Genetic Resources

REVIEW

Genetic Resources (2026), 7 (13), 169–180
DOI: 10.46265/genresj.OVEO3504
https://www.genresj.org
ISSN: 2708-3764

A comprehensive review of approaches for genetic improvement in foxtail millet (*Setaria italica* L.)

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Abstract: Foxtail millet (*Setaria italica* (L.) P. Beauv.) is a historically significant and resilient cereal crop known for its adaptability to diverse environmental conditions, nutritional benefits and economic potential. Despite its importance, foxtail millet remains underutilized compared to major cereals. Recent advances in breeding techniques and molecular marker technologies have substantially enhanced efforts toward its genetic improvement. Conventional breeding approaches, including selection, hybridization and mutation breeding, have contributed to trait improvement, while modern strategies such as marker-assisted selection (MAS), genome-wide association studies (GWAS), and quantitative trait loci (QTL) mapping have accelerated the identification of genes associated with desirable agronomic traits. The development of high-resolution genetic maps and the use of molecular markers, including simple sequence repeats (SSRs) and single-nucleotide polymorphisms (SNPs), have further facilitated genomic studies and breeding programmes. In addition, association mapping has emerged as an effective approach for identifying genomic regions linked to important agronomic traits, thereby supporting precision breeding. With the integration of genomics, transcriptomics and genome-editing technologies, foxtail millet improvement is progressing towards enhanced yield, stress tolerance and nutritional quality. This review summarizes recent advances in foxtail millet genetics, breeding strategies and molecular marker technologies, highlighting their significance for sustainable agriculture and global food and nutritional security.

Keywords: Foxtail millet, breeding approaches, molecular marker technologies, MAS, GWAS, genome editing

Citation: Pareek, S., Pheirim, R., Chetariya, C. P. and Soharu, A. (2026) "A comprehensive review of approaches for genetic improvement in foxtail millet (*Setaria italica* L.)", *Genetic Resources*, 7(13), pp. 169–180. doi: 10.46265/genresj.OVEO3504.

Introduction

Setaria italica (L.) P. Beauv., commonly known as foxtail millet, is among the earliest domesticated millet species and has a long history of cultivation in India since ancient times (Jia *et al*, 2013). Known locally as 'Kangni' in Hindi, foxtail millet is a hardy crop that is well adapted to a wide range of climatic conditions. It can thrive in both low-fertility and well-drained fertile soils and is commonly cultivated in semi-arid and rainfed regions (Fukunaga and Kawase, 2024). Owing to its ability to grow under low-input conditions, the crop is often regarded as a 'life-saving crop' for farmers in marginal environments (Zhang *et al*, 2022).

Among the minor millets, foxtail millet ranks as the second most important species and is recognized for its high nutritional value. The grain typically contains about 65% carbohydrates, 11% protein and 6% fat, and is rich in minerals such as iron and copper, as well as dietary fibre (Yousaf *et al*, 2021). It serves as a staple food in some regions of Southern India. Due to its immense nutritional value, millet is also considered one of the best weaning foods. In today's modern world, where growing consumer demand for healthier food, foxtail can serve as one of the best choices for the diet/weight-conscious, diabetic and people with heart disease, and holds great potential due to its unique phenolic content and roughage (Tripathi *et al*, 2021). In addition to human consumption, foxtail millet is used in the production of alcoholic beverages and also serves as fodder and feed for livestock in both temperate and tropical regions (Tomar *et al*, 2023).

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Received: 28.08.2025 | Accepted: 24.03.2026 | Published online: 12.05.2026

Despite its resilience, adaptability, and nutritional advantages, foxtail millet remains far less widely cultivated than major cereal crops. Historically, the crop has received limited research attention, leading to its underutilization and its perception as a 'forgotten crop,' often labelled as a 'poor man's food' (Singh *et al*, 2023). In contrast, major cereals such as rice, maize and wheat, which together contribute over 60% of the global plant-based dietary energy supply, are relatively poor sources of essential micronutrients. This heavy reliance on micronutrient-poor staple crops has significantly contributed to the problem of 'hidden hunger' (Vetriventhan *et al*, 2019).

With the rapidly increasing global population and the growing challenges of climate change, there is an urgent need to diversify agricultural systems to ensure sustainable food and nutritional security. In this context, foxtail millet has gained renewed attention due to its climate resilience, nutritional richness and potential role in sustainable agriculture. Therefore, this review provides a comprehensive overview of foxtail millet, with particular emphasis on its genetic resources, breeding strategies and molecular approaches that have been explored for its genetic improvement.

Morphological description of foxtail millet

Foxtail millet is a robust and upright annual grass that typically grows to a height of 0.6–1.2m (Brink, 2006). The plants are mostly slender with stem tillers but may occasionally branch, typically producing 1 to 25 culms, with an average of 3–4. It possesses a well-developed root system, with slender, wiry adventitious roots originating from the lower nodes (Rahayu *et al*, 1996). Leaves are simple and alternate with a glabrous or slightly hairy sheath measuring 10 to 25cm in length. The ligule is short and fimbriate, while the linear leaf blade varies from 15 to 50cm in length and 0.5 to 4cm in width, featuring an acuminate apex and a slightly rough, prominent midrib. It has a short vegetative growth period (Dekker, 2003), ranging from 80 to 120 days, though some cultivars mature within 60 days (Swamy, 2023).

Floral biology

The millet's inflorescence, measuring 6–30cm, consists of a central stalk surrounded by short, bristling, prickly lateral branches (Figure 1B). The terminal spike usually ranges from 8 to 32cm in length with a drooping appearance (Figure 1A), is thick with cylindrical, lobed structure and held up by a very tiny, slender pedicel (Sundararaj and Thulasidas, 1976). It consists of pairs of tiny blooms on each spikelet, which are enclosed by two glumes. The top bloom is fertile and bisexual, while the lower flower is sterile (Nirmalakumari and Vetriventhan, 2010). Each floret consists of three stamens with anthers that are white or yellow in colour (Jayaraman *et al*, 1997). The pistil of the flower consist of a smooth, round ovary with two long styles and feathery stigmas. The fruit is a caryopsis (grain), approximately 2mm in length and oval in shape. The colour varies from pale yellow to orange, red, brown, or black, with the lemma and palea tightly enclosing the grain with a 1,000-seed weight of around 2g (Figure 1C).

Anthesis and pollination

Foxtail millet is a self-pollinating species with a low average natural outcrossing rate of approximately 4%, occasionally spontaneous hybrids forming between wild and cultivated varieties (Till-Bottraud *et al*, 1992). Flowering commences when roughly three-quarters of the head protrudes from the sheath and proceeds to flower in a vertically aligned manner (Sundararaj and Thulasidas, 1976). The flowering process for a head takes between 8 to 16 days. Anthesis commonly

Figure 1. Structure of the foxtail millet plant. (A) Mature plant (B) Inflorescence (C) Grains. Created by the authors.

occurs early in the morning and around midnight, although this can vary widely based on environmental conditions (Siles *et al*, 2001).

Global status of germplasm resources

S. italica is predominantly grown in Asia, parts of Europe, and Africa, playing a vital role in the diets of people in China, India, Korea, Japan and Nepal (Dwivedi *et al*, 2012). Countries such as China, India, France and Japan have the most extensive collections of foxtail millet germplasm (Vetriventhan *et al*, 2016). The Crop Trust, along with other global organizations, is actively engaged in the ex situ and in situ conservation of foxtail millet genetic resources (Bramel *et al*, 2022). The Chinese National Gene Bank (CNGB) preserves a vast collection of 26,670 germplasm accessions (Wang *et al*, 2012). The International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) houses germplasm sourced from 26 different countries, while the Plant Genetic Resources Conservation Unit (PGRCU) in the USA and the National Institute of Agro-biological Sciences (NIAS) in Japan also maintain diverse germplasm collections (Upadhyaya *et al*, 2009; 2011). The formation of representative germplasm, which includes core and mini core collections (Upadhyaya *et al*, 2009; 2011), serves as valuable genetic resources for research at the genomic level.

Cytogenetics studies in foxtail millet

Foxtail millet is a C4 crop with a chromosome number of 2n = 2x = 18 (AA), belonging to Panicoid, characterized by a comparatively small genome size of 515Mb approx (Lata *et al*, 2013). It belongs to the Panicoideae subfamily and the tribe Paniceae. The wild ancestor of cultivated foxtail millet (*S. italica*) is the green foxtail millet, *S. viridis* (2n = 2x = 18, AA). Wild species *S. faberii* and *S. verticillata* consist of an AABB genome, thought to have arisen from natural crossing between *S. viridis* and *S. adhaerans*. A species from Mexico, *S. grisebachii*, is a diploid species detected to have a CC genome. The sole species that is autotetraploid in the *Setaria* genus with an AAAA genome was identified in *S. queenslandica*. Other polyploid species identified in *Setaria* are *S. pumila* and *S. pallidefusca* (Benabdelmouna *et al*, 2001a; 2001b; Benabdelmouna and Darmency, 2003).

Genetic diversity

Enhancing crop resilience, production, and adaptation in adverse environmental conditions is largely dependent on genetic diversity. Establishing breeding goals and comprehending the genetic diversity of foxtail millet are important initial steps in developing superior cultivars that can meet the growing global demand (Ramesh *et al*, 2023). A wide range of genetic variation in the population of foxtail millet has been reported based on traits such as the number of tillers, bristle length, panicle orientation, panicle compactness, anther colour, and seed size (Wang *et al*, 2012; Moharil *et al*, 2019). ICRISAT analyzed approximately 1,535 *S. italica* samples from 26 different countries to look at differences in height of plant, time of blooming, structure of inflorescence, and the shape of seed amongst the collection. The possibility of gene transfer between Setaria species appears to be significant, especially between cultivated and wild species, since the outcrossing rate was shown to range significantly (0.3–4%). The variation in the crop has been explored through several studies, including pedigree, morphological and biochemical assessment within foxtail millet (Murugan and Nirmalakumari, 2006; Nirmalakumari and Vetriventhan, 2010). The biochemical analyses done in foxtail millet were based on seed protein analysis, isozymes (Jusuf and Pernes, 1985), and analysis of molecular markers or DNA markers (Schontz and Rether, 1999; Van *et al*, 2008; Fukunaga *et al*, 2002; Jia *et al*, 2009; Radha *et al*, 2014). Foxtail millet's genetic diversity is protected and encouraged, which might strengthen our ability to assist international efforts to develop a stronger and fairer food system and to encourage agricultural innovation (Govindaraj *et al*, 2020).

Breeding approaches in foxtail millet

Improving grain yield, nutritional composition, drought tolerance and resistance to pests and diseases while adapting to evolving demands can be achieved through the strategic use of diverse germplasm in breeding programmes. Below is an overview of breeding approaches employed in foxtail millet improvement (Figure 2).

Conventional approaches

In the early stages of foxtail millet breeding, pure line selection was the predominant method for enhancing grain yield. Breeding approaches for foxtail millet encompass selection and hybridization utilizing male-sterile lines (Swamy, 2023). Genetically male sterile lines governed by dominant gene 'Ch A' (Hu *et al*, 1986) and photoperiod-sensitive male sterility (Wensheng *et al*, 1991) have been developed for heterosis breeding in foxtail millet to facilitate the development of hybrid varieties (Liu *et al*, 2014). Hybridizing foxtail millet (*Setaria italica*) with its wild counterpart *S. viridis* was reported to incorporate triazine resistance into the cultivated species (Darmency and Pernes, 1985). *S. viridis* acts as an important genetic reservoir for improving foxtail millet, offering a straightforward and efficient breeding strategy (Naciri *et al*, 1992). The main challenge in conventional breeding is inbreeding depression, which results in the loss of heterosis or hybrid vigour. Another issue is linkage drag, where undesirable genes are transferred and integrated into the genome.

Mutation breeding approaches

Mutation breeding has significantly contributed to crop enhancement on a global scale. Its primary goal is to amplify the frequency and range of mutations while enhancing the occurrence of viable mutations for targeted genetic modifications. Induced mutagenesis acts as a viable alternative breeding strategy to enhance variability and address specific shortcomings in existing cultivars. Various mutant varieties were listed in the MVD (Mutant Variety Database), among which a few were foxtail millet (*S. italica* L.) resulting from direct or indirect mutation breeding with chemical and

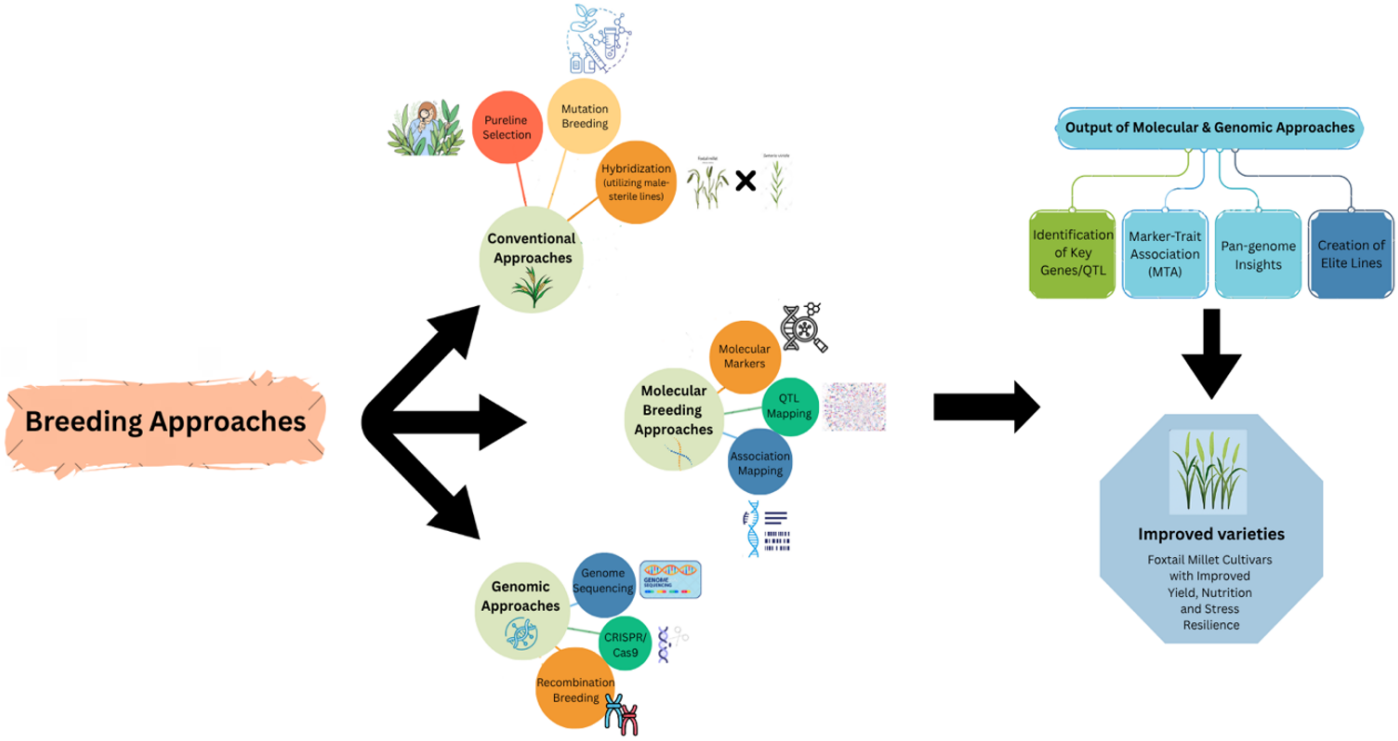

Figure 2. Overview of breeding approaches in foxtail millet. Created by the authors.

physical mutagens (IAEA, 2022). Some examples of mutant varieties released were Lugu 7, developed by irradiation of seeds with gamma rays with improved attributes of 10–15cm shorter stem and resistance to lodging, Jingu 47, officially approved in 2009, developed by treatment in aerospace, with main improved attributes of high yield and good quality. Also, mutagenesis techniques have been effectively combined with modern molecular biology tools, such as molecular marker analysis and high-throughput mutation screening, thereby increasing their efficiency and impact on crop improvement (Shu, 2009). Some examples in foxtail millet are SiDWARF2, a dwarf mutant gene (Xue *et al*, 2016), SiYGL1, a yellow-green leaf mutant (Li *et al*, 2016), and *siago1b*, a gene showing pleiotropic developmental defects (Liu *et al*, 2016).

Molecular breeding approaches

Conventional breeding often requires a long duration to develop and commercialize the cultivars, and several traits are easily influenced by environmental factors or exhibit low heritability. Advances in molecular biology led to the development of molecular marker technologies, which enable the study of plants based on polymorphic DNA sequences. Molecular markers are easily identified DNA fragments widespread in the genome with no environmental effect, and non-specific to tissue and stages of plants. It provides the most appropriate tool for the genetic diversity assessment, allowing the selection of suitable parental lines for further breeding programmes, efficient handling of plant genetic resources, and identifying varieties (de Vienne, 2003). The molecular approaches in foxtail millet are discussed broadly in the subsequent sections.

Molecular marker technologies

Molecular marker technologies have significantly advanced genetic studies and breeding programmes in foxtail millet, enabling precise identification of genetic variations. These markers are essential for assessing the genetic diversity, trait inheritance and crop improvement using marker-assisted selection (MAS). Among the molecular markers, restriction fragment length polymorphisms (RFLP) were the first molecular markers used in foxtail millet to analyze genetic differentiation across geographical diversity based on heterologous ribosomal DNA probes, providing foundational insights into domestication and diversity of foxtail millet and its wild ancestor *S. viridis* (Schontz and Rether, 1999; Fukunaga *et al*, 2002). RFLP map in the crop was constructed from an inter-varietal cross, Longgu 25 × Pagoda Flower green and reported nine linkage groups by Wang *et al* (1998). Doust *et al* (2004) expanded the work by using 257 RFLP markers from rice and foxtail millet to identify quantitative trait loci (QTL) in the aspect of branching and inflorescence architecture. Using F_2 plants derived from B100 (*S. italica*) and A10 (*S. viridis*) as a mapping population, the first functional dissection of morphological characters in foxtail millet using molecular mapping was developed. PCR-based molecular markers such as amplified fragment length polymorphism (AFLP), random amplified polymorphic DNA (RAPD), ISSR markers, and simple sequence repeats (SSRs) are widely used for genetic diversity studies, germplasm characterization, and linkage map construction (Gupta and Varshney, 2004; Jain *et al*, 2009; Kumari *et al*, 2011; Ardie *et al*, 2017). Among the molecular markers, SSR markers have been utilized to a great extent due to their reproducibility, high polymorphism and ease of use. This marker has been most extensively used in foxtail millet facilitating the study of diversity (Chander *et al*, 2017; Ramesh *et al*, 2023; Reddy *et*

al, 2025) for linkage map construction (Jia *et al*, 2009; Sato *et al*, 2013; Fang *et al*, 2016) and QTL mapping (Wang *et al*, 2017; Gao *et al*, 2025). The development of SSR markers based on the genomic resources of the draft genome in foxtail millet enables germplasm characterization, linkage mapping, phylogenetics and comparative mapping in foxtail millet (Pandey *et al*, 2013). Transposon display (TD marker) has been employed to examine the genetic structure of foxtail millet and wild green foxtail (*S. italica* subsp. *viridis* (L.) P. Beauv.) revealing geographical structuring (Hirano *et al*, 2011). The advent of single nucleotide polymorphism (SNP) has emerged as a powerful, high-resolution tool in molecular breeding and genomic research. The resequencing-based marker systems offers to detect SNPs and InDels and rapidly transitioned from low throughput to high throughput-based techniques and offers the construction of high-density linkage maps (Wang *et al*, 2017; Guo *et al*, 2023), genome wide association study (Jia *et al*, 2013; Jaiswal *et al*, 2019; 2024) and fine mapping of QTLs (Du *et al*, 2021; Li *et al*, 2022) in foxtail millet.

Methods for identification of QTLs in foxtail millet

Numerous chromosomal regions and QTLs have been identified that regulate a wide range of phenotypic traits in foxtail millet. According to Yu and Buckler (2006), the majority of the desirable features in plant breeding, such as height, quality, resistance to diseases, drought and salinity, are inherently quantitative in nature and are controlled by several genes. Such polygenic traits are regulated by specific genomic regions referred to as quantitative trait loci (QTLs). Phenotypic variations in complex traits arise from the combined effects of environmental factors, multiple QTL influences, QTL-QTL interactions, or QTL–environment interactions (Maloof, 2003). The primary goal of QTL identification is to locate genomic regions associated with complex traits and to identify tightly linked and neutral inherited molecular markers that can be used in breeding programmes (Agarwal *et al*, 2008). QTL identification involves the sequential arrangement of markers and determining genetic distances, assigning linkage groups based on recombination values. In order to address this complexity, high-resolution and accurate tools are required not only to decipher trait architecture but also to aid in the development of MAS tools for breeding programmes. QTL identification in plants is predominantly carried out using two approaches: (1) QTL mapping and (2) association mapping.

(1) QTL mapping in foxtail millet: Identified and genomic regions

The concept of QTL mapping was first introduced by Karl Sax in 1923. QTL mapping involves the analysis of an appropriate mapping population. Several QTL accounting for agronomic and yield attribute traits were reported in foxtail millet (Doust *et al*, 2004; Wang *et al*, 2013; Fang *et al*, 2016). QTL mapping was employed in the crop for *stb1* gene, for 'spikelet-tipped bristles' (Sato *et al*, 2013), variations in blooming time under various environmental circumstances (Mauro-Herrera *et al*, 2013), and germination and drought tolerance in early planting (Qie *et al*, 2014). The integration of next-generation sequencing enabled the development of high-density SNP based linkage maps. Map-based cloning was used to fine map and clone SiDWARF2 (a foxtail millet dwarf mutant) derived from Yugu1 (Xue *et al*, 2016), a recessive nuclear gene SiYGL1 encoding a magnesium-chelatase D subunit, responsible for yellow–green leaf mutant (Li *et al*, 2016), and Argonaute 1 (AGO1) mutant (*siago1b*) induced by ethyl methane sulfonate exhibiting pleiotropic developmental defects in foxtail millet (Liu *et al*, 2016). Liu *et al* (2024) identified QTLs associated with downy mildew resistance based on the specific locus amplified fragment sequencing with high-density linkage map and the phenotype data in four environments. They also concluded through collinearity analysis between genomes of pearl millet and foxtail millet that the genes were taxon-specific (Liu *et al*, 2024). Ma *et al* (2025) identified four important hull colour QTL and provided a basis for characterizing hull colour indices and contributing to the advancement of QTL mapping for grain colour. Liu *et al* (2022) identified 221 QTLs for 17 morpho-agronomic and yield-related traits, while Yoshitsu *et al* (2017) identified two QTLs (qDTH2 and qDTH7) regulating days to heading (DTH) using QTL-seq analysis. Ni *et al* (2017) performed resequencing of 184 recombinant inbred lines (RILs) of foxtail millet for QTL mapping of nine agronomic traits and identified a single gene controlling five traits, two QTLs for plant height and three QTLs for heading date. This provides an efficient way for constructing a high-resolution genome assembly and identifying genes. Han *et al* (2024) developed a genetic map for plant height based on re-sequencing, identifying 19 unconditional and 13 conditional QTLs. QTLs identified using molecular markers in foxtail millet are shown in Table 1.

(2) Advances in association mapping or association analysis in foxtail millet

Association mapping or association analysis uses linkage disequilibrium (LD) to investigate the connection between genotypic constitution and phenotypic expression in natural populations (Borba *et al*, 2010). It is typically conducted using two approaches – candidate gene-based and genome-wide association mapping. The major advantages of this approach are its use of natural populations, the elimination of bi-parental population requirements, and its ability to achieve high-resolution mapping due to recombination events accumulated over multiple generations (Agrama *et al*, 2007). GWAS was performed using the core collection of foxtail millet as an association mapping panel, which involves genome-wide screening of nucleotide sequence variation. Gupta *et al* 2014, evaluated 50 SST markers on 184 foxtail millet accessions across nine chromosomes and identified eight significant markers linked to agronomic traits and two markers with significant association for ubiquitin carboxyl-terminal hydrolase and phospholipid acyltransferase. GWAS by Upadhyaya *et al* (2015) identified several SNP loci associated, as well as a major genomic region of plant pigmentation and flowering time. The genomic regions of plant pigmentation were identified between 7.2 and 7.3Mbp on chromosome 4, which was also reported by Jia *et al* (2013) for the pigmentation-related traits such as colour of bristle, leaf sheath and pulvinus. Significant associations were identified on chromosome 6, specifically around 34.0 to 35.5Mbp.

Table 1. A summary of QTL identification in foxtail millet. Abbreviations: QTL, quantitative trait loci; RFLP, restriction fragment length polymorphism; SSR, simple sequence repeat; GWAS, genome-wide association study; SNP, single nucleotide polymorphism; GBS, genotyping-by-sequencing; RAD-seq, restriction site-associated DNA sequencing; MTA, marker–trait association; RIL, recombinant inbred line; BSR-seq, bulked segregant RNA sequencing; SLAF-seq, specific length amplified fragment sequencing; InDel, insertion–deletion; ICIM, inclusive composite interval mapping; MCIM, mixed composite interval mapping.

Germplasm	Mapping approach	Population type	Marker used	No. of markers	Genomic region(s) identified	Putative gene identified	Trait(s) studied	References
Cross between *Setaria italica* (B100) × *S. viridis* (A10)	QTL mapping (Composite Interval Mapping, comparative genomics)	F2:3 population (~120 families)	RFLP markers	119 markers (subset from 257 loci map)	Multiple QTL across chromosomes I–IX; major regions on chromosomes V, VI, IX	tb1 (minor effect), auxin & gibberellin pathway genes, monoculm1, dwarf-related genes	Tillering, axillary branching	Doust *et al*, 2004
Diverse germplasm panel	Association mapping	Diverse germplasm panel, 184 foxtail millet accessions	Genomic SSRs	50	Strong associations on chromosome 5	*SSR b129* (Ubiquitin carboxyl-terminal hydrolase) and SSR *p75* (Phospholipid acyltransferase)	Yield-related agronomic attributes	Gupta *et al*, 2014
Global Collection	GWAS Association Mapping)	181 accessions, including 155 from the core collection	GBS	17,714	Pigmentation and days to 50% flowering at chromosomes 4 and 6, respectively	-	Flowering time and plant pigmentation	Upadhyaya *et al*, 2015
Segregating population	Linkage mapping	F_2 population (Yugu1 × Longgu7, 167 individuals)	SSRs	10,598	QTLs distributed across all nine chromosomes	-	Agronomic and yield attributes	Fang *et al*, 2016
RILs	High-density linkage mapping and QTL analysis	184 RILs (Zhanggu × A2)	SNPs	483,414 SNPs; 3,437 recombination bins	QTLs on all nine chromosomes	*sd1* (gibberellin synthesis gene)	Agronomic traits	Ni *et al*, 2017
Segregating population	RAD-seq based QTL mapping	F_2 population from cross between Hongmiaozhangu × Changnong35 (124 individuals)	SNPs	9,968	11 QTLs on chromosome 1,2,5,7,8,9	-	Agronomic traits	Wang *et al*, 2017
Yuikogane × Shinanotsubuhime (F_2 population, 382 plants)	QTL-seq combined with Bulked Segregant Analysis (BSA) and Composite Interval Mapping (CIM)	F_2 population	SNPs, Indel markers, CAPS markers	~45,370 SNPs identified between parents; 24 Indel & CAPS markers used for validation	Two major QTLs: qDTH2 (Chr 2: 38.2–39.6Mb) and qDTH7 (Chr 7: 29.2–31.0Mb)	Candidate genes include Seita.2G286100 (OsPRR95 homolog), Seita.2G291300 (DLF1 homolog) and Seita.7G246700 (Roc4 homolog)	Days to Heading (DTH) / Flowering time	Yoshitsu *et al*, 2017
Cultivars	GWAS Association Mapping	142 diverse genotypes (core collection)	SNPs (GBS-ddRAD)	12,460	High-confidence MTAs on chromosomes 3, 6, 7, 9	27 candidate genes for 1,000-grain weight, grain yield and flag leaf width	Major agronomic traits	Jaiswal *et al*, 2019

Table 1 continued

Germplasm	Mapping approach	Population type	Marker used	No. of markers	Genomic region(s) identified	Putative gene identified	Trait(s) studied	References
Yugu1 × Longgu7	QTL mapping (linkage mapping using resequencing data)	RIL population	Bin markers + SSR markers	2297 bin markers + 74 SSR markers	221 QTL across genome; 22 QTL clusters; stable QTL qLMS6.1 (Chr 6)	Seita.6G250500	Morpho-agronomic and yield-related traits (plant height, tiller number, panicle traits, yield traits)	Liu *et al*, 2022
Aininghuang × Jingu21	QTL mapping (unconditional & conditional QTL analysis + transcriptome integration)	RIL population	Bin markers (resequencing-based)	4360 bin markers	19 unconditional QTL + 13 conditional QTL; 4 stable QTL across environments	8 candidate genes (identified via RNA-seq & WGCNA; specific names not mentioned in abstract)	Plant height (PH)	Han *et al*, 2024
Foxtail millet G1 × JG21	QTL mapping using high-density linkage map and BSR-seq validation	Recombinant Inbred Lines (F6:7, 158 lines)	SLAF-seq SNP bin markers	1031 bin markers	Major region on Chr8 (0.78 Mb interval) including qDM8_1, qDM8_2, qDM8_4	Seita8G.199800, Seita8G.195900, Seita8G.198300, Seita8G.199300 (NBS-LRR genes)	Downy mildew resistance	Liu *et al*, 2024
Foxtail millet Jingu28 × Ai88	QTL mapping using genetic linkage map	F_2 population (300 individuals)	SSR + InDel markers	215 (213 SSR + 2 InDel)	Major QTLs qHD9-1 (Chr9) and qPH5-1 (Chr5); 46 QTLs forming 13 clusters	Seita.9G020100 (CCT motif gene), Seita.5G404900 (GA20-oxidase)	12 agronomic traits including heading date and plant height	Gao *et al*, 2025
Foxtail millet Changsheng07 × Donggu218	QTL mapping using genetic linkage map	F_2 population with $F_{2:3}$ families	SSR + InDel markers	196 (159 SSR + 37 InDel)	Major QTLs qMPL3.1, qMPL5, qMPW2, qSD5, qTGW5.1, qTGW5.2, qGL5; 22 QTLs forming 4 clusters	-	Panicle-related traits (panicle length, width, grain length, TGW)	Li *et al*, 2025
Yugu18 × Hongjiugu19	QTL mapping (ICIM, MCIM, multi-method phenotyping)	RIL (F6, 250 lines)	SNPs, InDels, bin markers	~20,748 SNPs + 1,759 InDels (1420 bins)	Major QTL: qHC1.1, qHC1.2 (Chr 1); qHC9.1, qHC9.3 (Chr 9)	Not specifically identified (QTL regions validated; overlap with previous loci)	Hull colour (grain colour traits using 4 methods)	Ma *et al*, 2025

Advances in genomic research for foxtail millet improvement

Among minor millets, foxtail millet possesses the smallest genome (423–510Mb) and was the first millet crop to have its entire genome sequenced. Its compact diploid genome, rapid growth cycle and self-pollination make it a model for C4 species (Vetriventhan *et al*, 2020). Zhang *et al* (2012) made a major breakthrough, producing a draft genome (~423Mb) anchored to nine chromosomes. This provides marker discovery, gene annotation and comparative genomics with other cereals such as rice, pearl millet and sorghum. The reference genome allowed the development of a genome-wide scale of microsatellite markers across the nine chromosomes of foxtail millet. A diverse foxtail millet collection was genotyped through genotyping-by-sequencing (GBS) by ICRISAT in collaboration with Cornell University, identifying genome-wide SNPs and assessing population structure and diversity (Upadhyaya *et al*, 2015). Several gene families have been identified and characterised in foxtail millet, including NAC (NAM, ATAF, and CUC) (Puranic *et al*, 2013), MYB (myeloblastosis transcription factor) (Muthamilarasan *et al*, 2014b), WRKY (WRKY DNA-binding protein) (Muthamilarasan *et al*, 2015), AP2/ERF (APETALA2/Ethylene-Responsive Factor) (Lata *et al*, 2014), and C2H2 (Cys2-His2 zinc finger protein) (Muthamilarasan *et al*, 2014a), which play important roles in stress response, growth, and development. In addition, regulatory components such as DCL (Dicer-like), AGO (Argonaute), and RDR (RNA-dependent RNA polymerase) (Yadav *et al*, 2015) are involved in gene silencing pathways. Although these gene families are conserved across plant species, their characterisation in foxtail millet provides insights into mechanisms of stress tolerance and can aid genetic improvement.

The Beijing Genomics Institute, China and The Joint Genome Institute, USA, have recently sequenced the complete genome of two foxtail millet accessions. The comparative genome mapping through sequence alignment of foxtail millet demonstrated a strong syntenic relationship with both rice and sorghum, even though they have diverged over half a century years ago. With this genome-wide sequence resources and availability in public repositories, it is now possible to develop *in silico* molecular markers and large-scale validation to utilize them in various applications for genetic improvement in foxtail millet. Such a genome-wide scale may prove beneficial for other underutilized or orphan crop species with limited or no genomic information available.

Application of genome editing technologies in foxtail millet

Genome editing technologies have developed as a powerful tool because of their precision and simplicity in modifying targeted genomic regions by using engineered nucleases such as zinc finger nucleases (ZFNs), transcription activator-like effector nucleases (TAL-ENs), or RNA-guided engineered nucleases such as the CRISPR/Cas system. The first genome editing in foxtail millet was successfully demonstrated by Lin *et al* (2018) through mutating the *SiPDS* gene, which was achieved through protoplast transfection. Cheng *et al* (2021) targeted gene *SiMTL* by using CRISPR/Cas9 to generate a haploid inducer line. Although there are relevant reports of genome editing systems in foxtail millet, a highly efficient genome-editing system is limited. Liang *et al* (2022) first successfully applied base editing in foxtail millet by using CRISPR/Cas9 targeting the *SiALS* gene, and successfully created a homozygous mutant plant that is herbicide-tolerant.

Future directions and challenges

Foxtail millet is a significant crop with its climatic resilience and superior nutritional profile. With a potential role in food and nutritional security, it is necessary to harness its nutritional potential to meet daily needs for a healthy lifestyle. Addressing the challenges for breeding foxtail millets is necessary to accomplish this goal. An in-depth understanding of the floral biology of foxtail millet is necessary for developing standardized hybridization techniques to create variability, develop improved varieties and enhance tolerance to adverse climatic conditions, which shall serve the breeding efforts of the crop. Exploration of underutilized germplasm, including wild relatives, shall also enhance biotic and abiotic stresses and nutritional quality. The use of advanced genomic tools (e.g. marker-assisted selection and genome-wide association studies) has improved foxtail millet breeding. Collaboration among genebanks, researchers and policymakers is crucial for sustainable utilization of foxtail millet genetic resources (Vetriventhan *et al*, 2020).

Conclusion

Foxtail millet holds immense potential as a climate-resilient, nutrient-rich crop that can address global food security challenges. Advances in breeding methodologies, including molecular marker technologies and genomic selection, have enabled precise identification and introgression of desirable traits. QTL mapping and association studies have identified key genetic loci governing yield, stress tolerance, and disease resistance, laying the foundation for marker-assisted breeding. The availability of high-throughput sequencing and genome-editing tools such as CRISPR/Cas9 has further enhanced the scope of foxtail millet improvement. However, challenges such as limited genetic diversity in cultivated varieties, underutilization of wild germplasm, and the need for better characterization of genomic resources persist. Further research should prioritize integrating advanced genomic tools, promoting international germplasm exchange and developing climate-resilient cultivars. By leveraging genetic innovations and sustainable breeding approaches, foxtail millet can play an important role in uplifting global agricultural productivity and ensuring food security amid climate change.

Author contributions

Shivika Pareek: Compilation of the literature, preparation of the draft and preparation of figures/tables; Reginah Pheirim: Conceptualization and article revision; Chetariya Chana Pitha: Revision of article; Alka Soharu: Revision of article.

Conflict of interest statement

The authors have no relevant financial or non-financial competing interests to disclose.

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