

REVIEW ARTICLE

A Systematic Review of Thousand-Grain Weight Genes in Rice and Foxtail Millet: Toward Functional Markers for Yield Improvement

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Abstract

Foxtail millet (*Setaria italica* (L.) P. Beauv.) is a climate-resilient crop with high potential for cultivation in low-input agricultural systems. However, its genetic improvement lags behind major crops such as rice. The objectives of this study were to identify agronomic traits associated with grain yield and to determine candidate genes for thousand-grain weight (TGW) in foxtail millet using a systematic literature review (SLR) combined with sequence-based analysis. Rice was included in the SLR due to its close synteny with foxtail millet and its extensive genetic studies. In accordance with PRISMA 2020 guidelines, 116 articles were selected from the Scopus and PubMed databases. The results showed that TGW has a strong positive correlation with rice grain yield. Eight candidate genes (*GS3*, *GW5*, *TGW6*, *GW2*, *GS5*, *GW8*, *GS2*, and *GW5L*) controlling grain size and grain weight were identified based on their recurrence across studies and subsequently used to identify homologs in foxtail millet. The sequence of a foxtail millet homolog of *TGW6*, *SiTGW6* (*Seita.1G350400*), was further analyzed to find potential variants and co-inherited genes. Sequence analysis identified SNPs in the *SiTGW6* region, including a variant at 40,392,218 bp (MAF 0.17; moderate effect) that warrants further investigation for SNP-based marker development. Analysis within the linkage disequilibrium (LD)-decay region

identified *Seita.1G350500.1*, which contains BRCT, HAD-like, and FCP1 domains involved in transcriptional regulation. This study identifies *SiTGW6* as a potential genetic target, with both SNP-based and linkage-marker development serving as a foundation for gene-based functional markers and prospective precision breeding in foxtail millet.

Keywords: linkage marker, millet, PRISMA, SLR, SNP

Introduction

Foxtail millet is attracting increasing attention as a climate-resilient crop due to its tolerance of low-input environments (Kalsi & Bhasin, 2023). This crop exhibits resilience to drought, salinity, and poor soils, and has high nutritional value (Ardie et al., 2025; Arora et al., 2023). Despite these advantages, genetic improvement of foxtail millet remains limited compared with major crops such as rice, largely due to the relatively limited number of studies and the limited availability of comprehensive genomic resources (Kasule et al., 2024; Liang & Han, 2024). This bottleneck has contributed to slower progress in yield improvement in foxtail millet. To address this challenge, greater attention should be given to identifying and improving key yield-related traits. Among these, thousand-grain weight (TGW) is recognized as one of the key components of grain yield and

an important target for genetic improvement (Zhang et al., 2022). Therefore, improving TGW is a promising strategy to enhance productivity in foxtail millet. Achieving this objective requires more precise breeding approaches.

Precision breeding approaches are needed to accelerate foxtail millet improvement, particularly by developing gene-based functional markers that can efficiently enhance yield. Grain yield remains the main target for crop improvement in most cereals. However, yield is a complex trait controlled by multiple genes and influenced by environmental effects (Liu et al., 2020). Therefore, identifying reliable genes and understanding their genetic basis is necessary for advancing breeding efficiency (Gasparis & Miłoszewski, 2023). Gene-based markers offer benefits compared with traditional random markers, as they are derived from polymorphisms within functional genes and are closely associated with phenotypic traits (Salgotra & Stewart, 2020). For instance, gene-based markers targeting the waxy alleles (wx_a and wx_c) have been used to identify heterowaxy genotypes in local Indonesian sorghum to improve grain quality (Suroya et al., 2023). At present, only a limited number of gene-based markers have been reported in foxtail millet. For example, a SNAP marker derived from *SiDREB2* has been associated with salinity and drought tolerance (Lata et al., 2011; Widyawan et al., 2018), whereas SNPs in *SiCHLI* have been linked to photosynthetic capacity (Liang et al., 2023). In contrast, no significant association was observed between SNPs in *SiARGOS1* and yield-related traits (Wang et al., 2017). This limited set highlights the need to examine additional gene-associated traits, especially those related to yield, to support the development of functional markers for precision breeding in foxtail millet.

In contrast to foxtail millet, rice has been extensively studied, and provides a comprehensive source of genetic and genomic information. Rice shares a high level of genomic synteny with foxtail millet (Zhang et al., 2012). This enables the transfer of insights from rice to foxtail millet to identify yield-related traits and genes. A systematic literature review

offers a transparent and rigorous approach to synthesizing existing knowledge and identifying research gaps. By integrating findings across studies, this method minimizes bias and enhances comprehensiveness. It also supports evidence-based identification of key traits and candidate genes (Boell & Cecez-Kecmanovic, 2015; Brignardello-Petersen et al., 2025). Applying a systematic literature review across rice and foxtail millet enables cross-species comparison and supports the transfer of genetic knowledge. The objectives of this study were to identify agronomic traits associated with grain yield and to determine candidate genes for thousand-grain weight (TGW) in foxtail millet using a systematic literature review combined with sequence-based analysis. The results of this study are expected to provide a foundation for developing gene-based functional markers and to support precision breeding approaches to improve yield in foxtail millet.

Materials and Methods

This systematic literature review was conducted in accordance with PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) guidelines (Page et al., 2021). The literature search was conducted on March 7, 2025, using the Scopus and PubMed databases. Databases such as Scopus and PubMed were chosen because they are considered reliable and authoritative (Falagas et al., 2008). No publication year restriction was applied, and all eligible articles indexed in the databases up to March 7, 2025, were considered for inclusion. The search strategy used Boolean operators as follows: ("foxtail millet" or "*Setaria italica*" or "rice" or "*Oryza sativa*") and ("grain weight per plant" or "thousand grain weight" or "1000 grain weight") and "associat*" and ('QTL' or "gene*"). The operators were designed to retrieve articles reporting yield-related traits, quantitative trait loci (QTL), and genes associated with thousand-grain weight in rice and foxtail millet. Rice was included in the search because of its close genomic synteny with foxtail millet (Devos et al., 1998). Inclusion criteria were applied to

filter the search results: 1) fields of science limited to agricultural and biological sciences, biochemistry, genetics and molecular biology, and environmental sciences; 2) research articles; 3) final publication stage; 4) English language.

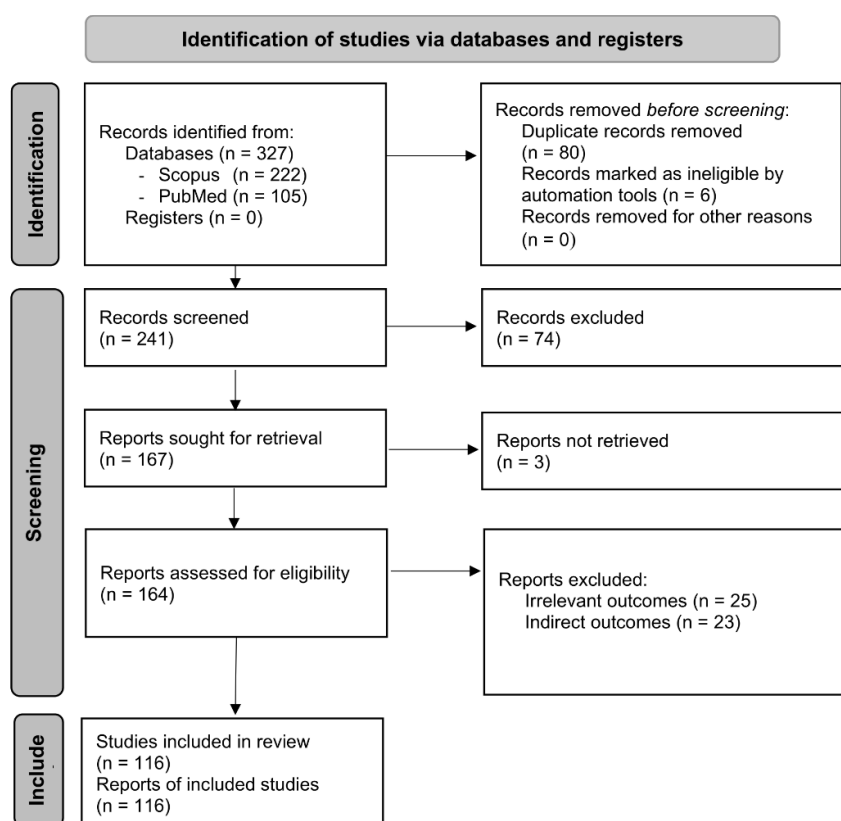
All data obtained were exported to Microsoft Excel for pre-screening, specifically to remove duplicates using title similarity. Furthermore, the data were exported to the Rayyan website for additional duplicate detection. Rayyan identified similarity based on title, authors, and abstract, and grouped articles by level of similarity (Ouzzani et al., 2016). The initial search identified 327 articles, which were reduced to 241 after duplicate removal during pre-screening. The screening process

was conducted in three stages. The first stage involved screening titles and abstracts to assess article suitability, resulting in the exclusion of 74 articles. In the second stage, three articles that could not be accessed or downloaded were excluded from the analysis. In the third stage, full texts were assessed for suitability, and 48 articles were excluded. Articles were excluded if they did not report traits related to yield or thousand-grain weight, did not identify QTL or genes associated with thousand-grain weight (irrelevant outcomes), or only reported genes or QTL not directly related to thousand-grain weight (indirect outcomes). A total of 116 articles were included for the final analysis (Figure 1).

Based on the reviewed studies, candidate

Figure 1

PRISMA 2020 Flow Diagram for Article Identification, Screening, Eligibility Assessment, and Study Inclusion



Notes. This diagram illustrates the study selection process conducted in accordance with the 2020 PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) guidelines (Page et al., 2021). Records identified through database searches were screened by title and abstract, followed by full-text eligibility assessment. Inaccessible articles and those that did not meet the inclusion criteria were excluded, resulting in the final set of studies included in the systematic review.

genes were selected if they were reported in at least two articles. Homologs in foxtail millet were identified using sequence similarity in the Phytozome database. One gene, *SiTGW6* (*Seita.1G350400*), was selected for further analysis based on the availability of studies in foxtail millet and its gene length. Genomic regions upstream and downstream of the *SiTGW6* gene were also examined in Phytozome (<https://phytozome-next.jgi.doe.gov/>), and SNP data for *SiTGW6* were retrieved from SetariaDB (<http://www.setariadb.com/>). All graphical visualizations were generated in RStudio, whereas the genomic position figure was created using Canva.

Results and Discussion

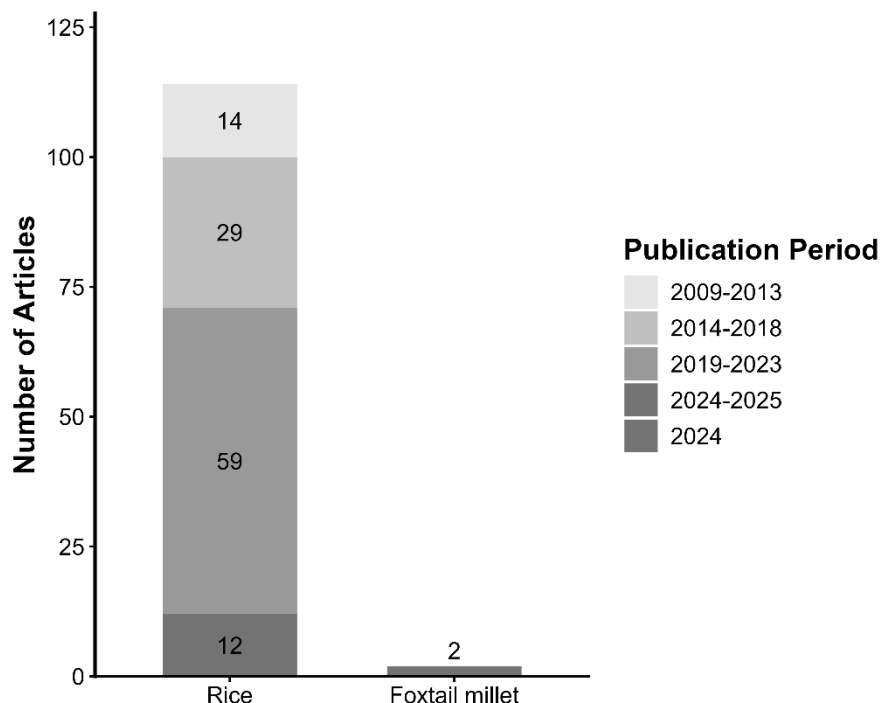
Publication Trends

The distribution of publications over time showed a strong dominance of rice over foxtail millet (Figure 2). A total of 114 publications on rice were identified, compared with 2 on foxtail millet. For rice, the years 2019–2023 had the most publications ($n = 59$), followed by 2014–2018 ($n = 29$), and 2009–2013 ($n = 14$). The fewest articles were identified in the 2024–2025 period ($n = 12$). However, this number cannot be interpreted as a downward trend in rice research, as the time span is relatively short and does not reflect the publication period (5 years). In contrast, foxtail millet had two publications in 2024.

This gap in publication output was reflected

Figure 2

Trends in Research Publications on the Thousand-Grain Weight of Rice and Foxtail Millet from 2009 to 2025



Notes. The figure shows the annual distribution of studies on rice and foxtail millet included in this systematic review. Publication years are grouped into approximately five-year intervals (2009–2013, 2014–2018, 2019–2023, and 2024–2025), with different bar colors representing each period. The 2024–2025 interval is included as the most recent publication period in rice, even though it covers fewer years. Studies on foxtail millet were reported only in 2024. Darker colors indicate more recent publication periods.

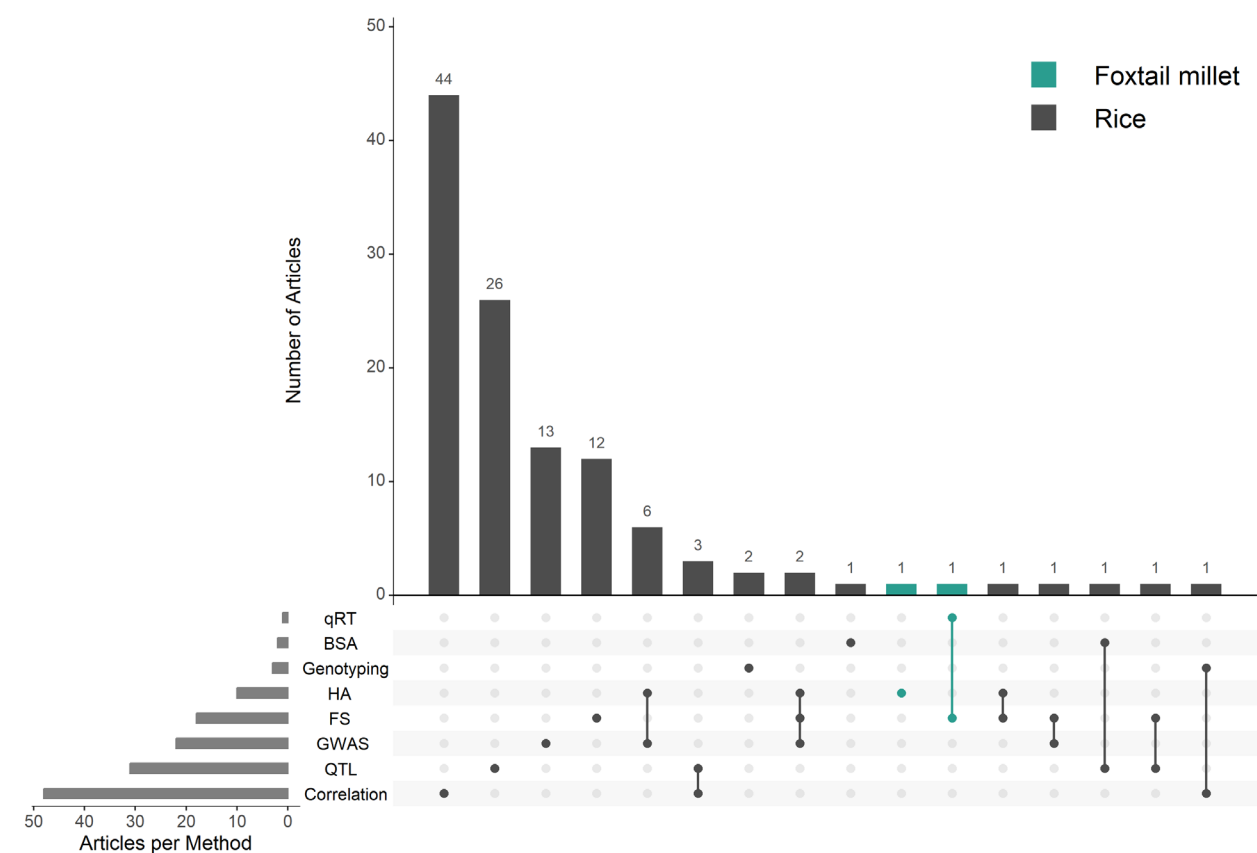
in global research trends in rice and foxtail millet. The global trend in rice research showed high output, with more than 8,000 published studies in 2020, whereas foxtail millet research remained very limited, with only 151 articles reported (Ardie et al., 2025; Ashfaq et al., 2025). These trends indicate that research is consistently focused on rice as a major staple crop and a model species in genetic studies. At the same time, foxtail millet remains underexplored despite its potential as a climate-resilient crop. Research has focused more on crops such as maize, rice, and barley, whereas climate-resilient cereals such as rye, oats, millet, and sorghum have received less attention (Manners & van Etten, 2018). The limited number of studies on foxtail millet indicates a considerable research gap and

suggests opportunities for future research.

Comparative Analysis of Research Methods in Rice and Foxtail Millet Studies

The distribution of research methods among all studies showed a clear dominance of rice studies (Figure 3). Rice studies employed nearly all available approaches to identify traits highly correlated with grain yield and to uncover genes or QTLs tightly associated with yield components, particularly thousand-grain weight (TGW). In contrast, only a limited number of studies focused on foxtail millet. Among the methods, correlation analysis was most frequently applied (n = 44) to establish trait-yield relationships, followed by QTL mapping (n = 26),

Figure 3
UpSet Plot of Research Methods used for Gene/QTL Identification Related to Thousand-Grain Weight in Rice (Dark Grey) and Foxtail Millet (Green)



Notes. Horizontal bars indicate the number of studies using each research method, whereas vertical bars represent the total number of studies for each method combination. Connected dots indicate studies employing multiple methods.

and GWAS ($n = 13$), which were used to locate genomic regions linked to yield traits. Functional studies ($n = 12$) further validated candidate genes, whereas other approaches, such as haplotype analysis, bulked segregant analysis (BSA), genotyping, and qRT-PCR, were rarely employed. In rice, research has advanced from correlation-based trait identification to functional validation of yield-related genes. By contrast, foxtail millet remains largely in the discovery phase, with limited use of advanced methods for dissecting yield traits.

The UpSet plot shows that single approaches were more common than combined ones. Nevertheless, several studies integrated multiple methods, particularly QTL, GWAS, and functional analyses, to strengthen their findings. The high frequency of correlation analysis shows its importance as an initial step in genetic studies. Correlation analysis is widely used in rice studies, serving as a standard approach for understanding trait interrelationships in multivariate evaluations of agronomic and grain-quality traits (Facchinello et al., 2023; Nagaraju et al., 2023; Semeskandi et al., 2024). Advanced approaches such as QTL mapping and GWAS are abundant in rice but absent in foxtail millet, reflecting the limited genomic resources available for this crop. Nevertheless, some studies on foxtail millet have employed approaches such as QTL mapping, GWAS, and correlation analysis in independent studies (Gao et al., 2025; Liu et al., 2022; Xue et al., 2025). However, these may not have been captured in the current PRISMA-based review, likely due to the restrictive use of Boolean operators that narrowed the search results.

Correlation Between Agronomic Traits and Grain Yield

The correlation between agronomic traits and grain yield in rice was extracted from 58 correlation analyses reported in 48 articles (Table 1). Correlation between traits varied across studies, and among the evaluated studies. TGW showed a strong positive correlation with grain yield, with 35 of 54 analyses displaying

significant results. Several traits showed substantial correlations with grain yield, including productive tiller number (89.7%), panicle number (84.6%), panicle weight (83.3%), filled grains per panicle (76.9%), and number of grains per panicle (63.6%). Traits such as plant height (27.5%) and days to flowering (20.0%–21.1%) showed weaker, more inconsistent relationships, suggesting that their effects may vary depending on genetic background and growing conditions.

The variation in correlation patterns across studies demonstrates the complex, polygenic nature of yield, in which multiple components interact to determine final productivity. The consistently strong correlation of TGW with yield supports its use as a primary target trait in genetic studies. Other crops, including sorghum, maize, and wheat, have shown a strong positive correlation between TGW and grain yield (Baye et al., 2020; Chibvongodze et al., 2025; Kumar et al., 2024). Given the strong, consistent correlation between TGW and grain yield across diverse studies and crops, it is important to explore the underlying genetic determinants that regulate this trait.

Candidate Genes Associated with Thousand-Grain Weight

Eight candidate genes associated with TGW were selected based on reports in at least two rice studies, providing recurrent evidence of their association with the trait across different studies (Table 2). The identified genes include *Grain Size 3 (GS3)*, *Grain Width 5 (GW5)*, *Thousand-Grain Weight 6 (TGW6)*, *Grain Weight 2 (GW2)*, *Grain Size 5 (GS5)*, *Grain Width 8 (GW8)*, *Grain Size 2 (GS2)*, and *Grain Width 5-Like (GW5L)*. These genes have been reported in rice, whereas only the *TGW6* homolog in foxtail millet (*SiTGW6*) has been reported by Zhang et al. (2024). Among these, *GS3*, *GW5*, *TGW6*, and *GW2* act as negative regulators of TGW, whereas *GS5*, *GW8*, *GS2*, and *GW5L* act as positive regulators. This indicates that TGW is influenced by the balance between growth-promoting and growth-suppressing factors. In Table 2, the foxtail millet homologs

Table 1

Summary of Reported Correlations Between Agronomic Traits and Grain Yield Across Studies with at Least Five Reports

Variable	No. of studies reporting	Significant positive	Significant negative	Non-significant	No data	% significant positive
Plant height	49	13	6	30	9	26.5
Tiller number	17	10	0	7	41	58.8
Total tillers per hill	5	3	0	2	53	60.0
Productive tiller number	29	26	0	3	29	89.7
Flag leaf length	10	4	0	6	48	40.0
Flag leaf width	7	3	0	4	51	42.9
Flag leaf area	8	6	0	2	50	75.0
Days to first flowering	5	1	1	3	53	20.0
Days to 50% flowering	19	4	4	11	39	21.1
Days to heading	5	1	2	2	53	20.0
Days to maturity	14	1	4	9	44	7.1
Panicle length	47	23	2	22	11	48.9
Panicle number	13	11	0	2	45	84.6
Grains per panicle	44	28	0	16	14	63.6
Filled grains per panicle	13	10	0	3	45	76.9
Unfilled grains per panicle	5	0	1	4	53	0.0
Spikelet fertility	17	10	4	3	41	58.8
Thousand-grain weight	54	35	5	14	4	64.8
Grain length	10	5	0	5	48	50.0
Grain width	10	0	0	10	48	0.0
Grain length breadth ratio	8	0	0	8	50	0.0
Panicle weight	6	5	0	1	52	83.3

Notes. Values represent the number of studies reporting significant positive, significant negative, and non-significant correlations between agronomic traits and grain yield. No data indicates unavailable or unreported information in the reviewed studies. The percentage of significant positive correlations was calculated as: (number of significant positive reports/number of studies reporting the trait) × 100.

of these rice genes are listed, most showing identity percentages greater than 70%. The identification of these homologs indicates high similarity and synteny between rice and foxtail millet, suggesting that rice genetic information can be applied to foxtail millet.

Among the eight identified genes, seven (*GS3*, *GW5*, *GW2*, *GS5*, *GS2*, *GW8*, *GW5L*) primarily regulate grain size, whereas only *TGW6* directly controls thousand-grain weight. Correlation studies (Table 1) demonstrated no significant relationship between grain width and

grain yield, and only half of the analyses reported a positive correlation between grain length and yield, indicating that grain size is not a consistent determinant of productivity. In contrast, the strong positive correlation between *TGW* and grain yield (64.8%) indicates that *TGW6* may act as a determinant of grain yield.

Studies in rice showed that *TGW6* (*LOC_Os06g41850*) encodes an IAA-glucose hydrolase that regulates early endosperm development in an IAA-dependent manner, thereby acting as a negative regulator of grain weight through

endosperm development rather than hull cell expansion (Akabane et al., 2024; Gasparis & Miłoszewski, 2023). The role of *TGW6* as a negative regulator of grain weight was further validated using CRISPR/Cas9-mediated editing, in which mutations in the coding region altered the protein sequence and increased TGW in mutant lines (~23.0 g) compared with wild-type (~21.1 g) (Han et al., 2018). Furthermore, allelic variation in *TGW6* appears to contribute to differences in grain weight, as the Nipponbare allele of *TGW6* was associated with higher TGW (~23.77 g) than the Kasalath allele (~22.19 g) (Zhong et al., 2020). A homolog of rice *TGW6* in foxtail millet, *SiTGW6* (*Seita.1G350400*), was identified as a key gene regulating grain weight, where elite haplotypes (H2 and H4) were associated with larger grain size and higher TGW. Similar to *TGW6*, *SiTGW6* also acts as a negative regulator, as lower *SiTGW6* expression was associated with higher grain weight (Zhang et al., 2024). In view of these functional insights, further analyses of nucleotide polymorphisms and the genomic position of *SiTGW6* provide valuable opportunities to develop SNP- and linkage-based markers to enhance its utility as a functional marker.

Genetic Variation and Gene Context of *SiTGW6*

A total of six single-nucleotide polymorphisms (SNPs), including both synonymous and missense mutations, were identified in the *SiTGW6* region by aligning sequences from 1,844 worldwide foxtail millet accessions available in SetariaDB (Table 3). The proportion of missing data (MISS) was minimal across all SNPs (0.00–0.01), indicating high data quality and the reliability of the identified variants. Among the identified SNPs, three were classified as missense variants with moderate predicted effects, whereas the remaining three were synonymous variants with low predicted impact. The presence of missense mutations suggests possible alterations in protein function that may affect *SiTGW6*'s role in regulating TGW. Similar functional implications of missense

mutations in which SNP variation contributes to phenotypic differences among cultivars have also been reported in rice genes such as *GS3*, *TAD1*, and *ABA8ox2* (Rachmandika et al., 2025). In terms of gene conservation, the minor allele frequencies (MAFs) of *SiTGW6* are relatively low (0.06–0.17), indicating high conservation among global foxtail millet germplasm. A similar pattern of conservation has been observed in rice, where *GS3* harbors only three SNPs (Rachmandika et al., 2025), supporting the idea that low SNP abundance reflects limited variability and strong gene conservation.

Notably, an SNP at position 40,392,218 had the highest MAF (0.17) and a moderate predicted effect, suggesting that this variant may contribute to the alteration of *SiTGW6*'s function. Although additional studies are required to validate its association with TGW, this SNP warrants further investigation to develop functional SNAP markers. A previously developed *SiDREB2*-based SNAP marker was associated with drought and salinity tolerance in foxtail millet (Widyawan et al., 2018). Therefore, establishing a SNAP marker linked to yield is expected to considerably accelerate the development of high-yielding, stress-tolerant foxtail millet varieties. It is also important to note that only one of the 1,844 foxtail millet accessions in SetariaDB is from Indonesia. Luthfiani et al. (2025) reported that Indonesian genotypes contained at least one unique variant in the *DUF-640* gene compared with those deposited in SetariaDB, indicating that Indonesian foxtail millet may harbor unique variants. Thus, further attempts should focus on characterizing variants in *SiTGW6* from Indonesian genotypes.

To further investigate the genomic content of *SiTGW6*, neighboring genes located upstream and downstream of the gene were identified using Phytozome (Figure 4). The *SiTGW6* gene is located on chromosome 1 at positions 40,391,499–40,392,549 bp on the forward strand. In the upstream region, a gene near *SiTGW6* was identified at 40,384,558–40,386,124 bp, designated *Seita.1G350300.1*. This gene showed no functional annotations, indicating that its role remains unclear. In

Table 2

Candidate Genes Associated with Thousand-Grain Weight Supported by Multiple Approaches Across Studies, and Foxtail Millet Homologs Identified through Phytozome

Gene name (abbreviation) / ID	Identification method	General function	Reference	Homolog of foxtail millet (Query coverage, Identity)	Chr: position	Gene length (bp)	Exon/ Intron
<i>Grain Size 3</i> (GS3) / LOC9269602/ Os03g0407400	QTL, GWAS, KO, BSA, Haplotype, Genotyping	Negative regulator	Xu et al. (2015), Feng et al. (2016), Liang et al. (2016), Gull et al. (2019), Yang et al. (2019), Badro et al. (2020), Ponce et al. (2020), Wang et al. (2020), Zhong et al. (2020), Cu et al. (2021), Niu et al. (2021), Usman et al. (2021), Yang et al. (2021), Zhong et al. (2021)	<i>Seita.9G369300</i> (37.93%, 76%)	9: 42,925,826- 42,931,050 (F)	5,224	5/4
<i>Grain Width</i> 5 (GW5) / LOC4338011 / Os05g09520	QTL, GWAS, KO, BSA, Genotyping, Haplotype	Negative regulator	Liang et al. (2016), Gull et al. (2019), Badro et al. (2020), Ponce et al. (2020), Wang et al. (2020), Niu et al. (2021), Liu et al. (2023), Zhao et al. (2023), Yang et al. (2024)	<i>Seita.3G109700</i> (100%, 72%)	3: 7,316,303- 7,320,277 (F)	3,974	3/3
<i>Thousand- Grain Weight 6</i> (TGW6) / Os06g0623700	KO, Genotyping, Haplotype, GWAS	Negative regulator	Wang et al. (2016), Han et al. (2018), Yang et al. (2019), Zhong et al. (2020), Zhang et al. (2024)	<i>Seita.1G350400</i> (88%, 77%)	1: 40,391,499- 40,392,549 (F)	1,050	1/0
<i>Grain Weight</i> 2 (GW2) / LOC4328856/ Os02g0244100	Genotyping, QTL, GWAS	Negative regulator	Gull et al. (2019), Badro et al. (2020), Hou et al. (2022), Zhao et al. (2023)	<i>Seita.1G020400</i> (100%, 85%)	1: 1,747,605- 1,752,816 (F)	5,211	8/7

Gene name (abbreviation) / ID	Identification method	General function	Reference	Homolog of foxtail millet (Query coverage, Identity)	Chr: position	Gene length (bp)	Exon/ Intron
<i>Grain Size</i> 5 (GS5) / Os05g0158500	QTL, Genotyping	Positive regulator	Gull et al. (2019), Zhong et al. (2020), Hou et al. (2022)	<i>Seita.7G269800</i> (92.12%, 83%)	7: 32,155,413- 32,161,591 (R)	6,178	12/12
<i>Grain Width</i> 8 (GW8) / Os08g0531600	GWAS, Genotyping	Positive regulator	Gull et al. (2019), Zhong et al. (2020), Zhong et al. (2021)	<i>Seita.6G223300</i> (69.67%, 69%)	6: 33,752,950- 33,758,240 (F)	5,290	3/2
<i>Grain Size</i> 2 (GS2) / Os02g0701300	GWAS, Genotyping	Positive regulator	Gull et al. (2019), Zhao et al. (2023)	<i>Seita.1G287100</i> (100%, 74%)	1:35,670,426- 35,674,285 (R)	3,859	5/4
<i>Grain Width</i> 5-Like (GW5L) / Os01g0190500	GWAS, QTL	Positive regulator	Yang et al. (2021), Zhong et al. (2021)	<i>Seita.5G135000</i> (100%, 69%)	5:11,758,132- 11,759,927 (F)	1,795	3/2

Notes. F = forward strand, R = reverse strand. QTL = quantitative trait locus, GWAS = genome-wide association study, BSA = bulked segregant analysis, KO = knockout. Foxtail millet homologs and information on gene length, exon/intron numbers, and chromosomal positions were obtained through BLAST analysis in the Phytozome database.

Table 3

SNP Variants in the SiTGW6 (Seita.1G350400) Gene Region Identified through Comparative Analysis of 1,844 Global Foxtail Millet Accessions Using SetariaDB

Position on Chr. 1 (bp)	Variant	Minor Allele	MAF	MISS	Effect
40,391,517	SNP (G/A)	A	0.10	0.00	Synonymous (low)
40,391,776	SNP (T/C)	C	0.07	0.01	Missense (moderate)
40,392,080	SNP (G/A)	A	0.07	0.00	Missense (moderate)
40,392,174	SNP (C/T)	T	0.06	0.00	Synonymous (low)
40,392,213	SNP (T/A)	A	0.17	0.00	Synonymous (low)
40,392,218	SNP (C/G)	G	0.17	0.00	Missense (moderate)

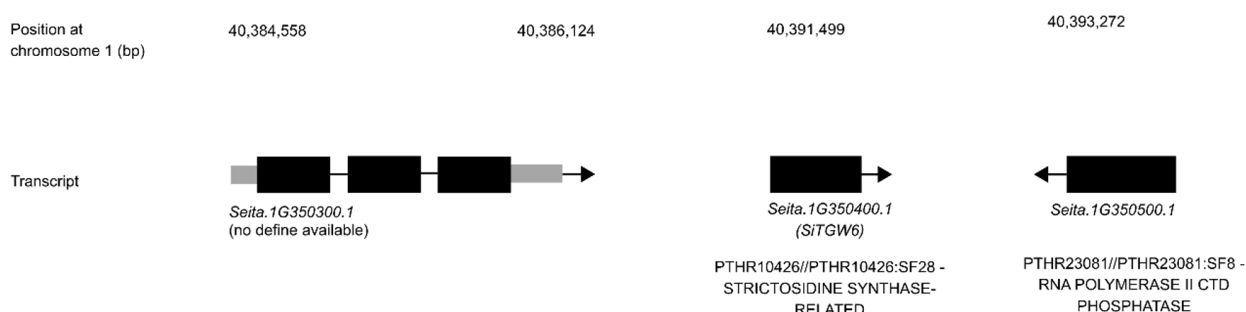
Notes. MAF, minor allele frequency; MISS, proportion of missing genotype data.

contrast, *Seita.1G350500.1*, located downstream at 40,393,272 bp, was annotated with several domains, including the BRCT domain, HAD-like domain, and FCP1 homology domain, all associated with transcriptional regulation. The distance between this gene and *SiTGW6* is approximately 700 bp. Linkage disequilibrium (LD) decay on chromosome 1 is 306 kb (Jaiswal et al., 2019), which means that this region is linked and may be co-inherited. Comparable observations have been reported in GWAS-based maize biofortification studies, in which

significant SNPs located near candidate genes within regions of LD decay have been predicted to be inherited together with the candidate genes (Suwarno et al., 2015). Genes surrounding *SiTGW6* may contribute to TGW phenotypic variation. Therefore, further studies are required to examine and integrate the combined effects of these genes on TGW.

Figure 4

Genomic Position and Transcriptional Orientation of *SiTGW6* (*Seita.1G350400*) and its Flanking Genes on Chromosome 1 of the Foxtail Millet Genome



Notes. The figure is based on genomic annotation data from Phytozome. Gene models are displayed according to their chromosomal coordinates. Black boxes represent exons, light gray boxes represent untranslated regions (UTRs), and black lines represent introns. Arrows indicate the transcriptional direction of each gene. The upstream gene (*Seita.1G350300.1*) and downstream gene (*Seita.1G350500.1*) are shown as the nearest flanking genes around the *SiTGW6* locus.

Future Direction and Implication

In Indonesia, foxtail millet is grown in several regions as an alternative food source, especially in West Sulawesi and Papua (Karamang et al., 2023; Ramlah et al., 2020). Considerable variability has been reported among Indonesian foxtail millet accessions (Ardie et al., 2017; Jannah et al., 2024; Ratnawati et al., 2024). Despite this genetic diversity, productivity improvement remains a major challenge. Ratnawati et al. (2024) reported that promising Indonesian accessions such as Hambapraing and Mauliru-2 produced 2.33 and 1.93 t/ha, respectively, which are substantially lower than the yield potential reported for cultivars in China, where productivity can reach up to 8 t/ha (Zhang et al., 2022). This yield gap illustrates the need for more efficient breeding approaches to improve genetic gain in Indonesian foxtail millet.

Foxtail millet breeding in Indonesia is still in its early stages. Previous studies have identified diverse local accessions, promising segregating populations, and potential high-yielding accessions for cultivar development (Butarbutar et al., 2024; Muzzayyanah et al., 2024; Ratnawati et al., 2024; Sintia et al., 2023). In addition, marker-assisted selection has been successfully demonstrated using

the *SiDREB2* marker for drought and salinity tolerance (Widyawan et al., 2018), indicating the feasibility of integrating molecular markers into foxtail millet breeding programs. These results show that molecular breeding approaches could support conventional selection and accelerate cultivar improvement.

In this context, since the previously developed *SiDREB2*-based marker was associated with drought and salinity tolerance, developing additional markers related to yield is of great importance, particularly for breeding foxtail millet varieties that combine stress tolerance with high yield. The present study provides a starting point for future gene mining and functional marker development for yield-related traits, particularly thousand-grain weight (TGW). Among candidate genes, *SiTGW6* is of particular interest, as several SNPs were identified within its genomic region. Future studies should validate the effects of these polymorphisms, assess allelic variation across germplasm collections, and elucidate on the contribution of *SiTGW6* to thousand-grain weight through association and functional analyses. Together with advances in genomic resources, including QTL mapping, genome-wide association studies, and molecular marker technologies, such integrated approaches may facilitate the development of functional markers

for precision breeding of high-yielding foxtail millet varieties in Indonesia and other regions (Gandhimeyyan et al., 2023; Pareek et al., 2026).

Conclusions

A systematic literature review analyzed 116 publications, of which 114 focused on rice and 2 on foxtail millet. Correlation studies in rice were the main approach for identifying yield-associated traits and consistently showed that thousand-grain weight (TGW) was the trait most positively correlated with grain yield. Eight genes were frequently reported to influence TGW: seven (*GS3*, *GW5*, *GW2*, *GS5*, *GS2*, *GW8*, *GW5L*) regulate grain size, whereas *TGW6* directly regulates TGW. These genes were subsequently used to identify homologs in foxtail millet. In foxtail millet, *SiTGW6* (*Seita.1G350400*), the homolog of rice *TGW6* contains a variant at 40,392,218 bp (MAF 0.17; moderate effect), warranting further investigation for SNP-based marker development. *SiTGW6* is located in a linkage disequilibrium (LD)-decay region that includes one unannotated gene (*Seita.1G350300.1*) and *Seita.1G350500.1*, which has transcriptional regulation domains such as BRCT, HAD-like, and FCP1. These features suggest potential linkage markers that may enhance the utility of *SiTGW6*. Overall, this study identifies *SiTGW6* as a potential genetic target, with both SNP-based and linkage-marker development aimed at improving selection accuracy in foxtail millet breeding.

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