



REVIEW ARTICLE

Insights into fodder quality enhancement in sorghum through genetic and molecular approaches

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Abstract

Forage sorghum (*Sorghum bicolor* L. Moench), a climate-resilient, drought-tolerant fodder crop with high adaptability and biomass potential, plays a significant role in addressing global livestock feed and fodder demands. However, its complex quantitative quality traits, such as crude protein, fibre fractions, crude fat, lignin and antinutritional factors like hydrogen cyanide (HCN) content, show considerable variation across genotypes and are strongly influenced by developmental stage, management practices and environmental conditions. This review comprehensively summarises the genetic and molecular strategies for improving forage quality traits in sorghum, highlighting key trait relationships, yield-quality trade-offs, harvesting effects and emerging genomic tools to accelerate the development of nutritionally superior and safer forage sorghum cultivars. Conventional breeding programs have contributed to the development of improved forage sorghum cultivars. Brown midrib lines have emerged as a successful breeding strategy, with average neutral detergent fibre (NDF) and acid detergent fibre (ADF) contents of 57.5 % and 33.67 % dry matter (DM), compared to 59.45 % and 36.51 % DM in conventional varieties. However, this is often accompanied by biomass yield penalties of approximately 14.33 %. Recent advances in molecular breeding, such as functional genomics, genome-wide association studies (GWAS), quantitative trait loci (QTL) mapping, marker-assisted selection and antisense-mediated downregulation, have enabled the precise identification of the genetic architecture of forage quality traits. In particular, QTL mapping uncovered 43 overlapping QTLs controlling various forage quality traits and biomass traits, demonstrating their interconnections and possibilities for their simultaneous improvement. The identified candidate genes and pleiotropic loci controlling forage quality traits offer new opportunities for genomic-assisted improvement, where gene-editing tools such as CRISPR/Cas9 can simultaneously enhance feed safety, biomass yields and nutritional quality.

Keywords: candidate genes; forage improvement; forage sorghum; genomic tools; lignin reduction; quality parameters

Introduction

Sorghum (*Sorghum bicolor* (L.) Moench) is considered the fifth largest cereal crop and is widely cultivated in the semi-arid tropics across the globe (1). Sorghum is believed to have originated in Africa, where it remains a major staple source of food (2). It has diversified into many forms, including grain sorghums for human consumption, grass sorghums for hay and fodder and broomcorn for making brooms and brushes. In India, sorghum is known as jowar, cholam or jonna; in West Africa as guinea corn; and in China as kaoliang. Globally, during 2023–24, sorghum production reached about 52.8 million tonnes. It is well adapted to hot and arid regions due to its tolerance to drought and heat (2). This inherent drought resistance of the crop makes it suitable for cultivation in dry agro-ecologies where water and sometimes other resource scarcity occurs. In many semi-arid and tropical regions, sorghum effectively competes with maize as forage under scarce water resources (3).

The rapid development of dairy and meat industries has increased the need for high-quality green and dry fodder, yet countries like India continue to face a significant deficit of 11.24 % and 23.4 % in green and dry fodder, respectively. In this context, dual-purpose sorghum has gained major interest as it allows simultaneous improvement of grain and biomass yield. Such crops increase the feasibility of mixed crop-livestock systems for smallholder farmers while reducing competition for land and water resources (4). Sorghum plays a major role in livestock nutrition, as nearly 20 % of the Indian livestock population depends on sorghum-based fodder for health and nutrition, either in the form of hay, fresh-cut fodder, or silage (5). The demand for nutritious, high-quality fodder is rising sharply, particularly in northeastern states like Assam. Sorghum is predominantly grown as a fodder crop in north India during kharif and summer seasons, while in south India it is mainly grown for grain purposes throughout the year. Due to its high biomass yield, palatability and digestibility, sorghum is highly

preferred by ruminants (1).

From a breeding perspective, sorghum possesses a small genome size and moderate linkage disequilibrium, making it a suitable model for identifying natural genetic variation linked to complex quality traits through genome-wide association studies (GWAS) (6). The effectiveness of GWAS has been enhanced through the application of multiple statistical models, such as fixed and random model circulating probability unification (FarmCPU), general linear model (GLM) and multilevel model (MLM), enabling a better understanding of the genetic architecture of forage quality traits. Such approaches provide valuable insights for improving forage sorghum cultivars suitable for specific agro-ecological conditions, thereby improving breeding efficiency, strengthening fodder security, supporting sustainable livestock production and ensuring food security (4). However, one major limitation in sorghum is the presence of the anti-nutritional compound dhurrin in leaves and stems, which releases hydrogen cyanide (HCN) and may cause cattle poisoning. To address this, an antisense approach has been used for the downregulation of cytochrome P450 *CYP79A1*, a key enzyme in the dhurrin biosynthesis pathway, effectively reducing the accumulation of the anti-nutritional glycoside and thereby suppressing the levels of HCN in sorghum cultivars (7). Although India accounts for only around 2 % of the global surface area, it supports 17 % of the global human population and 15 % of the world's animals, creating immense biotic stress on agricultural systems. The Indian livestock population is about 536.76 million, showing a 4.8 % increase since the 2012 livestock census (8). To address fodder demands and challenges, genetic resources are being conserved through initiatives such as All India Co-ordinated Research Projects (AICRPs) and native grasses and legumes are maintained in the Indian gene centre, representing a rich reservoir of genetic diversity (9). Nevertheless, the nation continues to face serious shortages in concentrate feed ingredients by 28.9%, dry crop residue (23.4 %) and green fodder (11.24 %), suggesting the urgent need for genetic and molecular improvement of forage quality traits in sorghum (10). While the genetic and molecular mechanisms underlying sorghum grain and bio-ethanol traits are well documented, a detailed review focusing entirely on the genetic and molecular mechanisms of forage quality traits remains limited. This review mainly addresses this gap by providing a focused molecular roadmap of the gene networks regulating various quality traits such as crude protein, fibre fractions, fat expression and dhurrin-associated toxicity mitigation.

A literature search was conducted across Google Scholar, Web of Science, PubMed and Scopus for peer-reviewed articles published. Search terms included *S. bicolor*, forage quality, dhurrin, HCN toxicity, *CYP79A1*, brown mid-rib (BMR), crude protein and GWAS. Articles were included if they directly addressed the genetic, molecular, or biochemical mechanisms of forage sorghum traits and breeding. Conference abstracts, non-English papers and studies strictly limited to grain processing or bio-ethanol production were excluded. Based on these criteria, a total of 100 core papers were selected and synthesised in this review.

Major forage quality parameters

Crude protein

Crude protein (CP) content is an important forage quality parameter, as it strongly influences forage palatability, digestibility, rumen microbial activity and animal performance. In animal nutrition, a

minimum of 7–8 % CP is needed to support efficient rumen microbial activity, good function and digestion of feed (11). Below this level, rumen microbial protein synthesis is limited, leading to degradation of structural carbohydrates and limiting the animal's voluntary intake. Nitrogen (N) content is generally higher in improved varieties than in local cultivars, indicating scope for quality enhancement through breeding (11). Crude protein shows substantial genetic variability among sorghum genotypes, making its genetic improvement feasible (12). Notably, crude protein showed high heritability associated with high genetic advance, implying that additive gene action plays a major role and that selection would be effective for improvement. Additionally, a positive correlation was found between crude protein and digestibility (1). Further, TKS_V 1171 showed high crude protein content but was on par with several elite genotypes; these mean differences may be due to the relation of leaves to total biomass and protein content (12). Crude protein is strongly influenced by harvesting stages, as it decreases with increasing growth stages, with maximum CP observed during the boot stage (13). Studies reported a reduction in CP in stay-green sorghum from 86 g kg⁻¹ at the boot stage to 67.2 g kg⁻¹ one month after grain harvest. Higher concentrations of CP at the boot stage increase ruminal microbial activity in cattle (14).

In addition, through GWAS, protein-associated loci on chromosomes 1, 2 and 9 were identified, confirming that protein accumulation is regulated by both genetic and molecular mechanisms, not solely by environmental factors, providing molecular targets that can be exploited for protein improvement in forage sorghum (15). Furthermore, hundreds of single nucleotide polymorphisms (SNPs) associated with amino acid biosynthesis traits were identified. Despite showing considerable genetic variability and identifying genomic loci associated with crude protein, translating these findings into validated markers and improved cultivars remains limited, highlighting the need for multi-environment validation and breeding integration.

Crude fat

Whole-plant crude fat is an important component of forage quality because of its contribution to energy density and the nutritive value of sorghum fodder. Comparative trials of 15 sorghum varieties, including sweet, dual-purpose and forage types, revealed significant variation in crude fat content, ranging from 1.32–2.53 %. This variation highlights clear potential for crop improvement through targeted selection (16). Furthermore, brown midrib lines exhibit a simultaneous increase in both crude fat content and dry matter digestibility, thereby improving overall forage quality, highlighting that mutations affecting lignin biosynthesis may also influence crude fat content (17). Therefore, genotypes combining higher fat concentration with superior digestibility represent promising breeding materials for enhancing overall forage value (18). At the molecular level, BMR lines arise from mutations in lignin biosynthesis genes and reduced lignification changes cell wall-lipid interactions, thereby improving energy availability by improving the ruminal accessibility of dietary fats to microbial enzymes, showing an indirect molecular effect on fat utilisation rather than lipid synthesis (17). Through GWAS, a significant lipid biosynthesis gene named *DGAT1*, responsible for the final step in triacylglycerol biosynthesis, has been identified as a potential breeding target for enhancing crude fat content (19). However, these grain-based markers cannot accurately predict forage quality because, in the case of *DGAT1*, leaves and

stems have an intrinsic capacity to store lipids; instead of storing fats permanently like seeds, they continuously break them down (20). Studies have reported a positive genetic correlation between fat and other quality traits such as fibre and protein, suggesting that they may share common inheritance (21).

A genetic linkage map was constructed across 10 linkage groups using 124 polymorphic simple sequence repeat (SSR) markers. Using these co-dominant markers, two major QTLs responsible for whole-plant fat content, namely *qWF1* and *qWF2*, were identified on chromosomes 1 and 2 respectively. Mapping the precise locations of these loci demonstrated that fat content in sorghum-sudan grass hybrids is controlled by both dominant and additive gene actions (21). Recent advances in sorghum genomic resources, including high-quality reference genomes and pangenome resources, are enabling increasingly precise mapping of lipid-related loci. The availability of genome-wide association studies, nested association mapping, multiparent advanced generation intercross populations, RNA-seq expression atlases and ethyl methanesulfonate mutant libraries provides powerful tools for identifying and validating candidate genes involved in lipid metabolism and forage energy quality improvement (22). Despite being a secondary quality trait, crude fat significantly contributes to forage energy density. Therefore, crude fat is a major breeding target that ensures high concentrations of caloric value per unit of dry matter consumed, which directly optimises feed conversion efficiency in ruminants. These findings suggest that crude fat content can be improved by dissecting genetic variability and QTLs through GWAS, thereby developing high-quality forage sorghum cultivars.

Fibre fractions

Crude fibre is an important quality component of forage, representing the fraction that is poorly digested by mammalian enzymes and largely depends on microbial fermentation in the rumen (23). Crude fibre is generally associated with reduced nutritive value, as strong negative relationships have been observed between crude fibre and energy-related parameters such as N-free extract, non-fibrous carbohydrates, total digestible nutrients, digestible dry matter, dry matter intake, relative forage quality and metabolisable energy requirement. Thus, an increase in crude fibre typically lowers nutrient availability, followed by poor digestibility and palatability, ultimately decreasing feed intake by ruminants (12). Genetic parameters confirmed the feasibility of fibre improvement through breeding. Crude fibre has shown high broad-sense heritability of 78.92 %, along with a substantial genetic advance as a percentage of the mean of 18.4 %, indicating that selection for lower fibre content will significantly improve forage quality in sorghum (12).

Although crude fibre has been an indicator of forage quality, it does not fully capture the complexity of plant cell wall composition. Neutral detergent fibre and acid detergent fibre provide a more precise representation of structural carbohydrates influencing intake and digestibility. Since crude fibre, neutral detergent fibre (NDF) and acid detergent fibre (ADF) originate from the same cell wall matrix, their regulation is governed by overlapping genetic mechanisms. Forage energy content is influenced by the fibre content of plant biomass, as higher concentrations of NDF and ADF are associated with digestibility. Unlike soluble plant components, fibre fractions show greater variability in digestibility and therefore serve as reliable predictors of forage energy value (24). Improving forage quality in sorghum depends on an understanding of the genetic variability and interrelationships of these fibre traits.

Studies have reported substantial variation, with NDF ranging from 0.38–0.75 g/g and ADF from 0.18–0.52 g/g, indicating considerable scope for genetic improvement (25).

Genetic parameter analyses further showed high heritability for both NDF (71.66 %) and ADF (69.82 %), suggesting that selection-based breeding approaches can effectively enhance these traits (26). Among molecular interventions, *BMR* mutation has been one of the successful tools for fibre modification, as *BMR* genotypes consistently showed reduced NDF and ADF compared to conventional types, averaging 57.50 % versus 59.45 % for NDF and 33.67 % versus 36.51 % for ADF (27). Trait association studies show a significant positive relationship between NDF and ADF, indicating a coordinated regulation of structural carbohydrate accumulation, whereas ADF exhibited a non-significant negative correlation with crude protein content (24). Molecular mapping studies have identified shared genomic control of fibre components, where NDF, ADF and cellulose were linked to a common quantitative trait nucleotide (QTN) on chromosome 5, while additional QTNs were detected on chromosome 8 influencing ADF and lignin (25). Complementary QTL analyses further detected five loci governing NDF and three controlling ADF, along with overlapping regions affecting multiple fibre traits such as lignin and hemicellulose (28). Further, two major acid detergent lignin (ADL) loci on chromosomes 1 and 5 (25.83 % and 30.67 % PVE; LOD 2.5 and 3.17), which did not replicate across consecutive seasons, highlighting that unstable genomic architectures limit the consistency of marker-assisted selection across environments (28). These findings collectively demonstrate that while fibre composition in forage sorghum is genetically regulated, it exhibits distinct environmental sensitivity and can be improved through both conventional selection and molecular breeding approaches, offering opportunities to enhance digestibility and thereby facilitate the development of high-quality cultivars.

Lignin content

Lignin is among the most abundant structural biopolymers in nature and constitutes a major component of secondary cell walls in vascular plants (29). It interacts with cellulose and hemicellulose, contributing to the rigidity, strength and hydrophobicity of plant tissues (30). However, in forage sorghum, lignin is negatively associated with fodder digestibility because it creates a physical and chemical barrier that restricts rumen microbial access to fermentable cell wall components. Genetic improvement targeting lignin biosynthesis has therefore become a major target for enhancing forage quality (31, 32). The *BMR* phenotype, characterised by reddish-brown pigmentation in leaf midribs and stem tissues, serves as a visual indicator of reduced lignin content and has been widely exploited in forage sorghum improvement programs (27, 33, 34). *Bmr12* is a key locus that encodes enzymes of the monolignol biosynthetic pathway, particularly those associated with lower lignin concentration and improved digestibility (35). More recently, the *bmr30* gene was identified using bulk segregation analysis and next-generation sequencing, which encodes chalcone isomerase (CHI), where a loss-of-function mutation resulted in reduced lignin content and a characteristic brown midrib phenotype (36).

Beyond structural gene mutations, molecular approaches have been widely used to regulate lignin biosynthesis more precisely. Downregulation of core monolignol pathway genes such as *PAL*, *C4H*, *4CL*, *HCT*, *COMT*, *CCR* and *CAD* has successfully altered lignin composition, even though it is often accompanied by

undesirable morphological effects (37, 38). At the regulatory level, transcription factors play a crucial role in lignin modulation. The *SbbHLH1* transcription factor, identified from *BMR* mutants, acts as a major repressor of lignin biosynthesis by directly downregulating key genes such as *4CL*, *HCT*, *COMT*, *PAL1* and *CCR1*, thereby reducing lignin deposition and improving digestibility (39). Emerging post-transcriptional strategies offer improved control. For example, overexpression of *sbi-miRNA397-5p* targets laccase transcripts, enabling fine-tuning of lignin levels without severe developmental penalties (40). Conversely, *SbWRKY51* functions as a positive regulator of lignin accumulation under salt stress conditions by activating genes such as *SbPAL*, *SbCOMT* and *SbC4H*, strengthening structural barriers such as the casparian strip to enhance stress tolerance (41). In this context, overexpression of *SbMYB60* enhances lignin accumulation through upregulation of monolignol pathway genes and increased synthesis of phenolic compounds (42). Collectively, these advances demonstrate that lignin content in forage sorghum can be effectively manipulated through structural gene mutations, post-transcriptional regulation and transcriptional control mechanisms, thereby offering promising opportunities for improving forage digestibility without compromising plant structural integrity.

Anti nutritional factor - hydrogen cyanide content

Hydrogen cyanide content is a critical forage safety trait in sorghum, largely determined by the presence of cyanogenic glucosides such as dhurrin. Cyanogenic glucosides are classified as phytoanticipins, meaning that the defensive compound is stored in an inactive form and is released when required (43). Dhurrin is a harmless compound that undergoes enzymatic hydrolysis to form HCN and during ingestion, HCN inhibits cytochrome c oxidase, disrupting cellular respiration (44). The HCN concentration above 600 mg kg⁻¹ is considered highly poisonous to ruminants. Despite being an anti-nutritional factor, dhurrin serves an ecological role by protecting sorghum plants against herbivores and microbial pathogens through the release of the toxic substance HCN (45). Hydrogen cyanide is typically highest during the early developmental stages of the plant and gradually declines with maturity (46). The higher levels of dhurrin in young developmental organs and growing regions are intended to provide protection (43). It has been widely reported that processing sorghum into silage or hay can reduce HCNp by approximately one-half, thereby improving fodder safety (44).

In addition, molecular approaches have been explored to directly lower dhurrin biosynthesis. To lower dhurrin content, experiments using antisense-mediated downregulation of cytochrome *P450 CYP79A1*, an important enzyme in the dhurrin biosynthetic pathway, produced transgenic plants with reduced HCN content, followed by their subsequent generations (7). Wild sorghum relatives also represent valuable genetic resources for reducing cyanide potential. Tissue-specific screening of leaves, sheaths and root tissues in *S. bicolor*, *Sorghum brachypodium* Lazarides and *Sorghum macrospermum* E. D. Garber plants across growing periods showed that HCNp was detectable but present in trace amounts, which was lower than that in cultivated *S. bicolor* (47). Screening for HCN under drought conditions is important because water stress can influence HCN accumulation. Hydrogen cyanide concentrations below 200 ppm are generally considered safe for ruminants (48). Recent comparative studies further confirmed that *S. macrospermum* exhibited negligible dhurrin levels in leaf and sheath portions of above-ground tissues, while

S. brachypodium maintained consistently low HCN potential even under water deficit. In contrast, *S. bicolor* can exceed 1000 ppm HCNp in leaf and sheath tissues. Interestingly, water limitation did not significantly affect leaf HCN levels in wild species, although drought stress increased N accumulation in *S. bicolor*, suggesting distinct physiological responses between wild and cultivated species (47). Overall, these findings highlight that integrating genetic resources, molecular strategies and wild germplasm offer promising avenues for reducing HCN content. Table 1 summarises a list of sorghum varieties and hybrids with good forage quality.

Morphological interaction with forage quality

Morphological traits such as plant height, stem proportion and leaf-to-stem ratio play a crucial role in determining forage quality and digestibility in sorghum. Genetically shorter varieties such as Asosa1 and Adukara exhibited higher mean leaf proportion and leaf-to-stem ratios and are considered nutritionally superior and likely to be digested faster than genetically taller varieties possessing a higher stem proportion (53). Although increasing plant height at harvest increases hay yield, it often results in reduced nutritive value, as taller plants tend to accumulate more structural biomass. Additionally, an increase in plant height has been linked with a substantial 54 % decrease in crude protein and a 34 % decrease in crude fat, while crude ash increased by 33 % and N content of stems also decreased as height increased (54). Environmental stress can also affect stem morphology and forage quality. Under water-deficit conditions, internode elongation may be reduced without a decrease in stem diameter, resulting in shorter but thicker internodes. These stress-expanded internodes often accumulate more soluble sugars with reduced lignin, thereby enhancing digestibility (55).

Mesophyll cells present in leaves are naturally more digestible than non-chlorenchymatous parenchyma cells dominant in stem tissues (56). Seasonal variation in crude protein concentration is also frequently explained by dilution effects associated with changes in the leaf-to-stem ratio (57). As the plant matures, nutrients such as crude protein are diluted from leaves to stems to support plant integrity, thereby causing a reduction in nutrient levels. Varieties exhibiting a higher leaf-to-stem ratio (LSR) not only absorb lighter but also enhance the photosynthetic rate, thereby producing forage of superior quality (58, 59). Higher LSR has been reported to lower ADF and NDF contents while simultaneously enhancing energy and protein content, which ultimately improves forage digestibility (59). Stem structural organisation further contributes to quality variation. The outer rind of the stem provides rigid support and contains higher levels of cellulose and arabinoxylan, whereas the inner pith serves as a storage site for carbohydrates enriched in (1,3; 1,4)- β -glucan, implying that a thicker, rind-dominated stem may reduce digestibility, while greater pith increases nutrient availability (60). Nutrient management also affects morphology and quality, as N improves forage quality by altering morphological traits, especially by increasing leaf number and leaf mass (61). Similarly, differences in silage quality have been associated with morphological composition. High dry matter content in genotypes such as BRS 716 and AGRI002E has been linked to a higher proportion of cell walls in the forage (62). Overall, these findings highlight that morphological architecture is closely linked with forage quality and represents an important selection target in sorghum crop improvement.

Table 1. List of sorghum varieties and hybrids with good forage quality

Sl. No.	Variety/hybrid	Nature of the cultivar	Release/notified year	Quality attributes	Reference
1.	Co (FS) 29	Variety (multi cut)	2001 (released and notified)	8.41 % crude protein and 50.30 % IVDMD, low HCN content	(49, 50)
2.	CSH 24 MF	hybrid	2009	High digestibility (55-58 % IVDMD), high protein (7.5–8.0 %) and low HCN (80–95 ppm)	(51, 50)
3.	Pant Chari 7	variety	2010	high protein content (7.70 %) and digestibility (56.90 % IVDMD)	(50)
4.	HJ 541 (Haryana Jowar Chari)	Variety (single cut)	2010	Popular fodder variety having good palatability, Low HCN and high digestibility	(51, 50)
5.	GAFS 11 (Gujarat Anand Forage Sorghum 11)	Variety (multi cut)	2012	CP- 7.5 %, IVDMD- 43.2 % and HCN content- 34.24 ppm;	(50)
6.	PSC 4	Hybrid	2014	HCN content is very low	(50)
7.	CO 31 (TNFS 0952)	Variety	2014	High crude protein (9.86 %) and dry matter yield Low HCN (172 ppm) and crude fibre (19.8 %)	(50)
8.	CSV 33 MF	Variety (multi cut)	2017	Better nutritive value, improved forage quality	(51, 52)
9.	CSH 40F	Hybrid (single cut)	2018	Low HCN, 8.4 % crude protein and 53 % IVDMD	(51, 52)
10.	CSH 43 MF	Hybrid (multi cut)	2021	superior fodder quality traits	(51, 52)

IVDMD: *In vitro* dry matter digestibility; HCN: hydrogen cyanide.

Yield vs quality relationships

The relationship between forage yield and quality traits in sorghum is complex and often influenced by environmental conditions. Under normal conditions, yield and quality traits showed weak or non-significant correlations, whereas under drought conditions, they exhibited positive correlations. Genetic studies have identified multiple loci underlying both productivity and quality traits, with 43 QTLs identified as controlling acid detergent lignin, acid detergent fibre, days to 50 % flowering, dry weight, fresh weight, grain weight, *in vitro* organic matter digestibility, metabolisable energy, neutral detergent fibre and plant height, indicating a shared genetic correlation between quality and yield traits. Although fibre fractions and digestibility traits are often negatively correlated, several studies have found no negative relationship between biomass yield and digestibility traits, suggesting that simultaneous improvement of yield and quality is feasible without many trade-offs (3). However, translating these favourable trait relationships into commercial cultivars introduces significant field-level breeding and environmental constraints. This operational barrier is evident in BMR sorghum, where reduced lignin levels result in higher NDF digestibility compared to conventional sorghum but often result in lower dry matter yield (57). Furthermore, yield penalties of around 14.33 % have also been observed in some BMR genotypes (30). At the molecular level, the *bmr12* mutation inhibits caffeic acid *O*-methyltransferase (COMT) enzyme activity, which disrupts lignin biosynthesis during cell wall development (63, 64). Physiologically, total biomass decreases as stem lignification declines because lignin content is positively linked to structural stem biomass density, especially in the internode parenchyma (65). To overcome these performance barriers, genetic and modern molecular methods are required to distinguish structural yield requirements from vegetative nutritive quality. Linkage mapping has revealed genomic regions where yield and quality traits co-localise. For example, flowering, plant height and acid detergent fibre were found to be associated with the LG10 linkage group, while digestibility and increased stalk mass were linked to LG6 (66). Overlapping QTL clusters such as *qPH7.1/qBX7.1* and *qPH7.1/qFBW7.1* have also been reported for plant height, fresh biomass weight and biomass yield. Similarly, morphological traits strongly influence this relationship, where NDF exhibited a significant positive correlation with plant height and

forage yield and a negative correlation with relative feed value and LSR, indicating that taller, stem-dominant plants may yield more biomass but exhibit lower nutritive value (61). In line with this, hay yield generally increases with greater plant height at the harvesting stage, while nutrient concentrations decline due to dilution effects associated with increasing biomass accumulation (54). This dilution effect explains how crude protein and metabolisable energy are often positively correlated with each other but tend to decline with increasing plant height and yield, largely due to reduced leaf proportion and increased stem fraction in taller plants (67, 68). Overall, these findings highlight that yield and quality are genetically interconnected and breeding strategies integrating multi-trait selection and stress-adaptive evaluation can help identify suitable sorghum genotypes that enhance biomass productivity with improved forage quality and nutritive value.

Harvesting time vs quality relationships

Harvest maturity stage is widely known as one of the most critical factors determining forage quality, as nutritional quality gradually declines with advancing maturity. This decline is due to a metabolic shift in the plant's physiology. As the crop matures, plant growth becomes increasingly focused on enhancing structural integrity, which increases lignin content and fibre concentration, with a decrease in digestibility and voluntary intake by animals, resulting in a reduction in overall feeding value (69). Sorghum × sudangrass hybrids showed increased crude protein when harvested at early stages, such as the boot stage, without reducing yield compared with later harvests at flowering or heading, thereby improving palatability in hay (70). This is because the leaf-to-stem ratio becomes higher, with leaves accumulating more N than stems. Notably, harvesting flowering can be done without substantial loss; it often leads to higher dry matter, starch and non-fibre carbohydrate accumulation, accompanied by a decrease in crude protein and fibre digestibility (71). Studies reported that dry matter, fresh forage yield, plant height, dry matter content, protein yield, lignin content and relative feed value (RFV) tend to increase with advanced maturity, whereas protein content, leaf proportion, cellulose and hemicellulose decline gradually (72). During maturation, NDF varies across different harvest times, but ADF shows similarity at certain early stages. Conversely, if the crop is intended for ensiling, harvesting cultivars too early is not preferred because premature

stages can compromise silage fermentation (73). In this context, the time of day also influences silage quality, as morning-harvested sorghum $\times$ sudan grass silage showed improved fermentation characteristics and microbial and metabolic activities, while harvesting late in the day showed a reduction in silage quality due to insufficient fermentable sugars and high moisture content. Furthermore, late-day harvesting can delay fermentation, causing an abnormal drop in final pH and converting plant nitrates to nitrogen dioxide (NO₂) inside silos. This NO₂ gas can cause serious hazards such as pulmonary oedema and bronchiolitis in both humans and livestock and can increase aerobic instability when the silo is opened, causing further spoilage (74). Overall, harvesting at the soft dough stage has been suggested, as the developing grain balances the declining digestibility of vegetative tissues, providing optimal levels of forage yield with acceptable quality (72). These findings collectively highlight that both harvest stage and time play vital roles in forage quality parameters.

Conventional breeding methods

The availability of adequate genetic variability is a prerequisite for successful crop improvement (75). As an often-cross-pollinated crop, mass selection, a conventional breeding approach, has been widely used for a long time to improve landraces and pass desirable traits from one generation to the next (76). Traits such as green biomass yield and dry biomass yield can be improved using mass selection, but quantitative traits including regeneration potential and tillering ability, which have low heritability, can be improved through progeny selection more effectively than through phenotypic selection (77). In India, forage sorghum breeding was initiated during the 1930s, with varieties like SSG 59-3, which was the first multicut variety released using pedigree selection, followed by various single-cut and dual-type varieties such as Pusa Chari (first single-cut variety), HC 136, HC 260, HC 308, PC 5, PC 7, etc. Pure-line selection, another conventional method for exploiting existing genetic variation, is widely used in forage crops (1). Later, in the 20s, to combine desirable genes from two or three varieties, hybridisation programmes were practised in forage sorghum, where CSH20MF and CSH24MF were CMS hybrids developed under the All India Coordinated Project on Sorghum at Govind Ballabh Pant University of Agriculture Science and Technology.

In 2017, a new multicut variety, CSV33MF, was released using mutation breeding from Co (FS)-29, which has an annual forage yield potential of more than 100 tons/ha from three cuts and has the potential for 7–8 harvests under favourable conditions (1). Line $\times$ tester analysis is an effective approach for studying heterosis and combining ability. The BMR lines such as BMR 7-4-1 and BMR 7-2-2 are potential donors for sorghum breeding programmes, as they possess low lignin content and better digestibility, which enhances fodder quality. MS 104B $\times$ BMR 7-8-1 and PMS 71B $\times$ BMR 7-2-2 showed superior performance along with positive specific combining ability effects, suggesting considerable potential for heterosis breeding and might be exploited directly as both lines are male sterile. Studies have reported that both additive and non-additive gene effects control fodder quality parameters (78). Conventionally, the intensity of BMR colouration does not directly quantify lignin reduction but is an indicator of the presence of the BMR gene.

For targeted quality traits, crop- and situation-specific breeding strategies are needed to develop improved varieties and ensure fodder security. Proper and effective utilisation of genetic

resources is vital since forage crops hold a small proportion of global germplasm collections. Systematic characterisation and evaluation of available germplasm sources, along with approaches like the focused identification of germplasm strategy (FIGS), increase the identification of existing useful variation (79). Additionally, pre-breeding practices are essential for transferring important traits from wild relatives that have crossability barriers to sorghum cultivars. Notably, secondary and tertiary gene pools were utilised to create variability and incorporate useful alleles, including *Pennisetum purpureum* Schumach., *Pennisetum squamulatum* Fresen., *Pennisetum pedicellatum* Trin., *Pennisetum polystachion* (L.) Schult. and *Pennisetum subangustum* (Schumach.) Stapf & C.E.Hubb. in pearl millet and *Sorghum halepense* (L.) Pers., *Sorghum propinquum* (Kunth) Hitchc., *Sorghum alnum* Parodi, *Sorghum drummondii* (Steud.) Millsp. & Chase and *Sorghum arundinaceum* (Desv.) Stapf in sorghum, which act as valuable reservoirs for developing improved forage cultivars with enhanced forage quality (79). Fig. 1 illustrates the overall breeding framework for improving forage quality traits and thereby developing improved cultivars by integrating conventional and molecular approaches.

Modern molecular approaches

Modern breeding approaches utilise molecular tools and genomic resources to accelerate genetic improvement, increase breeding programme efficiency and attain greater accuracy for targeted traits. These approaches are increasingly being applied for forage quality improvement in sorghum. For example, downregulation of *CYP79A1*, a key enzyme in the dhurrin biosynthetic pathway, was achieved by antisense-mediated suppression (Fig. 2). This process confirmed that HCN content was reduced in the transgenic plants obtained, demonstrating the feasibility of molecular interventions for forage quality improvement and thereby making forage safer for livestock consumption during their early growth stages (7). In addition to this, cinnamyl alcohol dehydrogenase (CAD) has been successfully targeted using clustered regularly interspaced short palindromic repeats (CRISPR-Cas9) genome editing delivered through biolistic bombardment in sorghum. Knockout of this gene represents a strategic approach to reducing lignin accumulation, thereby decreasing rigidity and increasing access for rumen microbes in forage, thus improving digestibility (80). Similarly, downregulation of another key lignin biosynthetic gene, *Sb4CL* (4-coumarate: CoA ligase), through RNA interference has been shown to significantly reduce total lignin content by up to 25 %, highlighting the effectiveness of post-transcriptional gene silencing for improving forage digestibility (81). Together, these studies demonstrate that both genome editing and gene silencing can be effectively used to manipulate lignin biosynthesis pathways for forage quality improvement in sorghum. It is also important to note that excessive reduction of lignin can lead to lower cell wall rigidity, making plants susceptible to lodging; therefore, it is important to find an equilibrium between lignin content and digestibility.

While gene editing targets known genes, genomic-assisted breeding enables the discovery of novel loci controlling complex traits (83). Multi-locus analysis detected SNPs and QTNs associated with major forage quality parameters, including crude protein (CP), cellulose, hemicellulose, NDF and ADF, with some loci showing pleiotropic effects, proving the interrelationships between quality traits and the possibility of their simultaneous improvement. A QTN on chromosome 5 is simultaneously associated with CP, NDF and ADF, highlighting shared genetic regulation of fibre and nutritional

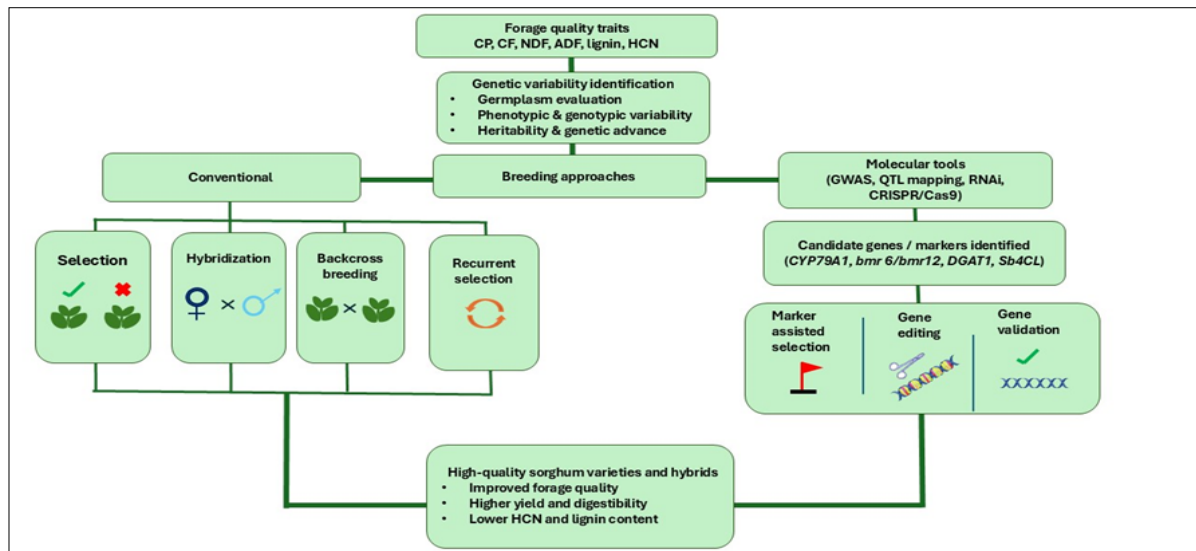


Fig. 1. Integrated approaches for forage quality improvement in sorghum.

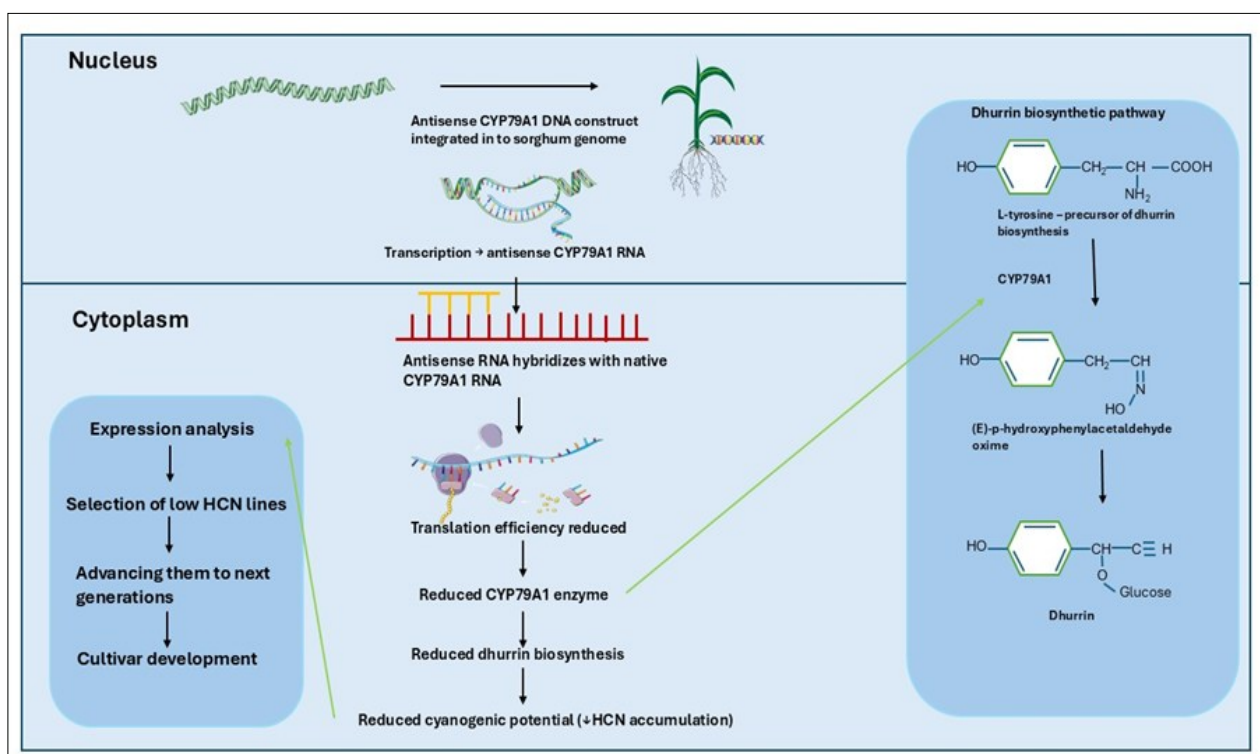


Fig. 2. Illustration of antisense mediated downregulation of hydrogen cyanide (HCN) in sorghum. Source: (82).

traits and demonstrating that simultaneous improvement can be achieved for biomass and nutritional traits (25). Integrating GWAS with transcriptomic profiling and weighted gene co-expression network analysis (WGCNA) provides refined candidate gene discovery for influencing sorghum architecture and quality parameters (84). Additionally, enzymes such as ferulate 5-hydroxylase (F5H) in the monolignol pathway offer promising opportunities to modify lignin composition, which is one of the major molecular targets for improving digestibility in forage sorghum (85). These advances demonstrate that combining transgenic approaches, GWAS and functional genomics provides a powerful framework for the genetic enhancement of forage quality and digestibility in sorghum. However, bringing these crops to market involves regulatory issues, including biosecurity concerns such as the creation of superweeds through gene flow, with commercialisation costs estimated at \$100–150 million and a timeline of 7–13 years for full approval (86). Finally, although reducing lignin enhances digestibility, it affects cell wall rigidity and

increases lodging risk, which remains a primary barrier to farmer's acceptance (87).

Marker assisted selection

Marker-assisted selection (MAS) has become an effective genomic tool for improving quantitative traits, such as forage quality, because it facilitates selection at early growth stages as well as accurate identification of the presence of the trait. Integrating MAS with other breeding approaches enables better and faster results in developing good cultivars. The BMR trait, which is strongly associated with reduced lignin content, improves the digestibility of forage for ruminants. Therefore, it can be extensively utilised in forage breeding programmes, especially with the known BMR loci *bmr6* and *bmr12* being majorly exploited. For further application in breeding, these genes are translated into breeder-friendly DNA markers using cleaved amplified polymorphic sequence (CAPS) and kompetitive allele-specific PCR (KASP), since the BMR trait is recessive and often difficult to select. Kompetitive allele-specific PCR markers are modern, breeder-friendly and much more efficient than CAPS. In this

context, two CAPS and 15 KASP markers were developed and provided accurate selection for the BMR trait and markers *bmr6*-132 and *bmr12*-129 effectively identified lines carrying the respective alleles (88). Similarly, bulked segregant analysis, which rapidly identifies SSR markers, is used to target low HCN content, leading to forage safety (89). Collectively, these studies demonstrate that marker-assisted selection provides a powerful framework for improving digestibility and lignin content and reducing HCN and other nutritional quality constraints in sorghum breeding programmes.

Genome wide association studies

Genome-wide association studies (GWAS) have become one of the most widely used genomic tools for identifying genomic regions and candidate genes, especially for quantitative traits such as forage quality in sorghum. By exploiting linkage disequilibrium in diverse germplasm panels, GWAS provides greater mapping resolution and broader genetic diversity coverage than conventional biparental mapping approaches. It accelerates breeding progress and enhances genetic gain (90). Genome-wide association studies has been used to identify forage quality traits such as NDF and ADF, including several candidate genes related to them, such as *Sbic.001G378300*, encoding sucrose synthase and also playing a vital role in cellulose biosynthesis (25). Apart from fibre traits, GWAS has also contributed to improving forage safety by identifying the genetic basis of HCN content.

Sudangrass, which is genetically closer to US commercial sorghums and exhibits significantly lower dhurrin levels, has provided important insights into understanding the genetic variation for HCN. A major QTL associated with HCN was identified that is tightly linked to SNPs in the 3' UTR of *Sobic.001G012300*, encoding *CYP79A1*, the key enzyme catalysing the first step of the dhurrin biosynthetic pathway (91). Targeting such QTLs enhances the accuracy of selecting lines with low cyanogenic levels. Integration of GWAS with transcriptomics enables researchers to confirm not only the gene location but also its activity, thereby improving candidate gene discovery and identifying genes that directly or indirectly influence forage quality traits. Association mapping using SNP markers across four environments identified QTNs for plant height, tiller number, stem diameter and fresh weight and combined GWAS and RNA-seq identified key candidate genes such as *Sobic.004G143900* and *Sobic.003G375100*, which help in understanding the regulation of biomass-related traits (84). Large-scale resequencing efforts have expanded genomic resources for the improvement of forage quality. Resequencing identified 14 million SNPs and 2 million INDELs, enabling the identification of loci associated with lignin content (92). Through GWAS, variation in ADF among Asian and American sorghum varieties has been identified and these varieties possessed greater diversity than European materials. Furthermore, genome-wide linkage disequilibrium (LD) analysis shows that decay rates vary widely among geographic subgroups, with European varieties having the slowest LD decay due to self-fertilisation. These differences directly influence the precision and consistency of detecting GWAS signals across diverse environments (92).

Along with this, eight QTLs harbouring 91 genes were associated with ADF content. In this context, identified molecular trait associations and favourable alleles are expected to accelerate the improvement of quality traits, thereby developing better-quality sorghum varieties and hybrids for forage (92). Collectively, these studies demonstrate the role of GWAS, especially when integrated

with functional genomics, which provides a powerful framework for improving forage quality and digestibility in sorghum, thereby supporting molecular breeding approaches.

Quantitative trait loci mapping

Most forage quality and biomass traits are governed by quantitative inheritance, which is controlled by multiple genes with complex patterns of inheritance. The genetic information of quality traits such as lignin, crude fibre, crude protein, digestibility and their linkage can be dissected using QTL mapping, which is very significant for modern breeding programmes (93, 94). In one comprehensive linkage mapping effort, a genetic map was developed and a total of 294 QTLs were identified along with 534 epistatic interactions across the traits evaluated. In line with this, the identification of 139 control and 155 drought-responsive QTLs, influenced by moisture variations, illustrates how different water conditions trigger distinct genetic pathways affecting fibre fractions, plant height and biomass yield (95). The discovery of epistatic interactions helps in understanding gene-to-gene communications that influence forage quality. Many candidate genes under these QTL regions are associated with N metabolism and cell wall-related biological functions, proving their importance in forage nutrition (95), such as crude protein, neutral detergent fibre, acid detergent fibre, acid detergent lignin and hemicellulose.

Notably, QTLs for fresh weight, dry weight and plant height were localised on linkage group 7, while QTLs controlling digestibility, particularly *in vitro* dry matter digestibility (IVDMD), were localised on LG1, LG2 and LG8. Furthermore, in a recombinant inbred line (RIL) population obtained from sorghum × Tx623A and Sudan grass Sa, 19 QTLs were successfully mapped and associated with forage quality, providing important genomic regions and insights for further breeding programmes aiming to improve fodder quality in sorghum (28). This specific genetic background was successfully incorporated into the elite cultivar 'Wancao No. 3', a commercial hybrid derived from the cross between Tx623A and Sa, which exhibits exceptional heterosis for both biomass yield and forage quality traits (21). Most recently, breeders have utilised Kompetitive Allele-Specific PCR (KASP) marker assays in early-generation F1 and BC1F1 screenings to effectively verify the transfer of *bmr6* and *bmr12* alleles into diverse sweet and high-biomass backgrounds. This marker-assisted strategy successfully generated advanced BC2F2 populations exhibiting improved cellulose content, earlier maturity for drought adaptation and shorter plant stature that reduces lodging without causing negative phenotypic trade-offs (96). The major QTLs/genes controlling key forage quality traits are summarised in Table 2.

Future prospects

Looking ahead, improvement of forage quality in sorghum will increasingly depend on advanced phenomics and genomics technologies to accelerate genetic gains for complex quantitative traits such as crude protein, fibre fractions, digestibility and nutritional content. Future research should prioritise the following areas:

Forage quality trait marker and QTL validation: Through GWAS, multiple quantitative trait loci associated with key forage quality traits have been identified, enabling the discovery of candidate genes that can be used in MAS and genomic selection strategies (25).

Predictive model development: Genomic selection, particularly multi-trait genomic prediction models, promises to shorten breeding

cycles by predicting the performance of unphenotyped individuals, thereby reducing the time and cost associated with conventional selection and has shown strong potential in sorghum and other crop breeding programmes (97).

Integration of emerging molecular breeding and omics tools: High-throughput phenotyping, along with machine learning, offers powerful tools for dissecting genotype-phenotype associations, facilitating the rapid evaluation of complex traits under field conditions (98). Additionally, emerging molecular breeding approaches, including CRISPR/Cas systems, transcriptomic and metabolic profiling and integrated omics approaches, offer opportunities for the precise modification of cell wall biosynthesis pathways and antinutritional factors such as dhurrin, enabling the development of sorghum cultivars with improved forage quality (99). However, despite progress, knowledge gaps remain in balancing trade-offs between grain and forage yield and quality, farmer preferences and sustainability outcomes, highlighting the need for integrated breeding approaches that balance both productivity and forage quality in sorghum (100).

Conclusion

Forage sorghum represents a climate-resilient and nutritionally versatile crop capable of addressing the growing global demand for quality livestock feed under resource-limited conditions. This review highlights that forage quality traits such as crude protein, fibre fractions (neutral detergent fibre (NDF), acid detergent fibre (ADF), acid detergent lignin (ADL)), digestibility, crude fat and hydrogen cyanide (HCN) content are quantitatively inherited and strongly influenced by genetic, developmental and environmental factors. Substantial genetic variability, moderate to high heritability estimates and identified quantitative trait loci (QTLs) demonstrate significant scope for targeted genetic improvement. Conventional breeding approaches, including mass selection, hybridisation, heterosis exploitation and brown midrib (BMR) incorporation, have laid a strong foundation for improving digestibility and nutritive value. However, the integration of modern molecular tools has considerably enhanced breeding precision. Genome-wide association studies (GWAS), QTL mapping, transcriptomics and marker-assisted selection (MAS) have identified key candidate genes such as *CYP79A1*, *bmr6*, *bmr12* and several SNP-associated loci governing crude protein, fibre fractions, lignin biosynthesis and dhurrin metabolism. These discoveries confirm polygenic control and shared genetic architecture of yield and quality traits.

Importantly, emerging evidence suggests that forage yield and quality are not necessarily mutually exclusive and multi-trait genomic selection approaches may enable the simultaneous improvement of biomass productivity and nutritive value. Advances in high-throughput phenotyping, genomic selection models and functional genomics—including gene-editing approaches—provide promising opportunities to accelerate genetic gains for complex quality traits. Nevertheless, challenges remain in validating stable QTLs across diverse environments, balancing yield–quality trade-offs under stress conditions and translating molecular findings into widely adopted cultivars. Future breeding programmes should emphasise multi-environment testing, integration of omics-assisted selection, exploitation of wild germplasm and development of breeder-friendly molecular markers. Ultimately, a holistic breeding

framework integrating conventional, genomic and physiological approaches will be essential to develop nutritionally superior, safe and climate-resilient forage sorghum cultivars that contribute to sustainable livestock production and global fodder security.

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Authors' contributions

JR prepared the initial draft and contributed to writing, review and editing. KD supervised the study and critically revised the manuscript. MKB contributed to visualisation and investigation. PR conceptualised the study. SA and TM contributed to the final revision and improvement of the manuscript. All authors have read and approved the final version of the manuscript.

Compliance with ethical standards

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Declaration of generative AI and AI-assisted technologies in the writing process

Generative AI was used solely for grammatical refinement and language polishing during the preparation of this manuscript; the authors retain full responsibility for all scientific content.

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Table 2. List of quantitative trait loci (QTLs)/genes controlling forage quality traits

Sl. No.	Trait	Molecular marker/gene ID	Cultivar improvement endpoints	Validation / discovery approach	Reference
1.	Crude protein	<i>Sobic.002G217100</i>	Nitrogen metabolism improvement: Encodes for serine /threonine -protein kinase. It is involved in nitrogen metabolism	Genomic database annotation: Discovered by comparing the DNA region against the official sorghum reference genome and the NCBI database to identify the matching candidate gene.	(25)
2.	Crude protein	<i>Sobic.002G397001</i>	Optimised protein quality: Encodes for cysteine proteinase and associated with protein quality traits.	Genomic database annotation: Discovered by comparing the DNA region against the official sorghum reference genome and the NCBI database to identify the matching candidate gene.	(25)
3.	IVOMD (Digestibility)	<i>Sobic.001G463900</i>	Digestibility under stress: It is Linked to N-terminal acetyltransferase and mapped for IVOMD under drought.	Validated by testing stability across multiple water regimes and seasons, verifying biological relevance through trait correlations, confirming positions by comparing known reference genes and demonstrating cross-species consistency with the maize genome.	(95)
4.	IVOMD (Digestibility)	<i>Sobic.002G335900</i>	Cyclin related gene associated with IVOMD tends to improve forage digestibility under drought conditions.	Validated by testing stability across multiple water regimes and seasons, verifying biological relevance through trait correlations, confirming positions by comparing known reference genes and demonstrating cross-species consistency with the maize genome.	(95)
5.	Lignin / ME	<i>Sobic.001G356000</i>	Maximising energy availability: It is an MYB-like DNA binding protein associated with lignin and metabolizable energy.	Validated by testing stability across multiple water regimes and seasons, verifying biological relevance through trait correlations, confirming positions by comparing known reference genes and demonstrating cross-species consistency with the maize genome.	(95)
6.	NDF	<i>Sobic.002G223200</i>	Stabilising fibre under stress: Significantly associated with NDF under drought conditions.	Validated by testing stability across multiple water regimes and seasons, verifying biological relevance through trait correlations, confirming positions by comparing known reference genes and demonstrating cross-species consistency with the maize genome.	(95)
7.	NDF	<i>Sobic.002G350600</i>	An Import in-beta gene associated with neutral detergent fibre content.	QTL mapping and database annotation: Statistical zones (QTLs) were first mapped across different treatments, their DNA sequences were extracted and then searched against the digital reference genome database to identify the matching candidate gene IDs.	(95)
8.	ADF	<i>Sobic.010G172100</i>	Improving rumen digestion: Encodes a Transcription factor BHLH. It has significant association with ADF levels.	Genomic database annotation: Discovered by comparing the DNA region against the official sorghum reference genome and the NCBI database to identify the matching candidate gene.	(25)
9.	Lignin (ADL)	<i>BMR30</i>	Enhancing forage digestibility: Disrupts the <i>BMR30</i> (Chalcone isomerase) gene to reduce lignin deposition in plant cell walls, making the biomass easier for livestock to digest and utilize."	Fully validated in the laboratory through genetic mapping of independent mutant lines, gene expression analysis, protein enzyme assays and 2D NMR cell wall chemical analysis.	(36)
10.	HCN / Dhurrin Synthesis	<i>CYP79A1</i>	Eliminating prussic acid risk in early vegetative forage through metabolic blockade: Antisense suppression blocks tyrosine conversion, preventing accumulation of cyanogenic glucosides and allowing safe grazing of young plants.	Validated using antisense down-regulation through particle bombardment, confirming multi-fold mRNA reduction through qRT-PCR and lower field HCN levels across advanced generations.	(7)

HCN: hydrogen cyanide; NCBI: National Center for Biotechnology Information; IVOMD: *in vitro* organic matter digestibility; MYB: myeloblastosis transcription factor; BHLH: basic helix-loop-helix transcription factor; qRT-PCR: Quantitative Real-Time Polymerase Chain Reaction; NMR: nuclear magnetic resonance; NDF: neutral detergent fibre.

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