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REVIEW ARTICLE

Advancements in abiotic stress resistance in sorghum (*Sorghum bicolor* L.): Integrating genomics, breeding and agronomic innovation

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Abstract

Sorghum (*Sorghum bicolor*) is highly resilient to abiotic stresses such as drought, heat, salinity, cold and nutrient deficiencies, making it an important crop for food security under changing climates. This adaptability is driven by morphological and physiological traits like deep root systems, stomatal regulation, osmotic adjustment and antioxidant defense, supported by molecular mechanisms involving stress-responsive genes and transcription factors such as DREB, NAC and LEA proteins. Advances in QTL mapping, GWAS, transcriptomics, proteomics and metabolomics have revealed key pathways and candidate genes for stress tolerance, while breeding approaches including marker-assisted selection, genomic selection and the use of wild relatives have enabled the development of stress-resilient lines with stable yields. Biotechnological tools such as CRISPR/Cas9, RNA interference and overexpression further offer precise genetic improvement. Together, these strategies are accelerating the creation of climate-smart sorghum varieties for sustainable agriculture. Future research should integrate multi-omics with machine learning to decipher complex stress-response networks and strengthen interdisciplinary collaborations to breed sorghum suited for diverse agro-ecological zones.

Keywords: abiotic stress; gene editing; omics; ROS; sorghum

Introduction

Sorghum serves as a staple food source for over 500 million people, primarily in Africa and Asia (1). First domesticated in sub-Saharan Africa, it later spread to regions such as India and China. Globally, it is the fifth most important cereal, with annual production ranging from 52 to 62 million tonnes over the past few years, but its productivity (average yield) remains low about 2.5 t/ha worldwide, significantly less in India, where it's grown mainly by smallholders in semi-arid regions and yields average close to 1 t/ha (2). As a nutrient-dense, annual diploid crop (2n=2x=20), it ranks as the fifth most cultivated cereal globally, following maize, rice, wheat and barley. Taxonomically, sorghum includes around 25 species and five subgenera. All cultivated forms belong to *S. bicolor* subsp. *bicolor*, within the *Eu-Sorghum* subgenus. Based on panicle morphology, it is classified into five main races bicolor, caudatum, guinea, durra and kafir and ten intermediate races resulting from inter-racial crosses (3).

Sorghum's ability to withstand extreme environmental stresses including drought and high temperatures makes it a climate -resilient crop. This adaptability is largely due to its well-developed root system, which includes seminal roots formed during germination and nodal (adventitious or crown) roots that emerge from the stem base (4). These roots enhance the plant's capacity to absorb water and nutrients, stabilize it in the soil and sustain growth under suboptimal conditions. Its leaves feature a protective waxy coating and can curl to reduce water loss under stress.

Sorghum is often grown in marginal lands that are highly susceptible to abiotic stresses such as drought, high temperatures and salinity, which can sharply reduce crop yield and quality (5). Abiotic stresses such as drought, salinity and heat majorly contribute to reduced productivity and substantial economic losses in both global and national contexts, with worldwide drought alone causing crop losses estimated around $30 billion annually across all crops (6). Sorghum has the capacity for deep-rooting, stomatal regulation, osmotic adjustment (e.g., proline accumulation) and activation of stress-responsive genes (such as DREB, NAC and LEA proteins) that allows it to maintain growth, yield stability and nutritional quality under stress, compared to more sensitive crops (7). The ability to tolerate abiotic stress is vital for stable productivity across diverse environments and years, especially for resource-poor farmers who rely on sorghum

as a staple crop (8). Breeding for abiotic stress tolerance increases crop resilience, with modified cultivars showing improved yield, grain quality and adaptation to extreme climates (9). Also, enhanced tolerance in sorghum reduces input requirements for water and fertilizer, lowering production costs and mitigating environmental impact (10).

Sorghum is renowned for its exceptional resilience to harsh climatic conditions, especially drought, heat and poor soils. It can survive and produce grain with much less water than crops like maize, owing to its deep, extensive root systems, high water extraction efficiency and capacity for osmotic adjustment and efficient photosynthesis (11). Sorghum fits well into mixed cropping and rotation systems, such as with legumes in dryland soils, enhancing soil health and reducing erosion. It is used for food, fodder, forage and industrial purposes (bioenergy, brewing), diversifying farmer income and food sources (12).

Major abiotic stresses affecting sorghum

Drought stress

Sorghum is widely recognized for its natural resilience to drought stress, exhibiting a set of adaptive mechanisms that allow it to maintain growth and productivity under water-limited conditions. Sorghum responds to drought by regulating stomatal conductance, which reduces water loss through transpiration. This process is controlled by hormonal signaling in particular, abscisic acid (ABA) and protein kinases that mediate stomatal closure and help conserve moisture (13). The crop accumulates osmolytes like proline and soluble sugars to lower cellular osmotic potential, enabling cells to maintain water absorption and turgor even as soil moisture decreases (14). Sorghum's extensive and deep root system enhances its ability to access water from deeper soil layers and the stay-green trait (delayed leaf senescence) supports continued photosynthesis and grain filling during drought periods (15). Drought -tolerant sorghum varieties upregulate antioxidant enzymes and stress-responsive genes including those encoding LEA proteins, NAC transcription factors and DREB genes which protect cells against dehydration and oxidative damage (16). The most drought-sensitive stages in sorghum are panicle development and flowering, where water deficit has the greatest impact on grain yield and reproductive success (17).

Heat stress

Sorghum demonstrates several key mechanisms enabling it to tolerate heat stress, which is crucial since high temperatures during sensitive stages like flowering can significantly reduce yields. Sorghum releases pollen in the early morning hours when temperatures are relatively cooler, protecting reproductive success. It bears perfect flowers (having male and female parts together) and has abundant pollen production which further reduces heat damage risk during fertilization. Sorghum maintains photosynthesis at higher temperatures (optimal net photosynthesis >38 °C) better than crops like maize, although extreme heat above ~32-35 °C can impair photosystem II, reduce chlorophyll content and decrease photosynthetic enzyme activities such as Rubisco activase. Heat-tolerant genotypes sustain photosynthetic rates better under heat shock, showing less decline in assimilation and photosystem II efficiency (18). Heat stress induces upregulation of Heat Shock Proteins (HSPs) that act as molecular chaperones protecting proteins and cellular structures, along with osmoprotectants and antioxidants to mitigate oxidative damage caused by Reactive Oxygen Species (ROS) (1). Sorghum increases stomatal conductance and transpiration under heat to cool leaves, though tolerant genotypes balance this to avoid excessive water loss, maintaining better intrinsic Water Use Efficiency (WUE) during heat stress. In sorghum, heat stress is most detrimental during the reproductive stages, particularly flowering and grain filling, when temperatures above 35-38 ℃ reduce pollen viability and grain set. Adjusting planting time so that these stages coincide with moderate temperatures in the range of 25-32 ℃ helps to minimize stress and improve yields. Breeding sorghum varieties with enhanced heat tolerance traits is vital for stable production under rising temperatures due to climate change (19).

Salinity stress

Sorghum exhibits a range of adaptive mechanisms to tolerate salinity stress, which is crucial due to its cultivation in soils with varying salt concentrations, especially in arid and semi-arid regions. Salt-tolerant sorghum genotypes maintain low sodium (Na^+) concentration in shoots by excluding or compartmentalizing Na^+ ions, while maintaining higher potassium (K^+)/Na^+ ratios, crucial for cellular functions and minimizing ionic toxicity (20). Sorghum adapts to saline environments by accumulating compatible solutes (osmolytes) to regulate osmotic pressure, helping cells retain water and maintain turgor under salt-induced osmotic stress (21). Increased activity of antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX) helps detoxify ROS generated due to salt stress, protecting membranes and cellular components from oxidative damage (22). Salt-tolerant genotypes maintain higher Membrane Stability Index (MSI) and lower malondialdehyde (MDA) levels, indicators of reduced lipid peroxidation and membrane damage under salinity. Specific genes like *SbTEF1* and *SbSOS1* play important roles in modulating salt tolerance by regulating ion transport and stress response pathways in sorghum (23).

Nutrient deficiency

Nutrient deficiencies, particularly macronutrients (such as nitrogen, phosphorus and potassium) and micronutrients (like iron and zinc), substantially affect sorghum growth, yield, grain quality and stress tolerance. Deficiencies reduce photosynthetic capacity, delay development and impair physiological functions, ultimately causing yield losses and poor nutritional quality of the grain (14). Nitrogen deficiency leads to stunted plant growth, pale yellow coloration especially on older leaves, reduced leaf area, delayed flowering, fewer tillers and lower grain protein content. Photosynthetic rate declines due to decreased stomatal conductance and chlorophyll levels (24). While phosphorus deficiency causes dark bluish-green leaves, purpling of stems and leaf undersides, poor root development, stunted growth and delayed or uneven flowering and potassium deficiency is characterized by marginal leaf chlorosis or necrosis on older leaves, weak stalks, reduced drought tolerance and poor grain filling. Sorghum exhibits genotypic variability for micronutrient content, especially iron and zinc. Modern breeding has narrowed genetic diversity in micronutrient accumulation, necessitating biofortification efforts using wild relatives with higher mineral contents. Nitrogen Use Efficiency (NUE) is a key physiological trait influencing yield; efficient partitioning of N to leaves and grains supports photosynthesis and grain formation (25). Significant variation exists among sorghum genotypes for NUE, with some lines showing greater yields and N assimilation than standard checks even at low N levels (24).

Cold and oxidative stress

Sorghum is generally sensitive to cold stress, but some varieties exhibit cold tolerance through several physiological, biochemical and molecular mechanisms. Cold stress negatively affects sorghum by reducing germination, growth, photosynthesis and development but cold-tolerant genotypes show higher survival, early vigor and better chlorophyll content under low temperatures (26). Cold inhibits sorghum growth by affecting photosynthesis and respiration. The reduction in growth is linked to the upregulation of C -repeat Binding Factor/Dehydration-Responsive Element-Binding (CBF/DREB) transcription factors that induce cold-responsive genes, causing growth inhibition and promoting survival (6). Cold stress also triggers ROS accumulation, causing oxidative stress. Sorghum responds by enhancing antioxidant enzyme activities (SOD, CAT and peroxidases) and increasing protective flavonoid and anthocyanin compounds to mitigate oxidative damage (27). Advances in molecular understanding are aiding breeding and biotechnological approaches to improve cold and oxidative stress resilience in sorghum, expanding its cultivation potential in cooler and temperate regions (6).

Physiological and morphological adaptations

Sorghum tolerates drought through physiological and molecular adaptations, including osmotic adjustment via accumulation of proline, betaine and glutathione, stomatal regulation to minimize water loss and deep root systems for soil moisture access. Drought-tolerant genotypes upregulate antioxidant and lipid metabolism genes, enhancing cellular protection (7). Under salinity, tolerant lines maintain photosynthesis, membrane stability and ionic balance by regulating antioxidant enzymes (SOD, CAT, APX) and K^+/Na^+ ratios (21). Morphological traits like leaf rolling, early flowering, deep roots and the *stay-green* phenotype support sustained photosynthesis and grain filling (7). Molecular mechanisms involve genes controlling osmolyte biosynthesis, antioxidant defense, membrane lipid remodeling and hormonal signaling (ABA, JA). Epicuticular wax deposition on leaves reduces cuticular water loss, protects chlorophyll and maintains relative water content, with genes such as *SbWINL1*, *FATB* and *CER1* linked to enhanced wax biosynthesis and drought tolerance. Increased wax accumulation reduces cuticular water loss, which complements other drought adaptations like root depth and stomatal control to enhance water retention (28). Thus, the integration of morphological, physiological, biochemical and molecular adaptations enables sorghum to endure drought and salinity stresses, making it a robust model for breeding climate-resilient cultivars.

Genetic and molecular mechanisms of stress tolerance

Sorghum's genetic and molecular mechanisms of stress tolerance involve complex, coordinated responses at physiological, biochemical and transcriptional levels that enable it to withstand abiotic stresses such as drought, salinity, heat and cold. Recent research has identified key genes, transcription factors and pathways that confer resilience by modulating antioxidant activity, osmotic adjustment, ion homeostasis and signaling networks. Genes encoding antioxidant enzymes such as superoxide dismutase (*SbSOB1)* ascorbate peroxidase *(SbAPX2)* and catalase *(SbCAT3)* are upregulated in response to oxidative stress caused by drought and salinity. These enzymes scavenge ROS, protecting cells from damage (29). Stress-tolerant genotypes accumulate osmolytes like proline and glycine betaine, regulated by genes such as *P5CS2,* contributing to cellular water retention and membrane stability under dehydration and salt stress (20). Ion transporter genes like *SbHKT1;4* help maintain high potassium/sodium ratios critical under salinity stress by excluding toxic Na⊠ ions from shoots and maintaining cellular ion balance (6). The transcription factors regulating stress responses are namely DREB (Dehydration Responsive Element Binding) family particularly *SbDREB2A* regulates gene expression under drought and salt stresses, activating downstream protective genes *SbNAC2* enhances tolerance by upregulating ROS-scavenging genes like *SbAP37*, improving antioxidant capacity and stress resilience in NAC transcription factors (30). Overall, sorghum's genetic and molecular networks driven by stress-responsive genes, ion transporters, osmolyte regulators and transcription factors coordinate antioxidant defense, osmotic balance and signaling pathways, collectively underpinning its resilience to diverse abiotic stresses. The transcription factors produced under various abiotic stresses are listed in Table 1.

QTL mapping and GWAS analysis

QTL mapping helps identify specific chromosomal regions associated with stress tolerance traits in crops. For instance, key QTLs responsible for the *stay-green* trait which delays leaf senescence and supports grain filling during post-flowering drought have been consistently located on several linkage groups, named *Stg1* through Stg4, including subregions like *Stg3A* and *Stg3B* (37). These QTLs account for a significant portion of phenotypic variation under drought conditions. Interestingly, *stay -green* QTLs from various genetic backgrounds, such as sorghum lines B35 and SC56, often map to the same genomic regions, some of which are syntenic with maize and rice, suggesting conserved mechanisms for drought tolerance among cereals (38). QTL mapping has also been instrumental in identifying genomic regions associated with various drought-related traits, such as pre -flowering drought tolerance, lodging resistance and maturity, supporting the simultaneous improvement of multiple traits (39). Additionally, QTLs linked to heat, salinity and cold stress covering traits like biomass production, root architecture and ion regulation have been discovered, offering valuable genetic markers for breeding stress-resilient sorghum varieties (40). Genome-Wide Association Studies (GWAS) further enhance this by utilizing diverse genetic populations to correlate Single Nucleotide Polymorphisms (SNPs) with stress tolerance traits at a higher resolution, helping to identify specific candidate genes and causal variants involved in drought response across different growth stages (41). Research shows considerable overlap between QTLs linked to different developmental phases (e.g., pre- and post-flowering drought), as well as shared genomic regions controlling photosynthesis and stay-green traits, highlighting pleiotropy and the complex nature of drought tolerance (38). Marker-Assisted Selection (MAS) and the stacking of multiple favorable QTLs such as several stay-green loci can significantly improve drought resilience, although this approach requires careful marker validation and is relatively time-intensive (37). Recent studies have also mapped QTL clusters associated with cold tolerance, particularly those influencing germination and early seedling vigor, advancing efforts to adapt sorghum for cooler environments (42).

Functional genomics: transcriptomics, proteomics, metabolomics

Sorghum's functional genomics approaches such as transcriptomics, proteomics and metabolomics, have significantly advanced the understanding of its molecular responses to abiotic stresses such as drought, salinity, heat, cold and combined stresses (Table 2). These

Table 1. Transcription factors produced under various abiotic stresses

Gene / Gene family	Function/role	Abiotic stress type(s)	Key notes & examples	References
DREB (Dehydration Responsive Element Binding)	Transcription factors regulating gene expression under drought, salt and cold stress	Drought, Salt, Cold	52 DREB genes identified; e.g.,SbERF027,SbERF025,SbERF100, major candidates for drought tolerance engineering	(31)
ERF (Ethylene Response Factor)	Regulate diverse abiotic stresses, hormone signaling	Drought, Heat, Combined stresses	158 ERF genes identified; specific genes likeSbERF040(heat-induced),SbERF147 (drought and combined stress) show strong differential expression	(32)
NAC Transcription Factors	Master regulators modulating multiple stress-responsive gene networks	Drought, Heat, Salt	e.g.,SbNAC2enhances abiotic stress tolerance through gene network regulation	(30)
WRKY Transcription tactors	Regulate abiotic stress signaling and biotic stress response	Drought, Salt, Heat, Pathogen	Associated with dehydration and stress responsecis-elements in promoters	(33)
bZIP (Basic Leucine Zipper Proteins)	Bind to stress-responsive elements, involved in ABA signaling and stress responses	Drought, Salt	Bind specific DNA elements (CACGTG), prevalent in abiotic stress gene promoters	(34)
LEA (Late Embryogenesis Abundant) proteins	Protect cells under dehydration, osmotic stress	Drought, Desiccation	Induced in drought, protect cellular structures during water deficit	(28)
Heat Shock Proteins (HSPs)	Protect protein integrity under heat stress	Heat	Upregulated under heat stress; molecular chaperones stabilizing proteins	(19)
Aquaporins	Facilitate water transport, supporting drought tolerance	Drought	Regulate water flow across membranes, implicated in osmotic adjustment	(32)
P5CS2 (Delta 1-Pyrroline-5-Carboxylate Synthetase 2)	Key enzyme in proline biosynthesis, osmotic adjustment	Drought, Salt	Proline accumulation mitigates osmotic stress; gene upregulated in drought	(33)
Ion transporter genes	Maintain ion homeostasis under salt and alkaline stresses	Salt, Alkaline	Regulate Na+/K+ balance; enhance salt tolerance	(33)
Flavonoid biosynthesis genes	Produce antioxidant metabolites that scavenge ROS	Salt, Drought	Related to antioxidant defense and stress mitigation	(35)
SbERF009 (ortholog of OsBIERF4)	Regulates both abiotic and biotic stress tolerance	Abiotic + Biotic	Downregulated by heat and combined stresses	(36)
SbERF011 (ortholog of OsRAF/OsLG3)	Involved in drought tolerance affecting root development	Drought	Downregulated under various abiotic stresses	(36)

Table 2. Different abiotic stresses and their research studies related to omics

Stress type	Key mechanisms & genes	Research approaches	Notable findings & insights	References
Drought	Deep root system, stomatal regulation, osmotic adjustment via proline accumulation, antioxidant enzyme activation, LEA proteins, P5CS2 gene	Transcriptomics, proteomics, metabolomics	Drought induces proline biosynthesis, carbohydrate metabolism genes; tolerant genotypes promote antioxidants and osmolytes; drought affects ~4 % of genes with root tissues showing stronger responses.	(43)
Salt & alkaline	Ion transporter gene upregulation, antioxidant enzymes, flavonoid biosynthesis pathways for ROS scavenging and ion homeostasis	Transcriptomic and metabolomic studies	Salt stress tolerance linked to enhanced flavonoid and phenylpropanoid pathways; salt-resistant cultivars show greater antioxidant activity.	(44)
Heat	Heat shock proteins (HSPs) expression, molecular chaperones for protein stabilization	Gene expression profiling	Up to 18 % of genes regulated under heat stress; HSPs play a crucial role in protecting cellular structures during high temperatures.	(31)
Combined drought + heat	Unique gene expression patterns; roughly 1/3 of differentially expressed genes exclusive to combination; distinct metabolic responses	Combined stress transcriptomic analysis	Combined stresses induce different molecular responses than single stresses, underscoring complexity of real field conditions for breeding.	(33)
Heavy metal stress	Detoxification pathways, antioxidant systems	Molecular and proteomic analysis	Heavy metal stress tolerance involves metal chelation, antioxidative protection; still an emerging area of research.	(31)

omics technologies help identify key genes, proteins, metabolites and pathways that confer resilience, enabling targeted breeding or genetic engineering for improved stress tolerance. Transcriptome profiling reveals large-scale differential gene expression in response to stresses. For example, drought induces expression of genes encoding Late Embryogenesis Abundant (LEA) proteins, proline biosynthesis enzymes (like P5CS2), antioxidant enzymes and HSPs under heat stress (4). Transcriptomic studies have shown that different stresses (e.g., drought vs osmotic stress, heat vs drought) elicit distinct gene expression patterns, with only partial overlaps in Differentially Expressed Genes (DEGs). Combined stresses tend to induce unique sets of DEGs not seen under single stresses. Field-based temporal transcriptomics in drought-tolerant versus sensitive genotypes reveal that a large portion of the sorghum genome (~40 %) alters expression under pre- and post-flowering drought stress. Genes related to photosynthesis, ABA signaling, ROS scavenging and symbiotic interactions are prominent (43). Important transcription factors such as DREB, NAC and bZIP families are frequently identified as key regulators modulating downstream protective genes under stress (44).

Proteomic approaches complement transcriptomics by confirming changes at the protein level, revealing post-translational modifications and activity of key enzymes involved in stress responses. Sorghum studies have identified proteins involved in antioxidant defense, osmolyte biosynthesis, membrane stability and signal transduction pathways, helping to understand how transcript levels translate into functional stress response. Proteomics also highlights variations between tolerant and sensitive genotypes in the abundance of stress-related proteins, supporting genotype-specific resilience mechanisms.

Metabolomic analyses identify changes in metabolites such as osmoprotectants (proline, sugars), phytohormones (ABA, jasmonic acid), antioxidants and secondary metabolites that help maintain cellular homeostasis under abiotic stresses (45). Metabolite profiling reveals stress-specific accumulation patterns, e.g., osmotic stress induces proline and certain carbohydrates, while salt stress elevates specific ion transport-related metabolites. Different abiotic stresses trigger distinct metabolite changes in sorghum. For example, drought and osmotic stress induce proline biosynthesis and carbohydrate metabolism genes accumulation to help maintain osmotic balance and energy supply. Salt stress elevates metabolites involved in antioxidant defense and ion transport to mitigate ionic and oxidative damages Under stress like salinity, expression of genes related to carbohydrate catabolism and enzymes such as phosphoglycerate kinase increase, reflecting a heightened energy demand to support protective mechanisms and repair systems (29). Comparative metabolomic profiling reveals that tolerant and sensitive sorghum lines differ markedly in metabolite abundance and regulation under stress. For instance, tolerant genotypes show enhanced accumulation of antioxidants, unsaturated fatty acids and certain amino acids that help maintain cellular functions (46).

Advances in breeding for abiotic stress tolerance

Conventional breeding approaches and trait introgression for abiotic stress tolerance in sorghum leverage natural genetic variation through hybridization, pedigree and backcross breeding to develop resilient varieties with stable yields under stresses such as drought, salinity, heat and cold. Sorghum has wide genetic diversity for traits like deep root systems, stay-green (delayed leaf senescence), osmotic adjustment and antioxidant capacity. Breeders select genotypes displaying these traits under controlled and field stress conditions to identify tolerant lines (47). Tolerant lines maintain higher biomass, harvest index, transpiration efficiency and leaf water status under water stress compared to sensitive lines. Traits like panicle exertion and peduncle length also contribute to improved grain yield and stress adaptability during reproductive phases (48). Multi-parent crossing strategies (e.g., 8-way, 4-way crosses) increase genetic diversity and enable accumulation of favorable alleles for drought and heat tolerance, resulting in high-yielding, stress-resilient lines (47).

MAS accelerates sorghum breeding by using DNA molecular markers closely linked to desirable traits, such as drought tolerance (e.g., stay-green traits), salinity tolerance and disease resistance, to select superior genotypes more precisely and rapidly than traditional phenotyping alone. Important QTLs for traits like stay-green *(Stg1, Stg2, Stg3, Stg4)* have been identified and introgressed into elite but sensitive sorghum varieties through marker-assisted backcrossing, improving post-flowering drought tolerance and yield stability (37). GS uses genome-wide marker information (such as SNPs) to predict the breeding values of individuals by capturing the effects of both major and minor genes influencing complex traits. Unlike MAS, which targets major effect QTLs, GS accounts for the aggregate effect of many small-effect loci, enabling better capture of genetic variance for traits like yield, drought tolerance and hybrid performance. GS enhances selection accuracy and accelerates genetic gains by predicting hybrid performances before phenotyping, thus saving time and resources in breeding cycles. Studies in sorghum demonstrate successful genomic prediction of grain yield, kernel weight and other agronomic traits using sequencing-based markers and cross-validation models (49). MAS is useful for traits with known major QTLs, while GS is powerful for polygenic traits requiring genome-wide evaluation.

Wild relatives and landraces have been used to create pre-bred lines and introgression populations, which have been evaluated for traits like grain yield, maturity, panicle density and stay-green (delayed senescence). Wild relatives of sorghum serve as a reservoir of genetic diversity lost during domestication due to the bottleneck effect. They often harbor unique alleles for important traits such as drought tolerance, disease resistance and nutrient use efficiency that are rare or absent in cultivated varieties. In Australia and Mali, thousands of lines involving wild relatives have been generated and tested, with several lines showing promise for farmer adoption and further breeding (50). Developed drought/heat-tolerant lines undergo multi-location trials under various stress conditions to verify stability. Successful cultivars combine stress tolerance with acceptable agronomic traits (yield, maturity, plant height) suitable for target agro-ecologies. Examples include advanced lines like SS22086RV and SS22085RV derived from multi-parent crosses showing superior tolerance and yield attributes (47). Continued integration of these genetic resources into mainstream breeding will be essential for developing climate-resilient sorghum varieties capable of sustaining productivity under future environmental challenges.

Biotechnological and genomic tools

Advances in biotechnology and genomics have revolutionized sorghum improvement by enabling precise dissection of stress-responsive pathways and targeted manipulation of key genes. Tools such as genome editing (CRISPR/Cas9), RNA interference (RNAi), gene overexpression, functional genomics and multi-omics integration have provided new avenues for enhancing stress resilience. The different biotechnological methods used for abiotic stress resistance in sorghum is mentioned in Fig. 1.

Gene editing

Sorghum breeding and improvement for abiotic and biotic stress tolerance have greatly benefited from advanced biotechnological and genomics tools, particularly from genome editing technologies like CRISPR/Cas9, high-throughput sequencing and omics integration. CRISPR/Cas9 has been successfully applied for targeted genome editing in sorghum, enabling precise mutagenesis of important genes affecting traits like flowering time *(SbFT),* plant growth regulators *(SbGA2ox5)* and seed protein quality (α-kafirin genes). CRISPR/Cas9 gene editing offers a powerful approach to improve sorghum's tolerance to drought, salinity and heat by precisely modifying stress-responsive genes involved in lignin biosynthesis, osmoprotectant accumulation, antioxidant regulation and hormonal signaling (51). Editing can be stably inherited across generations as long as the Cas9 transgene is present (52). Screening

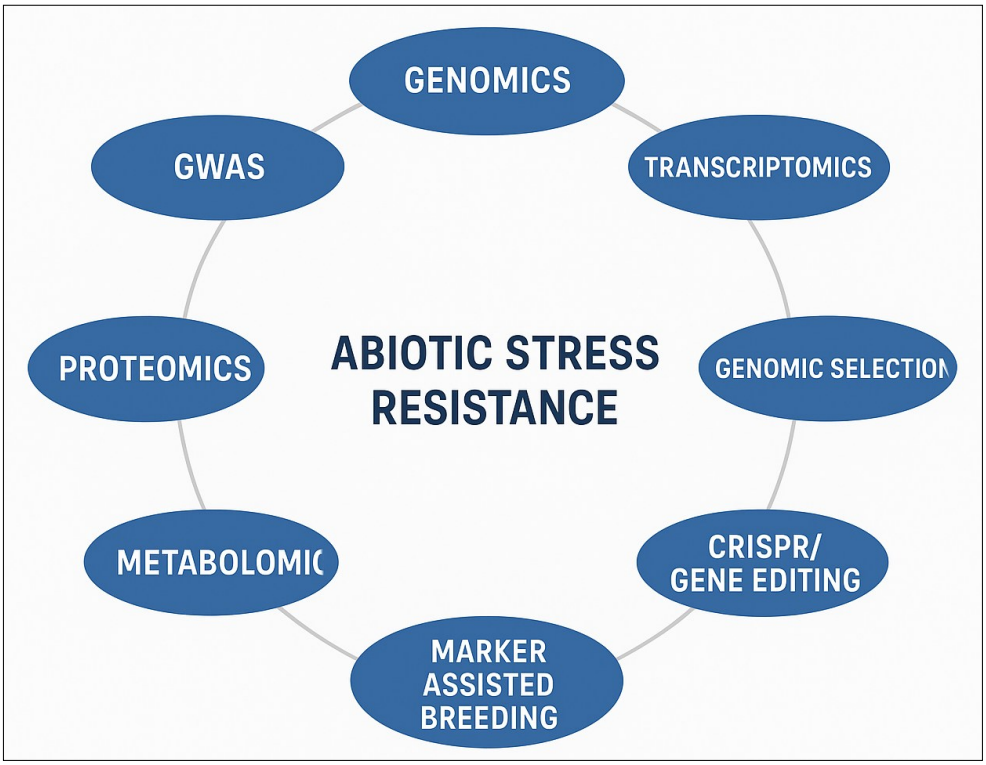

Fig. 1. Different biotechnological methods used for abiotic stress resistance in sorghum.

of single guide RNAs (sgRNAs) for genome editing in sorghum has been streamlined using transient protoplast transfection assays, allowing rapid testing of editing efficiency before stable transformation. DNA-free editing with preassembled Cas9-sgRNA ribonucleoproteins (RNPs) has shown promise to reduce off-target effects (53). Genome editing has improved nutritional quality by targeting kafirin seed storage protein genes, enhancing protein digestibility and lysine content without compromising seed development (51).

RNAi and gene silencing

RNAi is an innate mechanism of post-transcriptional gene silencing employed in sorghum to suppress the expression of specific target genes, aiding both functional gene studies and trait enhancement. RNAi, along with gene over expression techniques, provides a complementary approach allowing both loss-of-function and gain-of-function analyses. This dual strategy is crucial for validating the roles of candidate genes uncovered through transcriptomic and other omics-based investigations Sorghum possesses key RNAi machinery genes (DCL, AGO, RDR families) conserved with model plants, validating the presence of functional RNA silencing pathways (54). Sorghum possesses key RNAi machinery genes (DCL, AGO, RDR families) conserved with model plants, validating the presence of functional RNA silencing pathways. In sorghum, RNAi has been successfully utilized to silence kafirin seed storage protein genes, such as γ-kafirin, resulting in softer endosperm texture, enhanced protein digestibility and overall improved grain nutritional quality. Conversely, overexpression studies focus on increasing the activity of genes involved in stress responses such as transcription factors from the DREB, NAC and ERF families, antioxidant enzymes and genes related to osmolyte production to boost sorghum's tolerance to abiotic stresses like drought, salinity, cold and oxidative damage (55). Together, RNAi and overexpression approaches offer complementary tools for loss- and gain-of-function studies, playing a vital role in the functional validation of genes identified through transcriptomic and other omics-based research (55).

Gene overexpression and functional validation

Gene over expression in sorghum enhances drought, salinity and heat tolerance by upregulating stress-responsive genes such as antioxidant enzymes (SOD1, VTC1, MDAR1), regulatory proteins (CIPK1, CRK7) and hormone-signaling genes (JAR1, NACs), improving osmotic adjustment, defense and water-use efficiency (33). Functional validation of abiotic stress-responsive genes in sorghum is achieved through transgenic studies, transcriptome analysis and stress-based phenotyping. Drought-tolerant genotypes like SC56 inherently over express stress-related genes, enhancing biomass and homeostasis. Functional genomics tools such as GWAS, QTL mapping and association studies have identified key loci linked to transporters, ROS-scavenging enzymes and stay-green traits. These validated genes are being utilized in breeding, genetic engineering and MAS to develop stress-resilient sorghum varieties (32).

Genomic databases and bioinformatics tools for abiotic stress in sorghum are essential resources for understanding the genetic architecture, gene function and molecular pathways involved in stress tolerance, facilitating breeding and genetic improvement. The genomic databases are included in Table 3.

Challenges and future perspectives

Abiotic stresses like drought, heat, salinity and biotic stresses such as pests and diseases involve complex genetic control with significant genotype x environment interactions, making conventional breeding slow and less efficient. Traits such as drought tolerance and pest resistance are polygenic and environmentally sensitive, posing difficulties for selection and stable genetic gains (29). Sorghum transformation is technically challenging, genotype-dependent, costly and time-consuming, limiting the adoption of transgenic approaches and genome editing in commercial breeding. There are also environmental and regulatory concerns related to gene flow to wild relatives (e.g., Johnson grass), restricting widespread deployment of genetically modified sorghum (66).

Table 3. Various databases/bioinformatics tools related to sorghum

Database/Tool name	Description	Key features	Reference
SorghumBase	Community portal integrating genetic, genomic and breeding data for sorghum	Reference genomes, gene annotations, genetic maps, QTLs, variation data for trait discovery	(56)
Sorghum Functional Genomics Database (SorghumFDB)	Database of sorghum genomic sequences with functional annotations, transcriptomic & metabolomic data	Gene function info, expression profiles under abiotic stresses, omics integration	(57)
Sorghum Genome Science Database (SorGSD)	SNP and small indel variation data for >200 sorghum accessions including phenotypic and image data	Genomic variation data, genome browser, homologue search, ID conversion tools	(58)
SorbMutDB	Database of EMS-induced sorghum mutant lines linked to reference genome	Mutation locations, mutant line info for forward/reverse genetics	(53)
Gramene	Plant comparative genomics portal covering sorghum and other cereals	Genomic data, QTLs, gene families, conserved regions across species	(59)
Public Omics Repositories	NCBI GEO, SRA databases providing sorghum transcriptome, proteome and metabolome data sets	Raw and processed data for differential gene expression under abiotic stress	(60)
Bioinformatics tools	DESeq2, edgeR (gene expression analysis), Cytoscape (network analysis), KEGG Mapper, MapMan (pathway mapping)	Support differential expression, gene network, pathway enrichment for sorghum abiotic stress genes	(61-65)

Ideotypes serve as targets for both conventional and molecular breeding strategies, guiding trait introgression and selection to build climate-smart sorghum varieties. Candidate sorghum ideotypes have been modeled and experimentally validated to increase grain yield under projected future climates, notably in drought-prone regions such as Ethiopia. Increasing the length of the vegetative phase allows better biomass accumulation before reproduction, enhancing yield potential under variable climates (31). Delayed leaf senescence during grain filling sustains photosynthesis under drought and heat stress, supporting grain filling and improving yield stability (67).

Advances in MAS, GWAS, Genomic Selection (GS) and CRISPR-based genome editing provide powerful opportunities to accelerate sorghum improvement by enabling precise introgression and pyramiding of stress tolerance and yield traits (68). The integration of high-throughput phenotyping, remote sensing, AI and digital tools can enhance screening efficiency under complex multi-stress environments. Utilization of landraces, wild relatives and pre-breeding lines, combined with pan-genome analyses, will expand the genetic base and uncover novel alleles for abiotic and biotic stress resilience (35). Targeted focus on adaptive traits such as stay-green, root architecture, osmotic adjustment and heat tolerance through multilayered breeding approaches will strengthen sorghum's adaptability to future climates (7). Addressing biosafety concerns and gene flow issues is crucial for wider acceptance of biotechnological innovations (67). Strengthening breeding infrastructure and data management, particularly in developing countries, alongside international funding support for integrated multi-omics and gene-editing research, will be key to bridging knowledge gaps. Collectively, these advances are expected to accelerate the development of climate-resilient sorghum cultivars and reinforce its role in global food and nutrition security (69).

Conclusion

Sorghum stands out as a vital, climate-resilient cereal crop that underpins food and livelihood security for millions of people, especially in drought-prone and resource-limited regions. Its resilience to abiotic stresses such as drought, heat, salinity, cold and nutrient deficiency is underpinned by complex morphological, physiological, biochemical and molecular adaptations, including the stay-green trait, osmotic adjustment, efficient resource use and robust antioxidant systems. Advances in molecular breeding, QTL mapping, GWAS, functional genomics and genome editing technologies (e.g., CRISPR/Cas9) have greatly improved our understanding of stress tolerance mechanisms and facilitated targeted trait improvement. Marker-assisted and GS approaches are streamlining breeding pipelines, while biotechnological tools such as RNA interference and over expression studies are validating key candidate genes. Nevertheless, challenges such as genotype-dependent transformation efficiency, regulatory uncertainties and the polygenic and environment-sensitive nature of stress responses continue to hinder progress. To overcome these bottlenecks, broadening the genetic base through landraces, wild relatives and pre-breeding lines will be vital to harness novel alleles. Looking ahead, ideotype-based breeding is supported by high-throughput phenotyping, omics integration and AI-driven decision tools offers promising avenues for designing cultivars tailored to future climates. Strengthened global collaborations, improved infrastructure and sustained investment in sorghum breeding will be critical to fully realize its potential as a cornerstone crop for ensuring food and nutritional security under intensifying climate change.

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Authors' contributions

NS and DK prepared the design of the study and drafted the manuscript. BMK, AS and PM participated in its design and coordination and reviewed the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

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