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Genomics breeding approaches for developing *Sorghum bicolor* lines with stress resilience and other agronomic traits☆

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ABSTRACT

Sorghum, also known as great millet, is a major cereal crop that feeds over 500 million people in more than 100 countries, especially in Africa and Asia. It can grow well under harsh environmental conditions, such as drought, heat, salinity, and soils that are nutritionally poor. The crop is water- and nitrogen-efficient with C_4 photosynthesis system and a relatively small genome of about 730 Mb. Its genome has been sequenced and annotated, revealing significant genetic variation and genomics resources. Despite being drought tolerant, there is a great degree of variation among the diverse lines of germplasm for drought and drought associated traits, and hence resilience to drought and other stresses need to be studied through the integration of phenomics and genomics technologies. There is an urgent need to adopt advanced genomics and high-throughput technologies to find candidate genes and alleles for crop traits, develop molecular markers and genomic selection (GS) models, create new genetic variation and design sorghum ideotypes that suit to the changing climate.

1. Introduction

Climate change poses a severe threat to global food and nutritional security through the ongoing deterioration of soil quality, increase in temperature, CO_2 levels and increase in the frequency of extreme weather events like heat waves, flash floods, and prolonged dry spells during the regular monsoon season [1]. In addition, there is also less utilized or abandoned marginal crop land measuring about 320–702 million hectares which can be put into cultivation by using alternate crops [2]. Evidently, early evaluation of degree of sensitivity and vulnerability of the main agricultural landscape against the changing climatic conditions is essential to design and deploy suitable varieties that can adapt and grow [3]. There is a need to breed crops that are more resilient to harsh environmental conditions due to the growing population, diminishing land and water resources, and changing nutritional needs. Small seed millets and also great millet (sorghum) have been a staple food for the people in developing world, and these crops are cultivated in 93 countries with developing nations having major share of > 97% production and consumption [4]. Sorghum (*Sorghum bicolor*(L.) Moench) occupies a prime place among millets in the arid and semi-arid regions of the world that are particularly vulnerable to climate change. Sorghum, also known as the "camel of grains" or "great millet," is one of the best millets for crop diversification because of its ability to thrive in challenging environments.

Improvement of sorghum through breeding approach has led to the development of superior varieties however grain yield has been a major bottleneck to achieve comparable yield to that of cereal crops. Breeding efforts including selection have resulted in incremental yield but it is observed to be associated with genetic effects and, with reduced genetic diversity [5]. Often the effect is observed associated with genotypes and climatic factors under varied environmental milieu [6]. This context demands the intervention of new breeding technologies to fast-track the breeding of varieties with high genetic yield potential and resilience. Development of productive, diverse genotypes has been undertaken to investigate genotype-environment interactions, and genomics mediated selection for target traits [7], which emphasizes the need for

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establishment of diversity panels for genetic dissection and sorghum breeding. Furthermore, selection and improvement for resilience to biotic and abiotic stresses is a challenge since the traits, majorly, have a complex genetic control, with a wide range of associated effects.

Genome of sorghum has been assembled using several diverse sorghum types, and the new genome sequence references are expected to provide avenues to decipher genome structure and genomic diversity. The development and accessibility of a comprehensive reference genome sequence derived from an elite line, BTx623 have significantly expedited the progress of genetic and genomic investigations in the realm of sorghum research [8] and this reference genome facilitated resequencing of several cultivated and wild species of sorghum which led to the development of molecular markers in sorghum. The availability of these molecular markers will help in the construction of linkage maps and identification of quantitative trait loci (QTL) and Meta-QTLs associated with desirable agronomic traits as well as biotic and abiotic stress tolerance. The identified QTLs or Meta-QTLs can be exploited in marker-assisted backcross breeding for developing superior climate-resilient cultivars which can perform better under adverse climatic conditions [9]. Besides, DNA markers have various applications in the field of genetics. They can be used to assess the extent of genetic diversity and population structure in germplasm collections, identify cultivars, and test the genetic purity of hybrids and parental lines. Molecular markers, including SSR and EST(Expressed sequence tags)-SSR markers, are widely used for hybrid purity testing and DNA fingerprint profiles [10,11].

2. Molecular markers

DNA-based molecular markers have become very useful for the assessment of diversity among the germplasm collections besides, analyzing genetic variation underlying important agronomic and stress associated traits besides. These markers, independently or in combination with others, were efficiently used for sorghum improvement. Due to their abundance, high polymorphic nature, codominance and amenability to high-throughput genotyping, SSRs are the markers of choice for various genetics and mapping applications in sorghum. Forty-nine SSRs by using three different methods, (i) searching for sorghum SSRs in public DNA databases, (ii) using SSR-specific primers created for maize (*Zea mays* L.) and (iii) screening sorghum genomic libraries by hybridization with SSR oligonucleotides were identified [12]. Later, 13 SSR markers were found in sorghum [13]. Ten of these loci were detected by database searches, while the other three were found after screening sorghum genomic AG-enriched libraries with labelled poly (AG)/poly (CT). Other researchers discovered SSRs using cDNA sequences, EST sequences, and unigene sequences [14–17]. In whole-genome shotgun sequences of the sorghum line BTx623, 5599 non-redundant SSR markers, including areas bordering the SSRs were constructed [18]. Repeats of (AT/TA)n made up to 26.1% of all SSRs, followed by repeats of (AG/TC)n (20.5%), (AC/TG)n (13.7%), and (CG/GC)n (11.8%). Using computational analysis, the reference genome of *Sorghum bicolor* was analyzed, and 163,943 simple sequence repeats (SSRs) were predicted. This information is useful for identifying genetic markers and understanding the genetic diversity of *Sorghum bicolor* [19].

Single-nucleotide polymorphism (SNP) markers are currently at the top of the list of molecular markers for sorghum genotyping due to their great abundance and ability to accommodate the entire genome with higher throughput and precision than other markers. The rapid and extensive identification of SNPs has become achievable due to the progress in sequencing technologies, the presence of powerful computational tools, and the abundance of DNA sequence data, particularly in the form of expressed sequence tags (ESTs) and complete genomes. About 77,094 potential SNPs, 40,589 reliable SNPs were identified using the online SNP detection tool HaploSNPer [20]. Through short-read sequencing of eight diverse sorghum accessions, followed by their alignment with the reference genome, a total of 283,000 SNPs were identified [21]. By employing genotyping-by-sequencing (GBS) for 516 Nigerien sorghum accessions, 144,299 SNPs were identified [22]. Notably, in a study involving 304 sorghum accessions collected from various regions of Ethiopia, genotyping-by-sequencing evenly distributed 108,107 high-quality SNP markers across the sorghum genome [23].

Two sweet (Keller and E-Tian) and one grain (Ji2731) sorghum inbred lines were resequenced and aligned, which led to the discovery of 1057,018 SNPs and 99,948 insertions/deletions (InDels) [24]. Similar results were obtained when 44 *S. bicolor* representing all major cultivars of as well as its progenitors and *S. propinquum* were re-sequenced [25]. This study discovered 4946,038 genome-wide SNPs. When the genome sequences of two sorghum genotypes, Tx7000 and BTx642, were compared to the reference genome of BTx623, they revealed nearly 1.2 million SNPs and 120,969 InDels distinguishing Tx7000 from BTx623, and 1.6 million SNPs and 152,836 InDels distinguishing BTx642 from BTx623. [26]. By aligning more than 50 resequenced genomes from various sorghum genotypes to the reference genome [27], roughly 7.4 M SNPs and 1.9 M InDels were discovered.

A high-density genomic marker set of 43,983,694 variants was created using the whole-genome sequencing (WGS) of 400 sorghum accessions from the sorghum association panel (SAP) at an average coverage of 38x (25–72x). This included SNPs (about 38 million), InDels, and copy number variants [28]. Utilizing the compiled and annotated genome sequences of *Sorghum bicolor* (v2.1) the SNPs have been incorporated into the newly established Sorghum Genome SNP Database, known as SorGSD [29]. However, such precious data need to be exploited in breeding programs of sorghum for improvement.

3. Genetic maps

The initial stage for conducting genetic analysis of a trait with various DNA markers involves the development of a linkage map [30]. Despite the application of additional RFLPs (Restriction Fragment Length Polymorphism), which led to an expansion in both map length and marker density, it remained inadequate to comprehensively represent the entire genome [31–33]. A separate linkage map comprising 15 linkage groups was established by employing 38 sorghum and 33 maize genomic DNA probes, encompassing a map length of 633 cM [34]. Subsequently, the alignment and integration of five significant linkage maps based on RFLPs, which included a total of 1036 markers [35,36], with the existing 10 linkage groups [37], played a pivotal role in evaluating map precision and establishing connections between QTL markers within specific genomic regions. RAPDs (Random Amplified Polymorphic DNA) were initially used to create linkage maps [38–40], but were not widely used due to the inherent problem of reproducibility across laboratories. Subsequently, various researchers successfully used AFLP (Amplified Fragment lLength Polymorphism) markers to saturate linkage maps [41–43]. Initially, only a few SSR markers which were previously accessible were used to construct the linkage maps [13, 33, and 44]. Later, 31 and 113 more SSR markers were added [45,46], respectively, to the RFLP-based linkage map [47]. A high-density linkage map with additional 2926 markers, including 2454 AFLPs, 136 SSRs, and 336 RFLPs were obtained from rice, barley, oat, and maize cDNA and genomic clones. The average marker spacing in this augmented map was 0.5 cM [48]. Similarly, another high-density map with even tighter marker spacing (0.4 cM) was developed, incorporating 2512 RFLP loci [49].

Linkage maps were established using EST-SSR [42,50] and SSRs derived from unigenes [16,51], showcasing significant promise for comparative genome mapping. The emergence of high-throughput markers, such as Diversity Arrays Technology (DArT) and SNPs, has gained prominence thanks to rapid advancements in marker discovery. In constructing linkage maps, markers from both DArT and non-DArT sources, spread across all 10 chromosomes, were employed [52,53]. Based on 3418 bin markers that were found from resequencing of 244

RILs from the cross 654 x LTR108, an ultra-high density linkage map was created [54]. A linkage map was made using 3710 single nucleotide polymorphisms, discovered through restriction-site-associated DNA sequencing (RADseq), from 213 RIL individuals of the BTx623 and NOG (a landrace) cross [55].

Similarly, Jin et al. [56] generated a high-density genetic map for a RIL population resulting from a cross between Tx623A (sorghum) and Sa (sudangrass) utilizing RADseq. The genetic map comprised 1065 markers and had a cumulative length of 1191.7 cM. Within the set of 10 chromosomes, Chr2 exhibited the highest marker density, featuring an average marker interval of 0.88 cM, while Chr7 had the lowest marker density, with an average marker interval of 1.25 cM. Recently, Cuevas and Vermerris[57] constructed a highly saturated linkage map of 33,421 SNPs based on the genotyping of 205 RILs from a cross between SC1103 × RTx430. A consensus map was generated by amalgamating marker data from four mapping populations [58]. A grand total of 3449 unique polymorphic markers at the nucleotide level were employed to create a unified map spanning all 10 sorghum chromosomes. This study resulted in an exceptionally dense sorghum consensus map, encompassing a wide array of markers over a span of 1571.68 cM, with an average marker interval of approximately 0.46 cM.

4. QTL mapping

QTL mapping has become increasingly significant in plant breeding, particularly for addressing polygenic traits. This approach enables plant breeders to identify and track the various interacting genes that contribute to complex traits [59]. Additionally, it facilitates the incorporation of multiple component traits into a single genotype [60,61]. In sorghum, QTL studies identified several genomic regions linked to a number of agronomically important traits, including plant height [31,50,62–64], maturity [51,65], grain yield and related traits [51,63,65,66], post-flowering drought tolerance [67–69] and cold tolerance [40,70]. QTLs mapped for several biotic and abiotic stress tolerances in sorghum are given in Table 1.

LOD: logarithm of the odds-log10 of the ratio of the probability that a QTL is present to the probability that a QTL is absent; R^2: measure the proportion of phenotypic variation explained by molecular markers.

5. Genome-wide association study (GWAS)

Genome-wide association studies (GWAS), also known as association mapping or linkage disequilibrium (LD) mapping, leverage the substantial phenotypic diversity within a species and the numerous historical recombination events in natural populations. This approach offers an alternative to traditional quantitative trait locus (QTL) mapping for identifying the specific genetic loci associated with traits at a relatively high resolution [90]. Unlike conventional QTL mapping, which relies on bi-parental segregating populations, GWAS identifies causal genes for traits of interest within natural populations. A notable advantage of GWAS is the ability to use the same genotyping data and population for investigating various traits repeatedly. Another advantage of GWAS compared to mapping with bi-parental populations is that this method does not require development of bi-parental mapping populations such as RILs (Recombinant Inbred Lines), BILs (Backcross Inbred Lines), CSSLs (Chromosome Segment Substitution Lines), and DHLs (Doubled-Haploid Lines) which are highly time consuming (2–4 years).

GWAS has been used to study traits such as days to heading, panicle architecture, resistance to rice yellow mottle virus, fertility restoration, and other agronomic attributes in rice [91–94]. In maize, GWAS has shown genetic changes and evolution [95], and pasting properties [96], stalk biomass [97], and leaf cuticular conductance [98]. Additionally, GWAS and NAM (Nested Association Mapping) were used to develop joint linkage maps and further to map GBS (Genotyping-By-Sequencing) tags [99]. Similarly, in canola, GWAS has been employed to examine flowering time [100], while in brassica, it has addressed stress tolerance, oil content, seed quality [101], among others. Sesame GWAS studies have explored topics of significance [90,102–104].

In sorghum, GWAS has been applied for analyzing traits such as plant height and inflorescence [105], grain size [44] and grain quality [106] in sorghum. In order to map loci associated with stalk rot resistance in sorghum, Adeyanju et al. [107] used 79,132 SNP markers in a panel of 300 genotypes and found two SNPs that were significantly associated with low total lesion length and low major lesion length in *Macrophomina phaseolina* (S9_5816733, SNP1) and *Fusarium thapsinum* (S9_57222599, SNP2) respectively. A comparison of the performance of a marker-assisted selection-developed stay-green sorghum introgression line and its parental lines showed that stay-green QTL are functional during senescence, enhancing tolerance to water limitation after flowering [108]. Similarly for grain mould resistance, Cuevas et al. [109] performed genome-wide association scans using 268,289 SNPs in 331 sorghum association panel and found two loci on chromosomes 1 and 8 for low seed deterioration, with log (p-value) values of 6.18 and 6.88, respectively, and another with a log (p-value) of approximately 5.86

Table 1
List of QTLs mapped for various biotic and abiotic traits in sorghum.

Trait	Number of QTLs	Parents	LOD	R^2	References
Shoot fly	29	296B	2.6-	5.0-	[51,
Resistance	25	×IS18551	15.0	33.0	71–73]
		27B × IS2122	2.44-	4.3-	
			24.1	44.1	
Stem Borer	27	ICSV 745 × PB	3.01-	6.9-	[74]
		15520-1	8.16	17.5	
Sorghum	2	ICSV745 ×	2.40-	8.8-	[75]
midge		90562.	10.8	33.9	
Sorghum	10	S 34 × Malisor	2.08-	4.9-	[76]
Head bug		84-7	5.91	26.1	
Green bug	3	96-4121 ×	2.05-	0.09-	[39,
	4	Redlan	3.83	0.19	77–79]
		BTx623 × PI	2.5-	1.0-	
		607900	138.3	85.3	
Charcoal rot	9	IS22380 ×	2.19-	7.89-	[80,81]
	12	E36-1	4.47	19.29	
		SPV86 × E36-1	2.1-	5.9-	
			6.4	19.29	
Ergot	18	R931945-2-2	2.52-	0.05-	[82]
		× IS 8525	6.23	0.19	
Rust	4	QL39 × QL41	1.01-	6.8-	[33]
	2	296B ×	9.38	34.2	[83]
		IS18551	5.0-	15.3-	
			7.5	24.2	
Drechslera	1	296B ×	4.4	11.9	[83]
leaf blight		IS18551			
Grain mould	5	Sureno ×	2.79-	10-	[66]
		RTx430	6.63	23.6	
Drought	7	B35 ×Tx430	1.3-	7.7-	[38]
tolerance	4	B35 ×Tx7000	12.6	40.1	[84]
(staygreen	5	B35 × Tx7000	2.11-	9.7-	[68]
trait)	5	QL41 × QL39	6.23	24.5	[67]
	9	SC56 ×	1.81-	9.1-	[75]
	61	Tx7000	12.70	53.5	[85]
		M35-1 × B35	2.5-	10.3-	[86]
			3.88	15.3	[87]
			2.63-	9.9-	
			17.8	37.7	
			2.5-	4.0-	
			7.7	18.7	
Salinity	6	Shihong 137	2.00-	44.58	[88,89]
	9	× L-Tian	7.28	–	
		Tx7000 ×	3.32-	26.98	
		Sorghum	7.16	8.51-	
		propinquum.		14.34	
Cold tolerance	2	CT19 x TX430	2.44-	5.38-	[40,70]
	3	ICSV700 x	4.89	22.21	
		M81E	2.5-	6.26-	
			10.25	28.06	

linked to the emergence rate on chromosome 10. For cold stress, association analysis for five traits (shoot length, shoot weight, root length, root weight, and anthocyanin content) with 265 K SNPs was performed [110].

Marker-trait associations (MTAs) for anthocyanin content and root length were predominantly observed on chromosome 02 and chromosome 06. For shoot length (five SNPs), shoot weight (1 SNP), and root weight (1 SNP), the associations were primarily on Chr03 and Chr06. In the context of anthracnose resistance, eight significant MTAs ($P < 0.001$) were identified across chromosomes 1, 4, 6, 8, 9, and 10 among 313 sorghum collections, utilizing 11,643 SNPs [111]. In another study, 6186 SNPs were derived from resequencing data and utilized for GWAS in 354 sweet sorghum accessions. This analysis revealed 49, 5, and 25 significant SNP loci for drought tolerance traits in GLM, MLM, and FarmCPU models, respectively [112]. GWAS for 1171 Ethiopian sorghum landraces with 25,634 SNP markers uncovered trait-marker associations [116]. Thus, marker-trait associations (MTAs) serve as crucial tools for identifying genomic regions linked to various biotic and abiotic stress tolerances. The newly identified genetic markers from this GWAS study hold substantial value as genomic resources for future endeavors such as parental selection, QTL analysis, trait introgression, gene pyramiding, and marker-assisted selection (MAS) within sorghum breeding programs targeting biotic and abiotic stress tolerance.

6. Meta QTLs (MQTL) in sorghum

The transferability of QTLs across breeding programs is constrained by variations in population, environment, and marker choices. Additionally, it is crucial to validate the genetic impacts of QTLs identified in a single study across various genetic backgrounds and environmental conditions. QTL meta-analysis is a technique employed to identify shared genomic regions by consolidating QTL data from diverse populations and environments [9]. These shared QTLs, referred to as consensus QTLs or MetaQTLs (MQTL), represent stable and resilient regions where QTLs have consistently emerged in multiple experiments. Furthermore, when compared to the original QTLs, MQTL analysis reduces confidence intervals significantly. MQTLs have a shorter interval and are more reliable than QTLs, enabling more precise candidate gene identification and MAS. There have been few studies on MQTL in sorghum. A consensus map using nine previously mapped studies and identified 32 MQTLs for the stay-green trait in sorghum was generated [9]. Similarly, a consensus map by combining three mapping populations discovered five MQTLs for yield [113]. The list of MQTLs identified by different researchers is presented in the Table 2.

LOD: logarithm of the odds-log10 of the ratio of the probability that a QTL is present to the probability that a QTL is absent; R^2: measure the proportion of phenotypic variation explained by molecular markers.

7. Marker assisted selection (MAS) in sorghum

Phenotypic selection is a costly and time-consuming approach often followed by breeders and is influenced by environmental factors. Discovery and usage of PCR based molecular markers has revolutionized the MAS over phenotypic selection [117]. The microsatellite markers have been applied until the currently developed next generation sequencing (NGS) technologies have taken over for their application in MAS. Various types of markers have been developed including GBS for SNPs, Kompetitive Allele Specific PCR (KASP™ by LGC Biosearch Technologies) for SNPs, SNP chip arrays, whole genome sequencing, genome resequencing, and pan-genome sequencing. These markers have greatly advanced our ability to, track the inheritance of traits, and identify regions associated with key traits [7,27,105,118–120].

Sorghum is threatened by many challenges of biotic, abiotic stresses, mineral deficiencies, of which rust disease, shoot fly resistance, stem borer, drought stress have become serious. Most of the biotic, abiotic and mineral/nutrient stresses were mapped using molecular markers, QTL mapping and GWAS. Application of the mapped QTL introgression into elite varieties using molecular markers is defined as MAS. For MAS, trait specific populations need to be developed for trait introgression and recurrent parent recovery. Different populations including biparental mapping population, genetically diverse lines grouping into minicore collection, NAM population and multiparent advanced generation intercross (MAGIC) populations are necessary. For MAS G × E interactions, trait heritability, general combining ability (GCA) and specific combining ability (SCA) are also considered as important contributes for successful application of MAS in breeding [121].

Among the biotic stresses, shoot fly is considered as the most devastating pest in Asia, Africa and America and can cause severe damage to the crop during early growth. Many QTLs were reported for shoot fly resistance (SFR) [122]. The introgression effect of shoot fly QTLs studied in different genetic backgrounds confirmed the presence of SFR alleles from donor line IS18551 (SFR) in BTx623 (shoot fly susceptible) background [123,124]. The reported QTLs for SFR component traits present on three different chromosomes SBI-01, SBI-07 and SBI-10 were introgressed into elite post-rainy sorghum varieties (SPV1411 and ICSB 29004) using marker assisted back crossing. They selected six introgression lines based on SSR markers and phenotyping orved to be superior to recurrent parent SFR and grain yield [125]. It appears therefore that molecular markers are available in sorghum for biotic stress tolerance which needs to be utilized properly in breeding programs.

Sorghum resistance to parasitic weed Striga has been studied and the

Table 2
List of MQTLs identified for agronomic and other traits in sorghum.

Trait (Reference)	Number of MQTLs	Previous mapped studies	LOD	R^2	Number of QTLs identified	Parents of mapping population
Stay green trait [9]	32	[84]	9.0-20.3	41.2-66.5	7	B35 ×Tx430
		[75]	1.8-12.70	9.1-53.5	3	B35 × Tx7000
		[68]	2.63-17.8	9.9-37.7	14	SC56 ×Tx7000.
		[85]	2.63-17.8	9.9-37.7	19	IS9830 ×E36-1
		[37,67]	2.6-14.9	5.1-42.4	21	N13 × E36-1
		[69]	2.44-20.28	5.2-50.4	9	296B × IS18551
		[69]	2.5-8.1	3.8-18.7	43	M35-1 × B35
		[50]				
		[114,115]				
		[87]				
Agronomic and yield related traits [113]	25	[113]	2.53-5.35	2.00-25.00	27	76T1-23 × Baji,
			2.31-6.10		42	Meko × Birmash
			2.64-5.20	3.00-23.00	36	76T1-23 × 99 Birmash
				3.00-25.00		

QTLs have been mapped [127] which were utilized in MAS and introgression line development [128]. Striga resistant QTL originated from N13 was used in Sudanese sorghum breeding program and introgressed into Wad Ahmad and Tabat (cultivars) recurrent parents using SSR markers and DArT markers [129]. In Striga resistance breeding program of Kenya, Striga resistance QTLs originated from N13 were introgressed into Ochuti and were field evaluated for the resistance [130]. Other crosses with Nigerian lines Danyana and Samsorgh 39 cultivars were deployed as recurrent lines and made crosses with N13 as Striga resistance QTL donor line. Fore ground and background selection was carried forward with SSR markers and superior lines were selected and field evaluated [131]. QTLs for sorghum chilling tolerance were identified [132,133] for introgression and, studied under different genetic background using molecular markers. Recently GBS based SNPs have been identified for chilling tolerance QTLs which can be further utilized in sorghum breeding programs [134].

Among the abiotic stresses, post flowering drought tolerance has been considered as the most destructive, and results in reduced grain yields. But, stay-green genotypes retain green leaf area (GLA) under drought stress conditions and can help in more stable grain yield. QTLs for stay-green genotype have been identified and introgressed into several elite line backgrounds using MAS. Stg1, stg2, stg3, stg4, stg3A and stg3B QTLs from B35 stay-green donor and Q10GL QTLs from E36–1 (stay-green donor) have been utilized in several elite recurrent breeding lines [8,125-126]. Most of the QTLs were introgressed using SSR and SNP markers and the selected individuals are reported to be better performing for GLA with superior tolerance and yield performance to water deficit conditions.

Sorghum as a bioenergy crop; many QTL studies have been reported and *bmr6* allele was considered as significant for altering lignin composition. Such mutants play vital role in second generation ethanol production. The introgression of *bmr6* allele into elite lines of sorghum leads to lower lignin lines that can be used for bioenergy production. A donor line, CMSXS170 was used to cross with CMSXS652 and IS23777 recurrent elite lines. SNP markers were used to select the genotypes of interest using marker allele specific cleave amplified polymorphic sequences (CAPs). Nearly 30 lines were selected, and field evaluated, and these can be further utilized in sorghum bioenergy breeding programs.

8. Genomic selection (GS) in sorghum

NGS technologies, rapid low-cost genomic data generation and advanced computational analysis and improved artificial intelligence, deep learning and machine learning have evolved as a boon to researchers. Using prediction methodologies, we can now accurately predict genomic estimated breeding values (GEBVs) of the genotypes using only genomic data with the previous phenomics data sets. This GEBV estimation using computational tools will reduce the cost, time and improves the efficiency of the selection. GS or genome predictions [134] are potential breeding tools which have been successfully implemented in animal breeding but need to be effectively deployed into plant breeding programs. Initially breeders used conventional breeding methods until the markers evolved. Development of molecular markers and their linkage with QTLs enabled MAS of various traits in different crops.

Sorghum was the best studied, and various economically important traits were introgressed [125], fine mapped [126] in MABC (Marker--Assisted Backcrossing) programs. MAS was advantageous but requires both genotyping and phenotyping data for the trait specific population. The markers utilized were SSRs but the genetic coverage was very low. Recent advances in NGS technologies have brought whole genome coverage markers where major as well as minor QTLs have been identified and can also predict the non-phenotype individuals. Recently genomic selection has revolutionized the selection efficiency by reducing the number of breeding cycles and increasing the genetic gains. GS has been demonstrated to be more advantageous than conventional and MAS [135]. GS can also improve complex and less heritable traits in shorter time with lower budgets.

Selection of desired allele or desired trait is the major focus for any breeding program. The goal is to continuously improve the selection process to achieve greater gains. Prediction of non-phenotype individuals using phenotypic data of their ancestral pedigree, or a defined training set is involved. Several GS statistical models were used to predict accurately different families, their relatedness between families and the number of progenies within each family influencing the accuracy. GS has two population sets where one is a training population set and the other testing population set. Testing population is a subset of the training population. The information from the training population majorly contributes to the prediction accuracy, similarly like pedigree information used in genomic estimated breeding values (GEBVs) of the testing population [135].

In sorghum, grain yield phenotyping data from nearly 791 hyrids, from four different locations in Australia were studied. Out of 791 hybrids, 544 lines having 581 DArT marker genotyping data were utilized to predict the rest of the hybrids. This study shows improved prediction accuracy with combined pedigree and marker-based information. This might be achieved by testing and training population individuals. The prediction accuracies were cross validated and showed higher selection accuracy when compared to the pedigree-based models [136]. The Chibas sorghum breeding program in Haiti has developed a Practical Haplotype Graph (PHG) training population with 250 genotypes having phenotyping data for height, brix, juice weight, leaf weight, earliness, stem weight and grain weight [137]. The data of five different experimental conditions were utilized to build a practical haplotype graph (PHG) for sorghum genomic prediction usage. Nearly, 3849 GBS SNPs were called from the Chibas training population. Additionally, 207 genotypes from Chibas training population were sequenced and processed under PHG. Mean prediction accuracies with PHG, SNP calls range from 0.57–0.73 and are similar to GBS predictions. This study shows that PHG make genotyping more feasible to cost effective genomic selection in sorghum [137].

GS implementation has been found to be a better solution to increase genetic gains in Chibas breeding program but there were no standard estimation parameters established in sorghum [85]. A comparison was made between GS genetic gain, cost per unit gain, genetic variance and prediction accuracy and PS for each cycle of selection. A population size of 400 genotypes and a subset of 200 genotypes were used as a testing set for simulation studies. For oligogenic traits and small populations, cost per unit gain is lower in PS compared to GS. This study clearly demonstrated that GS is the best tool to increase genetic gains by accelerating breeding cycles.

Sorghum antioxidant properties make it a special grain but very few studies have focussed on sorghum total anioxidants, anthocyanins, polyphenols, flavonoids and condensed tannins which are health promoting. GS will be the best solution for increased genetic gains of sorghum grain antioxidant traits. A total of 114 sorghum genotypes were field phenotyped for two different seasons in Italy. Antioxidant concentrations were measured and calculated their trait heritability and genetic variance. A dataset of 114 genotypes underwent GBS, yielding 61,976 high-quality SNPs for subsequent genomic prediction and selection analyses. Model parameters were derived from a training set and then validated using a testing set. Across all models, genomic predictions ranged from 0.49 to 0.58 for various traits. These robust predictions support the feasibility of advancing sorghum antioxidant breeding, facilitating substantial genetic gains in terms of both time and cost efficiency [119].

Sorghum biomass is of economic importance and many studies focus on biomass improvement as it is used in second generation biofuel production. Biomass correlated traits include moisture, plant height measured at monthly intervals from planting to harvesting. Single, multi trait direct and indirect GS, a new strategy named trait assisted GS, where correlated traits were used along with marker data in the

validation population to predict biomass. The traits GP accuracy ranges from 0.33 - 0.65 using GBLUP model. In case of trait assisted GS, increased prediction accuracy up to 50% was noticed when using plant height in testing and training populations [138]. Efficiency of various GS strategies that use correlation traits to help predict biomass yield were compared and found that trait-based GS is the best for selection. Different models such as BayesA, BayesB, BayesCπ, BayesLasso, Bayes ridge Regression and RRBLUP have been employed, however the prediction accuracies vary substantially between different models and between traits. Predictive abilities obtained are high and range from 0.66–0.85. The lowest is the marker density; the minimum will be the predictive abilities and maximum, the variance. Genotype by environment interactions affect negatively to the prediction accuracies which are required for GS efficiency. Different models as above showed the potential of using GS for different environments and sub-panels. Functional enrichment analysis of marker effects has been correlated to synthesis and metabolism of biomolecules, secondary metabolites, cell division, and biosynthesis of macro molecules which are mostly relevant to the studied traits. This shows that genomic selection can be successfully applied in sorghum breeding programs aimed at improving biomass or fodder [139].

In sorghum, drought adaptation has been well studied. Recently, GS data for drought stress and grain yield parameters were compared with that of non-stress environments. Genomic predictions within the trait [136], across traits [140,141] and multi environment traits [140] from 2008 to 2014 covering Australian sorghum cropping regions have been performed. Phenotypic data of 2645 test cross hybrids with 1–5 testers were used for cross validation. Drought adaptability and productivity traits including grain yields, stay-green (delayed leaf senescence), and plant height and flowering time were taken into consideration. It has been suggested that multi-trait GBLUP evaluations were beneficial over that of single-trait GBLUP model. The combined pedigree and marker information were also utilized for optimizing multi-trait predictions. In case of multi-traits, predictive ability increased by 16–19% [140], and reduced prediction bias when GBLUP was used [141].

Traits with lower heritability like GY and stay-green were always benefitted by combining pedigree information with genomic models and can be used in optimizing genomic predictions of complex traits [141]. The impact of G × E and GEBV for grain yield within and across environments influenced by heterogeneous variances of marker effects were studied. The data set contains testcross yield performance under drought and well-watered environments with pedigree and genomic data. This combination with K-BLUP model produced clear increments ranging from 43–72% ability for grain yield in various environmental conditions and such predictions can improve sorghum adaptability [142].

Most of the minor alleles in the guinea and mixed subgroups of sorghum, and importantly, their diverse allelic contribution were observed towards prediction accuracy. The current sorghum association panel can only act as training data set, but more races from guinea and bicolor background need to be included to boost the prediction accuracy (142). Highly correlated grain yield components like amylose, fat, gross energy, protein, and starch from sorghum diversity panel of 389 lines and 191 RILs from a cross BTx642 Bayesian regression model were used in this study which showed accelerated genetic gains [144] (Table 3).

9. Next-generation sequencing (NGS) technologies

NGS (Next-Generation Sequencing) technologies represent a powerful tool for comprehensive DNA/RNA sequencing across different species, ushering in genomics revolution, particularly in the context of accelerating sorghum breeding programs. One of the major advantages of NGS is its ability to investigate the genetic mechanisms behind agronomically important traits within the vast and complex genomes of plants. By leveraging the smaller and less complex genomes of related

Table 3
Studies on genomic selection for various agronomic traits in sorghum.

S No	Objective	Traits	Population	Marker Type	Genotyping Platform	Statistical Method	Results	References
1	Genomic selection for antioxidant production	Antioxidant content	Panel of *S. bicolor* and *S. bicolor* x *S. halepense*lines	SNP	Illumina Infinium 50k SNP array	RR-BLUP	Accuracies ranged from 0.20 to 0.56 for different traits	[119]
2	Comparison of genomic selection methods for biomass sorghum	Biomass yield, plant height, stem diameter, and sugar content	Population of F_4 lines derived by a cross between two sorghum cultivars	SNP	GBS	GBLUP, BayesCπ, Bayesian Lasso, and BayesR	GBLUP had the highest accuracy for all traits	[138]
3	Genomic prediction for bioenergy production in high-biomass sorghum	Biomass yield and sugar content	Population of F_1 hybrids	SNP	GBS	GBLUP, BayesCπ, and Bayesian Lasso	GBLUP had the highest accuracy for biomass yield and sugar content	[139]
4	Impact of sorghum racial structure and diversity on genomic prediction of grain yield components	Grain yield and yield components (panicle length, grain number, and weight)	Association panel of diverse sorghum lines	SNP	GBS	RR-BLUP and Bayesian Lasso	Accuracy ranged from 0.17 to 0.68 depending on the trait and statistical method	[143]
5	Multi-trait genomic prediction for sorghum grain composition	Protein, fat, fiber, and ash content	Association panel of diverse sorghum lines	SNP	GBS	Multi-trait regressor stacking	Increased accuracy compared to single-trait models for all traits	[144]
6	Development of genomic selection	Grain yield, flowering time, plant height, stay-green	Association panel of 384 sorghum lines	389,547 SNPs	GBS	RR-BLUP, Bayesian LASSO	Demonstrated the feasibility and accuracy of genomic selection in sorghum using a diverse panel of lines	[136]
7	Facilitation of genome-wide imputation and genomic prediction	Not specified	Association panel of 973 sorghum lines	13,184,984 SNPs	GBS	Haplotype graph-based imputation	Developed a sorghum haplotype graph to facilitate imputation and genomic prediction	[137]
8	Optimization of genomic selection for a sorghum breeding program	Grain yield, flowering time, plant height, stay-green	Simulated population of 2000 individuals	10,000 SNPs	Simulated GBS	GBLUP, Bayesian LASSO	Optimized genomic selection methods to improve genetic gain in a sorghum breeding program in Haiti	[145]

plants, which share conserved regions, comparative genomics becomes a valuable approach. NGS technologies play a pivotal role in mapping the sorghum genome and identifying Quantitative Trait Loci (QTLs) through wide hybridization. These QTL-linked markers can subsequently be employed in selecting for specific traits of interest in sorghum through Marker-Assisted Selection (MAS). NGS technologies have also proven highly efficient in association genetics, population biology, and SNP identification [146].

NGS technologies have brought a revolution in sorghum genomics by enabling the production of complete sequences at the DNA/RNA level within and across species. These technological advances are instrumental in whole-genome research and are expected to simplify comparative genomics [146].

Key among these drawbacks is the bioinformatics and computational challenges related to data storage and gene function discoveries. Sorghum genome sequencing has been carried out using Sanger's method in sorghum inbred line BTx623, which covers ~10.5 million reads and ~8 × coverage and is freely available at the NCBI. The sorghum genome sequence is useful as a suitable substrate for a complete and high-quality annotation [147]. The genome alignment and assembly of sorghum reveal that more than 97% are protein-coding genes, which are captured into longest scaffolds (approx. 250), 2688 contigs, with a total assembly length of 732 Mbs. Plant genotyping can benefit plant breeding programs through the selection of individuals that are resistant to biotic stress that cause substantial losses in agriculture [147].

The Specificity Array Panel (SAP) stands out from other sorghum panels [28,105] due to its unique composition, meticulously crafted to encompass a broad spectrum of phenotypic and genetic diversity found in crucial U.S. breeding lines and adapted tropical varieties. This sets it apart from panels like the Bioenergy Association Panel, which was limited to specific traits like height, photoperiod sensitivity, and late maturity [148], or other multi-parent populations [28,53]. Subsequent to further refinement in genome alignment, the sorghum genome now contains approximately 204,000 expressed sequence tags, which are roughly organized into 22,000 unigenes, 34,118 genes, and 47,121 transcripts. These sequences exhibit an average length of 3714 base pairs [7,27].

The latest update, release v3.0, incorporated approximately 351 Mb of fully completed sorghum sequence. In this process, 349 clones underwent meticulous manual inspection, followed by finishing and validation using a range of technologies, including Sanger, 454, and Illumina. Consequently, 4426 gaps were successfully closed, adding a total of 4.96 Mb of sequence to the assembly. Emerging GBS technologies have initiated a revolution in plant genomics, enabling the identification and differentiation of sequences at the single-nucleotide level within large segregating populations. This facilitates rapid assessments of trait diversity. Next-generation DNA sequencing has been effectively applied in sorghum genotyping applications. Boatwright et al. [28] observed that the use of Whole Genome Sequencing (WGS) markers, rather than GBS markers, resulted in an average 30% increase in the predictive capability of genomic best unbiased linear predictor (GBLUP) models.

RNA-seq is a powerful technique used to analyze the transcriptome of an organism, providing insights into the genes that are actively expressed at a specific time and under certain conditions [149]. MicroRNAs (miRNAs) are small non-coding RNAs that play a crucial role in post-transcriptional gene regulation [150]. Several studies have identified novel miRNAs, drought-responsive microRNAs, and provided insights into the gene expression profile of sorghum under different conditions, including anthracnose infection and male fertility and may other traits mentioned briefly (Table 4).

Earlier studies provided an overview of transcriptome and proteome studies conducted with laboratory, greenhouse, or field-grown sorghum plants exposed to drought or osmotic stress [160]. Sorghum has a significant adaptation potential to drought, high salinity, and high temperature, which are important characteristics of genotypes. Drought stress affects sorghum growth and development from germination to reproductive and grain filling stages, as well as the plants' physicochemical properties, leading to a substantial reduction in grain yield and quality. Sorghum is considered a drought-tolerant crop and can be productive under low-input conditions, but drought stress due to water deficiency can still cause significant yield losses [154–159]. Drought interaction with other abiotic stresses, such as nutrient deficiency, aluminum toxicity, water logging, salinity, and low and high

Table 4
Studies on stress-induced novel miRNAs, drought-responsive microRNAs and differentially expressed genes in sorghum.

S No	Objective	Traits	Varieties	Key finding	Reference
1	Genome-wide mRNA and microRNA (miRNA) profiles of resistant and susceptible sorghum genotypes	Anthracnose, pathogenesis of *C. sublineolum*	SC283- resistance and TAM428 susceptible	75 miRNAs, including 36 novel miRNAs	[150]
2	Identification of novel drought-responsive microRNAs	Drought	M35-1 tolerant C43 susceptible	97 conserved and 526 novel miRNAs representing 472 unique miRNA	[151]
3	Transcriptomic analysis of field-droughted sorghum	Leaves and roots for drought	RTx430 BTx642	10 272 DEGs were accounting for 44% of totally expressed genes.	[152]
4	Transcriptomic analysis using Microarray, qRT-PCR	Leaves analyzed for heat and drought stress	R 16	28585 gene probes identified gene expression changes equating to ~4% and 18% of genes	[153]
5	Tolerance strategies studies by RNA-Seq in two sorghum genotypes	Drought	IS22330—tolerant IS20351—susceptible	Drought stress reveals different intergenic transcripts and novel splice sites	[154]
6	Dehydration stress-induced changes in mRNA accumulation in sorghum	Drought	TX 430	Dehydration-induced protein (dehydrin) revealed a rapid induction and increased accumulation of dehydrin mRNA species throughout the drought stress process	[155]
7	MicroRNA expression profiles in response to drought stress	Drought	11 Sorghum genotypes	Significant deregulation was observed with miR396, miR393, miR397-5p, miR166, miR167 and miR168.	[156]
8	Transcriptome analysis in response to water stress revealed an oxidative stress defense strategy	Drought	SC56 - tolerant Tx7000-sensitive	Under drought, SC56 upregulated stress tolerance genes that heighten the antioxidant capacity, regulatory factors, and repressors of premature senescence	[157]
9	MicroRNAs balance growth and salt stress responses in sweet sorghum	Salinity	M-81E - tolerant Roma-sensitive	miR-6225-5p reduced the level of Ca2 + in the miR-6225-5p-overexpressing line by inhibiting the expression of the Ca2 + uptake gene *SbGLR3.1*	[158]
10	Comprehensive meta-analysis on sorghum using RNA-seq data	Drought and salinity	-	meta-analysis identified 2139 and 2238 genes for drought, and salinity stresses and 1835 genes were common under drought and salinity stress conditions	[159]

temperature stresses, can aggravate the effects of drought-induced stress or enhance plant tolerance. Recent advances in the molecular regulation of abiotic stress tolerance in sorghum have been made using transcriptomic, proteomic, and metabolomic approaches, which help in understanding the molecular mechanisms of stress tolerance in crops and mining new genes for their genetic improvement of abiotic stress tolerance [160].

10. Conclusions

Climate change poses a severe threat to global food and nutritional security, highlighting the need for development and characterization of climate-resilient crops. Millets and sorghum, known for their resilience and water efficiency, play a crucial role in this effort. The United Nations' declaration of 2023 as the International Year of Millets aims to promote sustainable production and research in climate-resilient millet crops. Genetic and genomic research in sorghum has advanced significantly, thanks to its relatively simple genome. SNP markers, genetic maps, and GWAS which have provided valuable insights into key traits, and facilitated marker-assisted breeding for both biotic and abiotic stress tolerance. MQTL analysis, MAS, and GS have revolutionized the sorghum breeding, by improving the efficiency and trait selection. NGS technologies have been pivotal in advancing sorghum breeding through diverse germplasm and high-throughput variant discovery. Addressing bioinformatics and computational challenges is important to fully utilize NGS technologies in sorghum genomics. Nevertheless, ongoing efforts in genome sequencing contribute to a comprehensive understanding of sorghum genetics. Molecular breeding efforts integrated with high-throughput phenomics tools can be used to better comprehend the complexity of drought and other environmental stress responses and their associated traits and to screen diverse panel of genotypes for improvement. In conclusion, leveraging the genetic potential of sorghum through innovative genomic research and breeding strategies especially speed breeding and genome editing are crucial for achieving global food and nutritional security in the face of climate change.

CRediT authorship contribution statement

VKS, SP conceived the idea; VKS, DRSE, AG, KNSUK wrote the manuscript and analysed and contributed to the draft; JN, PBK, and SP coordinated, and refined the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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