H + antiporter 6
Gh_A01G0244	Tetratricopeptide repeat (TPR)-like superfamily protein
Gh_A01G0245	Di-glucose binding protein with Kinesin motor domain
Gh_A01G0246	WAG2 | Protein kinase superfamily protein
Gh_A01G0247	Chaperone DnaJ-domain superfamily protein
Gh_A01G0248	Protein kinase superfamily protein
Gh_A01G0249	PSBR | photosystem II subunit R
Gh_A01G0250	recA DNA recombination family protein
Gh_A01G0251	unknown protein
Gh_A01G0252	Tetratricopeptide repeat (TPR)-like superfamily protein
Gh_A01G0253	CBRLK1, SD1 - 13, RKS2 | S-domain- 1 13
Gh_A01G0254	S-locus lectin protein kinase family protein
Gh_A10G1751	SYP61, ATSYP61, OSM1 | syntaxin of plants 61
Gh_A10G1752	DNA-binding storekeeper protein-related transcriptional regulator
Gh_A10G1753	UBP12 | ubiquitin-specific protease 12

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surpassing traditional marker-assisted selection (MAS) in selecting desired individuals (Mubarik et al. 2020; Ahmed et al. 2024). Phenomics, the evaluation of fundamental attributes and their correlation with economic traits, is crucial for cotton breeding. High-throughput phenotyping aids in QTL mapping for cotton yield, fiber quality, and stress tolerance (Zhang et al. 2019b). However, further enhancements are still necessary in phenotyping, especially for abiotic and biotic stress resilience.

Despite millions of years of evolution, cotton genes remain highly conserved across cultivated and wild, diploid and tetraploid species (Tahmasebi et al. 2019). Tools like DNA microarrays and RNA-seq aid in large-scale transcriptome analysis, providing insights into gene expression variations during cotton development and under environmental stresses (Owusu et al. 2023; Xu et al. 2022; Kang et al. 2023). There are over 270 000 *Gossypium* ESTs in the NCBI database, reflecting extensive research in this area (Hasan et al. 2019). Notably, thousands of genes have been identified that control fiber yield, quality, and strength, shedding light on the regulatory mechanism of fiber development

(Padmalatha et al. 2012). Some of the identified candidate genes are given in Table 5.

Proteomics shifts the focus to protein synthesis and alteration, as proteins are essential cellular components (Bawa et al. 2022). Methods developed by Jin et al. (2019) allow for effective protein extraction from cotton fiber. A proteomic study in cotton under drought stress identified hundreds of proteins that may be involved in plant responses to drought stress (Xiao et al. 2020). A proteomic study also identified different protein dynamics in wild cotton species under heat stress, revealing critical post-translational alterations such as phosphorylation (Masoomi-Aladizgeh et al. 2022).

Metabolomics examines changes in primary and secondary metabolites during plant development (Zhang et al. 2023b). Mass spectrometry is employed alongside chromatography to identify different metabolite patterns among drought resistant and drought sensitive cotton lines in response to drought stress, revealed potential molecular regulatory mechanism involved in drought stress response (Han et al. 2022). It was reported that polyphenols increase under drought stress in cotton, aiding osmotic balance, and terpenoids provide defense against biotic and abiotic stress (Abdelrahman et al. 2018). The metabolomic analysis offers potential for breeding stress-resistant cotton varieties (Ren et al. 2022).

Role of epigenetics in climate-smart cotton varieties

Epigenetics plays an important function in plant abiotic stress response by controlling gene expression without DNA mutation (Williams 2023). During severe conditions, epigenetic modifications such as DNA methylation and histone modification may trigger or terminate the expression of stress-responsive genes, which control the physiological responses (Abdulraheem et al. 2024).

Epigenomics also provides a wider understanding of these modifications throughout the whole genome to recognize genes that are responsive to particular environmental stress (Ijaz et al. 2024; Wang et al. 2024). Through mapping these epigenetic alterations, researchers can identify the markers associated with stress tolerance. The knowledge of epigenomics may be introduced into breeding programs, which allows the selection of cotton germplasms to enhance the adaptation to climatic change and the development of resilient cotton (Khan et al. 2023; Manivannan et al. 2023). Although the epigenetic alterations are heritable, epigenetical adaptation in plants over generations is not a general phenomenon (Miryeganeh et al. 2025).

Genome editing and synthetic biology

Genome editing tools, including CRISPR/Cas, enable precise gene editing for trait improvement and functional analysis to address the challenges of climate change and food security (Chen et al. 2017; Ahmar et al. 2020; Martignago et al. 2020). In cotton, CRISPR/Cas toolkits have been used to enhance fiber quality byoptimized for targeted gene editing (Long et al. 2018). Molecular regulators involved in stress responsive are potential target loci of genome editing to improve abiotic stress resistance in cotton, such as cloned GhGAI3 and GhGAI4, encoding DELLA proteins, which are responsive to gibberellin, phytohormones, light, and stress signals (Wen et al. 2010). With the progress in omics data, the CRISPR/Cas system facilitates gene insertion and deletion and speed up the integration of target traits into elite breeding lines (Malzahn et al. 2017; Jaganathan et al. 2018; Bilichak et al. 2020).

Marker-assisted selection

Conventional plant breeding often relies on phenotypic selection of superior genotypes within segregation progenies but faces challenges like long breeding cycles and low selection efficiency (Kushanov et al. 2021). Phenotyping practices can be costly, time-consuming, and particularly challenging for traits like abiotic stress tolerance (Ijaz et al. 2019). Molecular marker-assisted selection (MAS) offers a solution by selecting genes associated with specific traits rather than relying solely on phenotype (Islam et al. 2020). Molecular markers are unaffected by environmental factors and can be detected throughout plant growth. This approach is promising for both qualitative trait loci (QTLs) and major gene-controlled traits due to the availability of diverse molecular markers and genetic maps (Darmanov et al. 2022). The effectiveness of molecular markers depends on their ability to detect polymorphism in nucleotide sequences (Lopes et al. 2020). Various molecular markers have been developed, such as SSR, AFLP, RFLP, RAPD, CASP, SSCP, SNPs, and so on, to reveal polymorphisms (Ujjainkar et al. Patel 2020).

The development of molecular markers has revolutionized crop breeding by minimizing the limitations of traditional methods, which could inadvertently transfer undesired genes due to genetic linkage, while molecular markers could facilitate identifying the undesired genes in the early progeny to speed up the breeding cycle (Hassan et al. 2021; Khan et al. 2022; Fang et al. 2021). The use of MAS has been found to be effective in enhancing fiber quality and stress resistance in cotton. Utilization of different molecular markers linked to the major QTL, MAS enables the detection of germplasm (Saud et al. 2022). Molecular markers linked to abiotic

Table 3 List of potential candidate genes related with salt tolerance in cotton identified through GWAS (Xu et al. 2021)

Chr	Gene	Trait	Annotation
A05	GH_A05G3644	RSDW16	Cytochrome c oxidase subunit 6b- 2
A05	GH_A05G3645	RSDW16	Transposon Ty3-G Gag-Pol polyprotein
A05	GH_A05G3646	RSDW16	Tetratricopeptide repeat protein 1
A05	GH_A05G3647	RSDW16	Putative clathrin assembly protein
A07	GH_A07G2207	RSFW16, RSFW17	no
A07	GH_A07G2208	RSFW16, RSFW17	Subtilisin-like protease SBT5.3
A07	GH_A07G2209	RSFW16, RSFW17	Ras-related protein RABB1c
A07	GH_A07G2210	RSFW16, RSFW17	Glucose- 1-phosphate adenylyltransferase small subunit 2, chloroplastic
A07	GH_A07G2211	RSFW16, RSFW17	no
A07	GH_A07G2212	RSFW16, RSFW17	no
A07	GH_A07G2213	RSFW16, RSFW17	Myb family transcription factor APL
A07	GH_A07G2214	RSFW16, RSFW17	Transmembrane 9 superfamily member 12
A07	GH_A07G2215	RSFW16, RSFW17	no
A07	GH_A07G2216	RSFW16, RSFW17, RPH17	Auxilin-related protein 1
A07	GH_A07G2217	RSFW16, RSFW17, RPH17	60S ribosomal protein L5
A07	GH_A07G2218	RSFW16, RSFW17, RPH17	Ribonuclease 2
A07	GH_A07G2219	RSFW16, RSFW17, RPH17	Mediator of RNA polymerase II transcription subunit 19a
A07	GH_A07G2220	RSFW16, RSFW17, RPH17	Acyl-coenzyme A thioesterase 9, mitochondrial
A07	GH_A07G2221	RSFW16, RSFW17, RPH17	UDP-glycosyltransferase 74 F2
A07	GH_A07G2222	RSFW16, RSFW17, RPH17	Probably inactive leucine-rich repeat receptor-like protein kinase At5 g48380
A07	GH_A07G2223	RSFW16, RSFW17, RPH17	FRIGIDA-like protein 3
A07	GH_A07G2224	RSFW16, RSFW17, RPH17	Ubiquitin-like-conjugating enzyme ATG10
A07	GH_A07G2225	RSFW16, RSFW17, RPH17	Glutamate receptor 2.7
A07	GH_A07G2226	RSFW16, RSFW17, RPH17	Glutamate receptor 1.3
A07	GH_A07G2227	RSFW16, RSFW17, RPH17	no
A07	GH_A07G2228	RSFW16, RSFW17, RPH17	Protein FAR1-RELATED SEQUENCE 5
A07	GH_A07G2229	RSFW16, RSFW17, RPH17	Calmodulin-like protein 7
A07	GH_A07G2230	RSFW16, RSFW17, RPH17	Probable linoleate 9S-lipoxygenase 4
A07	GH_A07G2231	RSFW16, RSFW17, RPH17	Uncharacterized protein
A07	GH_A07G2232	RSFW16, RSFW17, RPH17	Probable sodium/metabolite cotransporter BASS3, chloroplastic
A07	GH_A07G2233	RSFW16, RSFW17, RPH17	no
A08	GH_A08G0481	RSFW16, RSDW16	Zinc finger CCCH domain-containing protein 32
A08	GH_A08G0482	RSFW16, RSDW16	no
A08	GH_A08G0483	RSFW16, RSDW16	Protein TRANSPORT INHIBITOR RESPONSE 1

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Where *RSDW* Relative shoot dry matter weight, *RSFW* Relative shoot fresh matter weight, *RPH* Relative plant height; number 16 and 17 to distinguish the year of 2016 and 2017 of experiment

stress have been utilized in crops such as maize, rice, wheat, brassica, barley, tomato, and cotton (Darmanov et al. 2022; Majeed et al. 2021; Lopes et al. 2020; Lu et al. 2020). For example, waterlogged-tolerant varieties and improved agronomic traits have been successfully developed through MAS (Shehzad et al. 2019). Steps in marker-assisted selection have been illustrated in Fig. 4. The first step is the identification of plants with desired traits that emphasize superior agronomic attributes for stress resilience whereas parents with distinct traits are chosen, and genotypes are screened with molecular markers. Specifically, homozygous parents were preferred for MAS (Bolek et al. 2016). The second step is crossing the selected parents to obtain the F_1 generation. Then, the F_1 population is screened for specific marker alleles. The F_2 generation is developed to evaluate segregating patterns using similar screening techniques (Lopes et al. 2020). In the MAS procedure, DNA is extracted from the plant, preferably at the seedling stage to save time. Standard protocols are used for DNA extraction are used, followed by

Table 4 List of candidate genes in cotton associated with physiological traits under drought stress identified through GBS (Magwanga et al. 2020)

Gene Id	Description
Gh_A01G1935	Probable LRR receptor-like serine/threonine-protein kinase
Gh_A01G1936	NA
Gh_A01G1937	NA
Gh_A01G1938	NA
Gh_A01G1939	Neutral ceramidase
Gh_A01G1940	Probable sugar phosphate/phosphate translocator
Gh_A01G1941	Ataxin-3 homolog
Gh_A01G1942	OTU domain-containing protein
Gh_A01G1943	mRNA-capping enzyme
Gh_A01G1944	UPF0503 protein At3g09070, chloroplastic
Gh_A01G1945	Probable LRR receptor-like serine/threonine-protein kinase
Gh_A01G1946	Pentatricopeptide repeat-containing protein
Gh_A01G1947	NA
Gh_A01G1948	Laccase-4
Gh_A01G1774	GDSL esterase/lipase At5g03610
Gh_A05G2519	NA
Gh_A05G2520	Protein FLOWERING LOCUS D
Gh_A05G2521	U11/U12 small nuclear ribonucleoprotein 31 kDa protein
Gh_A05G2522	NA
Gh_A05G2523	NA
Gh_A05G3283	Probable WRKY transcription factor 28
Gh_A05G3284	NA
Gh_A05G3285	Probable receptor-like protein kinase
Gh_A05G3286	Protein NLP5
Gh_A05G3287	Callose synthase 7
Gh_D01G0174	Probable disease resistance protein
Gh_D01G0175	Probable disease resistance protein
Gh_D01G0176	RNA polymerase II subunit 5-mediating protein homolog
Gh_D01G0177	Leucine-rich repeat extensin-like protein 4
Gh_D01G0178	Protein TPX2
Gh_D01G0179	Non-specific lipid-transfer protein 13
Gh_D01G0180	Zinc finger CCCH domain-containing protein 2
Gh_D01G0181	Zinc finger CCCH domain-containing protein 2
Gh_D01G0182	26S proteasome non-ATPase regulatory subunit 2 homolog A

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digestion with specific restriction enzymes to produce DNA fragments (Khan et al. 2022; Sabev et al. 2020).

Genomic-assisted breeding pipelines and decision support system

Genomic-assisted breeding pipelines combine state-of-the-art genomic technologies and data analytics with traditional breeding programs to improve breeding efficiency and effectiveness. These pipelines utilise genetic information from the cotton genome to select and develop improved genotypes with desired traits, such as stress resistance, yield, and fiber quality (Conaty et al. 2022). Developing stress-resistant cotton genotypes requires a comprehensive approach that involves phenomics, genomics, and data analytics to identify and select resilient genotypes (Conaty et al. 2022). By incorporating advanced phenotyping, high-throughput genotyping, and data analytics techniques, these pipelines enhance the speed and accuracy of cotton breeding for stress resistance. The implementation of decision support systems and predictive models for the effective identification of superior germplasm with improved stress resistance requires the integration of phenomics and genomic data to make informed decisions on breeding (Manivannan et al. 2023). This technique speeds up the breeding process, decreases the utilization of resources, and enhances the development of stress-resistant varieties of cotton (Anilkumar et al. 2022) as shown in Figs. 5 and 6.

Omics data integration

Next-generation sequencing has generated a wealth of cotton omics data, but understanding and interpreting this data remains challenging. To effectively store, access, and analyze this data, it is crucial to have integrated databases and advanced bioinformatics tools. However, current cotton-specific databases lack user-friendly features (Yang et al. 2023b). Therefore, there is a need for a unified cotton information portal that has standardized layouts, metadata, and analysis workflows. This platform should integrate global datasets and utilize machine learning for intelligent querying and association. International collaboration is necessary to develop data standards, ontologies, and FAIR principles (Wilkinson et al. 2016). In addition, advanced tools such as natural language processing are needed to ensure data precision and to extract insights from historical literature. It is also important to have user-friendly bioinformatics pipelines for multi-step omics data analyses.

Unfortunately, cotton-specific platforms lack these pipelines (Afgan et al. 2018). What is needed are adaptable workflows for genetic prediction, expression quantification, and GWAS that incorporate graphical interfaces and cloud computing for accuracy (Mohanty et al. 2016; Manoj et al. 2022). To bridge the gap between phenotype and genotype in cotton, interdisciplinary tools from engineering, genomics, and data science are required. High-throughput phenotyping techniques generate vast amounts of data, but linking this data to genomic predictors is a challenge. Automation through machine learning, computer vision, and

Table 5 List of candidate genes involved in salt stress responses in cotton

Name	Gene_ID	DEG log2 (FoldChange)	DEP log2 (FoldChange)	Description
GhLEA14	Gh_A11G0835	4.53	0.55	Late embryogenesis abundant protein
GhKCS6	Gh_A03G1286	3.57	1.43	3-ketoacyl-CoA synthase 6
GhPRXR1	Gh_A05G1452	1.72	0.82	Peroxidase superfamily protein
GhPOD	Gh_A08G0714	1.58	0.41	Peroxidase superfamily protein
GhFIB	Gh_A05G1494	1.28	0.67	Fibrillin precursor protein
GhALDH7B4	Gh_D06G1578	2.48	0.31	Aldehyde dehydrogenase
GhUSP	Gh_A03G0386	1.2	0.37	Encodes universal stress protein
GhAVP1	Gh_D05G0122	1.42	0.62	Inorganic H pyrophosphatase family protein
GhADH1	Gh_A01G1605	2.03	0.34	Alcohol dehydrogenas

The log2(FoldChange) value indicates the relative change in abundance of candidate genes's transcripts at different time point is shown as a log2 ratio. Curtsey Chen et al. (2021) under a Creative Commons Attribution 4.0 International License

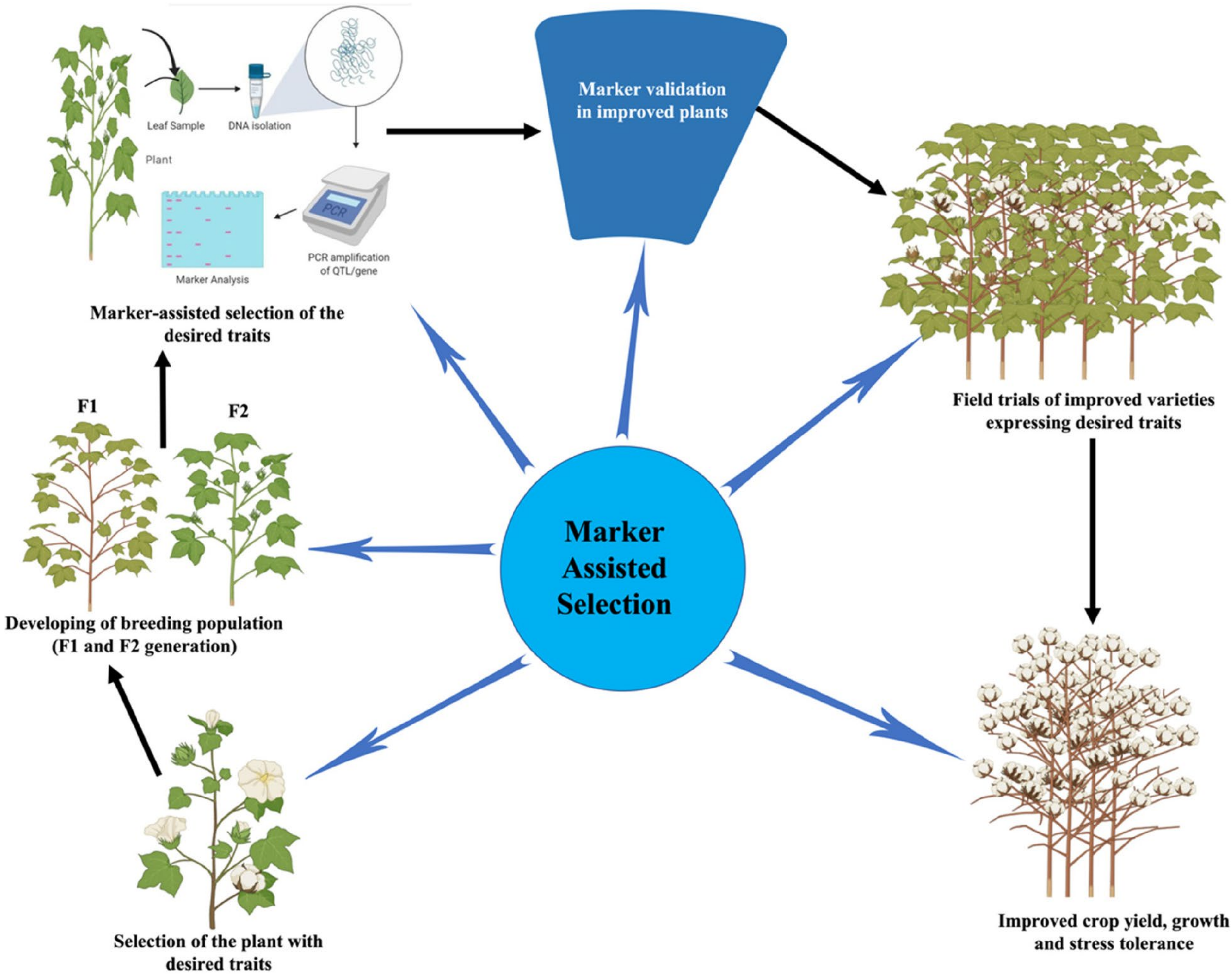

Fig. 4 Schematic diagram of different steps involved in marker-assisted selection in plants for abiotic stress tolerance

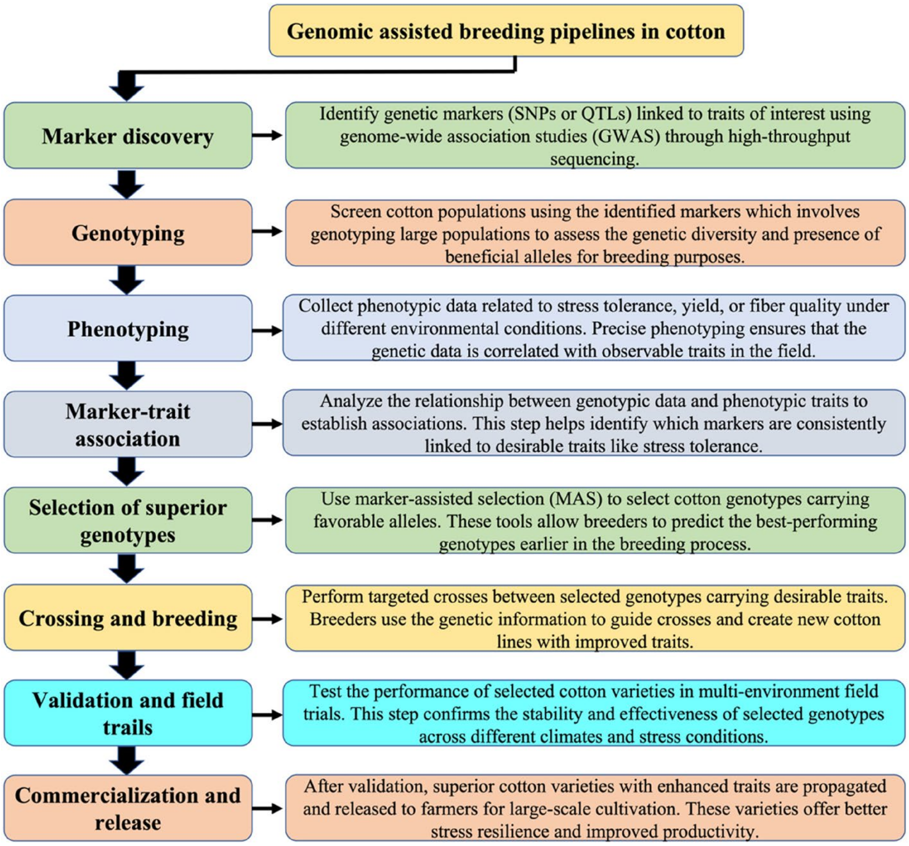

Fig. 5 Genomic-assisted breeding pipelines used to accelerate the development of stress tolerant cotton varieties

sensor integration can help with large-scale data collection and analysis. The future of cotton informatics lies in FAIR data ecosystems, community-driven standards, intuitive analysis platforms, and transdisciplinary collaboration. Open data sharing, collective development, and global partnerships are crucial for utilizing big data in cotton for fiber and environmental security. Achieving this vision will require creative skills, sustained funding, and active global collaboration.

Advantages and disadvantages of conventional breeding, pre-breeding, speed breeding and mutation breeding

Conventional breeding is cost-effective, which provides the advantage of exploiting natural genetic diversity as well as permitting the breeders to develop new crop varieties with desired attributes like environmental adaptability, disease resistance, and improved yield. However, it is time-consuming and laborious and mainly requires many growing seasons to develop the varieties with the desirable traits. And it lacks the accuracy in predicting the performance of progenies (Acquaah 2015). Similarly, pre-breeding introduces genetic variation by integrating desired traits into cultivated crops from wild relatives or landraces, which expands the gene pool and incorporate the traits of abiotic and biotic tolerance absent in domesticated germplasms (Sukumaran et al. 2022).

Speed breeding hastens crop development and allows breeders to produce numerous generations per year by adjusting light and temperature conditions, which assists quick selection for desired traits as well as considerably reduces the time. However, it requires controlled circumstances and expensive and specialized equipment, and not all crops respond well to the hastened conditions, which restrict application on certain traits, such as root development that requires long-term growth (Wanga et al. 2021). Similarly, mutation breeding develops new genetic diversity by subjecting plants to radiation or chemicals and directly incorporating favorable traits such as disease resistance and or improved yield. It permits the breeders to develop unique traits and avoid the need for current genetic variation. Although the mutation happens at random loci, which may be damaging or neutral, and requires extensive screening to recognize the favorable traits, which may be laborious and time-consuming, and having the risk of integrating unintentional negative traits that affects the plant growth and quality (Yali et al. 2022).

Interdisciplinary research and policy interventions for climate-resilient cotton production

The development of climate-resilient cotton varieties and cropping systems requires collaboration across a range of disciplines, including genetics, agronomy, climatology, and policy (Kusmec et al. 2021; Saad et al. 2022). This multidisciplinary approach allows for the integration of genetic knowledge into crop improvement, the assessment of breeding lines under future climate scenarios, and the consideration of economic returns when setting breeding goals (Antle et al. 2015).

Given the increasing threats posed by climate change, climate-resilient cotton cropping systems are essential (Rashid et al. 2020). Cotton is particularly vulnerable to abiotic stresses such as drought and floods, which necessitate innovative strategies such as adjusted sowing times, crop rotation, soil health improvement, crop diversification, and integrated pest management (Reddy 2015; International Trade Centre 2011; Plaza-Bonilla et al. 2016; Sprunger et al. 2021; Hinze et al. 2017; Naranjo et al. 2020). These practices, combined with early planting of heat-tolerant genotypes and Integrated Nutrient Management (INM), provide immediate and long-term resilience options (Kerns et al. 2016).

Despite the advantages of interdisciplinary collaboration, there are still obstacles to overcome, such as academic incentives that prioritize individual achievements and limited funding (Lyall 2012). Initiatives like grant programs and cyberinfrastructure tools can facilitate interdisciplinary collaboration (Biehl et al. 2017). Successful models like CGIAR and Excellence in Breeding demonstrate the potential of these collaborative efforts (Varshney et al. 2022). National initiatives like USDA's Triticeae Coordinated Agricultural Project (TCAP) and CIMMYT's Drought Tolerant Maize for Africa (DTMA) program provide effective strategies for enhancing crop resilience (TCAP 2022).

Policy plays a crucial role in promoting climate-resilient cotton varieties and cropping systems through incentives such as research grants, subsidies, and guaranteed prices (Kumari et al. 2020; Tiwari 2020). Subsidies for inputs, particularly for resource-poor farmers, can encourage the adoption of stress-tolerant varieties (van Asseldonk et al. 2023). Extension services, farmer incentives, and weather-index insurance further facilitate adoption and risk mitigation (Hansen et al. 2019; Serdeczny et al. 2017). International organizations like CGIAR play a vital role in guiding multinational breeding and cropping efforts (Abberton et al. 2016). Inclusive stakeholder engagement and gender-responsive policies are essential for effective policy interventions (Buehren 2023). Utilizing digital tools for localized breeding can accelerate the breeding of climate-resilient cotton (de Sousa et al. 2021; Fabregas et al. 2019).

Future prospects

Advanced genomic approaches

The field of genomics has revolutionized plant breeding by providing precise and efficient methods for developing crop varieties. Cotton breedings benefit greatly from the use of genomic tools as well, to enhance cotton resilience to both abiotic and biotic stresses. Some key advancements include genomic selection, gene editing, the integration of multiple omics datasets, high-throughput phenotyping, data-sharing platforms, and breeding strategies mediated with climate data. However, in order to fully realize the potential of these technologies, tailored research and strategic implementation in accordance with genetics and production challenges are essential.

Genomic selection

Genomic selection (GS) is a method that utilizes marker data from the genome to predict breeding values and identify superior genotypes, without the need for phenotyping every individual plant (Crossa et al. 2017). This approach allows for faster genetic gains by intensifying selection, shortening breeding cycles, and improving prediction accuracy compared with traditional phenotypic selection alone. Several studies have already demonstrated the potential of GS in improving traits such as fiber quality, yield, and drought tolerance in cotton (Islam et al. 2020; Liu et al. 2020; Sun et al. 2023; Ahmed et al. 2024).

Multi-omics integration

By integrating data from various omics datasets, we can gain a deeper understanding of the genetic mechanisms underlying stress tolerance in cotton. Omics data is essential for ensuring a sustainable and productive cotton industry. Metabolomics, for example, can identify stress-related metabolites, while proteomics can reveal stress-responsive proteins and pathways (Abdelrahman et al. 2018). When combined with transcriptomic data, these multi-omics analyses greatly enhance our understanding of cotton's molecular responses to stress (Lu et al. 2022; Xu et al. 2021). To further strengthen these approaches, it is important to develop tailored pipelines and databases that streamline the analysis of multi-omics data, ultimately bolstering systematic biology research in cotton (Hu et al. 2023).

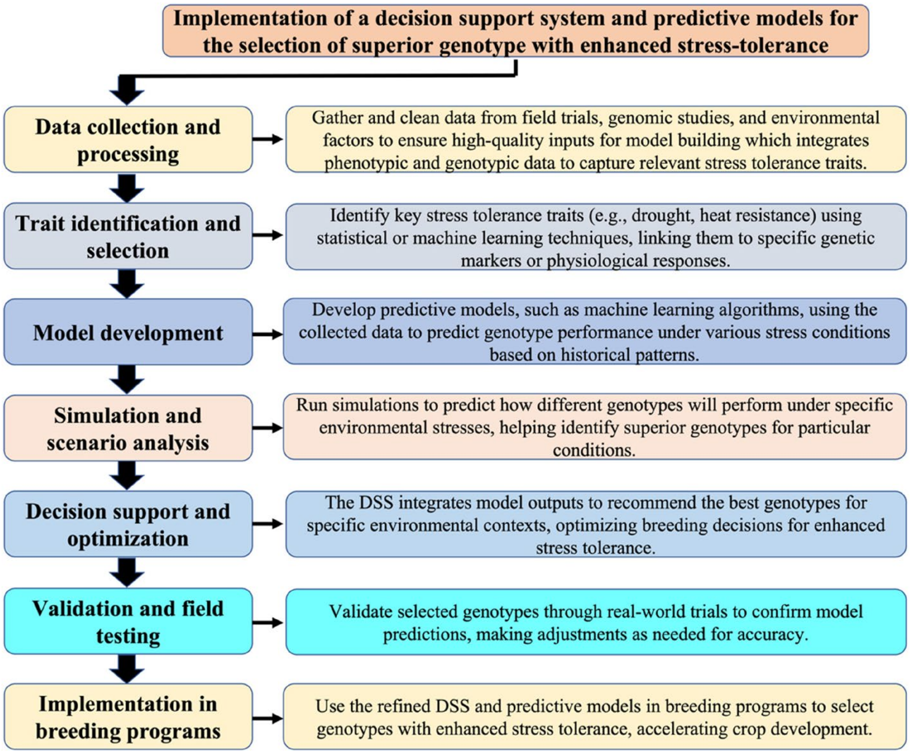

Fig. 6 Implementation of decision support system and predictive models for the selection of superior genotypes with enhanced stress tolerance

High-throughput phenotyping

High-throughput phenotyping (HTP) is a powerful tool that allows for rapid measurement of plant traits. When combined with genotypic data, HTP enhances genomic prediction and helps identify associations between traits and specific markers (Araus et al. 2018). Various technologies, such as automated imaging and sensors, can be used for monitoring plant traits like canopy temperature, plant architecture, and leaf area, as well as lysimeters that quantify crop water use and drought resistance (Deery et al. 2014; Fahlgren et al. 2015; Halperin et al. 2017). These HTP platforms are invaluable for assessing cotton genotypes in stress scenarios in the field, ultimately improving the speed of selection and genetic evaluation for stress resilience in cotton breeding programs.

Genomic data sharing

Public repositories like the US National Cotton Genome Database and CottonGen provide global access to important datasets for genomic research and breeding (Yu et al. 2021; Chen et al. 2021). By adopting the FAIR (findable, accessible, interoperable, reusable) principle and integrating predictive analytics and AI, we can enhance the use of collective information in real-time for cotton breeding, especially for climate resilience (Wilkinson et al. 2016; Dedeurwaerdere et al. 2016).

Climate-informed breeding

To develop climate-resilient varieties, we need to select improved varieties based on projected future environments, not just current conditions. Climate forecasting and crop growth modeling allow us to simulate target population environments, guiding breeding assessments (Lorenz et al. 2011). The genotype × environment × management (G × E × M) approach evaluates cotton genotypes across different sites and irrigation levels, helping us identify ideal germplasms and suitable cultivation areas (Sharif et al. 2019). Participatory varietal selection (PVS) and participatory plant breeding (PPB) involves farmer in the program to enhance biodiversity and adaptability.

Phenomics-assisted genomic selection

By incorporating phenomics data into genomic selection, we can improve the accuracy of predicting phenotypes (Zhu et al. 2021). Machine- and deep-learning-based MT-GS models have proven to improve prediction accuracy in large breeding programs (Sandhu et al. 2021). Integrating an inexpensive, high-throughput platform for stress tolerance selection can enhance prediction on the performance of genotypes under stress conditions. It is crucial to test and calibrate phenomics-enhanced GS models to diverse cotton production areas to maximize stress resilience traits.

To expedite the development of climate-resilient cotton germplasm, researchers should focus on improving predictive models that incorporate multi-omics data, and high-throughput phenotyping, expanding open-access genomic resources, incorporating climate analytics into breeding pipelines, and promoting strategic public–private partnerships.

Climate-smart agricultural practices

The concept of "climate-smart agriculture (CSA)" was introduced by the FAO during the Hague Conference on Agriculture in 2010. CSA is defined as agriculture that increases productivity sustainably, enhances resilience (adaptation), reduces or removes greenhouse gases (mitigation) where possible, and contributes to national food security and development goals (McCouch et al. 2013). The CSA approach involves integrating the need for adaptation into agricultural policies, planning, and investments (Imran et al. 2018). Farmers' willingness to adopt CSA is influenced by factors such as farming experience, access to credit, ownership of facilities, and availability of extension services (Jamil et al. 2021).

Climate-smart agriculture practices include soil health improvements, efficient water management, drought- and heat-resilient varieties, integrated pest management (IPM), efficient nutrient management, improvement of carbon storage and reduction of emission, and maintenance of diversity of crops and livelihoods. The adoption of climate-smart agricultural practices can reduce the negative impacts of climate change on the cotton crop. This can be achieved by ensuring profitability, addressing barriers in the adoption process, raising awareness about CSA, and implementing CSA regulations (Jamil et al. 2021). Farmers who have embraced CSA are using inputs more efficiently and achieving higher cotton yields per unit of irrigation water compared with those who do not practice CSA (Imran et al. 2019).

Conclusion

Climate change induces challenges to cotton production through an increase in the frequency of heat stress, drought, waterlogging, and salinity stress, as well as changing weather patterns that adversely affect crop yield and fiber quality. These different environmental stresses damage the developmental stages and growth of cotton plants, which makes it crucial to improve the stress resilience of plants. The advancement in genomic approaches like MAS, genomic selection, genome editing, and functional genomics provides an encouraging solution for enhancing stress resilience in cotton. These technologies facilitate the accurate identification and incorporation of key genes associated with stress resilience traits like heat, drought, salinity, and waterlogging. By incorporating these advanced genomic techniques into breeding programs, cotton production may become more sustainable and be well adapted to climate change.

Acknowledgements
We appreciate the kind help offered by our lab members to retouch the manuscript and provide constructive suggestions on the figure layout. We apologize to those faculties whose work cannot be mentioned due to limited space in this paper.

Authors' contributions

Khan MA, Anwar S, and Zhang R conceived and designed the study. Khan MA and Anwar S prepared the manuscript. Khan MA and Anwar S prepared the figures. Zhang R and Wei YX provided a critical review. Aneeq M, Abbas M, de Jong F, and Ayaz M revised the final manuscript. All authors contributed to the article and approved the final version of the manuscript.

Funding
This study was supported by major national R&D projects (No. 2023ZD04040-01), National Natural Science Foundation of China (No. 5201101621) and National Key R&D Plan (No. 2022YFD1200304). This work was performed at the China-Pakistan Joint Laboratory for Cotton Biotechnology, Beijing, China.

Data availability

The datasets and materials supporting this article are available upon request. Requests should be directed to Khan MA at maamir@bs.qau.edu.pk

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Received: 15 May 2024 Accepted: 18 November 2024
Published: 12 May 2025

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