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Unraveling the genetic basis of resistance traits for fungal diseases in sorghum

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Abstract

Sorghum is a versatile and resilient cereal crop known for its adaptability to a wide range of climatic conditions. In recent years, sorghum has gained attention in modern research due to its potential in bioenergy production and resilience to climate change. However, sorghum is susceptible to several fungal diseases, which pose significant threats to its productivity and profitability. Understanding the genetic control of disease resistance is essential for developing resistant sorghum cultivars to sustain global food production. Genetic and genomic resources play crucial roles in identifying and comprehending the genes responsible for disease resistance. This review delves into the available resources to elucidate fungal resistance mechanisms for crop improvement. The identification of fungal resistance genes forms the bedrock of breeding programs aimed at developing robust and sustainable crop varieties. Through quantitative trait loci mapping studies, numerous genomic regions linked to fungal disease resistance have been reported, providing crucial insights for targeted breeding strategies. Recent advancements in genotyping-by-sequencing, bioinformatics, and associated statistical methodologies have revolutionized genome-wide association studies, ushering in a new era of precision and efficiency in genetic research. Additionally, functional genomics techniques, such as transcriptomics, proteomics, and metabolomics, have played pivotal roles in sorghum research, enabling the identification of key genes and pathways implicated in defense responses against fungal pathogens. Genome editing of identified resistance genes holds promise for developing high-performing varieties to achieve food and nutritional security.

Keywords Genetic resources, QTL, GWAS, Functional genomics, RNA sequencing

Background

Sorghum bicolor, a dual-purpose food and fodder and a *rabi* season crop belonging to the Poaceae family, consists of five distinct genetic races predominantly grown in arid and semiarid environments, making it a crucial staple food for approximately 500 million people in Africa and Asia (Khoddami et al. 2023). According to the Food and Agricultural Organization (FAO), its cultivation spans 40.76 million hectares worldwide, yielding a total production of 57.58 million metric tonnes, making it the fifth most important cereal in terms of both area and production. The key contributors to global sorghum production include Nigeria, Sudan, the USA, Mexico, Ethiopia, and India. In India alone, sorghum is cultivated on 3.80 million hectares, producing 4.15 million metric tonnes annually (FAO 2023). Sorghum grains are rich in carbohydrates, proteins, vitamins, and minerals. In addition to its applications in

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human food, animal feed, and brewing, there is a growing demand for sorghum for grain-based ethanol production (Kumar et al. 2017). Owing to its high biomass yield, fast growth, C4 photosynthesis, stress tolerance, and compact genome, sorghum is ideal for bioenergy crop studies (Bushra et al. 2018). In 2021, global hunger affected 828 million people, increasing by 150 million since the onset of the COVID-19 pandemic, with 11.7% of this population facing extreme food insecurity. Embracing SMART agriculture and maximizing the use of germplasm and genetic resources are crucial for food and nutritional security (Ramya et al. 2013). A healthy diet was unaffordable for 3.1 billion people worldwide in 2020, a significant increase from 2019. It is projected that approximately 670 million people, constituting 8% of the world's population, will still be undernourished by 2030, deviating from the Zero Hunger Sustainable Development Goal (FAO April 2023). More than 60% of the energy obtained by humans from plant-based sources originates from essential cereals such as rice, wheat, and maize, posing a substantial risk of malnutrition and hidden hunger due to inadequate protein and micronutrient supplies (Ramya et al. 2013; Vetriventhan et al. 2020). The expansion of drylands and increasing groundwater levels threaten cereal production (Huang and Han 2014), necessitating resilient crops such as millet. Despite progress, sorghum cultivation faces challenges from biotic and abiotic stresses, notably fungal diseases (Ahn et al. 2023). Although the productivity of sorghum has progressed, sorghum cultivation is still constrained by several biotic and abiotic stresses (Kumar et al. 2017). The development of disease-resistant, high-yield cultivars is essential to avoid costly pesticides (Wang et al. 2014). Conventional breeding methods often lack polygenic traits, highlighting the need to understand genetic resistance. Identifying resistant sources, phenotyping, and genotyping are key. While molecular marker-based genotyping is hindered by cost and labor, the discovery of ESTs (Expressed sequence tags) and SNPs (Single nucleotide polymorphisms) has advanced this field (Deschamps et al. 2012). Next-generation sequencing (NGS) facilitates high-throughput genotyping, and GWAS (Genome-wide association analyses) is recommended for complex trait studies because of sequencing advancements and collaborative efforts (Michael and Jackson 2013). Over the past decade, GWAS has become a powerful tool for understanding plant traits (Xiao et al. 2017). This review examines sorghum's genetic and genomic resources and the methods used to elucidate the genetic control of fungal disease resistance.

Major fungal diseases affecting sorghum

Sorghum, which is the fifth most important cereal crop, following wheat, maize, rice, and barley, holds a pivotal position in global food security. Sorghum has excellent adaptability to various abiotic stresses, such as heat, salinity, cold, and drought (Behera et al. 2022). In addition to its resilience, sorghum cultivation faces challenges from a broad range of biotic and abiotic factors (Amelework et al. 2016). The most common sorghum diseases are fungal, bacterial, and viral diseases that can drastically compromise the yield and quality of the grain and fodder. Anthracnose (up to 86% yield loss), downy mildew, grain mold, leaf blight (up to 70% yield loss), smut, rust, ergot (up to 80% yield loss), charcoal rot, target leaf spot, zonate leaf spot, and gray leaf spot are the major fungal diseases that pose a significant threat to production and productivity (Cota et al. 2017; Tesema et al. 2022; Kazungu et al. 2023). The degree of crop loss caused by diseases depends upon the phase of the crop, the vulnerability of the cultivar, and the existing ecological conditions. Some fungal diseases (anthracnose, leaf blight, and charcoal rot) have reached epidemic magnitudes in sorghum-growing areas of the world. The development and use of resistant genotypes is a viable strategy for the efficient management of yield loss in sorghum due to fungal pathogens. Understanding the genetic basis of disease resistance is important for developing resistant sorghum cultivars and is crucial for sustaining global food production. The status of imperative diseases of sorghum was reviewed, and detailed information about disease symptoms, etiology, epidemiology, distribution, losses, and management options was reported (Sharma et al. 2015; Anitha et al. 2020; Singh et al. 2020). The major sorghum diseases (Fig. 1), causal organisms, and typical symptoms are given in Additional file 1: Table S1.

Genetic resources of sorghum

The conservation and effective utilization of diverse germplasms is crucial for SMART and sustainable agriculture. Sorghum, which originates from Africa, particularly Ethiopia and Sudan, is rich in genetic diversity. India, Sudan, and Nigeria are secondary centers of diversity, with extensive genetic variation (Acquaah 2009; Mamo et al. 2023). Sorghum is classified into primary races and intermediate types on the basis of panicle morphology (Harlan and de Wet 1972). Disease resistance relies on novel genetic sources, especially tropical germplasms (Uffelmann et al. 2021). The limited diversity of temperate germplasms underscores the need to explore new sources of resistance (Xin et al. 2021). Leveraging genetic resources is essential for enhancing sorghum's resilience to fungal diseases

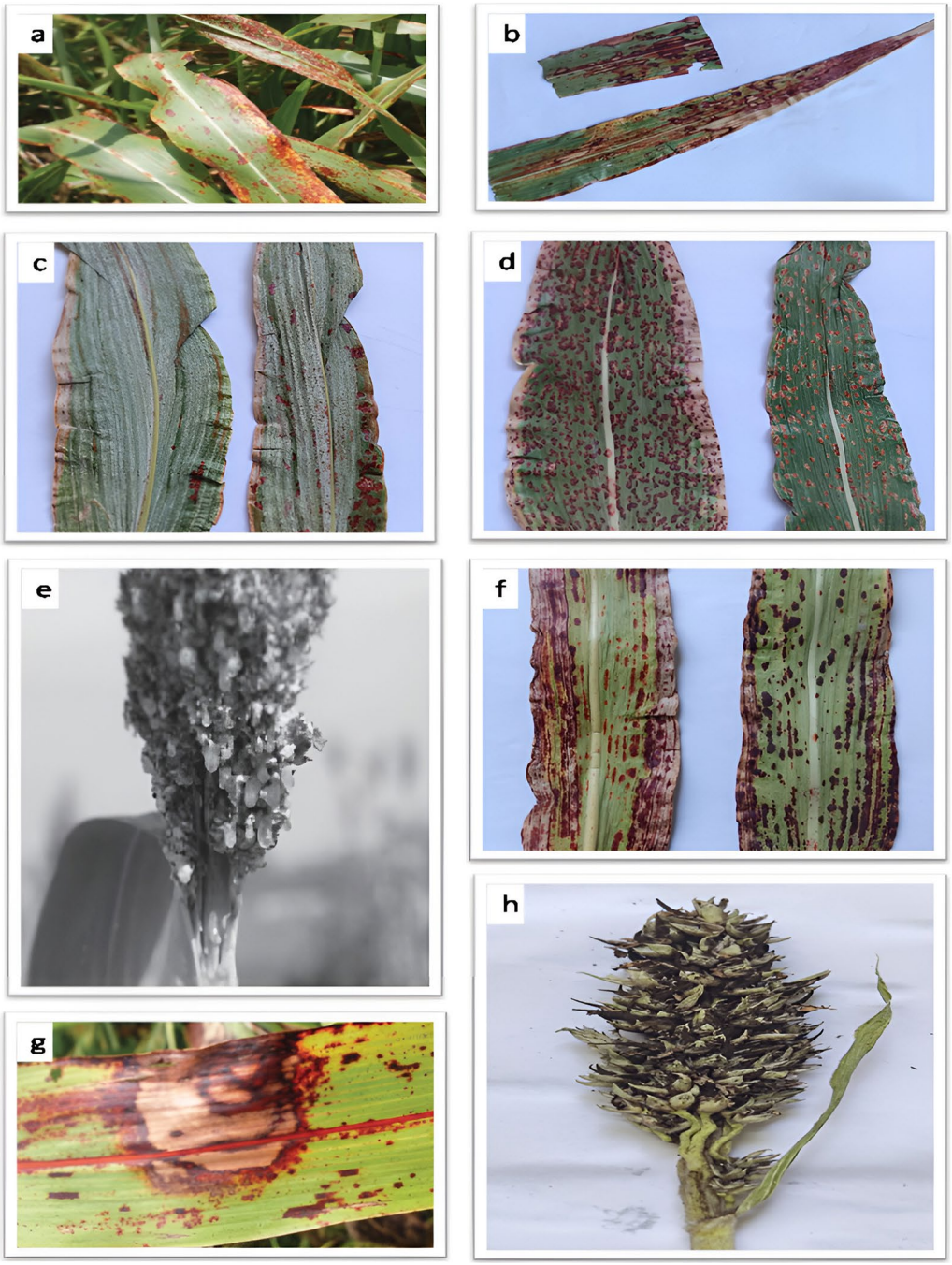

Fig. 1 Visible symptoms of major fungal diseases in sorghum. **a** Anthracnose, **b** Leaf blight, **c** Downy mildew, **d** Rust, **e** Ergot, **f** Target leaf spot, **g** Zonation leaf spot, **h** Smut. The source of a, e, and g—Singh et al. 2020

and ensuring global food security. Accessing updated information on various germplasm collections can be challenging. However, detailed data on major collections at the United States Department of Agriculture-Agriculture Research Service-Plant Genetic Resources Conservation Unit (USDA-ARS-PGRCU) in Griffin, GA, the International Crops Research Institute for Semi-Arid Tropics (ICRISAT) in Telangana, India, and the Indian Council of Agricultural Research-National Bureau of Plant Genetic Resources (ICAR-NBPGR) in New Delhi, India, are available. Within the USDA-ARS-PGRCU, 48,626 (92.93%) collections pertain to the *S.*

bicolor (L.) Moench subsp. *bicolor* taxonomic classification, and the remainder fall into 24 other categories (USDA-ARS-GRIN 2024). ICRISAT's gene bank manages 42,869 sorghum accessions from 93 countries, including traditional cultivars/landraces, breeding/research materials, advanced improved cultivars and wild relatives. Notably, 45.69% of the ICRISAT collections originate from specific countries, such as India, Ethiopia, Sudan, Cameroon, and Nigeria, with contributions from 82 other countries accounting for 27.49% of the accessions (ICRISAT 2024). A total of 20,459 sorghum accessions are available (ICAR-NBPGR 2024) and stored in the National Gene Bank, ICAR-NBPGR, which comprises 11,020 indigenous and 9004 exotic collections (Genebank 2024). Exotic collections of the National Gene Bank are mainly from African countries. The sorghum collections maintained in major gene banks are listed in Table 1.

Genomic resources of sorghum

Genomic resources are vital for understanding gene functions and assisting in genome-assisted breeding. The gene and feature statistics of the *S. bicolor* NCBIv3 reference genome are listed in Additional file 2:Table S2. Sorghum, a diploid C4 grass with 10 chromosomes, has been extensively studied (Price et al. 2005). Initial sequencing of the sorghum genome from the BTx623 inbred line via Sanger sequencing facilitated genome-wide analyses and identified genetic variations (Paterson et al. 2009). Comparative genomics of sweet (Keller and

Table 1 Sorghum collections conserved in major gene banks

Species	No. of accessions in USDA-ARS-PGRCU (GRIN-Global, Germplasm Resources Information Network accessed January 2024)	No. of accessions in ICRISAT, India	No. of accessions in National Gene Bank, India
Sorghum hybr	36	–	–
Sorghum spp.	127	–	47
S. angustum	8	–	–
S. bicolor (L.) Moench	2962	–	–
S. bicolor (L.) Moench nothosubsp. *drummondii*	88	–	–
S. bicolor (L.) Moench subsp. *bicolor*	45,186	42,786	20,408
S. bicolor (L.) Moench subsp. *verticilliflorum*	59	–	–
S. brachypodum	2	–	–
S. bulbosum	7	–	–
S. ecarinatum	1	–	–
S. exstans	3	–	–
S. halepense (L.) pers	72	37	1
S. interjectum	2	–	–
S. intrans	6	4	–
S. laxiflorum	6	1	–
S. macrospermum	1	1	–
S. matarankense	2	2	–
S. plumosum	12	1	–
S. purpureosericeum	3	9	–
S. stipoideum	3	5	–
S. timorense	4	–	–
S. venustum	1	–	–
S. versicolor	4	7	–
S. almum	30	–	–
S. rigidifolium	–	6	–
S. nitidum	–	1	1
S. affstipodeum	–	2	–
S. australiense	–	3	–
S. breviocallosum	–	1	–
S. arundinaceum	–	–	2
Total	48,626	42,869	20,459

Table 2 List of resistant genotypes identified for major fungal diseases in sorghum

Population	Target disease	Susceptible check	Resistant check	Resistant genotypes	References
335 Sorghum Association Panel (SAP)	Anthracnose	BTx623, RTx430, and PI609251	SC112-14	40 accessions including SC748, BTx378, and SC155	Cuevas et al. (2018)
163 Senegalese Sorghum Accessions	Anthracnose	BTx623, PI609251, and TAM428	SC748-5	44 accessions	Ahn et al. (2023)
358 Sorghum Accessions (SA)	Ergot	ATX623	–	E313, E111, E225, E200, E351, E352, E353, and E354	Kebede et al. (2023)
101 SA	Leaf blight	BTx623	SC748-5	N15, N43, N38, N46, N30, N28, and N23	Prom et al. (2023)
377 SAP	Grain mold	–	–	PI533871, PI576130, and PI656036	Prom et al. (2020)
655 SA	Grain mold	–	–	ETSL 100612 and ETSL 101178	Nida et al. (2021)

E-tian) and grain (Ji2731) sorghum varieties revealed various genetic variations, including SNPs, insertions/deletions (indels), present/absent variations (PAVs), and copy number variations (CNVs) (Zheng et al. 2011). Genotyping techniques characterize sorghum collections from Ethiopia, Sudan, Nigeria, and Senegal, revealing 1,057,018 SNPs, 99,948 indels, 16,487 PAVs, and 17,111 CNVs, differentiating sweet and grain sorghum (Zheng et al. 2011; Cuevas et al. 2019; Girma et al. 2019; Prom et al. 2020). While sorghum, pearl millet, and foxtail millet have reference genomes, studies on de novo assembly of sorghum lag compared with those in maize and rice (Zheng et al. 2011). Efforts to address the lag in de novo assembled genomes led to the assembly of a high-quality reference genome sequence, version 3, providing considerable improvements (McCormick et al. 2018). The current version, 3.1.1, contains over 34,000 annotated genes (McCormick et al. 2018). Genome assembly involves a robust approach combining PACBIO coverage and advanced bioinformatics tools, resulting in increased assembly accuracy and transcript assembly (Additional file 3: Table S3). These genomic resources are crucial for functional genomics and targeted breeding for sorghum improvement. Understanding gene function is vital for functional genomics, aiding in uncovering genetic traits such as drought tolerance and disease resistance for targeted breeding in sorghum improvement. In the Joint Genome Institute's *S. bicolor* BTx623 assembly version 5.1 (Additional file 3: Table S3), PACBIO coverage and advanced bioinformatics tools are employed utilizing syntenic markers and annotated genes for improved accuracy. The primary assembly, with 122.94×PACBIO coverage and an average read size of 11,008 bp, utilized MECAT for assembly and RACON for polishing. Nine breaks were identified, resulting in the reassembly of 10 chromosomes with 32 joins. Homozygous SNPs and indels were corrected with Illumina reads. Transcript assembly with PERTRAN and GSNAP yielded 748 k putative full-length transcripts from 12 M PacBioIso-Seq CCSs (Circular consensus sequences). PASA (Program to Assemble Spliced Alignments) constructed 581,006 transcript assemblies from ESTs, corrected CCS, and RNA-seq data. Gene models from assembly v3.1 were enhanced and mapped forward to v5.1, with PFAM, PANTHER, and transposable element domain filtering applied, and approximately 96% of nontransposable element-associated v3.1 models were mapped forward via JGI's locus name mapping pipeline.

Identification of disease-resistance genes for fungal diseases

Fungal pathogens cause devastating diseases in sorghum, leading to extensive yield losses. Sorghum germplasm cultivated in rainy and high-humidity regions of western and central Africa is a critical source of genes providing resistance to fungal diseases (Cuevas et al. 2018). Phenotyping natural variants of sorghum is essential for identifying resistant sources, and highly resistant accessions can serve as valuable sources of resistance genes for breeding (Nida et al. 2021). Mapping genes can facilitate the integration of identified genes into subsequent breeding programs. Fine mapping of ARG2 (Anthracnose Resistance Gene 2) via BSA-Seq revealed a 6.3 Mb region on chromosome 5 of sorghum corresponding to ARG2 (Mewa et al. 2023). The corresponding region harbors 20 putative genes. Gene annotations included domains of unknown function (DUFs), serine esterase (SE), and transcription elongation factor (TE), among others. ARG2 was later identified as NLR1. This gene is located in the plasma membrane and has conserved homologs in related crop species. Although ncRNAs have been identified as functional genes, they may play

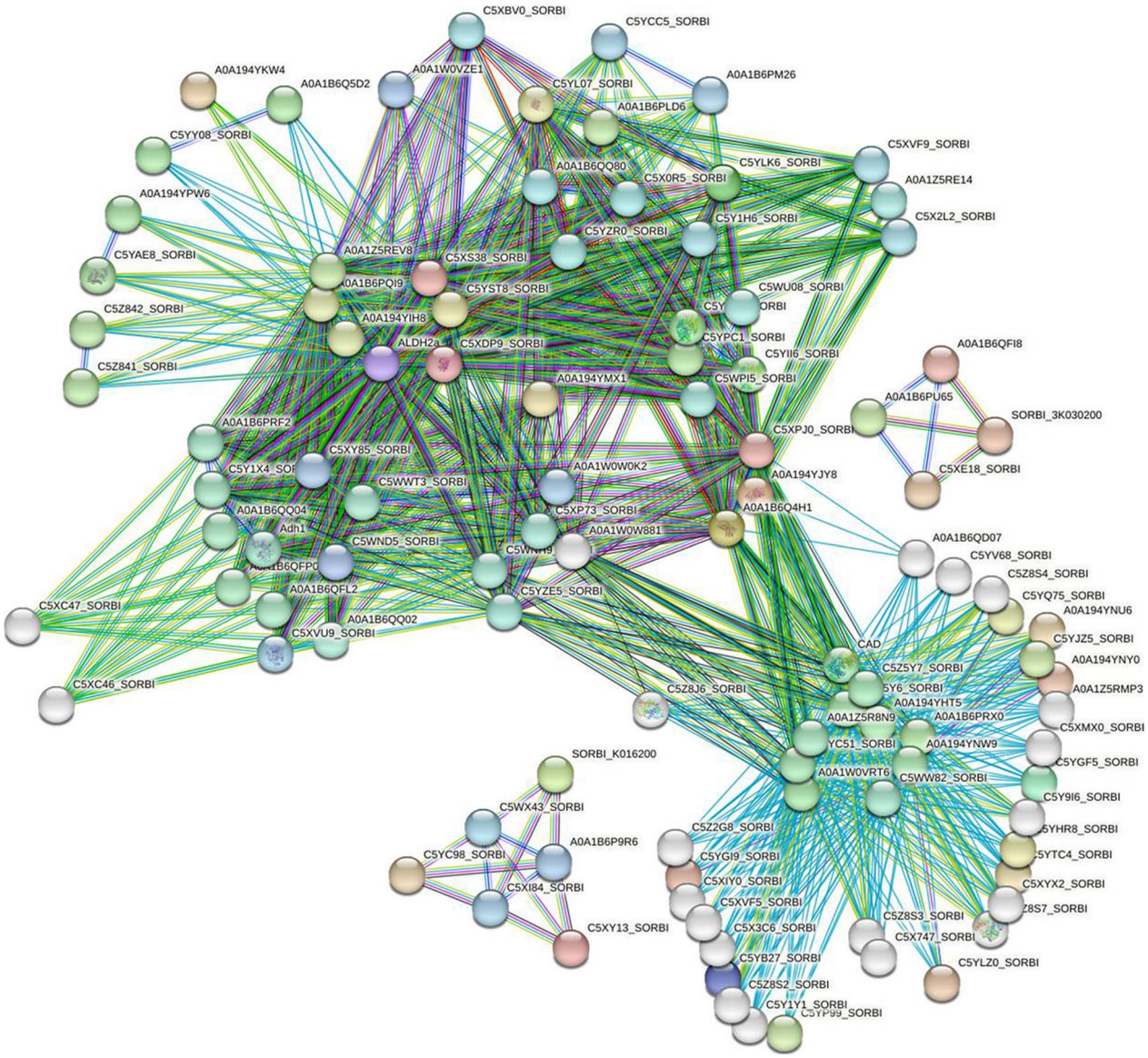

Fig. 2 Candidate genes associated with multiple diseases identified at ICAR-NBPGR (gene expression data)

Table 3 QTLs identified in some fungal diseases

Disease	Mapping population	Marker type	Linked markers/QTLs	References
Rust	ICSV745/R890562 RIL	DArT	txs387c/sPb-5892	Wang et al. (2014)
	IS8525/R931945-2–2 RIL	DArTs, RFLPs, and SSRs	2,651,978|F|0/1957225|F|0 1,949,016|F|0/1945627|F|0 2,207,675|F|0/2663674|F|0 1,925,698|F|0/2644849|F|0	
Charcoal rot/stalk rot	Mini core collection	EST-SSR	*Xiabt 210, Xiabt 527, Xiabt 301, Xiabt 37, Xiabt 77, and Xiabt 81*	Kumar et al. (2017)
Target leaf spot	BTx623/BTx642 RIL	SNP	3 QTLs in Chr.5, Chr.9, and Chr.6	Kimball et al. (2019)
	BTx623/SC155-14E	SNP	2 QTLS in Chr.3 and Chr.4	
Leaf blight	BTx623 × IS3620C RIL	SNP	c2.loc122, c3.loc128, and c7.loc125	Lipps et al. (2022)
	BTx623 × SC155	SNP	Chr01_11.7, c2.loc35, and c3.loc69	

a role in imparting this trait (Yasin et al. 2016). ARG1 is nested within the cis-natural antisense carrier (CARG) (Lee et al. 2022). These findings confirmed the presence of regulatory RNAs. Similar to ARG2, Anthracnose Resistance Genes (ARG4 and ARG5) encode canonical nucleotide-binding leucine-rich repeat (NLR) receptors. ARG4 and ARG5 are dominant resistance genes identified in the sorghum lines SAP135 and P9830, respectively, and are mapped on chromosome 8, which indicates broad-spectrum resistance to Cs (Nida et al. 2019). The different sources of resistance identified in earlier studies are listed in Table 2. In recent years, researchers have employed different molecular and genomic tools to identify loci associated with new mechanisms of resistance, providing fresh insight into the genetic control of disease resistance (Nida et al. 2021). Similarly, susceptibility to milo disease in sorghum is controlled by a single, semi-dominant gene known as Pc. The susceptible allele (Pc) can spontaneously convert to its resistant form (pc) at a gametic frequency of 10^3 to 10^4. A high-density genetic map around the Pc locus successfully narrowed the Pc gene to a 0.9 cM region on the short arm of chromosome 9 (Nagy et al. 2007). High-throughput sequencing technologies, genome-wide association studies (GWASs), and transcriptomic analyses play pivotal roles in revealing the genetic basis of fungal resistance.

Further exploration of resistance genes led to the analysis of a gene network, which we have presented in Fig. 2, to highlight the key genes involved. Network analysis of resistance-related and co-expressing genes was performed in sorghum, and the network is presented in Fig. 2. Contributing genes were found to be correlated and linked with the co-expression of the ARG1 gene. However, there are no public databases with reports on the *ARG1* gene and its expression levels.

Quantitative trait locus (QTL) mapping for resistance to fungal diseases

QTL mapping is a powerful tool used to identify genomic regions associated with complex traits, such as disease resistance. Unlike monogenic traits, the genetic architecture of complex traits is frequently controlled by multiple genes or alleles with small individual effects. Association analyses involving natural genetic variation, such as a diverse collection of sorghum germplasm or breeding materials, offer rich resources for QTL detection (Myles et al. 2009). The application of molecular markers in QTL mapping allows us to identify and understand QTLs involved in resistance and provide valuable insights into the molecular mechanisms of resistance (Kumar et al. 2017). In one study, two sorghum recombinant inbred line (RIL) populations, BTx623/BTx642 and BTx623/SC155-14E, were assessed for target leaf spot resistance in replicated trials. Four TLS (Target Leaf Spot) resistance QTLs were identified. Among these, three were previously unidentified, whereas a major QTL on chromosome 5 in the BTx623/BTx642 RIL population corresponded to the previously identified TLS resistance gene ds1. Additionally, a set of sorghum lines was assessed for reactive oxygen species (ROS) production induced by treatment with the microbe-associated molecular pattern (MAMP) flg22, a derivative of flagellin. Flg22-induced ROS production varied consistently between the lines. One QTL associated with variation in the flg22 response was detected in the RIL populations. However, no evidence was found to link variation in the MAMP response to variation in TLS resistance (Kimball et al. 2019). QTL detection involves the creation of mapping populations, such as recombinant inbred lines (RILs) or biparental populations. These populations are then phenotyped for disease resistance traits and genotyped via molecular markers. Statistical analyses are applied to identify associations between specific genomic regions and the observed resistance phenotypes. The QTLs identified for some sorghum fungal diseases via diverse germplasms and biparental populations are given in Table 3. Advanced technologies such as high-throughput genotyping and next-generation sequencing (NGS) have significantly enhanced the effectiveness and resolution of QTL mapping. Understanding the role of these QTLs is crucial for developing improved sorghum cultivars with resistance against a range of fungal pathogens. These significant associations are useful and suitable for marker-assisted selection for disease resistance.

Genotyping-by-sequencing (GBS)

Recent advancements in NGS technology have rendered DNA sequencing economically viable, enabling the implementation of the GBS approach for large-genome species with substantial genetic diversity, thereby avoiding ascertainment bias (Elshire et al. 2011). This strategy has rapidly expanded genomic resources across numerous crops, such as sorghum, where large-scale GBS data have been utilized to elucidate genomic diversity patterns and map genomic loci associated with complex trait variation in diverse germplasms, such as landrace accessions, breeding lines, and RILs, including those constituting a nested association mapping (NAM) population (Lasky et al. 2015; Bouchet et al. 2017). The GBS-based QTL analysis, which incorporates phenotype and marker data, identified nine QTLs, including qDMR1.2, qDMR3.1, qDMR5.1, and qDMR6.1, located on chromosomes 1, 2, 3, 5, 6, and 7 across three different environments. Further genome mining of qDMR3.1, qDMR5.1, and qDMR6.1 revealed putative candidate genes associated with resistance to sorghum downy mildew (SDM). The insights

Table 4 Candidate genes nearest to the SNPs associated with major fungal diseases in sorghum

Disease	Linked SNP	Chromosome position	Candidate gene and function	*P* value	References
Anthracnose	65,193,948	Chr.5	*Sobic.005G172300* F-box domain	1.39×10^{-7}	Cuevas et al. (2018)
	66,491,767		*Sobic.005G182400* Protein tyrosine kinase, leucine-rich repeat N-terminal domain, leucine-rich repeat	1.71×10^{-7}	
	71,578,176		*Sobic.005G228400* Oryzalide A biosynthesis	8.34×10^{-7}	
	66,554,507	Chr.1	*Sobic.001G1377200* Glucuronosyl transferases	5.66×10^{-5}	
	66,786,128		*Sobic.001G379400* Peroxidase	2.57×10^{-5}	
	60,609,133	Chr.6	*Sobic.006G274866* Leucine-rich repeat//Protein tyrosine kinase//Leucine-rich repeat N-terminal domain	2.2×10^{-4}	Ahn et al. (2021)
	70,974,745	Chr.3	*Sobic.003G401200* Selenium binding protein	2.3×10^{-4}	
	67,841,876	Chr.5	*Sobic.005G194700* Zinc finger, C3HC4 type family protein	2.3×10^{-4}	
	64,406,687	Chr.5	*Sobic.005G166700* Sulfotranferase family	2.4×10^{-4}	
	61,651,261	Chr.8	*Sobic.008G183100* Unknown function	2.4×10^{-4}	
	53,329,242	Chr.3	*Sobic.003G203500* Cytosolic aldehyde dehydrogenase RF2C Aldehyde dehydrogenase family	2.7×10^{-4}	
	65,282,291	Chr.2	*Sobic.002G268900* Single-strand DNA repair-like protein	2.8×10^{-4}	
	10,745,341	Chr.3	*Sobic.003G118600* F-box domain	2.8×10^{-4}	
Grain mold	3,764,910	Chr.3	*Sobic.003G040600* Similar to putative inositol polyphosphate 5-phosphatase	9.66×10^{-5}	Prom et al. (2020)
	62,334,957	Chr.4	*Sobic.004G281000* Similar to MADS-box protein	1.39×10^{-4}	
	5,326,968	Chr.7	*Sobic.007G052201* Weakly similar to Zinc finger (C3HC4-type RING finger) protein	1.5×10^{-4}	
	60,278,659	Chr.5	*Sobic.005G142101* Zinc finger, C3HC4-type (RING finger)	1.54×10^{-4}	
	54,729,155	Chr.6	*Sobic.006G194100* Similar to the H0307D04.12 protein zinc finger of the FCS-type C2-C2	2.21×10^{-4}	
	2,630,359	Chr.7	*Sobic.007G028900* Tetratricopeptide repeat coexpressed with genes in anthesis stage-specific coexpression subnetwork	2.27×10^{-4}	
	50,143,352	Chr.8	*Sobic.008G106700* Similar to isoflavone reductase, putative, expressed	1.76×10^{-4}	
	48,997,099	Chr.1	*Sobic.001G264000* Similar to alcohol dehydrogenase 2, zinc-binding dehydrogenase Alcohol dehydrogenase GroES-like domain	2.32×10^{-4}	
	62,085,849	Chr.7	*Sobic.007G187900* Weakly similar to putative uncharacterized protein P0681F10.18	2.47×10^{-4}	
	S4_62316425	Chr.4	*TAN1* gene biosynthesis of tannin	–	Nida et al. (2021)
	S1_51860558 S1_51860580	Chr.1	*Sobic.001G270200* *Cytochrome P450 CYP2* subfamily protein *Sobic.001G269900* *Sobic.001G270301* *KAFIRIN* Seed storage protein	–	
	S3_15689447	Chr.3	*Sobic.003G149100* *LATE EMBRYOGENESIS ABUNDANT 3 (LEA3)*	–	

Table 4 (continued)

Disease	Linked SNP	Chromosome position	Candidate gene and function	*P* value	References
Target leaf spot	7,332,596.1	Chr.5	*SORBI_3005G065100* F-box-like domain	1.4×10^{-8}	Samira et al. (2020)
			SORBI_3005G065050 Transmembrane helix, membrane component		
			SORBI_3005G065200 Uncharacterized protein		
			SORBI_3005G065300 SAM-dependent_MTases, Transmembrane transferase		
			SORBI_3005G065000 ds1/LRR, Ser/Thr protein kinase family		
			SORBI_3005G065400 DUF1618 domain-containing protein		
			SORBI_3005G064900 Cyt_P450, Fe binding transmembrane helix		
			SORBI_3005G064800 Aldehyde dehydrogenase		
Leaf blight	38,670,567	Chr.9	*Sobic.009G099450* Zinc finger, CCHC-type	7.0×10^{-9}	Prom et al. (2023)
	67,084,062	Chr.3	*Sobic.003G351501* Homeobox-leucine zipper protein anthocyaninless2-related	1.7×10^{-8}	
	9,250,700	Chr.8	*Sobic.008G070700* Protein suppressor of gene silencing 3 XS domain-containing protein/XS zinc finger domain containing protein-related	1.7×10^{-8}	
	5,849,212	Chr.9	*Sobic.009G057200* Electron transport oxidoreductase//Acyl-CoA dehydrogenase 4, peroxisomal	3.1×10^{-8}	
	48,064,154	Chr.5	No annotated gene	4.4×10^{-8}	
	37,426,140	Chr.2	*Sobic.002G147900* MYB/SANT-like DNA-binding domain	7.0×10^{-8}	
Head smut	55,470,704	Chr.4	*Sobic.004G202700* F-box and leucine-rich repeat protein	1.05×10^{-9}	Ahn et al. (2023)
	55,267,519	Chr.2	*Sobic.002G174700* Ankyrin repeats	1.2×10^{-8}	
	61,700,071	Chr.4	*Sobic.004G273200* Xyloglucan endotransglucosylase/Hydrolase protein 29-related	7.7×10^{-8}	
	65,477,983	Chr.4	*Sobic.004G319800* 10 kDa heat shock protein//20 kDa chaperonin, Chloroplastic	7.8×10^{-8}	
	73,084,958	Chr.3	*Sobic.003G427400* Similar to signal recognition particle 54 kDa protein 1	1.8×10^{-7}	
	70,919,811	Chr.1	*Sobic.001G430000* Similar to helix-loop-helix DNA-binding domain containing protein, expressed	2.4×10^{-7}	
	55,189,900	Chr.2	*Sobic.002G174300* Weakly similar to transcription factor WRKY74	3.2×10^{-7}	

gained from this study provide valuable resources for map-based cloning and marker-assisted selection in sorghum breeding programs, facilitating the development of SDM-resistant maize varieties (Jadhav et al. 2020). Notably, GBS, which concurrently involves SNP discovery and genotyping, eliminates the prerequisite for prior genomic knowledge of the species. However, challenges arise from variations in parameters or reference genomes employed for SNP calling in different projects, hindering the comparison and reuse of datasets. Consequently, the integration of public GBS data into a reference SNP dataset becomes imperative to facilitate cross-project comparisons and unearth previously unexplored biological information (Rung and Brazma 2013). The SNPs identified through GBS offer a valuable resource for analyzing genetic diversity and can be seamlessly integrated into genome-wide association studies (GWASs) aimed at

identifying candidate genes responsible for both quantitative and qualitative traits.

Genome-wide association studies (GWAS) in sorghum

Linkage analysis (LA) stands out as the primary genomic tool employed for the mapping of QTLs. An alternative methodology, GWAS or association mapping (AM), was introduced as a complement to traditional linkage-based QTL mapping. Unlike the biparental population utilized in linkage/pedigree-based QTL mapping, GWAS or AM relies on the principle of linkage disequilibrium (LD) to establish a significant association between DNA markers and the target trait. Cuevas et al. conducted a seed mycoflora analysis, revealing the presence of pathogenic fungi, including *Curvularia lunata, Fusarium thapsinum*, and *F. semitectum*, in both resistant and susceptible accessions. Through genome-wide association scans with 268,289 single nucleotide polymorphisms (SNPs), they identified two loci linked to low seed deterioration and another associated with the emergence rate. Candidate genes (Table 4) within these loci, such as Sobic.08G132000 and Sobic.01G349300, presented domains associated with systemic acquired resistance, indicating their involvement in pathogen recognition and downstream signaling cascades (Cuevas et al. 2019). The steps followed in GWAS (Fig. 3) are simplified. Although linkage analysis is instrumental in unraveling the genetic foundations of various crops, its markers suffer from limitations, such as population specificity of detected QTLs and the consideration of only two alleles per locus with a minimal number of meiotic recombination events for estimating genetic distances between marker loci and causal loci, thereby constraining mapping resolution. The identification of genetic linkage involves thorough genotyping of a panel of germplasm or breeding populations exhibiting diverse phenotypes across varying environments, highlighting its ability to pinpoint specific genes governing desired traits. Through genome-wide association studies (GWASs), several genes were identified as potential contributors to sorghum's defense against head smut. Notably, the F-box-encoding gene on chromosome 2 and a zinc finger protein on chromosome 9 are known for their roles in regulating cell death and defense responses. LOC8064738, which encodes Plasmodesmata Callose-Binding Protein 2 (PDCB2), was highlighted for its involvement in symplastic communication and pathogen defense. Additionally, two candidate genes related to the BZR1 protein were identified on chromosome 4, along with LOC8085202, encoding a mevalonate kinase, and LOC8082811, encoding CUP-SHAPED COTYLEDON1. Other important genes, including LOC8064189, encoding structural maintenance of chromosome protein 4 (SMC4); LOC8085201, encoding a phytosulfokine; and LOC8084627, encoding PIN-LIKES 7 (PIN7) (Ahn et al. 2024). These genes offer valuable targets for breeding programs aimed at enhancing disease resistance in sorghum. On the other hand, association mapping (AM) presents several advantages over linkage mapping, offering enhanced mapping resolution due to historical mutations and recombination events in genetic lineages. Through association mapping, two loci linked to grain

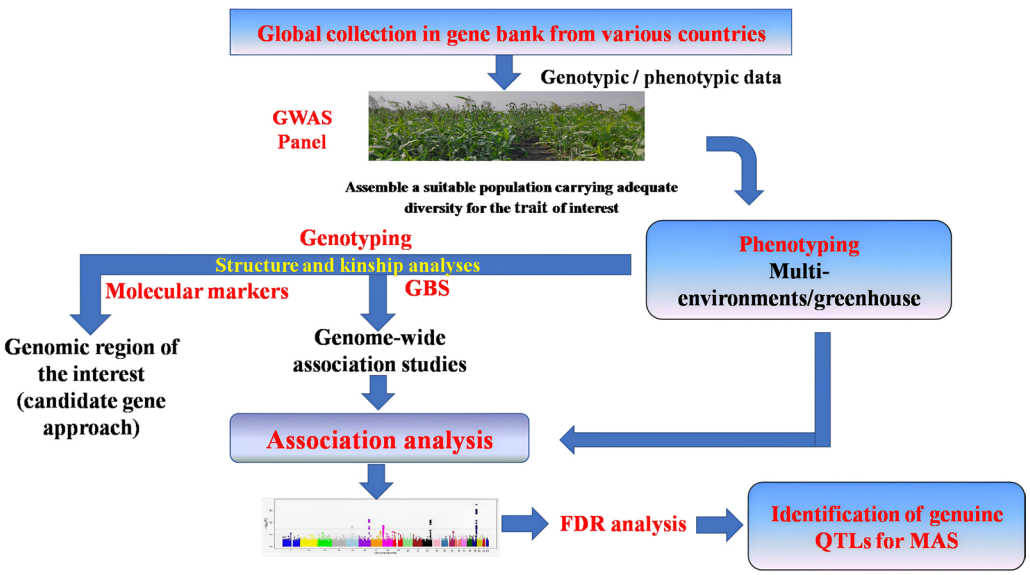

Fig. 3 Schematic representation of genome-wide association studies (GWASs). GBS-Genotyping by sequencing, FDR-False discovery rate, QTL-Quantitative trait loci, MAS-Marker-assisted selection

mold resistance and five loci linked to rust resistance were identified. Among the grain mold resistance loci, one contained a homolog of the maize nonhost resistance gene Rxo1. Two of the rust-linked loci each contained rust resistance genes homologous to the maize rust resistance gene Rp1-D (B locus) and the wheat rust resistance gene Lr1. The other loci included genes crucial for different steps of the defense response, such as cyclophilins, which mediate the resistance response preceding the hypersensitive response (HR), and Hin1, which is directly involved in producing HR. These findings will facilitate marker-assisted selection for enhancing host resistance to grain mold and rust in sorghum (Upadhyaya et al. 2013). This information facilitates the identification of markers proximal to governing genes, providing a more nuanced understanding of the genetic basis of traits. The expectation is that genetic polymorphisms strongly linked to a genomic locus, resulting in phenotypic differences, will exhibit substantial associations with target traits across a diverse panel of germplasms.

Functional genomics approaches

Functional genomics involves studying the function of genes and their interactions within the entire genome. Various techniques, such as genome sequencing, transcriptomics, proteomics, and metabolomics, have been utilized by sorghum researchers to identify key genes and pathways involved in the defense response against fungal pathogens. Through techniques such as genome-wide association studies (GWASs) and quantitative trait locus (QTL) mapping, researchers have pinpointed genomic regions associated with resistance traits. These identified genes can then be further characterized to understand their function and regulation. Researchers have employed RNA sequencing (RNA-Seq) to analyze the transcriptome of sorghum plants under fungal stress. This information helps identify key genes and signaling pathways involved in the defense response. Pathway analysis then allows scientists to understand the interconnectedness of these genes and how they collectively contribute to fungal resistance.

Transcriptomic analysis through RNA sequencing

The identification of the genetic, molecular, and biochemical components responsible for disease resistance relies on the study of transcriptome profiles. Transcriptomics, the study of RNA expression, provides insights into how genes are differentially expressed during fungal infection. Anthracnose (*C. sublineolum*) infection causes transcriptome changes in both resistant and susceptible sorghum cultivars, with thousands of genes being up-/down-regulated (Fu et al. 2020; Natarajan et al. 2021). Transcriptome analysis of salicylic acid (SA)-sensitive (BTx623) and tolerant (WHEATLAND) sorghum lines

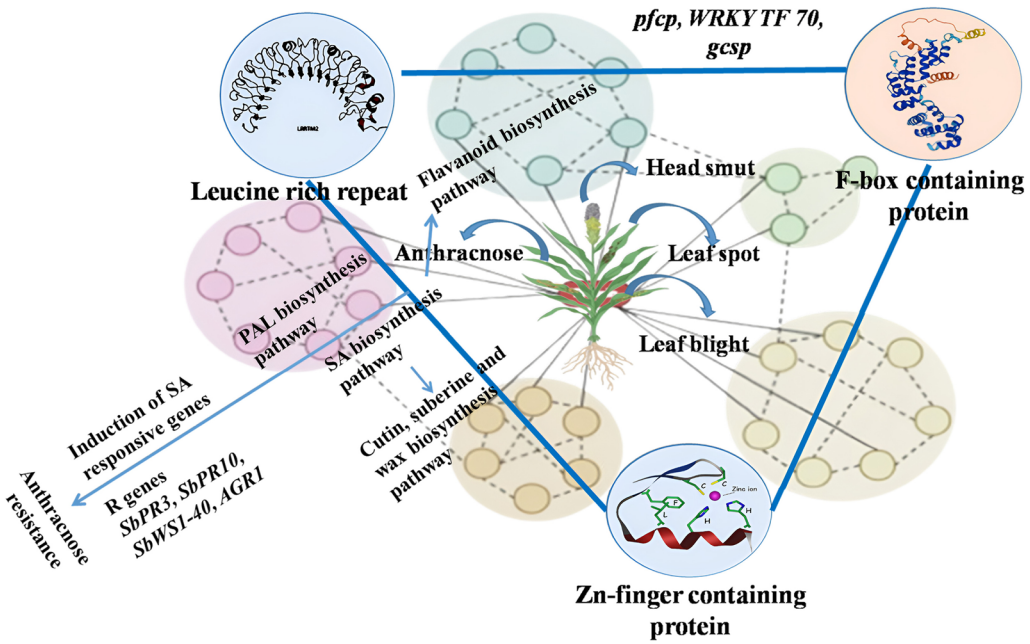

Fig. 4 Interaction network of stress signaling molecules and genes involved in the stress-tolerance phenotype. Pathways involved in plant defense mechanisms and anthracnose resistance were identified through transcriptome and pathway analyses. SbPR-sorghum pathogen related, SbWS-sorghum water stressed, pfcp-papain family cysteine protease, WRKF TF 70-WRKF transcription factor 70, and gcsp-glycine-rich cell wall structural protein

revealed that SA enhances anthracnose resistance by activating the expression of several immune-related genes and pathways (Sun et al. 2022). The extensive regulation of gene expression at the transcriptional level plays a crucial role in plant responses to pathogen infection. This is particularly important since numerous genes associated with disease resistance are known to be transcriptionally regulated. This approach can help identify genes that play a role in the response to pathogens, and among these genes, a subset is likely to directly contribute to resistance. Sun et al. 2022 reported that two pathways, the cutin, subernine, and wax biosynthesis pathways, which are involved in the plant immune response, and the flavonoid biosynthesis pathway, which is involved in the upregulation of specific genes (enriched in BTx623) induced through SA signaling, result in anthracnose resistance (Fig. 4). Nida et al. (2021) explored transcriptome changes related to various molecular and cellular processes and biological functions. Notably, differential regulation was observed in defense, secondary metabolism, and flavonoid biosynthesis during the development of kernels in two sorghum genotypes: the grain mold-resistant variety RTx2911 and the susceptible variety RTx430. Increased expression was noted in genes associated with pattern recognition receptors (PRRs), regulators of growth and defense homeostasis, antimicrobial peptides, pathogenesis-related proteins, zein seed storage proteins, and phytoalexins, and this increased expression correlated with resistance.

Conclusion and future perspectives

Sorghum, well known for its dual-purpose nature and resilience to water-stressed conditions, stands as a resilient crop amid the challenges of climate change. However, the onslaught of fungal pathogens threatens the productivity and sustainability of sorghum cultivation. Despite its importance, genetic and genomic research in sorghum is behind that in major cereals. While conventional strategies have revealed numerous QTLs associated with disease resistance, the advent of sequencing technologies offers new avenues for exploring SNPs linked to fungal resistance. Moreover, functional genomics and systems biology approaches have identified candidate genes and pathways governing plant immune responses, enabling genome editing (Andrew-Peter-Leon et al. 2021), although the focus has primarily been on major diseases. However, further exploration, particularly in gene expression profiling, is essential to elucidate the intricate genetic mechanisms underlying stress resistance in sorghum, including both genes and noncoding RNAs (Yasin et al. 2020, 2022). With concerted efforts and the application of new tools and techniques, sorghum can be fortified against fungal pathogens, ensuring its continued prosperity and supporting food and nutritional security.

Abbreviations

AM	Association mapping
ARG	Anthracnose resistance gene
CCSs	Circular consensus sequences
CNVs	Copy number variations
DArT	Diversity array technology
DUFs	Domains of unknown functions
ESTs	Expressed sequence tags
FAO	Food and Agriculture Organization
FDR	False discovery rate
GBS	Genotyping-by-sequencing
gcsp	Glycine-rich cell wall structural protein
GRIN	Global-Germplasm Resources Information Network
GWAS	Genome-wide association studies
HR	Hypersensitive response
LA	Linkage analysis
LD	Linkage disequilibrium
MAMP	Microbe-associated molecular pattern
MAS	Marker assisted selection
NAM	Nested association mapping
ncRNA	Non-coding RNA
NGS	Next generation sequencing
NLR	Nucleotide-binding leucine-rich repeat
PAVs	Present/absent variations
PDCB2	Plasmodesmata callose-binding protein 2
pfcp	Papain family cysteine protease
PRRs	Pattern recognition receptors
QTL	Quantitative trait loci
RFLPs	Restriction fragment length polymorphisms
RIL	Recombinant inbred line
RNA-Seq	RNA sequencing
ROS	Reactive oxygen species
SA	Sorghum accessions
SAP	Sorghum association panel
SbPR	Sorghum pathogen related
SbWS	Sorghum water stressed
SDM	Sorghum downy mildew
SE	Serine esterase
SMC4	Structural maintenance of chromosome protein 4
SNP	Single nucleotide polymorphism
SSRs	Simple sequence repeats
TE	Transcription elongation factor
WRKF TF 70	WRKF transcription factor 70

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42483-024-00309-x.

Additional file 1: Table S1. Major sorghum diseases, causal organisms, and their symptoms.

Additional file 2: Table S2. Gene and feature statistics of the *S.bicolor* NCBIv3 reference genome.

Additional file 3: Table S3. Genome information of the *S. bicolor* BTx623 assembly version 5.1.

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Author contributions

APM conceived and designed the study. APM and YJK assisted with the analysis and interpretation of the results. APM, SV, APL, and EH contributed to drafting the manuscript, designing the study, and supervising it. All the authors reviewed the results and approved the final version of the manuscript.

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Availablity of data and materials
The authors declare that the data supporting the findings of this study are available within the paper.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
All the authors reviewed the results and approved the final version of the manuscript.

Competing interests
The authors declare that they have no competing interests.

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References

Acquaah G. Principles of plant genetics and breeding. Hoboken: Wiley; 2009.
Ahn E, Prom LK, Hu Z, Odvody G, Magill C. Genome-wide association analysis for response of Senegalese sorghum accessions to texas isolates of anthracnose. Plant Genome. 2021;14: e20097.
Ahn E, Prom LK, Magill C. Multi-trait genome-wide association studies of sorghum bicolor regarding resistance to anthracnose, downy mildew grain mold and head smut. Pathogens. 2023;12:779.
Ahn E, Fall C, Prom LK, Magill C. A genome-wide association study of senegalese sorghum seedlings responding to pathotype 5 of sporisorium reilianum. Plants. 2024;11:2999.
Amelework BA, Shimelis HA, Tongoona P, Mengistu F, Laing MD, Ayele DG. Sorghum production systems and constraints, and coping strategies under drought-prone agro-ecologies of Ethiopia. S Afr J Plant Soil. 2016;33:207–17.
Andrew-Peter-Leon MT, Selvaraj R, Kumar KK, Muthamilarasan M, Yasin JK, Pillai MA. Loss of function of OsFBX267 and OsGA20ox2 in rice promotes early maturing and semi-dwarfism in γ-Irradiated IWP and genome-edited pusa basmati-1. Front Plant Sci. 2021;12:714066.
Anitha K, Das IK, Holajjer P, Sivaraj N, Reddy CR, Balijepalli SB. Sorghum diseases: diagnosis and management. In: Tonapi VA, Talwar HS, Are AK, Bhat BV, Reddy CR, Dalton TJ, editors. Sorghum in the 21st Century: food – fodder – feed – fuel for a rapidly changing world. Singapore: Springer Singapore; 2020. p. 565–619.
Behera PP, Saharia N, Borah N, Devi SH, Sarma RN. Sorghum physiology and adaptation to abiotic stresses. Int J Environ Clim Change. 2022;12:1005–22.
Bouchet S, Olatoye MO, Marla SR, Perumal R, Tesso T, Yu J, et al. Increased power to dissect adaptive traits in global sorghum diversity using a nested association mapping population. Genetics. 2017;206:573–85.
Bushra S, Faisal Saeed A, Fozia S, Hafeez Ahmad S, Sarmad Frogh A, Haseeb S. Genetic improvement of sorghum for biomass traits using genomics approaches. In: Madhugiri N-R, Jaya RS (eds). Advances in biofuels and bioenergy. Rijeka: IntechOpen; 2018. p. Ch. 2.
Cota LV, Souza AGC, Costa RV, Silva DD, Lanza FE, Aguiar FM, et al. Quantification of yield losses caused by leaf anthracnose on sorghum in Brazil. J Phytopathol. 2017;165:479–85.
Cuevas HE, Prom LK, Cooper EA, Knoll JE, Ni X. Genome-wide association mapping of anthracnose (Colletotrichum sublineolum) resistance in the U.S. sorghum association panel. Plant Genome. 2018;11:170099.
Cuevas HE, Prom LK, Cruet-Burgos CM. Genome-wide association mapping of anthracnose (Colletotrichum sublineolum) resistance in NPGS ethiopian sorghum germplasm. G3 Genes Genomes Genet. 2019;9:2879–85.
Deschamps S, Llaca V, May GD. Genotyping-by-sequencing in plants. Biology. 2012;1:460–83.
Elshire RJ, Glaubitz JC, Sun Q, Poland JA, Kawamoto K, Buckler ES, et al. A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. PLoS ONE. 2011;6: e19379.
FAO. FAOSTAT. Rome: Food and Agriculture Organization of the United Nations; 2023.
Fu F, Girma G, Mengiste T. Global mRNA and microRNA expression dynamics in response to anthracnose infection in sorghum. BMC Genomics. 2020;21:760.
Girma G, Nida H, Seyoum A, Mekonen M, Nega A, Lule D, et al. A large-scale genome-wide association analyses of ethiopian sorghum landrace collection reveal loci associated with important traits. Front Plant Sci. 2019;10:691.
Harlan JR, de Wet JMJ. A simplified classification of cultivated sorghum1. Crop Sci. 1972;12:172–6.
Huang X, Han B. Natural variations and genome-wide association studies in crop plants. Annu Rev Plant Biol. 2014;65:531–51.
ICAR-NBPGR. Indian Council of Agricultural Research-National Bureau of Plant Genetic Resources. 2024. http://pgrportal.nbpgr.ernet.in. Accessed January 2024
ICRISAT. Genetic resources. International Crops Research Institute for the Semi-Arid Tropics. 2024. http://genebank.icrisat.org. Accessed January 2024
ICRISAT. ICRISAT Genebank. Patancheru, Telangana, India: International Crps Research Institute for the Semi-Arid Tropics; 2024.
Jadhav KP, Saykhedkar GR, Tamilarasi PM, Devasree S, Ranjani RV, Sarankumar C, Bharathi P, Karthikeyan A, Arulselvi S, Vijayagowri E, Ganesan KN. GBS-based SNP map pinpoints the QTL associated with sorghum downy mildew resistance in maize (Zea mays L.). Front Genet. 2020;13:890133.
Kazungu FK, Muindi EM, Mulinge JM. Overview of sorghum (Sorghum bicolor L.), its economic importance, ecological requirements and production constraints in Kenya. Int J Plant Soil Sci. 2023;35:62–71.
Kebede D, Dramadri IO, Rubaihayo P, Odong T, Edema R. Resistance of sorghum genotypes to ergot (Claviceps Species). Agriculture. 2023;13:1100.
Khoddami A, Messina V, Vadabalija Venkata K, Farahnaky A, Blanchard CL, Roberts TH. Sorghum in foods: functionality and potential in innovative products. Crit Rev Food Sci Nutr. 2023;63:1170–86.
Kimball J, Cui Y, Chen D, Brown P, Rooney WL, Stacey G, et al. Identification of QTL for target leaf spot resistance in sorghum bicolor and investigation of relationships between disease resistance and variation in the MAMP response. Sci Rep. 2019;9:18285.
Kumar B, Harsha BS, Borphukan B, Fakrudin B. Association analysis of charcoal rot disease component traits in sorghum minicore germplasm with EST-SSR markers. Indian J Genet Plant Bree. 2017;77:74–82.
Lasky JR, Upadhyaya HD, Ramu P, Deshpande S, Hash CT, Bonnette J, et al. Genome-environment associations in sorghum landraces predict adaptive traits. Sci Adv. 2015;1: e1400218.
Lee S, Fu F, Liao CJ, Mewa DB, Adeyanju A, Ejeta G, Lisch D, Mengiste T. Broad-spectrum fungal resistance in sorghum is conferred through the complex regulation of an immune receptor gene embedded in a natural antisense transcript. Plant Cell. 2022;34(5):1641–65.
Lipps S, Rooney WL, Mideros SX, Jamann TM. Identification of quantitative trait loci for sorghum leaf blight resistance. Crop Sci. 2022;62:1550–8.
Mamo W, Enyew M, Mekonnen T, Tesfaye K, Feyissa T. Genetic diversity and population structure of sorghum [Sorghum bicolor (L.) Moench] genotypes in Ethiopia as revealed by microsatellite markers. Heliyon. 2023;9: e12830.
McCormick RF, Truong SK, Sreedasyam A, Jenkins J, Shu S, Sims D, et al. The Sorghum bicolor reference genome: improved assembly, gene annotations, a transcriptome atlas, and signatures of genome organization. Plant J. 2018;93:338–54.
Mewa DB, Lee S, Liao CJ, Adeyanju A, Helm M, Lisch D, Mengiste T. Anthracnose resistance gene2 confers fungal resistance in sorghum. Plant J. 2023;113(2):308–26.
Michael TP, Jackson S. The First 50 Plant Genomes. The Plant Genome. 2013; 6:plantgenome2013.03.0001in.
Myles S, Peiffer J, Brown PJ, Ersoz ES, Zhang Z, Costich DE, et al. Association mapping: critical considerations shift from genotyping to experimental design. Plant Cell. 2009;21:2194–202.

Nagy ED, Lee TC, Ramakrishna W, Xu Z, Klein PE, SanMiguel P, Cheng CP, Li J, Devos KM, Schertz K, Dunkle L. Fine mapping of the Pc locus of Sorghum bicolor, a gene controlling the reaction to a fungal pathogen and its host-selective toxin. Theor Appl Genet. 2007;114:961–70.
Natarajan P, Ahn E, Reddy UK, Perumal R, Prom LK, Magill C. RNA-sequencing in resistant (QL3) and susceptible (Theis) sorghum cultivars inoculated with johnsongrass isolates of colletotrichum sublineola. Front Genet. 2021;12:722519.
Nida H, Girma G, Mekonen M, Lee S, Seyoum A, Dessalegn K, Tadesse T, Ayana G, Senbetay T, Tesso T, Ejeta G. Identification of sorghum grain mold resistance loci through genome wide association mapping. J Cereal Sci. 2019;85:295–304.
Nida H, Girma G, Mekonen M, Tirfessa A, Seyoum A, Bejiga T, et al. Genome-wide association analysis reveals seed protein loci as determinants of variations in grain mold resistance in sorghum. Theor Appl Genet. 2021;134:1167–84.
Paterson AH, Bowers JE, Bruggmann R, Dubchak I, Grimwood J, Gundlach H, et al. The sorghum bicolor genome and the diversification of grasses. Nature. 2009;457:551–6.
Price HJ, Dillon SL, Hodnett G, Rooney WL, Ross L, Johnston JS. Genome evolution in the genus sorghum (Poaceae). Ann Bot. 2005;95:219–27.
Prom LK, Cuevas HE, Ahn E, Isakeit T, Rooney WL, Magill C. Genome-wide association study of grain mold resistance in sorghum association panel as affected by inoculation with Alternaria alternata alone and Alternaria alternata, Fusarium thapsinum, and Curvularia lunata combined. Eur J Plant Pathol. 2020;157:783–98.
Prom LK, Botkin JR, Ahn EJS, Sarr MP, Diatta C, Fall C, et al. A genome-wide association study of nigerien and senegalese sorghum germplasm of exserohilum turcicum, the causal agent of leaf blight. Plants. 2023;12:4010.
Ramya K, Abdul Fiyaz R, Yasin J. SMART agriculture for nutritional security. Curr Sci. 2013;105:1458.
Rung J, Brazma A. Reuse of public genome-wide gene expression data. Nat Rev Genet. 2013;14:89–99.
Samira R, Kimball JA, Samayoa LF, Holland JB, Jamann TM, Brown PJ, et al. Genome-wide association analysis of the strength of the MAMP-elicited defense response and resistance to target leaf spot in sorghum. Sci Rep. 2020;10:20817.
Sharma I, Kumari N, Sharma V. Sorghum fungal diseases. In: Lichtfouse E, Goyal A, editors. Sustainable agriculture reviews: cereals. Cham: Springer International Publishing; 2015. p. 141–72.
Singh Y, Sharma D, Kharayat B. Major diseases of sorghum and their managment. In: Srivastava J, Singh A (eds). Diseases of field crops diagnosis and management. Volume 1: Cereals, Small Millets and Fiber Crops: Apple Academic Press; 2020.
Sun X, Li A, Ma G, Zhao S, Liu L. Transcriptome analysis provides insights into the bases of salicylic acid-induced resistance to anthracnose in sorghum. Plant Mol Biol. 2022;110:69–80.
Tesema ML, Mengesha GG, Dojamo TS, Takiso SM. Response of sorghum genotypes for turcicum leaf blight [*Exserohilum turcicum* (Pass.) Leonard and Suggs] and agronomic performances in southern Ethiopia. Int J Sci Res Arch. 2022;05:77–95.
Uffelmann E, Huang QQ, Munung NS, de Vries J, Okada Y, Martin AR, et al. Genome-wide association studies. Nat Rev Methods Primers. 2021;1:59.
Upadhyaya HD, Wang YH, Sharma R, Sharma S. SNP markers linked to leaf rust and grain mold resistance in sorghum. Mol Breed. 2013;32:451–62.
USDA-ARS-GRIN. U.S. National Plant Germplasm System. USDA; 2024.
Vetriventhan M, Azevedo VCR, Upadhyaya HD, Nirmalakumari A, Kane-Potaka J, Anitha S, et al. Genetic and genomic resources, and breeding for accelerating improvement of small millets: current status and future interventions. Nucleus. 2020;63:217–39.
Wang X, Mace E, Hunt C, Cruickshank A, Henzell R, Parkes H, et al. Two distinct classes of QTL determine rust resistance in sorghum. BMC Plant Biol. 2014;14:366.
Xiao Y, Liu H, Wu L, Warburton M, Yan J. Genome-wide association studies in maize: praise and stargaze. Mol Plant. 2017;10:359–74.
Xin Z, Wang M, Cuevas HE, Chen J, Harrison M, Pugh NA, et al. Sorghum genetic, genomic, and breeding resources. Planta. 2021;254:114.
Yasin JK, Tyagi H, Singh AK, Magadum S. Abiotic stress tolerance in soybean: regulated by ncRNA. J AgriSearch. 2016;3(1):1–6.
Yasin JK, Mishra BK, Pillai MA, Verma N, Wani SH, Elansary HO, et al. Genome wide in-silico miRNA and target network prediction from stress responsive Horsegram (Macrotyloma uniflorum) accessions. Sci Rep. 2020;10:17203.
Yasin JK, Mishra BK, Arumugam Pillai M, Chinnusamy V. Physical map of lncRNAs and lincRNAs linked with stress responsive miRs and genes network of pigeonpea (Cajanus cajan L.). J Plant Biochem Biotechnol. 2022;31:271–92.
Zheng L-Y, Guo X-S, He B, Sun L-J, Peng Y, Dong S-S, et al. Genome-wide patterns of genetic variation in sweet and grain sorghum (Sorghum bicolor). Genome Biol. 2011;12:R114.