Review article

Foxtail millet research in supporting climate change resilience efforts: Bibliometric analysis and focused literature review

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ABSTRACT

Foxtail millet is part of the millet group but is less popular than sorghum and pearl millet. Nevertheless, the potential of this plant is considered promising for diversifying food nutrition, health products, feed, biofuel, and several other uses, as indicated by various publications, including review articles. However, studies, analyses, and development trends of foxtail millet are lacking, and the current development status of foxtail millet and future projections cannot be systematically identified. Bibliometric analysis offers a method to clarify the current state of the development and interaction of a study topic for systematic analysis. Therefore, this study conducted a bibliometric review to examine the development, interaction, and projections of foxtail millet research regarding publication trends, countries involved, and keywords. Publications related to foxtail millet were first mined from the Scopus database and analyzed using Biblioshiny R Studio and VOSviewer software, with 2091 Scopus documents identified as being associated with the topic of foxtail millet. A significant development occurred in 2012 when the entire foxtail millet genome was explored. The main countries that focus on developing foxtail millet are China and India. The development of foxtail millet is focused on optimizing omics-based approaches to support the use of its potential, especially in research efforts involving climate change tolerance systems. Therefore, innovation, exploration, and potential use of foxtail millet in the future will continue to develop along with submarginal land and public health problems, including in Indonesia, which has the fourth largest population globally.

1. Introduction

A substantial global caloric intake is derived from cereals dominated by wheat, rice, and maize [1]. The Green Revolution has enabled the domination of wheat, rice, and maize over other cereals. A remarkable increase in the global cultivation of these crops has been recorded since 1961, whereas the cultivation of other minor cereals, including barley, sorghum, and millet, has declined

dramatically [2]. Maintaining and preserving indigenous species such as millet is crucial for sustainable food production in a changing climate [3]. Millets are a group of small-grained cereals belonging to the Panicoidae subfamily of the Poaceae family [4]. Foxtail millet (*Setaria italica* L. Beauv.) is the second most cultivated small millet after pearl millet [1]. The economic significance of foxtail millet has increased as a nutritious food crop [5], feed and fodder [6], biofuel [7], and a model crop for other cereals [8]. Foxtail millet is considered a climate-resilient crop [9] as this demonstrates outstanding performance under adverse environmental conditions, including drought [10], salinity [11], and limited nitrogen and phosphate availability [12]. Thus, foxtail millet is an important crop in many areas, such as Africa, where water scarcity is a major limiting factor for crop production [13]. Moreover, foxtail millet is gaining increased recognition as a nutricereal because of its nutritional attributes, including a low glycemic index, high protein and dietary fiber content, and high antioxidant activity [14] and its health-promoting features, such as cardiovascular risk factor reduction [15], hypertension prevention [16], and therapeutic capacity against various cancers [17,18] and neurological disorders [19]. Foxtail millet is naturally gluten-free [20], thus providing valuable alternatives for people with celiac disease. Furthermore, foxtail millet has potential for biofuel purposes because of its genetic proximity to the biofuel crop switch grass (*Panicum virgatum*) [21]. These attributes indicate a high potential for foxtail millet, which requires proper attention. A considerable number of reviews on foxtail millet have been published with emphasis on particular areas of interest, such as adaptation to unfavorable environmental conditions [12,22–26], nutritional and health benefits [5,27–32], and genetics and genomics [4,33–36]. However, to our knowledge, no comprehensive report on the foxtail millet research trend is currently available.

Bibliometric analysis is an increasingly popular method that effectively analyzes large volumes of scientific papers to map and identify research trends and gaps as the basis for strategies for the future development of a particular field of interest [37,38]. Bibliometric analysis of major crops such as rice [39–43], wheat [39], and maize [44], as well as several other minor cereals, such as sorghum [45] and pearl millet [46], have been conducted to provide valuable information for directing the development of these crops. A bibliometric analysis of millet as a group showed an increasing trend in millet research over the years [47]. However, based on the PubMed database, the previously available bibliometric study on millet only provides a simple overview, where foxtail millet ranked second in published research articles after pearl millet. Herein, we applied bibliometric analysis to conduct a more advanced and detailed analysis to identify key research trends, potential challenges, and opportunities to improve foxtail millet as a climate-resilient crop for sustainable food production.

2. Materials and methods

This study employed a systematic methodology using bibliometric analysis to examine the progression and trends in foxtail millet across three principal phases (Fig. 1). The primary phase encompasses data mining via subject-specific literature exploration. The subsequent phase involved a comprehensive bibliometric analysis incorporating various parameters. The final stage focuses on presenting the outcomes. The literature review exclusively incorporated pertinent references identified through bibliometrically derived keywords. The methodological approach adopted for each phase was elaborated and delineated in subsequent sections and was slightly modified from those of Djalal et al. [48] and Anshori et al. [40].

2.1. Literature search strategy

This information was obtained via document mining of Scopus on January 29, 2024. Scopus was chosen because of its extensive coverage and accessibility to research publications across various fields [49]. This bibliographic data mining focused on foxtail millet (ARTICLE TITLE, ABSTRACT, KEYWORDS (foxtail AND millet)) within Scopus. The search identified 2091 documents, comprising 1884 articles, 8 books, 57 book chapters, 29 conference proceedings, and other document types. The mined data encompassed article titles, abstracts, and keywords.

2.2. Bibliometric analysis

The concept and procedure of bibliometric analysis in this research refer to the working concept of Anshori et al. [40], especially regarding the use of Biblioshiny and VOSviewer. Three methods were employed for the bibliometric analysis: general data analysis, global topic development, and keyword-based topic development. This analysis used VOSviewer (Leiden University, Leiden, Netherlands) and RStudio (version 3.6.1, R Studio Inc., Boston, MA, USA) to leverage the bibliometrix package. Each software program has specific functions for creating bibliometric analysis.

VOSviewer software is commonly used in bibliometric analyses. This software primarily deals with document data and interrelated knowledge units to construct a scientific knowledge map depicting the interconnectedness within the literature on the subject [50].
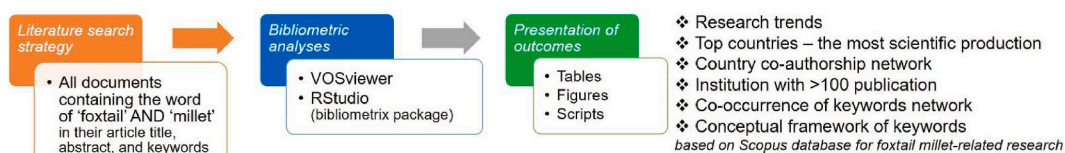

Fig. 1. Flow chart of the bibliometric review process.

VOSviewer provides extensive graphical representation and versatile adaptability with diverse database formats [51]. This software identifies clusters of interactions and collaborations across nations, keyword interactions, and citation interactions among the publishers. The depicted items are visualized through a label and a circle, where the circle's size indicates the item's frequency of appearance. To prevent overlap, some items were omitted from the analysis. The colors used in the network visualization or text maps indicate clusters of similar items determined by the program. The distances between items reflect the intensity of their relationships [52].

RStudio, coupled with the bibliometric package, supports bibliometric concepts and is free of cost. This software can access various data mining sources, enhance reference clarification through string-based algorithms, perform direct and tri-cited analyses, and employ a hybrid approach that combines bibliometric and semantic methodologies. From a technical perspective, we used Biblioshiny to facilitate the generation of informative figures and summary information tables, as previously described by Aria and Cuccurullo [53].

3. Results

3.1. General trends in foxtail millet-related documents in Scopus

Data mining results in Scopus identified 698 journals involved in publishing studies on foxtail millet, with an average annual increase of 3.44 %. The mining results included 5554 authors with an average of 5.92 coauthors per document and an international rate of 20.23 %. The average citation rate per document was 21.84. These results provide fundamental data for assessing the overall research development on foxtail millet.

General trends in the publication of research findings on foxtail millet from the Scopus database began in 1942 and continued until 2024 (Fig. 2). The highest increase occurred in 2022 with nearly 300 articles, reaching 75 % of articles from the previous year, followed by a slight decline in 2023, then experienced a steep drop in early 2024 because the data obtained was only from January. Meanwhile, several peaks occurred in the average quotations per year, with the highest peak in 2012, followed by 2009. However, after 2012, the number of articles published per year decreased drastically by 2023 and 2024.

3.2. Country trends in foxtail millet-related documents in Scopus

Based on country trends for the foxtail millet topic, China and India were the most productive countries in generating scientific publications, totaling 7121 and 1,906, respectively, far exceeding the USA as the third-ranked country, with only 858 publications (Table 1). Many citations accompanied a significant number of publications. The top three countries with the highest citations in foxtail millet publications were China, India, and the USA, with 15,268, 7,198, and 4569 publications, respectively. However, Canada, with only 88 publications in the last eight decades, had a total citation count of 2,478, and the UK, which produced only 168 publications with a total citation count of 1334. Consequently, the highest article citation average was in Canada at 95.30, followed by the UK at 53.40, significantly higher than China (only 18.10).

The roles of institutions determined the results of this study. Seven of the eight institutions with the most relevant publications were from China, where Shanxi Agricultural University had the highest publication output on this topic (Table 2). In contrast, India has only one representative institute, the National Plant Genome Research Institute (NIPGR), which focuses on developing foxtail millet research topics and is ranked fifth.

Analysis of the publication interactions between countries (Fig. 3A) identified two major clusters (red and blue) and three minor
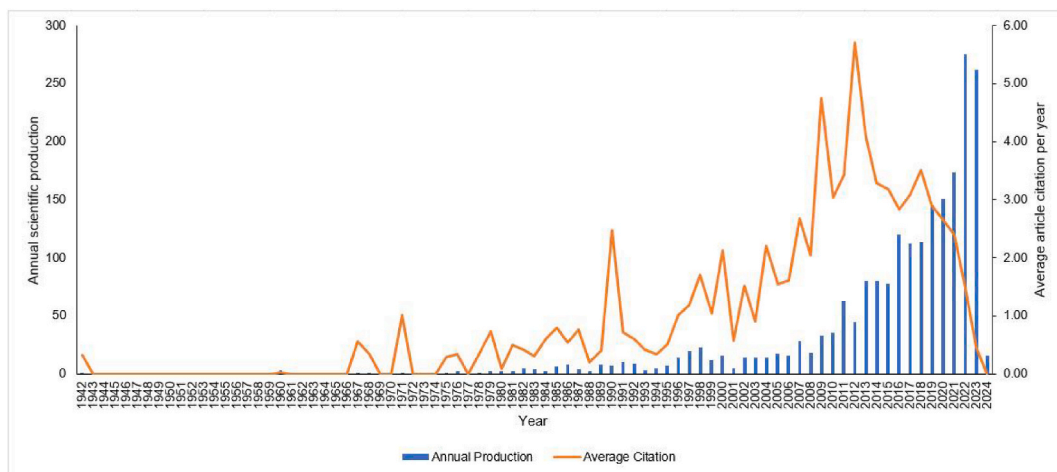

Fig. 2. Annual publication rate and average citation per year based in the Scopus database (1942–2024) for foxtail millet-related research.

Table 1
Top 15 countries with the highest scientific production based on the Scopus database (1942–2024) for foxtail millet-related research.

Country	Total publication	Total citation	Average article citations
China	7121	15,268	18.10
India	1906	7198	21.10
USA	858	4569	38.70
Japan	512	1269	20.80
South Korea	250	1007	28.00
United Kingdom	168	1334	53.40
France	157	523	30.80
Australia	117	175	12.50
Iran	110	112	5.30
Germany	92	552	42.50
Canada	88	2478	95.30
Indonesia	83	99	4.70
Argentina	68	90	11.20
Brazil	60	63	7.00
Pakistan	53	21	3.50

Table 2
Institutions with 100 or more publications based on the Scopus database (1942–2024) for foxtail millet-related research.

Institution	Total publications	Country
Shanxi Agricultural University	945	China
Institute of Crop Sciences, Chinese Academy of Agricultural Sciences, China	575	China
China Agricultural University	373	China
Shanxi University	258	China
National Institute of Plant Genome Research (NIPGR)	178	India
Northwest A&F University	154	China
Shandong Agricultural University	129	China
Lanzhou University	114	China

clusters (yellow, purple, and green). The first major cluster (red) was centered on China, followed by the USA, UK, Canada, and Denmark, which had strong relationships. The next major cluster (blue) was centered on India, encompassing South Korea, Spain, and Brazil. The minor green cluster focuses on Japan, connecting Australia and Indonesia. From 2010 to 2012, research was centered on Japan, France, and Canada (Fig. 3B), shifting to the USA and India in the following years. Publications in 2018 were predominantly from China and recently expanded to include Indonesia and Spain.

3.3. Foxtail millet thematic research area

Analysis of thematic research areas is a key aspect of bibliometrics. Based on this analysis, three main clusters related to the scope of keywords in publications were identified in Scopus for foxtail millet research (Fig. 4A). The first cluster (red) had a central point in foxtail millet research. It was related to China, rice, chemistry, and *Panicum miliaceum*, which revolved around foxtail millet keywords related to millet plant scope and the general sciences associated with this. The green cluster focuses on metabolism and encompasses controlled studies, genetics, and physiology. The blue cluster revolved around Setaria plants and their genetics. The yellow cluster focused on maize and sorghum, closely related to cereal plants, especially foxtail millet.

Fig. 4B shows that, near the beginning of 2014, research focused on the general scope of cereal plants/Poaceae, including *Panicum miliaceum* and *Triticum aestivum*, and then shifted to molecular genetics, nucleotide sequence, variability, and chromosome mapping in the following years. Subsequently, the research was expanded to other species closely related to foxtail millet (e.g., maize and sorghum) in 2016 and then moved toward controlled study components, plant proteins, plant genes, and physiology related to foxtail millet. Since 2018, research has focused on genetics and metabolism, especially abiotic stress.

After adjusting related keywords, grouping similar terms, and removing unrelated keywords (article, female, moisture, non-human, priority journal, procedures, review, and unclassified drug), two keyword clusters were identified based on multiple correspondence analysis (Fig. 5). Keywords related to species close to foxtail millet, including sorghum, rice, *T. aestivum*, *P. miliaceum*, and antioxidants, exhibited significant diversity in the red cluster. Foxtail millet was in the red cluster's center, signifying the keywords' stability in that cluster. The blue cluster was determined using keywords related to foxtail millet studies, such as genotype, chemistry, physiology, physiological stress, *Arabidopsis*, and plant genomes.

Table 3 displays publications with the most citations over the past 82 years. We found that publications on genome sequencing are a fundamental topic to which authors frequently refer. This correlates with the data presented in Fig. 2, and the high average number of citations per year in 2012 is due to the abundance of publications on genome sequencing that year. This research was published in several well-known journals, where Nature published the most primary documents related to foxtail millet, followed by PNAS.
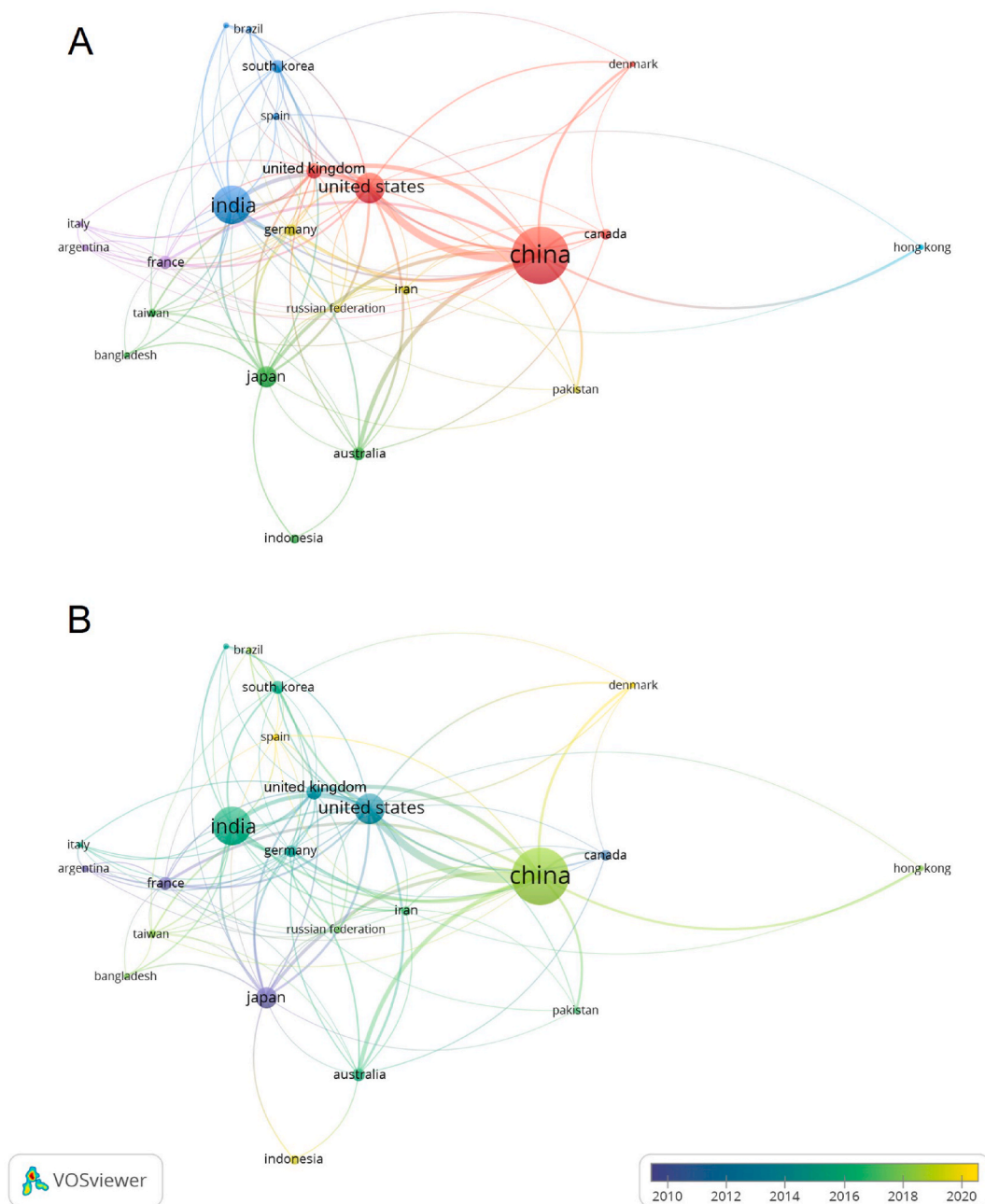
Fig. 3. Country coauthorship network (A) and time frame (B) based on the Scopus database (1942–2024) for foxtail millet-related research.

4. Discussion

4.1. Trends and insights into foxtail millet research

Over the past 20 years, the number of scientific papers related to foxtail millet has increased noticeably (Fig. 2), indicating a growing scientific interest in foxtail millet-related research. Nevertheless, there is a lag in the scientific production of other millet, such as sorghum and pearl millet. A bibliometric analysis of global research on millets based on research articles published in PubMed (NLM) between 1857 and 2023 showed that the total number of papers on sorghum, pearl millet, and foxtail millet were 3,801, 634, and 273, respectively [46]. A more detailed bibliometric analysis of sorghum using research articles available on Scopus showed that the total number of publications on sorghum-related research per year was almost 500 in 2000 and increased dramatically to almost 1600 in 2020 [45]. However, only 16 publications in 2000 and 151 in 2020 were related to foxtail millet-related research (Fig. 2),
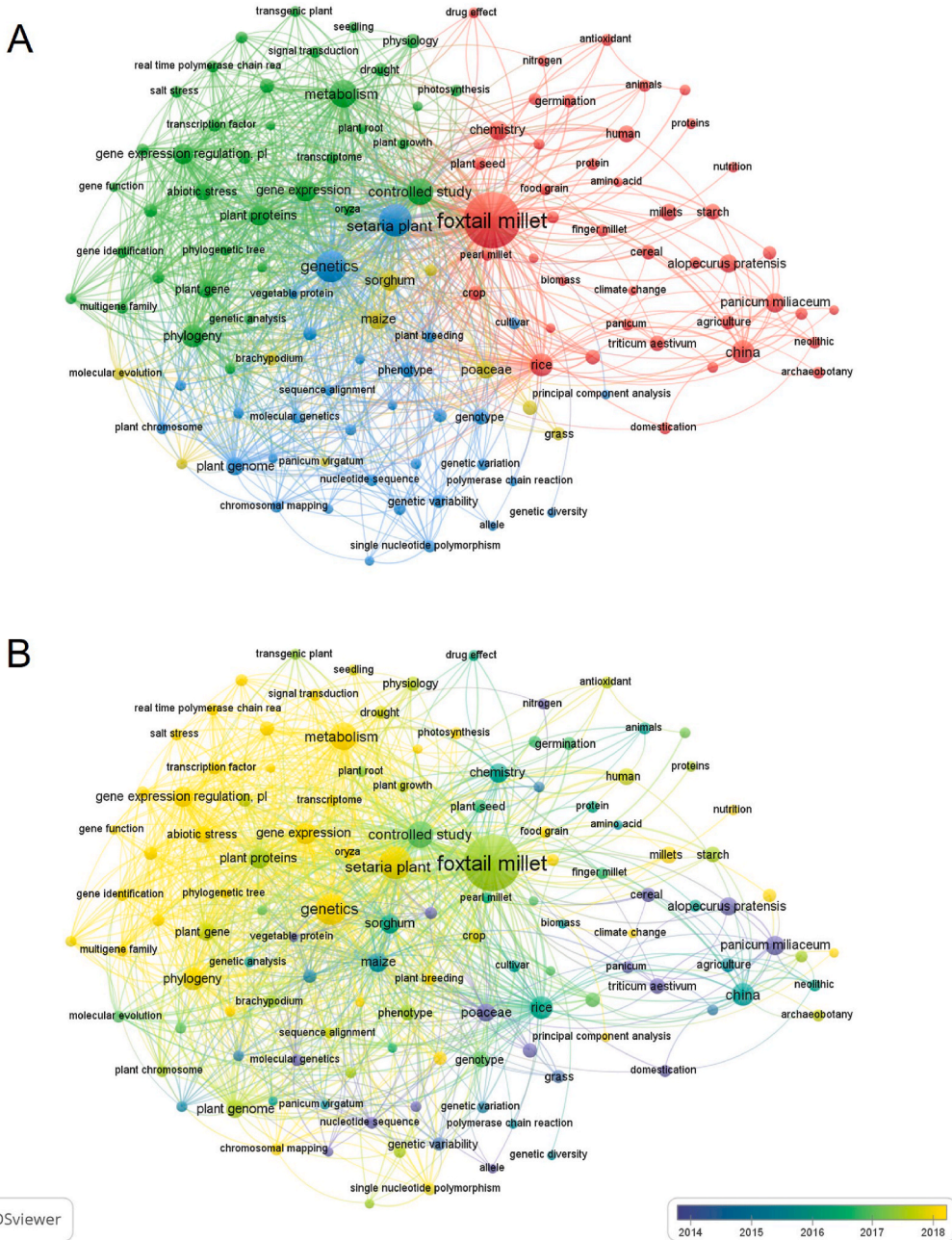
Fig. 4. Network visualization of the co-occurrence of keywords (A) and its time frame (B) based on the Scopus database (1942–2024) for foxtail millet-related research.

showing the delayed development in foxtail millet-related research compared to sorghum-related research. Scientific interest in particular crops may reflect their global economic importance.

Sorghum and pearl millet are categorized as major millets because of their larger grain size and wider cultivation region. In contrast, foxtail millet is categorized as a minor millet because of its smaller seeds and smaller area of cultivation [13]. Consequently, foxtail millet has significantly lower yield and productivity and thus, has lower economic importance. To illustrate, in India alone between 2010 and 2019, pearl millet was cultivated in 7.89 million hectares with a productivity of 1.15 tons/ha, followed by sorghum, with 6.04 million hectares with a productivity of 0.88 tons/ha. In contrast, the cultivation area of foxtail millet was only 0.67 million hectares, together with other minor millets (Kodo millet, little millet, barnyard millet, and proso millet), with only 0.63 tons/ha productivity [54]. However, in China, foxtail millet cultivation is increasingly developing, reaching 0.9 million hectares in 2017 [55]. Therefore, this crop will be a secondary important crop supporting food and feed security worldwide.
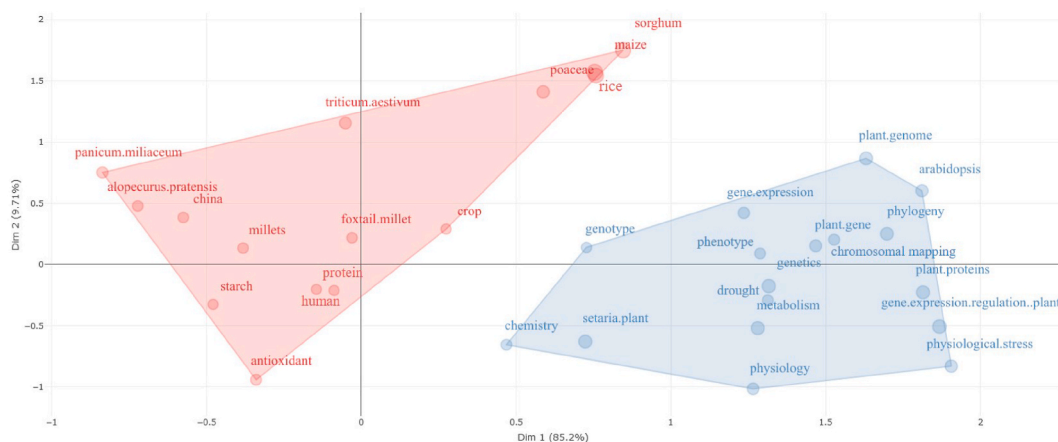
Fig. 5. Factorial map of keywords in the Scopus database (1942–2024) for foxtail millet-related research.

Table 3
Top 15 most cited scientific publications from the Scopus database (1942–2024) for foxtail millet-related research.

No	Title	Journal	Year	Total citations	Total citations per year
1	Reference genome sequence of the model plant Setaria [OA] [a]	Nature Biotechnology	2012	657	54.75
2	Earliest domestication of common millet (*Panicum millaceum*) in East Asia extended to 10,000 years ago [OA] [a]	PNAS	2009	583	38.87
3	How important are transposons for plant evolution?	Nature Reviews of Genetics	2013	573	52.09
4	The genome sequence of foxtail millet (*Setaria italica*) provides insights into grass evolution and biofuel potential [OA] [a]	Nature Biotechnology	2012	531	44.25
5	Switchgrass genomic diversity, ploidy, and evolution: Novel insights from a network-based SNP discovery protocol [OA] [a]	PLOS Genetics	2013	511	46.45
6	Content of insoluble bound phenolics in millets and their contribution to antioxidant capacity	Journal of Agricultural and Food Chemistry	2010	381	27.21
7	Agricultural origins and isotopic identity of domestication in northern China [OA] [a]	PNAS	2009	381	25.4
8	Early millet use in northern China [OA] [a]	PNAS	2012	363	30.25
9	Antioxidant activity of methanolic extracts from some grains consumed in Korea	Food Chemistry	2007	349	20.53
10	Haplotype map of genomic variations and genome-wide association studies of agronomic traits in foxtail millet (*Setaria italica*)	Nature Genetics	2013	325	29.55
11	Differential response of antioxidant compounds to salinity stress in salt-tolerant and salt-sensitive seedlings of foxtail millet (*Setaria italica*)	Physiologia Plantarum	2000	324	13.5
12	Mechanisms of plant salt response: insights from proteomics	Journal of Proteome Research	2012	316	26.33
13	Rapid reorganization of resistance gene homologs in cereal genomes [OA] [a]	PNAS	1998	315	12.12
14	New archaeobotanic data for the study of the origins of agriculture in China [OA] [a]	Current Anthropology	2011	314	24.15
15	Nitrogen-to-protein conversion factor for ten cereals and six legumes or oilseeds. Reappraisal of its definition and determination. Variation according to species and seed protein content	Journal of Agricultural and Food Chemistry	1990	294	8.65

[a] [OA] = open access.

The number of foxtail millet-related scientific outputs also indicates the country-based significance of this crop. China and India are the two most productive countries in generating foxtail millet-related scientific publications (Table 1), reflecting the important role of foxtail millet in these countries. The importance of foxtail millet in China is based on its historical origin. Archaeological evidence indicates that foxtail millet was first domesticated in the Chisan and Yellow River Valleys in the northern province of China [55,56]. Between 2014 and 2016, China was the leading producer of foxtail millet (1.74 million metric tons, MMT), followed by India (0.07 MMT) [1,57,58]. The genetic diversity and varietal development of foxtail millet in these two countries likely contributed to their high production in China and India. The Chinese Gene Bank (China) holds the most extensive collection of foxtail millet germplasms (~28, 000 accessions) [6]. In contrast, approximately 1535 cultivated foxtail millet germplasms are stored at the International Crop Research Institute for the Semi-Arid Tropics (ICRISAT, India) [59]. Approximately 870 foxtail millet cultivars have been released in China since 1950, including several leading cultivars such as the super cultivars "Yugu 1" and "Zhaogu 1," which have improved grain yield and food quality [57] and "Jigu 3," which provides a stable high yield under stress conditions [60]. At least 23 foxtail millet cultivars have been released in India, with "GPUF 3" as the latest variety developed from pure line selection from germplasm "IC 479864" [61]. Thus, institutions with ≥100 publications on foxtail millet-related research are dominated by those in China, with the National Plant Genome

Research Institute (NIPGR) being the only Indian institution listed (Table 2). However, the two countries appear to work less collaboratively on crops. China collaborates strongly with the USA and the UK in foxtail millet-related research. In contrast, India works independently with some collaboration with South Korea, Spain, and Brazil (Fig. 3A). We suspect that the reasons for the infrequent research collaboration between the two countries are as follows: 1) both countries have well-established research institutions; 2) each has an abundant collection of germplasm and does not require the exchange of germplasm between them; 3) they have breeding objectives from different germplasm sources and technologies; and 4) student exchanges between China and India are limited. We find it challenging to provide literary evidence; these are merely observations and speculations by the author.

Several countries, including Spain, Denmark, and Indonesia, have recently begun to research foxtail millet (Fig. 3B). Indonesia cultivates foxtail millet [56,62], although foxtail millet-related publications only began to increase in early 2020. Indonesia is among the top 15 countries producing the most scientific papers on foxtail millet in Scopus (Table 1). Foxtail millet is considered underutilized in Indonesia, and no superior foxtail millet variety has been released in the country to date [63]. However, the crop has gained significant scientific interest in recent years. The involvement of more countries and research groups in studying foxtail millet is essential for accelerating foxtail millet development, especially considering the lag in research advancement compared to other major cereals.

Canada had a very high average citation count despite having only the eleventh-highest number of publications. Canada had an average citation >95, which was far higher than the country with the second-highest average citation, the UK, which did not reach 55. The titles of articles with high citation numbers are generally related to phenolics or antioxidants, which are often cited in other publications, especially in the Introduction section on the excellence of foxtail millet [64], with some appearing in the Discussion sections of publications on the content of foxtail millet seeds [65]. Several high-citation publications from Canada include "Content of insoluble bound phenolics in millets and their contribution to antioxidant capacity" and "Determination of antioxidant activity in free and hydrolyzed fractions of millet grains and characterization of their phenolic profiles by HPLC-DAD-ESI-MSn."

Furthermore, the co-occurrence of keywords and multiple correspondence analysis based on keywords in foxtail millet-related

Table 4
Database resources for genomic, transcriptomic, and proteomic research in foxtail millet.

Database	Database URL	Description/Specific Information for Foxtail Millet		References
Phytozome	https://phytozome-next.jgi.doe.gov/	**Comparative Plant Genomic Database** Database of high-quality assembled and annotated plant genomes, including *S. italica*. General features for genomic studies include genome browser, gene search, sequence alignment using BLAST, and synteny analysis.	*S. italica* v2.2. *Setaria italica* cv. Yugu1 https://phytozome-next.jgi.doe.gov/info/Sitalica_v2_2	[66,160]
Gramene	https://www.gramene.org/		*S. italica* v2.0. Source*: JGI, Setaria italica* cv. Yugu1 https://ensembl.gramene.org/Setaria_italica/Info/Index	[66,69, 72–74]
NCBI	https://www.ncbi.nlm.nih.gov/		*S. italica* Source: JGI, *Setaria italica* cv. Yugu1; Academia Sinica, *Setaria italica* cv. TT8 https://www.ncbi.nlm.nih.gov/datasets/genome/?taxon = 4555	[66,68]
PlantTFDB 5.0	http://planttfdb.gao-lab.org/	**Transcription Factor Database** Genome-wide transcription factors, with physical map, tissue specific-expression data, and their functional annotation. The new version PlantTFDB 5.0 has been incorporated into PlantRegMap. The PlantRegMap (plant transcriptional regulatory map) provides a comprehensive, high-quality resource of plant TFs, regulatory elements, and interactions between them, advancing the understanding of plant transcriptional regulatory system	Source: JGI, *Setaria italica* cv. Yugu1 http://planttfdb.gao-lab.org/index.php?sp = Sit	[22,75–77, 161]
PlantRegMap	http://plantregmap.cbi.pku.edu.cn/			
MDSi	http://foxtail-millet.biocloud.net/home	**Multiomics Database for *Setaria italica*** Integrated and visualized genomics, transcriptomics, and metabolomics data from whole-genome resequencing (WGS) data of 360 foxtail millets (including the "*xiaomi*" genome) and 38 green foxtails germplasms		[78,107, 132,162]
FmMDb	http://www.nipgr.res.in/foxtail.html	**Molecular Marker Database for *Setaria italica*** A comprehensive online database for information retrieval, visualization, and management of large-scale marker datasets (DNA markers such as genomic- and genic SSRs with ILP markers) with unrestricted public access		[89]
FmMiRNADb	59.163.192.91/FmMiRNADb/index.html	**miRNA Database for *Setaria italica*** A web-based, searchable, and downloadable database with unrestricted public access to the complete miRNA information (chromosomal location, length, MFE, AMFE, sequences of pre-miRNA and mature miRNA, secondary structure, and target gene information) with interactive physical map viewing and miRNA information browsing chromosome-wise.		[83]
FmTEMDb	59.163.192.83/ltrdb/index.html	**Transposable Element-based Marker Database for *Setaria italica*** An open-access database of identified TE and TE-based markers (retrotransposon-based insertion polymorphisms, inter-retrotransposon amplified polymorphisms, repeat junction markers, repeat junction-junction markers, insertion-site-based polymorphisms, and retrotransposon-microsatellite amplified polymorphisms)		[82]

research (Figs. 4 and 5) provide important insights into the key research areas of this crop. We identified two key research areas that have sparked the greatest interest in foxtail millet research: (i) foxtail millet use as a crop plant and its genetic relationship with other cereal crops and (ii) foxtail millet genomics (especially functional genomics that links genomic data to abiotic stress tolerance in foxtail millet). While the first key research area seemed to have gained significant interest until around 2015, the second key research area received growing attention in the last decade and is likely to become an important research area in the future, considering the rapid advancement of molecular biotechnology and increasing environmental challenges due to the changing climate.

4.2. Progress in foxtail millet genomics

The availability of the first draft genome for foxtail millet in 2012 [66,67] led to a sharp increase in the publication of foxtail millet-related research (Fig. 2) and is considered a milestone in foxtail millet genomics. The Beijing Genome Initiative (BGI, China) and the United States Department of Energy-Joint Genome Initiative (USDOE-JGI, USA) independently sequenced the foxtail millet genome using different cultivars and genome-sequencing approaches [7,66,67]. The foxtail millet cultivars "Zhang gu" and "A2" accession were sequenced by BGI using a genome shotgun combined with Illumina next-generation sequencing, producing an ~423 Mb draft genome, with ~28 Mb (6.6 %) gaps and a predicted genome size of ~485 Mb [7,67]. Meanwhile, the foxtail millet cultivar "Yugu 1" and a green foxtail (*Setaria viridis*) accession "A10" were sequenced using the Sanger ABI3730xl platform, the 454 FLX platform, and the Illumina Genome Analyzer II platform, producing an ~400 Mb draft genome with a genome coverage of ~80 % and covering >95 % of the gene space [7,66], which is currently used as a reference genome in many databases. The availability of foxtail millet genome sequences has supported the discovery of novel genes associated with important traits, high-density linkage maps, and molecular marker development to accelerate foxtail millet breeding. Multiple databases that provide sequence information on foxtail millet are summarized in Table 4. Phytozome, Gramene, and NCBI provide high-quality assembled and annotated foxtail millet genomes to facilitate genomic studies with user-friendly features, including genome browsers, gene searches, sequence alignment using BLAST, and synteny analysis [66–74]. Approximately 2410 foxtail millet transcription factors (TFs) have been identified and classified into 56 families from the annotated genes in JGI (v2.2) and deposited in PlantTFDB 5.0. The incorporation of PlantTFDB 5.0 into PlantRegMap (plant transcriptional regulatory map) provides a comprehensive, high-quality resource of TFs in foxtail millet, as well as the regulatory elements and interactions between them, advancing the understanding of the transcriptional regulatory system of foxtail millet [75–80]. The sequenced foxtail millet genome also showed that ~46 % of the "Zhang gu" genome and ~40 % of the "Yugu 1" genome comprise transposable elements (TEs) [66,67]. TEs play significant roles in the evolution and function of the genome and act as significant endogenous gene expression regulators that determine phenotypic variations in plants [81]. The fact that foxtail millet has relatively lower TEs than other Poaceae members, including sorghum (~62 %), wheat, and maize (>80 %) ([66,67], favors the use of foxtail millet as a model. The foxtail millet transposable element database (FmTEMDb) provides publicly available identified TEs and TE-based markers to enable large-scale genotyping applications in foxtail millet and related grass species [82].

The availability of the foxtail millet genome sequence also provides the opportunity to identify microRNAs (miRNAs), important post-transcriptional gene regulators, in foxtail millet [66,83]. Up to 355 mature miRNAs have been identified, classified into 53 miRNA families, and made publicly available in the Foxtail millet miRNA Database (FmMiRNADb) [83]. The development of molecular markers for foxtail millet began before the release of the genome sequence [84,85], which further enabled the development of large-scale molecular markers, including SSRs [86], EST-SSRs [87], and ILP markers [88]. The foxtail millet marker database (FmMDb) was developed to provide complete marker information, an important step in improving breeding strategies for this species. As many as 21,315 genomic SSRs, 447 genic SSRs, and 96 ILP markers were publicly available in the database when it was launched [89]. The significant progress in foxtail millet genetics and genomics studies has prompted other omics approaches to study this crop. The first transcriptome of foxtail millet was released together with the draft genome sequence by sequencing the total RNA from four different tissues (root, stem, leaf, and spike) of the "Zhang gu" cultivar [66]. Multiple transcriptome analyses of foxtail millet have since been conducted to provide insights into the molecular mechanisms underlying abiotic stress tolerance, such as drought [75,90,91], salinity [92,93], low light [94], biotic stress resistance [95–97], and yield traits [98]. Proteomics and metabolomics studies are emerging to explain post-translational modifications that cannot be inferred at the transcript level [99,100]. Most proteomic studies in foxtail millet have emphasized the proteomic changes occurring under abiotic stress, particularly drought and salinity stresses [11,101–103], implying a particular interest in post-translational protein modification in response to these stresses. A multi-omics study that integrated transcriptome, proteome, and metabolome data into a metabolic reconstruction captured key metabolic entities at different developmental stages of foxtail millet [104]. Comprehensive profiling of primary and secondary metabolites in hybrid progenies and their parental lines has provided insight into the inheritance patterns of the foxtail millet metabolome [105]. Integrative transcriptome and metabolite analysis revealed key genes and metabolites involved in phenylpropanoid-related pathways as prominent regulators under drought stress during germination [75]. A widely targeted metabolomics analysis using liquid chromatography-tandem mass spectrometry of 150 millet germplasms revealed significant differential accumulation patterns of primary and secondary metabolites between Indian and Chinese foxtail millet [106]. A high-throughput multi-omics study using 398 foxtail millet accessions revealed the associations between metabolites and anti-inflammatory effects. It provided a valuable foundation for increasing the health benefits of foxtail millet through molecular breeding [107]. Recently, genomic, transcriptomic, and metabolomic data from whole-genome resequencing of 360 foxtail millet cultivars and 38 green foxtail germplasms were integrated and visualized using the Multiomics Database for *Setaria italica* (MDSi) to accelerate foxtail millet research [107]. These databases and advanced omics approaches are valuable for further exploration to enhance functional gene studies and genetic alterations in foxtail millet.

Genetic engineering and genome editing allow researchers to decipher gene functions and generate plants with desired traits [108]. *Agrobacterium*-mediated gene delivery remains the main technique used to facilitate functional gene studies and genetic engineering in

plants [109]. Attempts at gene transformation and genome editing in foxtail millet have been summarized in Table 5. The strenuous nature of callus induction and *in vitro* regeneration of foxtail millet is considered the main challenge for efficient genetic transformation system development in this crop [4]. Early optimization efforts of the *Agrobacterium*-mediated transformation protocol used immature inflorescences, which produced a low transformation efficiency (~5.5 %) [110,111]. The latest efforts in *Agrobacterium*-mediated transformation used secondary embryogenic calli induced from the mature foxtail millet seeds to produce a ~27 % transformation efficiency [112]. Several genetic engineering studies on foxtail millet have focused on the development of drought- and salt-tolerant cultivars [111,113–115] and phosphate transporter characterization [116], emphasizing the breeding direction of foxtail millet toward climate-resilient crops. Genome editing should further accelerate the breeding of classical foxtail millets. CRISPR/Cas9 is considered the most effective gene editing system and is widely applied in major cereals, including rice [117], maize [118], and wheat [119], for gene functional studies and crop improvement. The first CRISPR/Cas9 mutagenesis in foxtail millet targeted the *phytoene desaturase gene* using protoplasts with ~50 % transfection efficiency and ~10 % mutagenesis efficiency [120]. Knocking out *SiMTL*, the ortholog of maize's *MATRILINEAL/NOT-LIKE-DAD/PHOSPHOLIPASE A* (*MTL/NLD/ZmPLA*), using CRISPR/Cas9 base editing successfully produced double haploid (DH) lines of foxtail millet cv. "Ci846" with a haploid induction rate (HIR) of ~2.8 % [167]. These DH lines could serve as important genetic materials for foxtail millet breeders after further improvement of the HIR. The latest improvements in CRISPR/Cas9 base editing showed the efficiency of the Cytosine Base Editor (CBE) and Adenine Base Editor in targeting the *SiALS* (*Seita.1G169700*) and *SiACC* (*Seita.7G030200*) genes of foxtail millet. A homozygous herbicide-tolerant mutant plant was generated using CBE to induce missense mutations at the *SiALS-P170* site [121]. Later, identifying key genes for complex traits, such as grain yield, followed by comprehensive gene functional studies and improved cultivar generation, was made possible by combining map-based cloning, transgenic engineering, and CRISPR/Cas9 genome-editing technologies. Studies on *DPY1* (*droopy leaf1, Seita.5G121100*) and *SGD1* (*small grain and dwarf1, Seita.9G123200*) are two examples of such comprehensive approaches that offer a promising future for crop yield improvement [122,123]. *DPY1* encodes a leucine-rich repeat receptor kinase (LRR-RK) to control leaf architecture in brassinosteroid signaling. Increased yield was obtained by overexpressing *DPY1* in foxtail millet due to the upright leaf phenotype, enabling more efficient light capture and photosynthesis [122]. *SGD1* encodes a RING-type E3 ubiquitin ligase that orchestrates the genetic module along with *SiUBC32* (encoding an E2 ubiquitin-conjugating enzyme) and *SiBR1* (encoding a brassinosteroid receptor) to control the grain yield of foxtail millet. The study also employed a whole-genome selective sweep analysis to identify the *SGD1^{H1}* elite haplotype, and further overexpression of this haplotype resulted in a 12.8 % higher grain yield per plant compared to the wild type [124].

The rapid increase in foxtail millet genomics opens vast opportunities for using this species as a climate-resilient crop and a model plant for other cereals and C4 grasses. For instance, the extensive synteny between foxtail millet and sorghum, rice, and maize [4] and the maximum homology between foxtail millet and switch grass (*Panicum virgatum*) [125] showed the potential use of the foxtail millet genome to improve other cereals and C4 grasses with larger genome sizes or those with no reference genome available. However, compared with the model plant *Arabidopsis*, the relatively larger size and longer life cycle of foxtail millet impede its use as a C4 model species. Previous functional gene studies in foxtail millet have been performed in *Arabidopsis*. Most functional gene studies have focused on abiotic stress tolerance, which aligns with the breeding direction of foxtail millet as a future crop in the face of increasing climatic threats. Phospholipase D (PLD) from foxtail millet, *SiPLDα1*, is an important component of ABA signaling during drought

Table 5
Summary of genetic engineering (e.g., transformation, genome editing) efforts in foxtail millet.

Method	Main results	Foxtail millet cultivar	Functional gene used	Reference
Agrobacterium-mediated transformation	Optimization of transformation protocol	n.a.	–	[110]
		cv. "Jigu11"	*SBgLR*	[111]
		cv. "Jigu11" cv. "Yugu 2"	–	[163]
		cv. "IC-403579," cv. "IC-480117"	–	[112]
	Alteration in the growth and development events	cv. "Jigu1 1"	*Si401*	[164]
			Promoter *pF128*	[165]
	Alteration in abiotic stress tolerance: Drought and salinity stresses, phosphate uptake	cv. "Maxima"	*SiPHT1;1,2* and *3*	[116]
		cv. "Jigu1 1"	*SiLEA14*	[111]
			SiARDP	[60]
			SiLTP	[114]
			SiASR4	[115]
		cv. "Ci846"	*SiPLATZ12*	[146]
			SiBZR1	[166]
	Alteration in grain yield: leaf architecture, seed size	cv. "Ci846"	*DPY1*	[122]
			SGD1^{H1}	[124]
Biolistic	Alteration in the growth and development events	cv. "3661"	*SiPf40*	[167]
Genome editing by CRISPR-Cas9	Optimization of genome editing system protocol	Protoplast	*SiPDS*	[120]
	Development of *in planta* haploid inducer line	cv. "Ci846"	*SiMTL*	[168]
	Optimization of genome editing system protocol; resulted in herbicide-tolerant mutant plant	cv. "Yugu 1" cv. "*xiaomi*"	*SiALS*, *SiACC*	[121]
	Gene functional studies; site-directed mutagenesis	cv. "Ci846"	*DPY1, SGD1^{H1}*	[122, 124]

stress [126]. ABA-responsive DRE-binding protein genes from foxtail millet, *SiARDP,* and *SiREM6* are thought to be critical in drought and salinity tolerance [60,113]. Autophagy, the degradation process of intracellular components for nutrient recycling, has been suggested to be involved in low-nitrogen and drought stress responses based on the characterization of *SiATG8a* from foxtail millet in *Arabidopsis* [127]. *SiGRF*, a general regulatory factor in foxtail millet, was further identified as a member of the 14-3-3 protein family that mediates signal transduction during flowering and salinity stress in *Arabidopsis* [128]. The receptor-like kinase from foxtail millet, *SiERECTA*, was suggested to be a potential target for biotechnological intervention in biomass and thermotolerance improvement based on an overexpression study in *Arabidopsis* [129]. Recently, the overexpression of a transcription factor from foxtail millet, *SiMYBS3*, induced drought tolerance, ABA insensitivity, and earlier flowering in *Arabidopsis* [130]. Although many biological processes are conserved across flowering plants, several are family, genera, or species-specific. As a monocotyledonous C4 plant, the morphological, physiological, and developmental processes of foxtail millet are highly distinguishable from those of dicotyledonous C3 *Arabidopsis*. Despite the many advantages of using *Arabidopsis* as a model plant species, its specific characteristics may limit its use for understanding the biological processes of distantly related species [131], such as foxtail millet. Recently, a mini foxtail millet, "*xiaomi*," with an *Arabidopsis*-like life cycle, has been made available to accelerate functional studies of this species and other cereals. The short stature (~29 cm) and short life cycle (~70 days) of "*xiaomi*" were caused by an EMS-induced point mutation in the *Phytochrome C* (*PHYC/Si9g09200*) gene in the "Jingu21" cultivar [132]. The availability of the 429.94-Mb "*xiaomi*" genome in the MDSi database [107] and a transformation efficiency of ~23 % [132] indicates the potential of "*xiaomi*" as a C4 model crop.

Although the rapid increase in genetic, genomic, transcriptomic, and proteomic studies on foxtail millet is commendable, most studies have focused on abiotic stress tolerance in crops [4,60,111,114,115,133,134]. More attention is yet to be given to developing biotic-resistant cultivars [95–97], especially since the evolution of pathogens and their interaction with the host plant have been significantly altered by the changing climate [135]. Blast caused by *Pyricularia grisea* (teleomorph: *Magnaporthe grisea*) is one of the major diseases for many cereals that results in severe yield losses in foxtail millet [136]. Three QTLs for blast resistance in foxtail millet were identified by ultra-density genetic linkage map in the "Yugu 5" cultivar Recently, SLAF-seq and BSR-seq were employed to identify major QTLs and predict candidate genes associated with downy mildew resistance in foxtail millet [137]. These studies have shown notable progress in developing biotic-resistant cultivars for the crop. Improving the nutritional value and increasing the health benefits of foxtail millet [78,138,139] should also receive more attention in the coming years. Despite having a high total protein content, the unbalanced amino acid profile, low protein digestibility, and antinutrient content of foxtail millet hinder its robust development as a functional food [5,30]. A protein's nutritional value and digestibility are evaluated based on whether its essential amino acid content and ratio satisfy human requirements according to the FAO/WHO-recommended pattern [25]. The overall amino acid composition of foxtail millet flour is considered unbalanced for food sources, with lysine, tryptophan, methionine, and cysteine as limiting amino acids [30]. Furthermore, some anti-nutritional factors, such as polyphenols, tannins, and saponins, in foxtail millet may interfere with protein and starch digestibility and mineral bioavailability [140]. Various food-processing techniques can mitigate these unfavorable features [5,30] or further improve these unfavorable features by applying advanced technologies such as genetic engineering and genome editing [141]. Foxtail millet accessions with high zinc (107.1 mg/kg) and iron (70.52 mg/kg) contents, as well as high variation in the β-carotene contents, were identified from foxtail millet landraces in the Philippines [142], suggesting a considerable biodiversity potential for micronutrient and vitamin contents improvement. A study on yellow ("Jingu-21) and white ("Zhiseng") foxtail millet varieties showed that *SiPSY1* upregulation and *SiCCD1* downregulation were responsible for the higher carotenoid accumulation in yellow foxtail millet [55], implying potential target genes for vitamin A content alteration in foxtail millet. Future improvements could also be made towards flavor quality traits, such as aroma. Although there has been noticeable advancement in aromatic rice development studies [143], the aromatic trait seems missing from natural foxtail millet germplasms [123]. Ground-breaking research employed CRISPR/Cas9-mediated genome editing to modify the *SiBADH2* gene in cv. "Ci846" and created foxtail millet with a popcorn-like aroma [123]. Moreover, because the use of foxtail millet is less attractive due to the low productivity associated with tiny seeds, studies on panicle-related trait improvement are indispensable. A study utilizing 333 recombinant inbred lines (RILs) derived from "Ai88" and "Liaogu1" crosses, which were evaluated under 13 environmental conditions, identified important QTLs related to panicle architecture or grain yield and the associated candidate genes in foxtail millet [144]. Later, high-throughput whole-genome resequencing was employed on a RIL population generated from the "Longgu7" and "Yugu 1" crosses, producing a high-density bin map, which helped identify 47 QTLs, including three stable QTLs related to yield components in foxtail millet [145]. Recently, characterization of the *lp1* (*loose panicle 1*) mutant from the EMS-treated "Yugu 1" cultivar revealed that LP1 is a novel WRKY transcription factor that orchestrates the regulation of panicle development, stem elongation, and seed size in foxtail millet [146]. The increasing demand for global bioenergy [147] has led to the potential use of foxtail millet as a bioenergy crop. Muthamilarasan et al. [125] employed an integrative approach to identify the genes involved in the secondary cell wall as potential targets in lignocellulose bioengineering. Lignocellulosic biofuel production has become a key research area for generating bio-renewable energy, and this area needs further exploration in foxtail millet research. The direction of foxtail millet breeding should be targeted to address these traits, which can be promoted by developing a pan-genome of *Setaria*. Pan-genomic research propels functional genomics, studies in evolution, and exploration of biodiversity and has significant promise for enhancing crops, conserving the environment, and promoting sustainable agriculture [148]. The availability of super pan-genomes has accelerated functional genomics and molecular breeding of rice [149]. A similar approach can be implemented for foxtail millet, especially because *de novo* reference-level genome assemblies of 110 highly diverse core-set accessions of *S. italica* and *S. viridis*, selected from 1844 *Setaria* accessions with a vast range of diversity, have been made available by He et al. [150]. The development of the graph-based pan-genome for *Setaria* by He and collaborators represents significant progress in foxtail millet genomic research as it integrates a huge spectrum of genetic variations, including structural variants (SVs), single nucleotide polymorphisms (SNPs), insertions and deletions into the "Yugu 1" reference genome. Variations in the *Setaria* pan-genome will enable researchers to map key genes and develop

powerful markers for the precision breeding of foxtail millet. Studies utilizing the pan-genome in rice and pearl millet have revealed how particular SVs affect the expression of genes associated with environmental adaptation or yield [149,151]. Likewise, the *Setaria* pan-genome enabled a large-scale SNP- and SV-GWAS to identify 1084 signals associated with 226 sets of high-quality foxtail millet phenotypes, resulting in a prediction precision of more than 0.7 for 97 % of phenotypes [150]. The availability of the *Setaria* pan-genome provides a valuable foundation for accelerating the molecular breeding of foxtail millet.

Exploring various aspects, including omics, genome sequencing, genetic engineering, genome editing, and developing a new super cultivar, has significantly advanced foxtail millet breeding. Integrating biotechnology and technological advancements has paved the way for innovative approaches to enhance foxtail millet traits. Therefore, the prospects for foxtail millet breeding seem promising, with ongoing advancements likely to contribute to developing improved varieties with enhanced nutritional content, stress tolerance, and overall crop productivity. The synergy between biotechnology and cutting-edge technologies holds immense potential for shaping the future landscape of foxtail millet cultivation and meeting the evolving demands of agriculture and food security.

5. Conclusion and future perspectives

Foxtail millet is projected to attract significant scientific interest because the number of papers related to foxtail millet has been steadily increasing. As the top three most populated countries globally [152], China, India, and the US will continue to be leading countries in foxtail millet-related research. The historical origin of foxtail millet defines the vital role of this species as an important food crop in the arid and semiarid regions of China. In contrast, several rural areas in India depend on small millet crops as the staple food because of environmental pressure [153]. Unlike China and India, foxtail millet in the US is primarily grown for hay and bird food [154]. Climate change-driven abiotic stresses may trigger affected countries to pay more attention to climate-resilient crops. Indonesia is one of the countries most affected by climate change [155], with the fourth-highest population globally [152], and has shown a striking increase in foxtail millet-related research in the last decade, making this country a potential contributor to future foxtail millet research. Greater international collaboration and transdisciplinary studies are essential to address the unique features of foxtail millet in diverse agrometeorological regions and variations in crop use. The bibliometric analysis demonstrated the importance of omics studies on abiotic stress tolerance in foxtail millet. It will help shape the breeding direction of foxtail millet as a climate-resilient crop. Although research on the nutritional aspects, biotic stress resistance, and bioenergy potential of the crop remains in the initial phase, these subjects will most likely become critical aspects of research in the future. As collaborative initiatives continue to grow, involving countries such as China, India, and the US, as well as emerging contributors such as Indonesia, the trajectory of foxtail millet research is poised to shape a more sustainable and resilient agricultural future. Thus, future research should emphasize nutritional aspects, biotic stress resistance, and its use as a bioenergy source, further solidifying the role of foxtail millet as a crucial climate-resilient crop.

Climate-resilient crop varieties and innovative breeding techniques are among the top strategies emphasized at the local and regional levels, which later define the success of global adaptation to climate change [156]. Since agricultural productivity is highly dependent on climate stability, significant implications for sustaining agricultural productivity in a changing climate can be expected from the expanding scientific interest and global research efforts surrounding foxtail millet. Integrating genomic-enviromic prediction (iGEP), which requires multi-omics information, big data, and artificial intelligence, termed Smart Breeding [157], should now be possible to accelerate foxtail millet breeding. More importantly, the elucidation of conserved genetic regulations beyond species boundaries on economically important traits, such as grain yield and abiotic and biotic stress resistance, will soon be made possible by the availability of *Setaria* pan-genomes [150] and other major cereal crops, including rice [149] and maize [158]. For instance, the development of major cereal crops with C3 metabolism to be highly efficient in photosynthesis should be within the bounds of possibility with the introduction of C4 metabolism from *Setaria* [159]. We envision advanced progress in the revitalization of foxtail millet as a climate-resilient crop and the expeditious development of other crops to sustain agricultural productivity in the imminent challenges of climate change.

CRediT authorship contribution statement

Sintho Wahyuning Ardie: Writing – original draft, Validation, Software, Methodology, Investigation, Formal analysis. **Rizki Bagus Nugroho:** Writing – original draft, Visualization, Formal analysis. **Andi Dirpan:** Writing – review & editing, Validation, Software, Resources. **Muhammad Fuad Anshori:** Writing – review & editing, Validation, Supervision, Methodology, Funding acquisition, Data curation.

Data availability statement

Data will be made available on request. For requesting data, please write to the corresponding author.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to

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