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REVIEW ARTICLE

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Finger millet (*Eleusine coracana*) improvement: Challenges and prospects—A review

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Abstract

Finger millet is a climate-resilient and highly nutritious small grain crop widely grown in the semi-arid tropics. It has multiple uses, including for food, feed and beverage preparations. However, finger millet is an under-utilized and under-researched crop with a mean yield of <1.0 t/ha despite a potential productivity of up to 8 t/ha. The yield gap is attributed to several production constraints, such as biotic and abiotic stresses, a lack of access to improved seeds and production inputs and poor agronomic management practices. There are valuable genetic resources and genetic variability of finger millet in its centres of diversity and global gene banks for variety design, product development and commercialization. The genetic variability can be harnessed further to integrate essential traits into candidate varieties through conventional and modern breeding methods. Breeding and genetic innovations such as genomics-assisted breeding, mutation breeding and genome editing would accelerate finger millet breeding and new variety design and deployment. The objective of this review was to document the opportunities, challenges and prospects of finger millet improvement as a guide for variety development and deployment with enhanced grain yield and nutritional contents. The first section describes global production status and yield gains, major production and productivity challenges in finger millet. This is followed by an in-depth presentation on breeding and genetic progress on variety development with improved agronomic and nutritional quality traits, drought and salinity tolerance, and fungal diseases, weeds and insect pest resistance. Further, the review summarized finger millet's genetic and genomic resources, reference genomes, whole genome re-sequencing and transcriptomics of finger millet technologies, genetic engineering and genome editing and their integration with conventional breeding methods for variety design with desired end-use traits. The review provides foundational information to expedite the development of new-generation finger millet cultivars with desirable product profiles, including high grain yield potential, early maturity, desirable seed colour, compact head type, food and feed nutrients quality and high marketability through modern breeding approaches.

KEYWORDS
finger millet breeding, finger millet global production, genetic engineering, genetic gain, genome editing, production constraints, skim sequencing, whole genome re-sequencing

1 | INTRODUCTION

Finger millet (*Eleusine coracana* [L.] Gaertn.) is an allotetraploid ($2n = 4x = 36$, AABB) species belonging to the Poaceae family. It has a C_4 photosynthesis and is adapted to growing in the semi-arid tropics. The crop has exceptional genetic plasticity with tolerance to extreme temperatures (Kudapa et al., 2023; Yogeesh et al., 2016), moisture stress (Ceasar et al., 2018; Hittalmani et al., 2017), aluminium toxicity (Brhane, Fikiru, et al., 2017) and salinity (Divya et al., 2022; Rahman et al., 2014). The gluten-free grain has multiple uses, such as food and beverage preparations. The stalk is used as livestock feed, thatching and bedding material. The grain has extended storage quality (Ceasar et al., 2018), with unique nutritional composition, including high levels of Ca, Fe, Zn, K, Mg, Mn, dietary fibre, phenolic compounds, essential amino acids (e.g., cystine, methionine and tryptophan) (Backiyalakshmi et al., 2023; Devi et al., 2011; Kudapa et al., 2023; Maharajan et al., 2022). Finger millet food products are believed to lower blood cholesterol levels and blood pressure (Anitha, Botha, et al., 2021) and possess anti-cancer (Chandrasekara & Shahidi, 2011; Devi et al., 2011); and anti-ageing properties (Puranik et al., 2020; Kumar, Rani, et al., 2021). Further, finger millet diets prevent osteoporosis (Puranik et al., 2017; Anitha, Givens, et al., 2021), rickets (Maharajan et al., 2021), diabetics (Anitha, Botha, et al., 2021; Devi et al., 2011; Murtaza et al., 2014), obesity (Murtaza et al., 2014), anaemia (Karkada et al., 2019), celiac (Tadele, 2018), liver disorders and asthma (Shobana et al., 2009). It also boosts immunity against malaria (Assefa et al., 2013; Tsehaye et al., 2006) and diarrhoea (Assefa et al., 2013; Tsehaye et al., 2006). The human health benefits of finger millet make it a superfood to combat malnutrition and other ailments.

In sub-Saharan African and Asian countries, finger millet is mainly grown by smallholder farmers for household consumption, and the surplus is sold in the local and regional markets. It has a niche market opportunity due to its popularity among rural and urban populations for its human health advantages and food quality. However, limited information and dissemination about its commercial value and human-health benefits hindered product development and marketing. Integrating finger millet production into the existing cropping systems will diversify the food systems and ensure food and nutrition security and cash income along the value chains (Jerop et al., 2018).

The global total area and production of finger millet are not known because the data from pearl millet (*Pennisetum glaucum* [L.] R. Br.), finger millet, foxtail millet and other minor millet types are reported together by the Food and Agriculture Organization of the United Nations (FAOSTAT (Food and Agriculture Organization of the United Nations STAT), 2020; Gebreyohannes et al., 2021). In some countries such as India, Ethiopia, Nepal, Uganda and Rwanda, data are available on total area coverage and production of finger millet owing to the economic value of the crop (Orr et al., 2016; CSA (Central statistical agency), 2020; Indiastat, 2020; MoALD, 2020; Gairhe et al., 2021). India is the leading producer of finger millet in the world, with an annual production of 1.8 million tons, followed by Ethiopia (1.2 million tons), Nepal (.31 million tons), Uganda (.20 million tons) and Tanzania (.10 million tons) (CSA, 2020; FAOSTAT, 2020; Gairhe et al., 2021; Indiastat, 2020; MoALD, 2020; Orr et al., 2016). Finger millet is an under-utilized and under-researched crop with a mean yield of <1.0 t/ha compared with the potential productivity reaching up to 8 t/ha (Joshi et al., 2023; Oduori, 2008; Padulosi et al., 2015). The low average global yield of finger millet is attributed to several production constraints: biotic stresses (fungal diseases, insect pests, weeds and bird damage) and abiotic stresses (drought, heat, poor soil fertility and salinity). Global finger millet production and productivity are severely constrained by the combined effect of drought and blast disease, whose impact hinges on a complex interplay of varietal susceptibility, crop stage, stress severity, environmental factors and their intricate interactions. Drought alone wreaks havoc, with landraces like Kala Mandua and Safed Mandua in India and TZA-01 in Tanzania experiencing marked yield losses of up to 77% (Khatoom & Singh, 2016; Maqsood & Ali, 2007). Globally, finger millet yield exhibits a substantial reduction in the range of 7% to 90% due to blast disease, driven by a complex interplay of weather conditions and host genotype susceptibility (Akech et al., 2016; Lule et al., 2014; Mbinda et al., 2021; Mbinda & Masaki, 2021; Nagaraja et al., 2007). The severe limitations imposed by drought and disease underscore the critical need to develop highly resilient finger millet cultivars. A lack of access to improved seed and production inputs, poor agronomic management practices and poor market access are the foremost socio-economic factors hindering finger millet production, especially in less developed countries. Likewise, limited agricultural land for crop production, lack of access to extension services and absence of integrated disease, insect pest and weed management and under-developed pre- and post-harvest technologies and products have a detrimental impact on finger millet productivity and value chains (Jerop et al., 2018; Mbinda & Masaki, 2021).

The major impediments to finger millet productivity include a lack of locally adapted, drought-tolerance, disease-resistant and high-yielding varieties (Gebreyohannes et al., 2021; Mbinda et al., 2021; Owere et al., 2014). In most finger millet production areas, notably in sub-Saharan Africa (SSA), including Ethiopia, unimproved traditional varieties or landraces are commonly used for cultivation (Kasule et al., 2023; Mulualem & Melak, 2013). The landrace varieties have excellent eating quality and nutritive value and are highly preferred by growers, consumers and markets (Gebreyohannes et al., 2021). Also, landraces have better insect and disease resistance due to their co-evolution with major insect pests and diseases (Dida et al., 2021; Mbinda & Masaki, 2021; Vetriventhan et al., 2020). However, landraces are low yielders, susceptible to drought and lodging with low grain threshability (Gebreyohannes et al., 2021). Therefore, germplasm maintained by local farmers, regional and international research centres and gene banks could be an excellent source of novel genetic variation for finger millet pre-breeding and breeding programs.

There are valuable genetic resources and genetic variability of finger millet in its centres of diversity and global gene banks. About 40,182 finger millet accessions have been collected and conserved by different gene banks (Dwivedi et al., 2012; PGRC (Plant Genetic Resource Center), 2016; ICRISAT (International Crops Research Institute for Semi-Arid Tropics), 2017; EBI (Ethiopian Biodiversity Institute), 2023). The largest proportions of finger millet accessions are conserved in Asia and African countries, North America, by the International Crop Research Institute for the Semi-Arid Tropics (ICRISAT) in India, Kenya and Mozambique. Ethiopia is the centre of origin and diversity for finger millet (Harlan, 1971; Hilu et al., 1979; Tesfaye & Mengistu, 2017). The Ethiopian Biodiversity Institute (EBI) and Ethiopian Institute of Agricultural Research (EIAR) - Melkassa Agricultural Research Center (MARC) maintain around 1809 and 400 finger millet accessions, respectively (EBI, 2023). The germplasm is a valuable source of economic traits including grain yield and its component traits (Anteneh et al., 2019; Assefa et al., 2013), nutritional quality (Tsehaye et al., 2006), disease (e.g., blast), heat and drought tolerance, (Assefa et al., 2013; Manyasa et al., 2019), aluminium and acidic toxicity tolerance (Brhane, Fikiru, et al., 2017), bird damage tolerance (Tsehaye et al., 2006) and excellent fermentation quality for breeding (Tsehaye et al., 2006).

The genetic variability of the existing finger millet genetic resources can be harnessed further to integrate winning and essential traits into candidate varieties through conventional and modern breeding methods. Breeding and genetic innovations such as genomics-assisted breeding, mutation breeding, transgenic approaches and genome editing would accelerate finger millet breeding and new variety design and deployment. Considering the above background, this review aims to provide current and detailed information on the opportunities, challenges and prospects of finger millet improvement to guide variety development and deployment with enhanced grain yield and nutritional contents. The first section offers detailed data on global production status and yield gains and major production and productivity challenges in finger millet. An in-depth presentation on breeding and genetic progress on cultivar development with improved agronomic and nutritional quality traits, drought and salinity tolerance and major fungal diseases, weeds and insect pest resistance follows this. This review is supported by several data sets on finger millet breeding and genetic improvement and presents the crop's current breeding and genomic tools and genetic resources. Information presented in the review guides the development of new-generation finger millet cultivars with desirable product profiles, including high grain yield potential, early maturity, desirable seed colour, compact head type, food and feed nutrients quality and high marketability through modern breeding and genomic tools.

2 | GLOBAL PRODUCTION AND PRODUCTIVITY OF FINGER MILLET

Finger millet is grown in more than 50 different countries worldwide, including 27 African countries (Backiyalakshmi et al., 2021; Maharajan et al., 2021; Mirza & Marla, 2019; Radchuk et al., 2012). Figure 1 presents countries of finger millet production. Eastern and Southern Africa are the leading finger millet producers in Africa. It is also grown in Southern Chad, Senegal, Ghana, Cameroon, North-Eastern Nigeria and West-Central Africa to a lesser extent. There are 17 main finger millet-producing countries in Asia, including India, Nepal, Sri Lanka, Maldives, Pakistan, Malaysia, China, Bhutan, Taiwan, Myanmar, Iran, Afghanistan, Philippines and Japan (Maharajan et al., 2021). The crop is also grown in some areas of the Americas, specifically in Mexico and the USA. Finger millet is reportedly grown in minor quantities in Europe, such as in the United Kingdom, Germany, Italy and Ukraine (Backiyalakshmi et al., 2021; Mirza & Marla, 2019; Radchuk et al., 2012).

The area and production of finger millet on a global scale are comprehensively collected, analysed and summarized in Table 1 and Figure 2. Finger millet is globally produced in more than 2.1 million ha of land, with an annual production of 3.7 million tons when compared with the total area (11 million ha) and annual production (14.6 million tons) allotted to millets (FAOSTAT, 2020; Gairhe et al., 2021; Indiastat, 2020; MoALD, 2020; Orr et al., 2016). The values correspond to finger millet's share of 20% and 26% of the global millets in total area coverage and production, respectively (Table 1). India is the world's foremost producer of finger millet, with a total production area of 1 million ha (Gebreyohannes et al., 2021; Indiastat, 2020), accounting for 46% of the global share, followed by Ethiopia (with a total production area of 480,511 ha and 22% global share) (Figure 2).

2.1 | Genetic gains for agronomic traits and nutritional compositions

Genetic gain refers to the increased performance of genotypes achieved through genetic improvement, resulting in desirable gains for economic traits (Ganapathy et al., 2011; Krishnappa et al., 2009). Genetic gain estimation and documentation support breeding decision-making by highlighting potential features for future improvement and guiding breeding strategies to maximize production (Marefia et al., 2022). Panicle length, number of fingers per ear, plant height, number of productive tillers per plant, 1000 seed weight, threshability, early maturity, large head size, compacted head shape and harvest index are essential traits for finger millet improvement and genetic gains of yield and component traits (Manyasa et al., 2016; Marefia et al., 2022; Owere et al., 2015).

Realized genetic gains reported for agronomic traits in finger millet are presented in Table 2. In the past there were limited breeding efforts that reported the improvement of economic traits, including yield and nutritional compositions in finger millet. Yield reports from

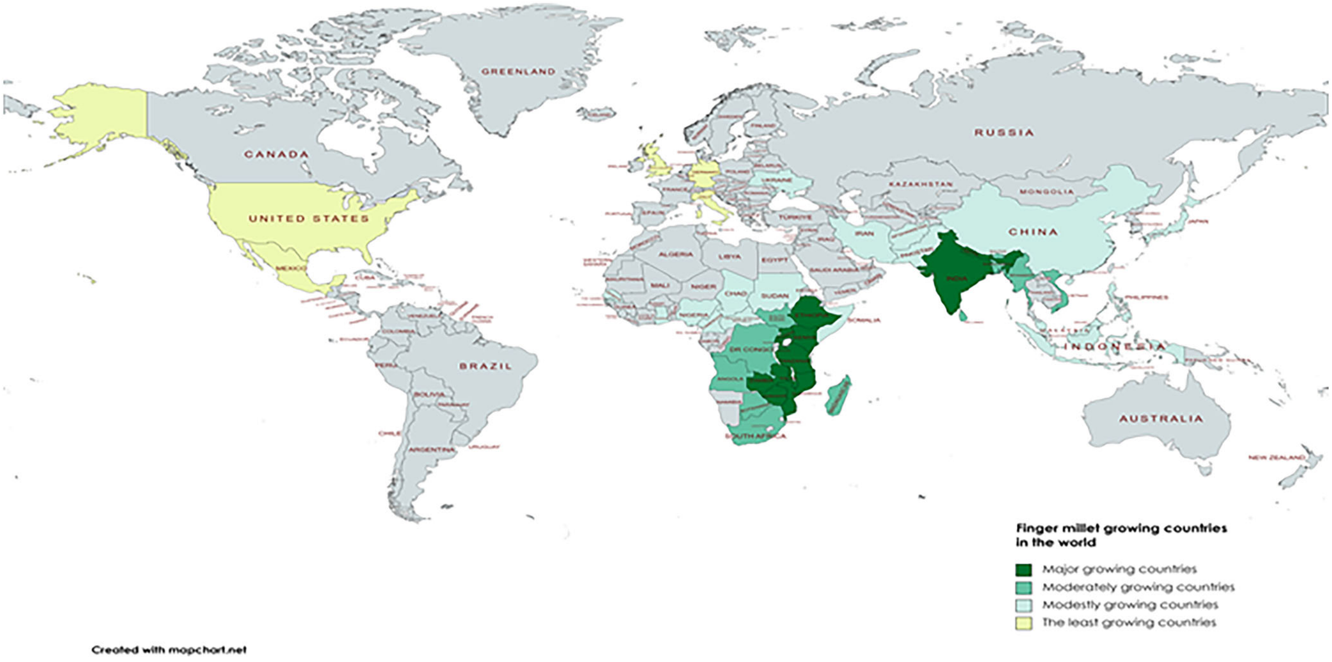

FIGURE 1 Map of finger millet growing countries in the world. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Total area coverage, production and mean yield of finger millet and its relative importance compared to other millets (e.g., pearl, finger, foxtail, proso, little, barnyard, kodo and fonio millets) in various major growing countries.

Countries	Relative importance (%)[a]	Total production area (ha)	Total production (tons)	Yield (t/ha)	References
India	1.3[b]	1,004,460	1,755,060	1.75	FAOSTAT (2020); Indiastat (2020)
Ethiopia	100	480,511	1,218,582	2.54	Orr et al. (2016); CSA (2020); FAOSTAT (2020)
Nepal	100	263,261	314,225	1.19	FAOSTAT (2020); Gairhe et al. (2021)
Uganda	94	141,600	197,091	1.39	Orr et al. (2016); FAOSTAT (2020); MoALD (2020)
Tanzania	30	81,000	97,500	1.2	
Kenya	45	53,285	68,850	1.29	
Zimbabwe	30	43,349	13,023	.3	
Zambia	60	39,454	27,003	.68	
Malawi	60	34,423	29,359	.85	
Eritrea	20	15,000	5000	.33	Orr et al. (2016); FAOSTAT (2020)
Mozambique	20	10,695	4420	.41	
Rwanda	100	10,637	5067	.48	
Finger millet Total/mean		2,177,675	3,735,180	1.03	
The importance of finger millet relative to other millets					
Millets global total/mean		11,140,318	14,585,766	1.32	FAOSTAT (2020)
Finger millets global total/%/mean		2,177,675(20)	3,735,180(26)	1.03	

[a] Finger millet's production and area coverage compared to other millets.

[b] Relative importance (%) = (finger millet area/total millet area) × 100, numbers in parenthesis is the percent share of finger millet in relation to other millets.

Ethiopia (Table 2) suggest high yield potential is achievable in finger millet through breeding. Yield-related traits including ear weight plant^{-1} (g), 1000 grain mass(g), straw yield (kg plant^{-1}), number of ears plant^{-1}, number of fingers ear^{-1} and plant height (cm) recorded meagre genetic gains (Table 2). Hence, there is a need for breeding and modern production technologies to harness the genetic

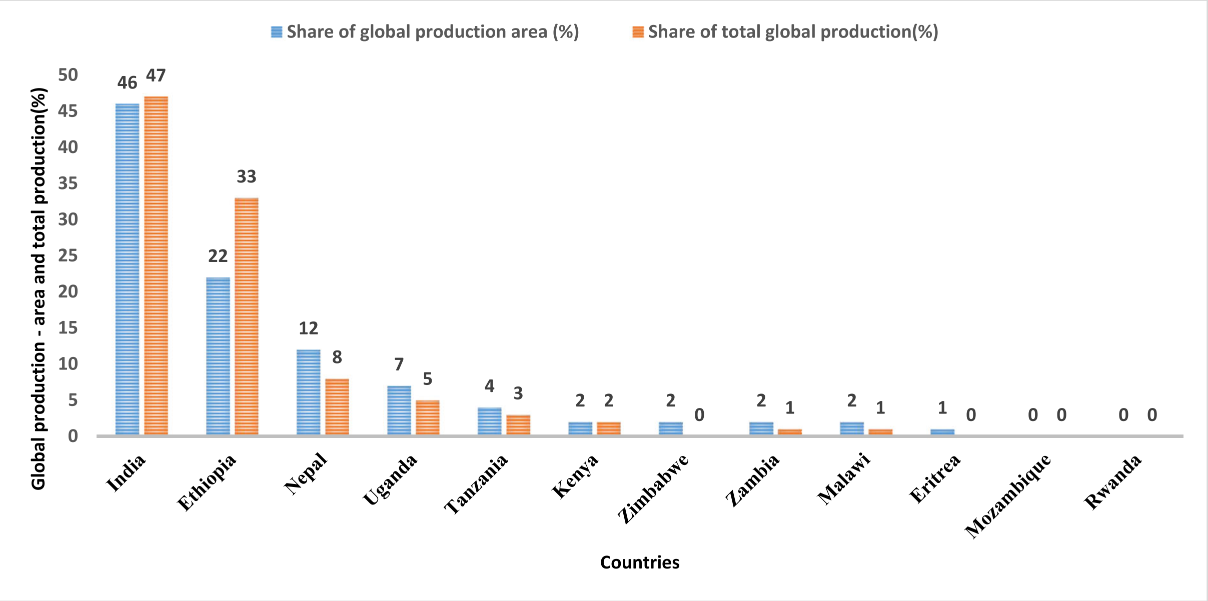

FIGURE 2 Global area and total production (%) of finger millet in major growing countries. [Color figure can be viewed at wileyonlinelibrary.com]

expression of these vital traits. Finger millet grains composed of the following macro-nutrients in mg/100 g: P (130.0–250.0), K (430.0–668.8), Ca (50.0–589.0), S (106.1–149.0), Na (6.3–41.6) and Mg (78.0–201.0) (Backiyalakshmi et al., 2023; Kumar, Rani, et al., 2021; Puranik et al., 2020; Teklu et al., 2024). Also, vital micro-nutrients are found in the grains (mg/100 g): Fe (2.5–53.4), Mn (17.6–201.0) and Zn (1.0–36.6) (Anitha, Givens, et al., 2021; Kumar, Rani, et al., 2021; Puranik et al., 2020). Except for calcium content, genetic gains for grain protein, iron and zinc contents are minimal (Table 2). High grain yield of finger millet appears to be closely associated with reduced zinc and protein content but has a positive association with increased calcium content (Table 2). For instance, among Indian finger millet cultivars released between 1953 and 2019 (Udamala et al., 2020; Vadivoo et al., 1998), genetic increase for protein content ranged between −0.048 mg/100 and −0.073 g/100 g year^{-1} indicating a negative association with yield gains. Likewise, a negative association between grain yield and zinc content were reported (Backiyalakshmi et al., 2023). The genetic gain of protein content was −0.001 mg/100 g year^{-1} for Indian finger millet cultivars released between 1976 and 2019 (Table 2). Conversely, a positive association has been reported between grain yield and iron and calcium content (Udamala et al., 2020; Vadivoo et al., 1998). The authors reported a genetic gain ranging from 1.336 to 4.110 mg/100 g year^{-1} for iron and .022 mg/100 g year^{-1} for calcium contents. Selection response for high yield and Ca and Fe contents can be enhanced through simultaneous trait selection, enabling the creation of finger millet varieties that fulfil the demands of both farmers and consumers. Gene discovery targeting yield and yield components and nutrient profiles using genome-wide association study (GWAS), marker-assisted selection (MAS) and genomic selection methods enable speed and precision breeding. Also, improved farming technologies such as soil fertilizers and water management systems will bolster sustainable crop production and productivity.

3 | CONSTRAINTS TO FINGER MILLET PRODUCTION

Global finger millet production and productivity are challenged by several biotic and abiotic factors and a lack of modern crop management practices (Asargew & Shibabawu, 2014; Jerop et al., 2018; Lule et al., 2014; Manyasa et al., 2019; Mulualem & Melak, 2013). In sub-Sahara African countries, farmers are still using low-yielding finger millet varieties, which has resulted in lower crop productivity (< 1 ton/ha). The average productivity of finger millet is 2.5 and 1.4 t/ha in Ethiopia and Uganda, respectively. This highlights the need for targeted breeding to unleash the crop's true potential on yield and nutritional value (Hussein, 2017). Different studies reported that high grain yield, early maturity, desirable seed colour, compact head type, threshability, end-use quality and high marketability are preferred traits by finger millet growers and consumers (Gebreyohannes et al., 2021; Mbinda et al., 2021; Mbinda & Masaki, 2021; Owere et al., 2014).

In some countries, there are modest breeding efforts and the development of improved varieties, including selections from landraces. For example, NGRC04789, NGRC04849 and NGRC06490 are landrace selections of finger millet favoured in Nepal for blast resistance, drought tolerance and medicinal value (Luitel et al., 2020). In Zimbabwe, most finger millet production is based on unimproved landrace varieties (Mbanyele et al., 2022). Landraces such as Tsa'ada, Tselim and Keyih with different seed colours are widely preferred finger millet in Northern Ethiopia, meeting consumers' needs and market demands (Tsehaye et al., 2006). Gangabali, Dengsameli and Kada are commonly grown finger millet landraces in India (Panda et al., 2021). High-performing and locally adapted varieties, better agronomic management practices, and favourable production conditions can achieve higher yield gains of 4.0 to 8.0 tons/ha in finger millet (Joshi

TABLE 2 Genetic gains for agronomic traits and nutritional compositions in finger millet.

Traits	Country	Years of cultivar release	Mean increase/decrease (unit^{-1} year^{-1})	Genetic gain (% year^{-1})	References
Grain yield (kg ha^{-1})	Ethiopia	1999–2019	27.64	1.35	Marefia et al. (2022)
		1998–2022	43	1.87	MOA (Ministry of Agriculture) (2022)
Ear weight plant $^{-1}$ (g)	India	1959–2016	0.026	0.0005	Aralikatti and Chaturvedi (2020)
1000 grain mass (g)		1959–2016	0.003	0.0001	
1000 grain mass (g)	Kenya	2000–2015	0.43	0.028	Manyasa et al. (2016)
Straw yield plant^{-1} (kg)	India	1959–2016	−0.001	−0.00001	Aralikatti and Chaturvedi (2020)
Number of tillers plant^{-1}	Ethiopia	1999–2019	0.11	0.005	Marefia et al. (2022)
	India	1959–2016	−0.005	−0.0001	Aralikatti and Chaturvedi (2020)
	Kenya	2000–2015	3.02	0.201	Manyasa et al. (2016)
Number of ears plant^{-1}	Ethiopia	1999–2019	0.1	0.005	Marefia et al. (2022)
Number of fingers ear^{-1}	India	1959–2016	−0.012	−0.0002	Aralikatti and Chaturvedi (2020)
	Uganda	1969–2017	0.83	0.017	Owere et al. (2015)
	Kenya	2000–2015	3.39	0.226	Manyasa et al. (2016)
Plant height (cm)	India	1959–2016	−0.006	−0.0001	Aralikatti and Chaturvedi (2020)
Days to maturity		1959–2016	0.027	0.001	
Days to maturity	Ethiopia	2002–2022	−0.58	−0.029	MOA (2022)
Days to 50% flowering	India	1959–2016	−0.033	−0.001	Aralikatti and Chaturvedi (2020)
	Uganda	1969–2017	4.43	0.092	Owere et al. (2015)
Ear head length (cm)	India	1959–2016	0.009	0.0002	Aralikatti and Chaturvedi (2020)
Flag leaf length (cm)		1959–2016	0.029	0.0005	
Finger length (cm)		1959–2016	0.017	0.0003	
Finger length (cm)	Kenya	2000–2015	5.15	0.344	Manyasa et al. (2016)
Panicle exertion (cm)		2000–2015	1.4	0.094	
Protein content (mg/100 g)	India	1976–2019	−0.048	−0.001	Udamala et al. (2020)
Protein content (g/100 g)		1953–1989	−0.073	−0.002	Vadivoo et al. (1998)
Calcium content (mg/100 g)		1953–1989	1.336	0.037	
		1976–2019	4.11	0.096	Udamala et al. (2020)
Iron content (mg/100 g)		1976–2019	0.022	0.001	
Zinc content (mg/100 g)	India	1976–2019	−0.001	−0.00002	

et al., 2023; Maqsood & Ali, 2007; Oduori, 2008; Padulosi et al., 2015; Puranik et al., 2017). Nonetheless, the actual yield of finger millet in SSA is low (Table 1) due to the various production constraints outlined below.

3.1 | Biotic factors

3.1.1 | Fungal diseases

Blast disease is the major bottleneck to finger millet production in wet and humid environments. The disease is caused by the heterothallic ascomycete fungus, with two stages of the same pathogen, [teleomorph: *Magnaporthe grisea* (Hebert) Barr] and [anamorph: *Pyricularia grisea* (Cook) Sacc.] (Zhang et al., 2016). Blast inflicts yield loss varying from 7.32% to 90% in finger millet (Akech et al., 2016; Lule et al., 2014). A yield loss of 28% to 36% is reported in India (Nagaraja et al., 2007); 60% to 90% in Uganda (Akech et al., 2016); 7.32% to 54.07% in Ethiopia (Gashaw et al., 2014; Lule et al., 2014) and up to 80% elsewhere (Mbinda & Masaki, 2021). When environmental conditions are favourable, the pathogen infects all parts of finger millet, including the leaves, stem, collar, node, neck, fingers and roots, resulting in significant crop losses. High temperatures, relative humidity and rainfall conditions enhance blast infection and disease development. Leaf wetness, alternate hosts, weeds, crop debris and high planting density promote the spread of blast disease (Gashaw et al., 2014; Lule et al., 2014; Mbinda et al., 2021). Additionally, other fungal diseases that threaten finger millet production include banded sheath blight, caused by *Rhizoctonia solani* Kühn, and foot rot, by *Sclerotium rolfsii* (Nagaraja & Das, 2016; Patro et al., 2018). These pathogens exhibit distinct pathological races. Banded sheath blight manifests as oval lesions on lower foliage, progressing to characteristic brown bands, while foot rot presents with basal stem necrosis, profuse mycelial growth and sclerotia formation (Nagaraja & Das, 2016).

The use of blast-resistant finger millet varieties is an effective, economical, ecologically friendly and sustainable control strategy (Manyasa et al., 2019; Mbinda & Masaki, 2021). Other blast-controlling options include adjustment of sowing during the first onset of rainfall, intercropping with legumes, weed control, use of fungicides (e.g., tricyclazole, edifenphos, carbendazim and mancozeb), clean seed (Mbinda et al., 2021; Mbinda & Masaki, 2021) and biocontrol methods. Fungal bio-control agents, such as *Trichoderma viride* and *T. harzianum* supress the causative agent of finger millet blast disease (Gashaw et al., 2014).

3.1.2 | Insect pests

The most economically important insect pests of finger millet include grasshoppers (Caelifera), shoot flies (*Atherigona soccata* [Rondani]), pink stem borer (*Sesamia inferens* [Walker]), root aphid (*Tetraneura nigriabdominalis* [Sasaki]) and aphids (Aphidoidea) (Mulualem & Melak, 2013; Sasmal, 2018). Insect pests caused yield losses ranging from 23% to 56% in finger millet (Mulualem & Melak, 2013; Sasmal, 2018). Host-plant resistance, pesticides, cultural practices (e.g., managing planting time, field sanitation, crop rotation, deep and frequent ploughing), silicon amendment and bio-control agents (e.g., predatory spiders and ladybird beetle [coccinellids]) are widely used in insect pests management (Gahukar & Reddy, 2019; Gebreyohannes et al., 2021; Jadhao et al., 2020). Integrating insect pest control involving resistant variety, cultural practices and biological control methods is the most efficient, cost-efficient and environmentally friendly option for smallholder farmers to control insect pests of finger millet.

3.1.3 | Weeds

Weed infestation causes a yield loss varying from five to 73.5% in finger millet production (Asargew & Shibabawu, 2014; Mahapatra et al., 2021). The notable weed species recorded in finger millet production include *Striga hermonthica* (Delile) Benth, *Digitaria ternata* (A. Rich.), Stapf, *Guizotia scabra* (Vis.) Chiov and *Cyperus rotundus* [L.] (Asargew & Shibabawu, 2014; Owere et al., 2014). Also, other wild relatives of finger millet, such as *Eleusine indica* (L.) Gaertn., and *E. africana* (L.) Gaertn are regarded as noxious weeds of finger millet. Wild relative weeds are remarkably similar to finger millet and are only distinguishable at the flowering stage.

Finger millet cultivars resistance to the major weeds are the most economical control options. Few *Striga*-resistant cultivars were developed and released by the Kenya Agriculture and Livestock Research Organization (KALRO (Kenya Agriculture and Livestock Research Organization), 2021). Also, other weed control options include cultural practices (e.g., early planting with the onset of the first rain, crop rotation and trap crops), enhancing soil fertility through the application of nitrogen and phosphorous fertilizers (Mgonja et al., 2013), hand weeding (Asargew & Shibabawu, 2014), application of pre- and post-emergent-herbicides (e.g., butachlor and 2,4-D Na salt) (Mgonja et al., 2013). Integrating weed management, such as resistant variety, bio- and chemical-herbicides and cultural control practices, is the most effective and economical approach to reducing yield and quality losses in finger millet production (Mbinda et al., 2021; Mgonja et al., 2013).

3.2 | Abiotic factors

3.2.1 | Drought stress

Recurrent drought is the major cause of yield and crop losses (Mukami et al., 2019). Drought stress can occur pre-flowering or post-flowering, and its impact is directly related to the crop growth stages (Maqsood & Ali, 2007; Mukami et al., 2019). Pre-flowering drought is associated with reduced leaf number, short plant stature and low canopy size (Maqsood & Ali, 2007). The extent of yield loss varies depending on cultivar susceptibility, the severity and duration of the stress (Mukami et al., 2019). High yield loss is recorded when severe drought occurs at flowering and grain-filling stages (Talwar et al., 2020). Drought at the flowering stage resulted in significant yield loss varying from 40% to 70% in various crops such as tef, finger millet and pearl millet (Maqsood & Ali, 2007; Numan et al., 2021; Tadele, 2018).

Developing and deploying finger millet varieties with drought tolerance and enhanced agronomic traits is a novel mitigation approach to drought stress. To pursue food security under drought, farmers adopted some indigenous knowledge systems. For instance, by diversifying the cropping system and integrating finger millet, farmers in the Indian Himalayas safeguarded their food supply even during droughts and famines (Gururani et al., 2021). Other drought mitigation strategies used by farmers include adjustment of sowing date, zero tillage, tie-ridging, mulching and supplemental irrigation.

3.2.2 | Salinity stress

Salinity stress threatens finger millet's resilience in arid and semi-arid regions, affecting its development throughout the growth cycle. At the seedling stage, salinity hinders germination, causing chlorosis, leaf scorching, delayed growth and stunted leaves in finger millet (Mbinda & Mukami, 2021; Mukami et al., 2020). At the vegetative stage, salinity inhibits root and shoot lengths, fresh and dry weights, leaf water potential and chlorophyll content of finger millet (Divya et al., 2022; Mukami et al., 2020; Satish et al., 2016). Also, salinity disrupts essential physiological and metabolic processes. For example, salinity drastically affected the crop's nutrient and water uptakes (Theerthana et al., 2022). Furthermore, salinity increases root and shoot necrosis, reducing internode lengths (Parida & Das, 2005). These alterations trigger biochemical and molecular changes, impacting functional genes and overall photosynthetic capacity (Rahman et al., 2014).

Climate change and unsustainable agricultural practices exacerbate soil salinity. Rising temperatures and altered precipitation patterns increase salt accumulation, particularly in arid regions. Published data (Mbinda & Mukami, 2021; Mukami et al., 2020) indicated the detrimental effects of salinity on finger millet, but yield loss is not well-quantified. Developing salinity-tolerant finger millet varieties is the most feasible, low-cost and eco-friendly approach (Divya et al., 2022; Mbinda & Mukami, 2021). Use of fluorescent pseudomonad inoculants as plant growth-promoting rhizobacteria is another approach for a sustainable and economical management of salinity stress in finger millet production. Agronomic management systems (e.g., increasing the soil water content through frequent irrigation, sub-surface drainage, application of calcium or magnesium with nitrate or chloride, and integrated agro-forestry systems) are widely used to mitigate against the effect of salinity stress (Mbinda & Mukami, 2021; Theerthana et al., 2022).

3.3 | Lack of production inputs and resources and poor access to markets

Smallholder farmers form the major component of the food systems in SSA. Limited resource access, encompassing finance, land, fertilizers, labour and draught power, hamper crop productivity (Gebreyohannes et al., 2021). Access to and adoption of scientific innovations and technologies that enhance crop production is vital to promoting sustainable finger millet cultivation (Jerop et al., 2018). Limited market access also poses a significant barrier to smallholder finger millet producers. Unfavourable market conditions, characterized by low prices, price volatility, high transportation costs and limited access to market information, discourage investment and impede production expansion (Mwema et al., 2017). Marketing bottlenecks can be circumvented through infrastructure development, streamlined information dissemination and fair trade, which are crucial to unlock the full potential of finger millet in the global food system and marketplace.

4 | BREEDING GOALS AND VARIETY DEVELOPMENT IN FINGER MILLET

Reportedly, the main goals of finger millet breeding are high grain yield potential (Gebreyohannes et al., 2021; Mwema et al., 2017; Owere et al., 2014), enhanced nutritional quality (Backiyalakshmi et al., 2023; Puranik et al., 2020), tolerance to biotic and abiotic stresses (Gebreyohannes et al., 2021; Mbinda & Masaki, 2021; Mbinda & Mukami, 2021; Mwema et al., 2017; Owere et al., 2014) and high marketability (Gebreyohannes et al., 2021; Mwema et al., 2017). Consumer preferences are increasingly shaping finger millet breeding programs, promoting the selection of traits that expand market appeal and ensure the crop's continued relevance in a changing lifestyle and food environment. Targeted breeding efforts focus on key market-driven factors such as grain colour, popping quality and brewing suitability. For instance, white grain varieties excel in the Indian processing industry, while in Ethiopia, diverse culinary traditions necessitate specific grain colours for traditional staples like “injera” (Tsehaye et al., 2006). Furthermore, finger millet has high popping potential and offers additional value in India, enabling diverse food applications (Sai & Meera, 2023). This targeted approach maximizes marketability and secures the crop's economic value. Other selection criteria include compact head type, medium plant height, a higher number of fingers per plant, longer and wider fingers, increased harvest index, bigger seed weight and a higher number of productive tillers.

Despite the socio-economic importance of the crop, there is a significant yield gap in finger millet compared to other major cereal crops such as maize, wheat and sorghum (Sood et al., 2016). Finger millet breeding programs in developing countries focus on selection from the landraces to develop improved finger millet varieties. Over 235 improved finger millet varieties have been released globally, with India releasing 149 and Africa 72 (AICSMIP [The All India Coordinated Research Project on Small Millets], 2014; Vetriventhan et al., 2020; Dida et al., 2021; MOA, 2022). Globally, the dominant number of improved finger millet varieties (62%) were developed through pure-line selection techniques, while another 32% have emerged from a recurrent selection approach (Dida et al., 2021; Joshi et al., 2022;

MOA, 2022; Gupta, Sood, Khulbe, Joshi, & Chandrashekhara, 2023; Gupta, Sood, Khulbe, Joshi, & Rajashekhara, 2023; Sood, Joshi, Gupta, et al., 2023).

Widening the genetic base of finger millet through artificial hybridization presents a critical challenge due to the floral biology (e.g., cleistogamous flower, small florets and poor synchronization of anthesis) (Nagaraja et al., 2023; Owere et al., 2016). Controlled crosses are the main approach in finger millet breeding programs, especially for genotypes with dominant traits (Owere et al., 2016). However, this method had a limited success rate (2% to 3%), necessitating alternative approaches (Nagaraja et al., 2023). Treating flower buds with hot water (e.g., 52°C, 3–5 min) and synthetic chemicals such as maleic hydrazide, gibberellic acid and ethyl induce temporary male sterility in finger millet (Nagaraja et al., 2023). Molecular markers have been used to assess emasculation efficiency and identify the true hybridity of crosses in finger millet. Krishna et al. (2020) compared hand emasculation and hot water male sterilization methods and assessed the hybrid purity in finger millet using simple sequence repeat (SSR), random amplified polymorphic DNA (RAPD) and inter-simple sequence repeat (ISSR). The authors reported that hot-water treatment of the flowers provided a high success rate (52% to 80% success) than hand emasculation (16% to 40%). The genetic purity of derived hybrids varied from 16% to 80% when assessed using RAPD and SSR markers (Krishna et al., 2020). Seventy-two finger millet varieties were released worldwide using the recurrent selection method with routine crossing and selection (Table 3). Another strategy to enhance hybridization is through the use of male sterility. Developing effective male sterility systems could be vital to harnessing the benefits of heterosis breeding (Vetriventhan et al., 2020). The authors developed INFM 9500, a genetic male-sterile line, through chemical mutagenesis. Developing male sterility systems boosts finger millet production and commercialisation through hybrid breeding.

Mutation breeding is an alternative method for genetic enhancement for finger millet breeding and genetic analysis. Finger millet has small bisexual florets, making artificial emasculation and pollination tedious and time-consuming for genetic recombination and selection.

TABLE 3 Finger millet varieties bred and released in different countries.

Country	Number of released varieties	Breeding methods	Characteristic features	References
India	72 66 9 2	PR RS MB SC	High-yielding, drought, salinity, lodging and cold tolerance, diseases (blast, blight, mosaic, brown spot, viral) and insects (tolerance to stem borer, aphids and tobacco cutworm, myllocerus weevil, earhead caterpillars and grass hopper), better nutritional quality, photo-insensitive, suitable varieties for irrigable and hilly areas	AICSMIP (2014); Patil and Patel (2018); Madhavilatha et al. (2019); Joshi et al. (2022); Gupta, Sood, Khulbe, Joshi, and Chandrashekhara (2023); Gupta, Sood, Khulbe, Joshi, and Rajashekhara (2023); Sood, Joshi, Gupta, et al. (2023)
Ethiopia	27 1	PR RS	High-yielding, drought and lodging tolerance, blast, grain mould and insect (stem borer) resistance and excellent nutritional quality	MOA (2022); Teklu et al. (2024)
Kenya	15 4	PR RS	High-yielding, drought, heat, high temperature, striga and bird damage tolerance, blast and insect resistance and good nutritional quality	Dida et al. (2021); Vetriventhan et al. (2020)
Uganda	9 4	PR RS	High-yielding, drought and lodging tolerance and resistance to blast	Owere et al. (2014); Vetriventhan et al. (2020)
Nepal	5	PR	High-yielding, drought and lodging tolerance and resistance to blast	Joshi et al. (2017)
Sri Lanka	5	PR	-	FAO (2011)
Bhutan	3	PR	-	FAO (2011)
Tanzania	3	PR	High-yielding, drought tolerance and better threshability quality	Ojulong et al. (2016)
Zimbabwe	2	PR		Mirza and Marla (2019)
Zambia	2 2	MB PR	High-yielding and brewing	IAEA (2022); Vetriventhan et al. (2020)
Malawi	3	PR		ICRISAT (2019)
Ukraine	1	SC	High-yielding	Radchuk et al. (2012); Mirza and Marla (2019)
Total	235			

Note: PR = pure line selection; RS = recurrent selection; MB = mutation breeding; SC = somaclonal selection.

TABLE 4 Drought-tolerant finger millet varieties reported globally.

Variety name	Trait description	Breeding method	Days to maturity	Year of release	Yield (t/ha)	Country	References
Mereb-1 (KNE#622)	Drought tolerance	PR	83–121	2016	2.5–3.2	Ethiopia	MOA (2022)
Kako-1 (ACC#203351)			139	2016	2.6–3.0		
Axum (ACC#229355)			147	2016	2.2–3.6		
Dibya Sinha	Drought tolerance	MB	90–100	1971	2.0–2.5	India	Hatakeyama et al. (2018); Aralikatti and Chaturvedi (2020)
K6			100–105	1982	2.3–2.5		
K1 (Kolar Gidda Ragi)		PR	130–135	1939	0.9–1.0		
CO2			110–115	1942	2.0–2.5		
CO1			120–125	1942	2.5–3.0		
Aruna			95–100	1956	1.5–1.8		
Vzm1			105–110	1958	2.0–2.5		
CO8			90–95	1963	1.5–2.0		
CO10			110–120	1976	3.5–4.0		
PR202 (Godavari)			110–115	1976	2.5–3.0		
CO11 (EC4849)			110–115	1982	3.5–4.0		
VL204			90–100	1985	1.8–2.0		
Paiyur1			100–110	1985	2.3–2.5		
CO12			120–125	1985	3.5–4.0		
KM13			95–110	1989	2.5–3.0		
PES400 (Pant Mandua3)			95–100	1989	1.8–2.0		
VR520 (Suraj)			85–90	1992	2.0–3.0		
PR230 (Maruthi)			90–100	1998	2.5–3.0		
VR708 (Champavathi)			90–95	1998	2.5–3.0		
Udaya		RS	90–95	1959	2.5–3.0		
Akp2			80–90	1960	2.0–2.2		
CO 9			100–105	1970	2.5–3.0		
INDAF5			105–110	1977	4.5–5.0		
K5			105–110	1982	2.6–3.0		
INDAF8			120–125	1982	2.0–2.5		
INDAF9 (Chitta)			95–105	1985	2.0–2.5		
CO13 (Tnau294)			95–100	1989	2.5–3.0		
ML365			110–115	2008	5.0–5.5		
VL347			90–105	2010	2.0–2.2		
VL352			95–100	2012	3.3–3.5		
KMR340			90–95	2016	3.5–4.0		
KM65	Drought tolerance and blast resistance	PR	95–100	1994	1.8–2.0		
VL146		RS	95–100	1995	2.5–3.0		
GPU26			95–100	1997	3.0–3.5		
GPU45			95–100	2001	2.8–3.0		
Maseno60D (MSUFM60D)	Drought tolerance	RS	80–90	2016	3.1	Kenya	Dida et al. (2021); KEPHIS (2023)
Kacimmi42 (Kak-Wimbi3)			87–130	2016	1.3–6.4		
Kacimmi49 (KAK-Wimbi5)			92–132	2021	1.2–5.7		
P-224		PR	90–120	1981	2.0–5.0		
Kat/FMI			90	2000	1		
KNE741 (EUFM-401)			65–75	2018	1.0–1.4		
GBK029646A (Kis-Wimbi1)			89–119	2021	1.4–4.4		
AGRY-2 (Mavuno)			90–120	2021	1.8–2.5		

(Continues)

TABLE 4 (Continued)

Variety name	Trait description	Breeding method	Days to maturity	Year of release	Yield (t/ha)	Country	References
Eufm-8			95–115	2021	1.8–2.2		
U-15 (Maridadi)	Drought tolerance, and blast and striga resistance	PR	90–120	2015	1.1–4.9		
I.E. 4115 (Kak-Wimbi2)			88–131	2016	1.3–6.1		
Okhale-1 (Kak-Wimbi1)			88–138	2016	1.1–6.7		
Kacimmi65 (KAK-Wimbi6)		RS	92–120	2021	1.2–4.3		
SDFM1702 (EUFM-503)	Early maturity, blast resistance and bird damage tolerance		90–98	2018	1.5–2.5		
IE-980 (Dalle-1)	Drought tolerance	PR		1980	3.3	Nepal	Joshi et al. (2017)
NE1304–43 (Okhle-1)				1980	3.3		
NF-6401-26 (Kabre Kodo-1)				1990	1.8–4.8		
PR-202 or GE-5176 (Kabre Kodo-2)				2015	2.5		
U-15			90–100	2019	2	Tanzania	Ojulong et al. (2016)
Gulu-E	Drought tolerance, and blast resistance	PR	75–80	1970		Uganda	Mwema et al. (2017)
Seremi2 (U15)			70–80	1999	2		

Note: PR = pure line selection; RS = recurrent selection; and MB = mutation breeding.

Through mutation breeding, 11 varieties were released and registered in India and Zambia (AICSMIP (The all India coordinated research project on small millets), 2014; IAEA (International Atomic Energy Agency), 2022). The varieties were reported to be tolerance to stem borer, blast, brown spot and drought. Finger millet variety designated as FMM175, which was derived through mutation breeding, was released in Zambia in 2009 with brewing quality (IAEA, 2022).

Somaclonal variants selected through the tissue culture method were developed and released in India and Ukraine from 2006 and 2017. Cultivars denoted as GN 4 and Dapoli-2, were released in India in 2006 and 2017, respectively, while cultivar, Yaroslav-8(SE7) was released in Ukraine in 2012 (Radchuk et al., 2012; AICSMIP (The all India coordinated research project on small millets), 2014). Several genes were reported conditioning economic traits in finger millet (Ganapathy et al., 2011; Krishnappa et al., 2009). Nevertheless, genetic engineering has not been pursued to stack candidate genes in desirable varieties due to technical limitations and a lack of priority and support for breeding, genetic research and innovations. Developing male sterility systems is a potential research area to exploit heterosis in finger millet breeding (Vetriventhan et al., 2020). A genetic male-sterile line of finger millet designated as INFM 95001 has been developed through chemical mutagenesis (Vetriventhan et al., 2020).

Finger millet varieties bred and released globally have enhanced yield potential, adaptability to drought and saline conditions, improved lodging resistance, resistance to insect pests and diseases, and enriched nutritional composition (Tables 3–6 and S1–S3). There is a need for research and development investments to develop and promote the adoption of climate-resilient, consumer-preferred cultivars tailored to the specific needs of SSA. Advanced and precision breeding techniques and innovations such as marker-assisted breeding, genomic selections, genome editing and genetic engineering can be integrated with classical breeding for impact.

4.1 | Breeding for drought tolerance

Modest selection progress has been made regarding breeding for drought-tolerant finger millet varieties (Table 4). In six countries, including India, Kenya, Ethiopia, Uganda, Nepal and Tanzania, 59 finger millet varieties have been developed with enhanced drought tolerance. Some 35 drought-tolerant finger millet varieties were released in India, followed by Kenya (13), Ethiopia (03), Nepal (3), Uganda (2) and Tanzania (1) (AICSMIP, 2014; Owere et al., 2014; MOA, 2022; Joshi et al., 2017; KEPHIS (Kenya Plant Health Inspectorate Service), 2023). Yield levels of the drought-tolerant varieties vary from .9 to 5.5 in India (AICSMIP, 2014), 1.0 to 6.7 in Kenya (KEPHIS, 2023) and 2.2 to 3.6 in Ethiopia (MOA, 2022). The varieties reportedly possess drought-adaptive traits, including stay-green, robust root system, purple pigmentation, early flowering and maturity. Globally, the highest number of finger millet varieties have been released in India, with K1 being the first drought-tolerant variety developed in 1939. Varieties such as PR202, Dibya Sinha, Udaya, KMR340 and ML365 are early maturity types (80 to 135 days to maturity). Likewise, varieties Axum, Mereb-1 and Kako-1 are popular drought-tolerant finger millet varieties released in Ethiopia in 2016, with 83 to 147 days to maturity. Early maturing (65 to 138 days) finger millet varieties in Kenya, namely, KNE741, Maseno60D, SDFM1702 and Kat/FM I were developed. Finger millet varieties such as Seremi2 and Gulu-E in Uganda (with maturity of 70 to 80 days) and U-15 in Tanzania (90 to 100 days) have been released for their remarkable earliness. Early maturity is a proxy trait for breeding drought escape genotypes.

4.2 | Breeding for salinity tolerance

Finger millet is a highly preferred crop in arid and semi-arid regions. Reportedly, it possesses polygenes for salinity tolerance and has a unique cellular pathways and environmental plasticity (Mbinda & Mukami, 2021). A limited number of salinity-tolerant finger millet varieties were released. For instance, finger millet variety designated as CO 11 (EC 4849) is reportedly high-yielding (3.5 to 4.0 t/ha), drought- and salinity-tolerance, photoperiod-insensitive and early maturing (110 days) (AICSMIP, 2014). Another variety, referred to as Nirmal, has blast resistance and is suitable for production under saline soils with a short maturation period of 110-day (AICSMIP, 2014). Inbred lines such as GBK043094 and GBK043137 were selected by Mukami et al. (2020) for breeding programs. Divya et al. (2022) identified some genotypes (e.g., ML 365, GPU 28 and GPU 67) with salinity tolerance under controlled environment conditions. Transcriptome analysis through RNA-sequencing was used to identify a finger millet genotype, Trichy 1, for salinity tolerance (Rahman et al., 2014).

4.3 | Breeding for resistance to fungal diseases

Finger millet blast caused by the fungus *Magnaporthe oryzae* poses a significant threat to global production and productivity. The disease causes a yield loss reaching up to 100% in susceptible varieties. Breeding new varieties with durable blast resistance and product profiles is an overriding goal. For instance, five elite lines were identified (IE 2883, IE 2871, IE 6240, IE 2710 and IE 3767) with adequate resistance to finger and neck blasts and desirable agronomic traits. Manyasa et al. (2019) assessed 81 Eastern African finger millet accessions and found three lines (Kafumbata, GBK-00351A and GBK-011119A) resistance to leaf, neck and panicle blasts. Among these accessions, GBK-011119A, recognized for its blast resistance and superior yield, was released in Ethiopia as Meba in 2016 (MOA, 2022), marking a significant advancement in disease management and crop production. Blast-tolerant genotypes (e.g., GBK000702, GBK000513, GBK029869, GULU-E, GBK000752 and Busibwabo) were identified in Western Kenya, priming them as donor parents for resistance breeding programs. Lule et al. (2014) reported exceptional blast resistance in cultivated accessions (e.g., Acc. 214,995 and PW-001-022) and a wild accession (AAU-ELU-15) among Ethiopian germplasm collections.

Globally, 20 blast-resistant finger millet varieties (Table 5) have been developed and released (AICSMIP, 2014; Dida et al., 2021; Madhavilatha et al., 2019; MOA, 2022). About 50% of the released varieties were bred by the All-India Coordinated Research Project on Small Millets (AICSMIP). Five blast-resistant finger millet varieties were released in Ethiopia, one in Nepal and two in Kenya and Uganda from 1999 to 2020.

4.4 | Breeding for resistance to insect pests

The major insect pests of finger millet are lower pink stem borer, jassids, aphids and shootflies (Mulualem & Melak, 2013). Five genotypes were identified (e.g., PRM 9002, KOPN 933, OEB 28, RAU 8 and Champabati) exhibiting resistance to lower pink stem borer infestation serving as valuable genetic resources for breeding. Reportedly, a few finger millet genotypes exhibited tolerance to the major insect pests (Table S1). Genotypes, such as PES 110, VR 847 (Srichaitanya), and OEB 532 had, tolerance to broad insect pest resistance. The reported insect pest tolerant genetic resources (Table S1) had grain yield variability, ranging from 2.2 t/ha (OEB 532) to 6.3 t/ha (Ikhule) and other contrasting agronomic traits. Eight insect pest-tolerant finger millet varieties were reported in India. Of these, five were developed through recurrent selection, two through mutation breeding and one with pure line selection methods (Table S1). Genotype Ikhule, identified and released in Ethiopia, had a marked tolerance to shoot fly (MOA, 2022).

4.5 | Breeding for *Striga* resistance

Striga is a parasitic weed of economic importance ravaging finger millet production in SSA. In SSA there is limited research on *Striga* resistance breeding in finger millet (Sood et al., 2019). Recently, Kunguni et al. (2023) reported *Striga* resistance in the wild finger millet (e.g., genotype LESK10) and the cultivated variety (Okhale-1) with reduced *S. hermonthica* parasitism. Nyongesa et al. (2018) identified three genotypes (e.g., GBK029661, I. E 2217 and I. E 6537) with an immune reaction to *S. hermonthica* infestation. Makani et al. () reported pre-attachment *Striga* tolerance in the genotype SDMF1702 for *S. asiatica* under controlled environments. In Kenya, the following cultivars were released with *Striga* resistance: U-15 (MARIDADI), OKHALE-1 (KAK-WIMBI 1), IE 4115 (KAK-WIMBI 2), KACIMMI 65 (KAK-WIMBI 6) and KACIMMI 42 (KAK-WIMBI 3). These lines were mainly developed through pure line selection, except KACIMMI 42, which was bred through the recurrent selection method. The Kenyan varieties possessed blast and lodging resistance and drought tolerance (KALRO, 2021).

4.6 | Breeding for nutritional quality traits

Various basic and applied research have characterized finger millet genetic resources for their mineral and protein contents. However, there is no single variety released with unique grain nutrient profiles. Finger millet's nutritional values have not yet been explored and deployed for the marketplace. Some pre-breeding progress have been reported on nutrient profiling and dietary value addition (Table S2). India released six varieties, followed by Ethiopia (2), Kenya (1) and Zambia (1) based on finger millet pre-breeding for biofortification (Table S2). Early maturing genotype CO 9, selected in India, had a remarkable protein content of 9.6%, making it an ideal candidate for

TABLE 5 Reported global finger millet varieties with blast resistance.

Variety name/ designation	Breeding method	Release year	Yield (t/ha)	Country	Trait descriptions	References
AKP7 (Sarada/ IE901)	PR	1971	2.5–3.0	India	Resistance to blast and mosaic diseases	AICSMIP (2014); Patil and Patel (2018); Madhavilatha et al. (2019); Joshi et al. (2022); Gupta, Sood, Khulbe, Joshi, and Chandrashekhara (2023); Gupta, Sood, Khulbe, Joshi, and Rajashekhara (2023); Sood, Joshi, Gupta, et al. (2023)
BM2 (Birsa Marua2)	PR	1995	2.5–2.6		Resistance to neck and finger blast	
GPU28	RS	1998	3.5–4.0		Highly resistance to finger and neck blast	
CO14(Tnau946)	RS	2004	2.6–2.8		Resistance to neck and finger blast	
GPU48 (Ratna)	RS	2005	2.8–3.0		Highly resistance to finger and neck blast	
GPU66	RS	2009	3.5–4.0		Resistance to neck and finger blast	
PRM2	PR	2010	2.5–2.8		Resistance to finger and neck blast and *Cercospora* leaf spot	
VL 380	RS	2018	1.9		A medium maturing and blast-tolerance	
VL 386	RS	2023	-		Resistance to leaf blast, neck blast, finger blast, foot rot, high harvest index and grain yield.	
VL 399	RS	2023	-		Broad resistance to finger blast and neck blast	
VL 400	RS	2023	3.5		Early maturing and resistance to leaf blast, neck blast, finger blast and foot rot, rich in calcium content	
CFMV1(Indravathi)	PR	2020	3.5–4.0		Resistance to neck and finger blast	
CFMV2(Gira)	PR	2020	3.2–3.5		Resistance to blast and stem borer	
Kacimmi42(Kak-Wimbi 3)	PR	2016	1.3–6.4	Kenya	Blast resistance	KEPHIS (2023)
SDFM1702 (EUFM-503)	PR	2018	1.5–2.5		Blast resistance	
Seremi3(SX17–88)	PR	1999	2.5–3.0	Uganda	Resistance to blast and tolerance to stem lodging	Mwema et al. (2017)
Seremi2 (U15)	PR	1999	2.0		Resistance to blast and tolerance to stem lodging	
PR-202 or GE-5176 (Kabre Kodo-2)	PR	2015	2.53	Nepal	Resistance to blast	Joshi et al. (2017)
Addis-1 (ACC#203544)	PR	2015	2.5–3.5	Ethiopia	Moderately resistance to blast	Manyasa et al. (2019); MOA (2022)
Wama (KNE#392)	PR	2007	1.7–3.5		Tolerance to major finger millet diseases	
Diga-1 (ACC#216036)	PR	2016	2.2–2.8		Tolerance to blast	
Meba (GBK-011119A)	PR	2016	2.1–3.5		Tolerance to major finger millet diseases	
Metekili (ACC.05pw-2012)	PR	2020	2.8–3.8		Resistance to blast under natural conditions	

Note: PR = pure line selection; RS = recurrent selection.

early harvest and boosting the dietary protein. Genotypes HAMSA and PRM 2 had higher protein levels (>9%), good candidates for quality breeding and deploying nutritionally rich finger millets.

Geneotype EUFM-8, selected in Kenya is valued for early maturity and higher contents of calcium and iron. A variety designated as FMM175 and selected in Zambia was recommended for its unique quality in brewing traditional beverages. The diverse products and unique nutrient content of the crop indicated the socio-economic value and the crop's broader significance for product development and commercialisation. Hence, continued breeding efforts are needed to focus on biofortification to develop cultivars rich in essential macro- and micro-nutrients and protein content. Finger millet is a candidate and nutritious solution to global food and nutrition challenges.

5 | GENETIC AND GENOMIC RESOURCES OF FINGER MILLET

5.1 | Genetic resources

Plant genetic resources are the foundation for variety development to meet the increased food demand and mitigate climate change (Ron & Rodiño, 2022). Globally, about 40,182 finger millet accessions have been maintained by various gene banks of different countries and institutions (Dwivedi et al., 2012; EBI, 2023; ICRISAT, 2017; PGRC, 2016). Most accessions are maintained in Asian gene banks. For example, India maintains the largest germplasm of 16,379 accessions, followed by Nepal (869), Japan (565), Sri Lanka (462) and China (300) (Dwivedi et al., 2012). ICRISAT is the highest germplasm repository of finger millet (Table 6). ICRISAT in India, Mozambique, and Kenya each maintained 7519, 2068 and 651 accessions, respectively (ICRISAT, 2017). In Africa, Kenya Agricultural and Livestock Research Organization (KALRO) in Muguga maintained the highest number of finger millet accessions (2875), followed by 2209 accessions by the Ethiopian Biodiversity Institute (EBI) in Addis Ababa and Melkassa Agricultural Research Center (MARC) in Adama (Dwivedi et al., 2012; EBI, 2023). A higher number of finger millet accessions is also maintained in the USA, including the University of Georgia (1500), the United States Department of Agriculture (USDA) Agricultural Research Service (ARS) in Griffin, Georgia (1425), and the National Center for Genetic Resources Preservation in Fort Collins (702) (Dwivedi et al., 2012). Most of the collected genetic resources are mainly landrace varieties, which are useful for variety design and development targeting high yield potential, nutrient compositions and biotic and abiotic stress tolerance.

Crop wild relatives (CWR) possess unique genes for various biotic stress tolerance, including insect pest and disease resistance and enhanced nutritional value (Hajjar & Hodgkin, 2007). The 335 wild species of finger millet are maintained in various gene banks. These include at ICRISAT in India, Mozambique and Kenya, EBI in Addis Ababa, Maseno University in Kenya, and Addis Ababa University in Ethiopia, maintaining 205, 41, 4, 11, 18 and 56 wild species, respectively (Dida et al., 2021; EBI, 2023; ICRISAT, 2017). The species (e.g., *E. coracana* subsp. Africana) and hybrid progenies derived from *subsp. coracana* and *subsp. Africana* are cross-compatible with cultivated finger millet (Dida et al., 2021; Lule et al., 2018). The gene flow

TABLE 6 Important gene banks and databases of finger millet.

Gene banks	Location, country	Number of accessions maintained	References
International Crops Research Institute for the Semi-Arid Tropics	Patancheru, India	7519	ICRISAT (2017)
	Nairobi, Kenya	651	
	Bulawayo, Mozambique	2068	
National Bureau of Plant Genetic Resources	New Delhi, India	9522	Dwivedi et al. (2012)
All India Coordinated Minor Millet Project	Banglore, India	6857	
Kenya Agricultural and Livestock Research Organization	Muguga, Kenya	2875	
Plant Genetic Resources Centre of Sri Lanka	Peradeniya, Sri Lanka	462	PGRC (2016)
Ethiopian Biodiversity Institute and MARC	Addis Ababa and Adama, Ethiopia	2209	EBI (2023)
University of Georgia, USA	Georgia, USA	1500	Dwivedi et al. (2012)
USDA Agricultural Research Service	Griffin, Georgia, USA	1425	
Serere Agricultural and Animal Production Research Institute	Soroti, Uganda	1231	
SADC Plant Genetic Resource Centre	Lusaka, Zambia	1037	
Central Plant Breeding and Biotechnology Division	Kathmandu, Nepal	869	
National Center for Genetic Resources Preservation	Fort Collins, USA	702	
National Institute of Agrobiological Sciences	Kannondai, Japan	565	Dwivedi et al. (2012)
Mt. Makulu Central Research Station	Chilanga, Zambia	390	Dwivedi et al. (2012)
Institute of Crop Germplasm Resources, Chinese Academy of Agricultural Sciences	China/Beijing	300	Dwivedi et al. (2012)
Total		**40,182**	

between the cultivated and wild accessions would result in genetic admixtures, causing linkage drag or novel genetic combinations for selection (Dida et al., 2021; Lule et al., 2018; Pendergast et al., 2022). Several finger millet varieties known as the "Indaf" series were created through controlled crosses between Indian and African genetic resources. The series possessed desirable traits such as blast and drought tolerance, and enhanced nutritional composition (Hittalmani et al., 2017). There is a need for introgression of farmers' desired traits between the wild and cultivated finger millet varieties. Wild relatives must be collected and conserved for future use in breeding for biotic and abiotic stress tolerance. This requires funding, international cooperation and public awareness of the importance of CWR.

Phenotypic heterogeneity in finger millet genotypes has been documented for numerous attributes. Marked genetic variation has been recorded on yield and yield component traits, seed colour, glume coverage, tolerance to *Striga*, bird damage and insect pests and disease (blast) (Madhavilatha et al., 2019; Owere et al., 2015; Patil & Patel, 2018; Tsehaye et al., 2006). Finger millet varieties with fist-like ear shapes were reported to be tolerance to bird damage in Kenya (KEPHIS, 2023). Finger millet genotypes with different seed colours are utilized for different purposes. For example, white seeded types are preferred to prepare fermented pancake-like flatbread "injera" in Ethiopia and for the baking and food industries in India (Joshi et al., 2021; Tsehaye et al., 2006). Contrastingly, black and brown seeds have exceptional brewing quality (Tsehaye et al., 2006). Furthermore, the black-seeded types are tolerance to bird damage due to their high tannin content (Xiang et al., 2019).

Finger millet exhibits remarkable genetic variability for agronomic traits, nutritional compositions and root attributes. Reports indicate variability for grain yield (.7–8.0 t/ha), plant height (50–180 cm), flowering time (51–96 days), inflorescence dimensions (40–180 mm width, 30–190 mm length), panicle exsertion (0–215 mm), number of tillers (3–7 basal tillers), number of fingers (6–9 per ear), root length (68–126 cm) and root weight per plant(14–33 g) (David et al., 2021; Oduori, 2008; Upadhyaya et al., 2010).

Marked genetic diversity were reported in finger millet for nutritional composition, including the contents of dietary fibre (15%–20%), protein (5%–16%), carbohydrate (72%–79%), amylose (29%–34%), iron (3–53 mg/100 g), magnesium (78–201 mg/100 g), zinc (1–37 mg/100 g) and potassium (430–490 mg/100 g) (Backiyalakshmi et al., 2023; Maharajan et al., 2022; Puranik et al., 2020; Upadhyaya et al., 2010). Higher calcium content was reported in Ethiopian finger millet varieties designated Diga-2 (BKFM0010) and Bareda (BRC-356-1) with 550 to 589 mg/100 g (Lule et al., 2020; Teklu et al., 2024), surpassing the previously reported value of 344 mg/100 g (Backiyalakshmi et al., 2023; Maharajan et al., 2022; Puranik et al., 2017, 2020; Upadhyaya et al., 2010). The substantial genetic diversity present in finger millet forms the foundation for successful breeding programs. Through targeted selection and hybrid development, cultivars can be tailored for farmer-preferred traits (e.g., yield, drought tolerance) and desirable nutritional attributes.

5.2 | Impact of in situ collections and gene banks for finger millet varietal development

In situ and gene bank collections are genetic reservoirs for finger millet improvement programs. These collections preserve genetic diversity and facilitate selection of adapted and resilient genetic resources for sustainable plant breeding. Landraces and wild relatives maintained at gene banks are novel source of genes for drought tolerance, disease and insect pest resistance and nutritional value (Upadhyaya et al., 2010). Over 150 finger millet varieties have been directly selected from the landrace accessions and released from 11 countries on the African and Asian continents (Table S3 and Figure 3). The following gene banks maintain genetically diverse accesssions of finger millet: ICRISAT/India, NBPG R/India, All India Coordinated Minor Millet Project, KALRO and EBI. Access to genetically diverse germplasm is the fuel for breeders to develop new varieties that meet local demands and adapt to specific or broad environmental conditions.

5.3 | Genomic resources of finger millet

5.3.1 | Reference genomes, whole genome re-sequencing and transcriptome analysis

Genomic resources are complementary tools for finger millet cultivar design and genetic gain under changing climatic conditions. Genomic tools and databases are essential for trait discovery, gene mining and markers-assisted breeding. There are three published reference genomes of finger millet, the most recent of which is chromosome-scale (Devos et al., 2023) and is publicly available in Phytozome (Table 7). Hittalmani et al. (2017) and Hatakeyama et al. (2018) reported two other scaffold-level reference genomes that were made available in NCBI (Table 7). Finger millet's chloroplast genome has been developed, generated and applied for phylogenetic analysis within the grass family (Liu et al., 2021). Devos et al. (2023) estimated the genome size of finger millet genotype KNE796-S at 1.1 Gb, which was significantly smaller than what was estimated for genotypes ML365 (1.45 Gb) (Hittalmani et al., 2017) and PR202 (1.5 Gb) (Hatakeyama et al., 2018). The availability of the reference genomes enabled the implementation of skim sequencing (Kumar, Choudhary, et al., 2021) and the use of high throughput Single Nucleotide Polymorphism (SNP) markers. Devos et al. (2023) reported the whole genome re-sequencing (WGRS) data from 35 accessions of the subsp. coracana, 11 from subsp. africana and two genotypes of *E. indica*. The WGRS data enabled a better understanding of the gene flow between finger millet and progenitors and to discern the genome evolution within the genus *Eleusine*.

Transcriptomics has been used in finger millet for genome annotation, marker and candidate gene discovery. Hatakeyama et al. (2018) generated transcriptome reads to aid in the PR202 genome annotation, while Hittalmani et al. (2017) used transcriptome data to identify drought-induced candidate genes. Devos et al. (2023) used

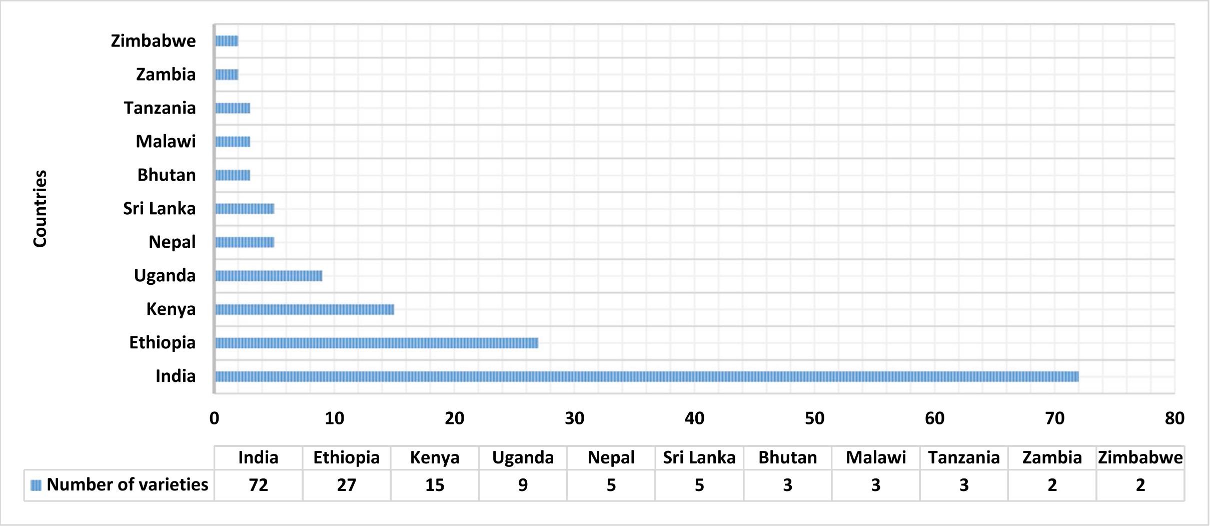

FIGURE 3 Number of globally released finger millet varieties selected from landraces. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 7 Whole genome resources for finger millet.

Database	Website	References
Phytozome	https://phytozomenext.jgi.doe.gov/info/Ecoracana_v1_1	Devos et al. (2023)
NCBI	https://www.ncbi.nlm.nih.gov/assembly/GCA_002180455.1	Hittalmani et al. (2017)
NCBI	https://www.ncbi.nlm.nih.gov/assembly/GCA_021604985.1	Hatakeyama et al. (2018)
NCBI	https://www.ncbi.nlm.nih.gov/nuccore/MW262987.1/	Liu et al. (2021)

Note: NCBI = the National Center for Biotechnology Information.

transcriptome data that was publicly available in NCBI to annotate the KNE796-S genome. Kumar et al. (2014) studied the transcriptome of developing spikes and discovered 43,928 and 36,652 SNPs and 24,748 and 21,276 SSRs in the high and low-grain calcium genotypes, respectively. Further, Chandra et al. (2020) used transcriptomics to study Fe and Zn homeostasis of finger millet and identified 15 putative iron and zinc homeostasis pathway candidate genes. Li et al. (2021) deployed transcriptomics and proteomics to determine drought response mechanisms and identified 113 associated differentially expressed genes (DEGs) and differentially expressed proteins (DEPs). Brhane, Haileselassie, Tesfaye, Ortiz, Hammenhag, Abreha, Vetukuri, and Geleta (2022) exploited transcriptomics for both marker and trait discovery. They reported differentially expressed genes between Al-tolerant and Al-susceptible finger millet and SNPs and SSR markers. Jadhao et al. (2020) used transcriptomics in finger millet to mine silicon transporter genes linked with defence against pink stem borer (*Sesamia inferens* [Walker]).

The availability of the three finger millet reference genomes, including a recent chromosome-scale assembly, revolutionizes cultivar design and genetic gain under changing climates and market prefernces. These resources, complemented by transcriptome data, equip scientists with a powerful toolkit for trait discovery, gene mining, marker development and understanding genome evolution (Ceasar et al., 2018; Devos et al., 2023; Hatakeyama et al., 2018; Hittalmani et al., 2017; Krishna et al., 2022; Sood et al., 2016). Genomic and proteomic tools with advanced breeding techniques will improve the pace and precision of finger millet cultivar development with enhanced nutrient content, stress tolerance and improved yields.

5.3.2 | Molecular markers and quantitative trait loci (QTL) mapping in finger millet

Various molecular markers have been used to characterize the genetic diversity and population structure of finger millet. These include Random Amplified Polymorphic DNA (RAPD) (Bezaweletaw, 2011; Pandian et al., 2018), Sequence-Characterized Amplified Region (SCAR) (Reddy et al., 2010), Inter-Simple Sequence Repeats (ISSR) (Brhane, Haileselassie, & Tesfaye, 2017; Pandian et al., 2018), Simple Sequence Repeat (SSR) (Babu et al., 2018; Gimode et al., 2016; Lee et al., 2017), Expressed Sequence Tag-derived Simple Sequence Repeat markers (EST-SSR) (Brhane et al., 2021; Bwalya et al., 2020) and SNP (Backiyalakshmi et al., 2021; Brhane, Haileselassie, Tesfaye, Ortiz, Hammenhag, Abreha, & Geleta, 2022; Gimode et al., 2016).

Venkatesan et al. (2021) employed ISSR markers for the accurate identification of traditional and hybrid varieties of finger millet, while Krishna et al. (2020) used SSR, RAPD and ISSR to examine the genetic purity of F1 hybrids. Several studies reported the association of SSR markers with traits of interest (David et al., 2021; Lule et al., 2018; Ramakrishnan et al., 2018). The existing finger millet SSR markers can be integrated into the robust SNP linkage map (Pendergast et al., 2022) to further validate their associations with economic traits.

Marker-trait association (MTA) studies in finger millet have been undertaken using whole genome SNP markers from different skim-

TABLE 8 A summary of marker-trait association studies in finger millet that used at least 100 genotypes.

Traits	Mapping methods	Marker types	Number of significant MTAs	Population size	References
Days to 50% flowering, plant height, panicle number, leaf blast severity and panicle blast incidence at maturity	Bi-parental QTL mapping	SNPs and insertion–deletions	8	151	Pendergast et al. (2022)
Primary root length, shoot dry weight and total phosphorous content in shoots	Bi-parental QTL mapping	SSRs	92	100	Maharajan et al. (2023)
Stigma, and anther colour	Bi-parental QTL mapping	SNPs	-	294	Devos et al. (2023)
Days to 50% flowering, basal tiller number, flag leaf width and plant height	Association mapping	SSRs	5	190	Babu, Agrawal, Pandey, Jaiswal, and Kumar (2014)
Finger blast and neck blast resistance	Association mapping	SSRs	7	190	Babu, Dinesh, Agrawal, Sood, et al. (2014)
Protein and tryptophan contents	Association mapping	SSRs	3	190	Babu, Agrawal, Pandey, and Kumar (2014)
Days to maturity, finger number, grain yield per plant, number of grain per spikelet, productive tiller number and thousand grain weight	Association mapping	SSRs	16	138	Lule et al. (2018)
Days to 50% flowering, days to maturity and grain yield	Genome wide association mapping	SNPs	111	113	Sharma et al. (2018)
Grain yield, days to maturity and seed protein content	Genome wide association mapping	SNPs	81	113	Tiwari et al. (2020)
Iron, zinc, magnesium, sodium and potassium contents	Genome wide association mapping	SNPs	418	190	Puranik et al. (2020)
Calcium content	Genome-wide association mapping	SNPs	44	202	Sharma et al. (2022)
Days to 50% flowering, days to maturity, plant height, number of basal tillers, flag leaf length, flag leaf width, ear length, ear width, number of fingers, green fodder weight, dry fodder weight and neck blast	Genome-wide association mapping	SNPs	132	186	Sood, Joshi, Rajashekara, et al. (2023)
Zinc and iron contents	Genome-wide association mapping	SNPs	45	202	Chandra et al. (2024)

sequencing techniques. Through GWAS, SNP markers associated with flowering days (Sharma et al., 2018; Sood, Joshi, Rajashekara, et al., 2023), grain yield (Sharma et al., 2018; Sood, Joshi, Rajashekara, et al., 2023; Tiwari et al., 2020), neck blast (Sood, Joshi, Rajashekara, et al., 2023), micronutrient (Chandra et al., 2024; Puranik et al., 2020; Sharma et al., 2022) and protein contents (Tiwari et al., 2020) were reported. Studies at the University of Georgia have characterized a bi-parental interspecific population (MD-20 × Okhale 1) (Qi et al., 2018) to map for days to flowering, plant height, panicle number per plant and blast disease resistance (Pendergast et al., 2022), and colouration of stigma and anthers (Devos et al., 2023). A mapping population between IE-2606 and PR-202 consisting of 100 individuals was characterized for agro-morphological traits and protein content, identifying several QTLs (Maharajan et al., 2023). Table 8 summarizes MTAs conducted in finger millet that used at least 100 genotypes and a minimum of 100 markers in the trait characterization. Future MTA studies in finger millet would require validating the reproducibility of generated datasets. Furthermore, there is a need to deploy larger, genetically diverse, bi-parental populations evaluated across representative environments.

6 | GENETIC ENGINEERING AND GENOME EDITING

Genetic engineering is the transformation of DNA sequence(s) of genomes by a variety of molecular biology methodologies (Lanigan et al., 2020; Ye et al., 2022), notably electroporation, biolistics, microinjection and *Agrobacterium tumefaciens* (Mir & Patel, 2018). Genetic engineering enables the introduction of a range of traits that may not be transferable through conventional breeding methods. The success of genetic transformation in any crop depends on the ability of the target crop cells to be cultured in vitro. Developing an optimum and reproducible tissue culture technique has been a challenge in finger millet, leading to slow progress in genetic engineering. Both somatic embryogenesis and organogenesis have been tested successfully for the regeneration of finger millet plants in vitro. Somatic embryogenesis is the formation of an embryo from a cell other than a gamete (Merkle et al., 1995), while organogenesis is the process in which adventitious roots are generated from detached or wounded plant tissues or organs (Chen et al., 2014).

Eapen and George (1989) reported the first finger millet plant regeneration through somatic embryogenesis. Several studies reported the use of somatic embryogenesis in finger millet (Eapen & George, 1989; Ngetich et al., 2018; Venkatesan et al., 2022), using embryoids for genetic engineering. There are successful finger millet plant regeneration using organogenesis (Mukami et al., 2018; Kansara et al., 2023.) and a combination of both organogenesis and somatic embryogenesis (Kansara et al., 2023; Kashyap et al., 2018). The somatic embryogenesis method is the most preferred method of regenerating cereals due to the single-cell origin of embryoids that enhances the stability and genetic uniformity of resulting transformants (Kumar et al., 2001). These successful plant regeneration reports have made it possible to genetically engineer finger millet, albeit with low reproducibility across labs.

Both biolistics and *Agrobacterium*-mediated transformation have been tested for the genetic engineering of finger millet. Gupta et al. (2001) used biolistics and successfully tested the efficiency of various gene promoters in finger millet. Latha et al. (2005) also used biolistics to insert an antifungal gene to improve leaf blast resistance in finger millet. Bayer et al. (2014) used a combination of both biolistics and *Agrobacterium*-mediated transformation to generate finger millet plants with herbicide resistance. Ignacimuthu and Ceasar (2012) reported successful transformation of finger millet using *A. tumefaciens*. The authors pinpointed successful introduction of *rice chitinase* gene into finger millet for leaf blast resistance. Other workers such as Ramegowda et al. (2013) reported successful transgenics for improved zinc concentration; introduced *mannitol-1-phosphate dehydrogenase* (mtlD) for improved multiple stress tolerance (Hema et al., 2014); and Jayasudha et al. (2014) and Anjaneyulu et al. (2014) for improving salinity tolerance. The biggest challenge is the reproducibility of the transformation methods across different labs.

Genome editing enables targeted alteration of both the genotypes and phenotypes of the edited organisms. Genome editing, as opposed to genetic engineering, involves the modification of endogenous plant DNA at specified loci by the deletion/insertion and replacement of essential DNA segments. Among several gene editing tools, clustered regularly interspaced short palindromic repeats (CRISPR) and CRISPR-associated protein 9 (Cas9) tools are the most successful in several organisms, including plants (Chen et al., 2019). There are currently no known reports on the use of CRISPR-Cas9 in finger millet, partly due to the lack of an efficient and reproducible transformation system. Genome editing in millets has been extremely slow, except for the recent momentum (Ceasar, 2022). More efficient transformation methods, such as those reported by Satish et al. (2017) and Mukami et al. (2018), will continue to enhance reproducibility across labs and subsequently enable routine genome editing in finger millet in the future. Comparative studies with other more successful cereals, such as rice, will further benefit the application of genome editing in finger millet. An example is deploying methods established in rice to generate male sterile lines (Barman et al., 2019; Zhou et al., 2016), which will be game-changing towards producing hybrids in finger millet. The current well-annotated chromosome-scale reference genome reported by Devos et al. (2023) will be valuable for future genome editing applications in finger millet.

7 | CONCLUSION AND OUTLOOK

Finger millet is a gluten-free, high potential and niche opportunity crop for its climate resilience, extended storage quality, rich nutritional compositions and different health benefits. Despite the socio-economic importance of the crop, genetic gains for yield and nutritional compositions of finger millet are low due to the limited research and development support compared with other staple crops. Globally, only a few improved finger millet varieties have been released for consumer-preferred traits, including high grain yield potential, enhanced nutritional quality, high marketability and tolerance to different biotic and abiotic stresses. Almost all finger millet improvement programs in SSA focus on conventional breeding for pure line selection through germplasm introduction, collection, characterization, selection and variety recommendation. Very limited research work has been conducted on variety development through mutation, tissue culture and trait integration using controlled crosses. Investing in robust male sterility systems for finger millet is key to accelerating its breeding progress and enabling its potential to address food security challenges. A male sterility system is an essential strategy for developing hybrid seeds in self-pollinating crop species such as sorghum and rice. Substantial amounts of finger millet genetic resources (cultivated and wild types) are maintained by different gene banks useful in variety design and product development with end-user preferences. The long-term availability of these genetic resources requires germplasm collection and conservation, which depends on availability of funding, international collaboration and public awareness. A limited number of reported functional genes, QTLs, molecular markers linked to various economic traits and the recently published chromosomal scale reference genome can be employed in finger millet breeding programs. Concurrently, enhancing genomic research and capacity development in developing countries and international collaboration is paramount. There is a need to develop new climate-smart finger millet cultivars tolerance to biotic and abiotic stresses, rich in nutritional value that meet consumers' needs and market demands. Therefore, current and future finger millet improvement programs should integrate yield, nutritional value-attributing traits and local adaptation. This can be achieved by integrating conventional breeding methods with advanced genomic techniques such as marker-assisted selection, genomic-assisted breeding and genome editing.

AUTHOR CONTRIBUTIONS

Conceptualization and methodology: AG, HS, JM and DAO. Data collection: AG. Data analysis: AG under the guidance of HS. Original draft preparation: AG, HS, JM and DAO. Review and editing: AG, HS, JM, TT, DAO and COO. Project funding acquisition and administration: HS, TT and COO. All authors contributed to the article and approved the submitted version.

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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