



Mutation breeding in small millets: approaches, advances, challenges, and prospects

S. Monika¹ · C. Vanniarajan¹ · M. Vetriventhan² · K. Sakthivel¹ · T. Ramesh¹ · S. Meena³

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Abstract

Small millets are the tiny seeded members of the Poaceae family, which include crops such as finger millet, foxtail millet, barnyard millet, proso millet, kodo millet, little millet, teff, fonio, brown top millet, job’s tears, guinea millet, etc. Small millets play potentially significant roles in nutritional food security, climate resilience, and sustainability. Genetic improvement and scaling up of cultivation of improved varieties are expected to sustain millets production and productivity in the changing climate. Despite the availability of considerable small millets germplasm conserved in gene banks, their use has been limited due to many reasons including inadequate characterization, evaluation, data availability, and difficulty in hybridization resulting in limited opportunity for creating required variation through recombination breeding. Induced mutagenesis has been an alternate and important breeding approach used not only in the improvement of small millets through the creation of novel and useful variation but also nourishes the existing germplasm resources. Mutagenesis methods have evolved from creating random mutation to introduce site-specific gene modifications to become integral to any modern genetic and genomic study including gene/genome editing. Due to the challenges posed by regulatory policies, random conventional mutagenesis combined with next-generation sequencing could be still considered promising to detect genetic variations induced by mutation and in high throughput functional annotation of the mutated genes. Several mutation-based forward and reverse genetic techniques help in the development and characterization of novel mutant genotypic and phenotypic resources, which would accelerate the small millets improvement. This review furnishes the role of mutation in widening the genetic base by creating novel variations, its application in gene mapping, advancements in mutation using next-generation sequencing, different approaches, challenges, and prospects in small millets mutagenesis research.

Keywords Small millets · Physical and chemical mutation · Targeted mutation · Mutant gene mapping · TILLING · EcoTILLING

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✉ C. Vanniarajan
vanniarajan.c@tnau.ac.in

¹ Anbil Dharmalingam Agricultural College and Research Institute, Tamil Nadu Agricultural University, Tiruchirappalli, Tamil Nadu 620027, India

² International Crops Research Institute for Semi-Arid Tropics (ICRISAT), Patancheru, Hyderabad, Telangana 502324, India

³ Department of Soil Science and Agricultural Chemistry, Tamil Nadu Agricultural University (TNAU), Coimbatore, Tamil Nadu 641003, India

Introduction

Millets are the members of the grass family Poaceae which include crops of small-sized grains in contrast to major cereals. They are the oldest domesticated crops (Das et al. 2020) and are staple food crops even before rice and wheat (Lu et al. 2009). Millets are relatively tolerant to adverse environmental conditions including biotic and abiotic stresses and are known to be climate-smart crops. The nutritional significance of these crops makes them “miracle grains/Nutri cereals”. To rejuvenate the importance of these millets, India celebrated the year 2018 as the “National Year of Millets” and the UN announced the year 2023 as “The International Year of Millets”. These nutri cereals have the potential to nourish and alter the present narrow food basket which depends on wheat, rice, and maize (Das et al. 2020).

Small millets include the crops, finger millet [*Eleusine coracana* (L.) Gaertn], foxtail millet [*Setaria italica* (L.) P. Beauv], barnyard millet [*Echinochloa frumentaceae* (Roxb.) Link], proso millet [*Panicum miliaceum* L.], kodo millet [*Paspalum scrobiculatum* L.], little millet [*Panicum sumatrense* Roth. Ex. Roem & Schult], teff [*Eragrostis tef* (Zucc.) Trotter], fonio [*Digitaria exilis* Stapf], brown top millet [*Brachiaria ramosa* (L.) Stapf], job's tears [*Coix lacryma jobi* L.], and guinea millet [*Brachiaria deflexa* (Schumach.) C. E. Hubb ex Robyns]. These millets have C₄ physiology, wider adaptation to harsh environments, minor incidence of pests and diseases, tolerance to abiotic stresses, and demand limited water which makes them recommended for semi-arid and arid regions of the globe. Small millets are reservoirs of nutrients including vitamins and minerals as listed in Table 1. However, the cultivation of these nutri cereals has been limited only to certain regions of the world (Fig. 1) and has been minimized due to the transition of traditional crops to cash crops and high yielding varieties (Vetriventhan et al. 2020).

Genetic resources of small millets have been used in the breeding programmes to develop varieties either through direct selections or use in hybridization followed by selection of the individuals with desired gene combinations. Hybridization in small millets is difficult due to their floral biology and anthesis behaviour, therefore creating genetic variability through hybridization is challenging. The problem of genetic erosion exists due to the selection pressure, leading to loss of desirable segregants. Today, emerging food and energy crises demand rapid crop improvement processes (Ray et al.

2013). To prevail over these issues and to generate individuals with multiple novel beneficial traits, mutation breeding would be an excellent choice (Shanwar et al. 2023). Mutagenized populations not only generate new genetic resources but also serve as valuable genetic materials for studying gene functions (Sun et al. 2019). Mutation indicates the sudden heritable changes occurring in the genome, either spontaneous or induced by mutagenic agents. Spontaneous mutation is a rare event and thus, induced using agents like radiations or chemicals to create useful mutations. Mutations are used not only to get desired variations in phenotype but also to find the mutant SNP or INDEL variations at the genotypic level and functional annotation of the gene. Mutation breeding has evolved from a conventional non-targeted method to targeted mutagenesis. MutMap and its modified approaches are genome sequence-based mutation breeding approaches that facilitate rapid gene identification, variations, and isolation (Lydia Pramitha et al. 2023). However, the use of these techniques in small millets for gene identification is only to a limited extent, compared to other cereals.

Bottlenecks in breeding for small millets

Varietal development in small millets makes use of breeding methods followed for self-pollinating crops such as pure line selection, mass selection, pedigree selection, and mutation breeding. Recombination breeding in small millets is hindered by their small floret size, floral morphology, and anthesis behaviour (Gupta et al. 2012; Nagaraja et al. 2023).

Table 1 Nutrient composition of small millets

Small millets	Nutritional composition	References
Finger millet	Rich in calcium (344 mg/100 g), iron (3.9 mg/100 g), zinc (2.3 mg/100 g)	Maharajan et al. (2021); Gopalan et al. (2004)
Foxtail millet	Balanced nutrients; carbohydrates (55–69 g/100 g), crude fat (4.3 g/100 g), protein (12.3 g/100 g)	Kumar et al. (2021); Sharma and Niranjana (2017); Muthamilarasan et al. (2016); Kalsi and Bhasin (2023)
Barnyard millet	High dietary fibre (23.25–31.70 g/100 g), iron (2.28–22.98 mg/100 g), zinc (0.44–5.92 mg/100 g)	Kim et al. (2011); Panwar et al. (2016)
Proso millet	Rich in protein (10–14 g/100 g), high essential amino acids (methionine, leucine, phenylalanine, lysine), crude fibre (5.5 g/100 g flour)	Rajasekaran and Francis (2021)
Kodo millet	Increased phenol content, iron (2.34 mg/100 g)	Deepak et al. (2018); Longhavi et al. (2017)
Little millet	Contains polyunsaturated fatty acids, flavonoids, high phosphorus, magnesium, protein, iron (1.26 mg/100 g), zinc (1.82 mg/100 g)	Indirani and Devasena (2021); Longhavi et al. (2017)
Teff	High iron content (9.5 to > 150 mg/100 g), zinc (2.3–6.8 mg/100 g), calcium (17–178 mg/100 g)	Abebe et al. (2007); Baye et al. (2014); Gebremariam et al. (2012); Kebede (2009); USDA (2015)
Fonio millet	Rich in dietary fibre (15.70–20.70 g/100 g), good protein content (7.40–9.50 g/100 g), iron (0.80–10.00 mg/100 g), zinc (1.9–3.8 mg/100 g)	Koreissi-Dembélé et al. (2013); Stadlmayr (2012)
Brown top millet	Rich in protein (8.93–19.33 g/100 g), iron (3.70–15.32 mg/100 g), zinc (1.36–2.80 mg/100 g)	Anitha et al. (2024)
Job's tears	High protein content (10.53–13.82 g/100 g)	Ramadhan et al. (2023)

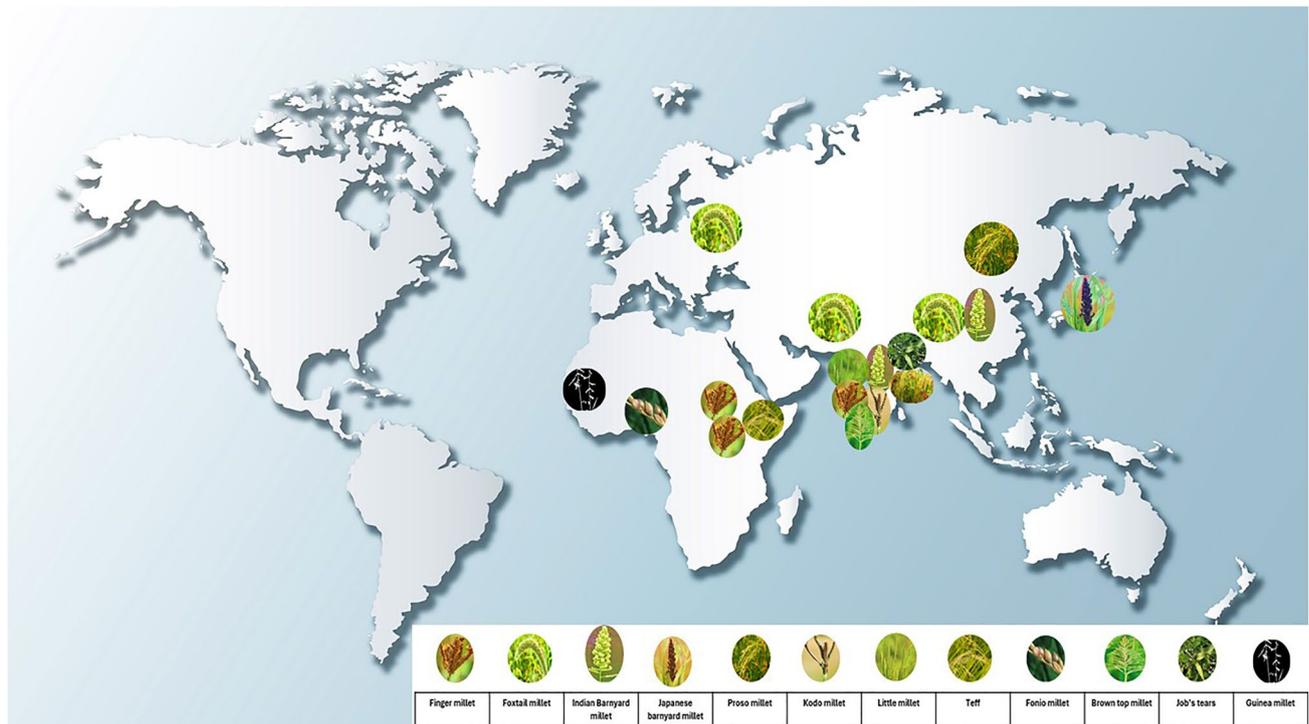


Fig. 1 Map depicting the domestication sites of different small millets (Based on Muruganatham et al. 2025)

The success rate of crossing is very low in small millets, even for experienced hands. Despite few successful artificial hybridization techniques developed and followed in small millets, the method which would yield more crossed seeds is yet to be identified (Nagaraja et al. 2024). The above-mentioned factors also limit the use of heterosis for commercial hybrid production in small millets (Vetriventhan et al. 2020). These reasons account for the limited number of improved varieties and lower productivity in small millets in contrast to major cereals (Ibrahim et al. 2021). In small millets where hybridisation is hard to create variability, mutation breeding, would be one of the alternate methods to create new variability and for cultivar development (Ahloowalia et al. 2004).

History of mutation breeding in small millets

Among all the crops, rice has the highest use of mutation approaches for cultivar development (<https://mvd.iaea.org>). Mutation breeding programs in small millet crops first began with finger millet. X-rays was used for developing a commercial finger millet cultivar Hagari 1 (Krishnaswami and Ayyangar 1941). Then, mutation using gamma rays and EMS was done in finger millet cultivars, Purna and Hamsa (Goud et al. 1969, 1971). Early finger millet mutants were identified using EMS and Nitrosoguanidine mutation of AKP-7 (Sinha and Sahoo 1971). Gamma ray mutant of HES 927 was

selected and released as blast resistant finger millet M21 (Shivashankar et al. 1973). Nayar et al (1979) developed a short-duration and bold-grain finger millet mutant cultivar, Hamsa. Tikka (1985) used gamma rays, EMS, MMS and DES (Diethyl Sulphate) to induce mutation in genotypes PR 202, CO 10, Indaf 9, HR 24, IE 744 and GN1. High yielding mutants were identified from CO 9 using EMS (Devkota 1987). In foxtail millet, mutation breeding was initiated in 1970s. Male sterile line, SuanHSi 28 was developed using induced mutation (Cui et al. 1979). Gamma radiation of Jinfen 52 led to the development of cultivar Jingu 21 (Chen and Wei 1992). Another mutant variety in foxtail millet, Jigu 14 was developed in China in 1996 from cultivar Lusuigu. Smut resistant mutants were identified in proso millet (Konstantinov et al. 1991). Non-waxy gamma ray mutant was isolated from cultivar Noghie (Hoshino et al. 2010). Further, many induced mutation studies have been carried out till the present day in small millets using several physical and chemical mutagens which is presented in this article. The Joint FAO/IAEA Mutant Variety Database (MVD) provides information on the registered, officially released small millet varieties worldwide (Table 2). Using mutation breeding 16 small millet cultivars have been developed in India, including Seven finger millet, five kodo millet, THREE little millet, and one foxtail millet varieties (Table 3).

Table 2 Varieties released by mutation breeding in small millets (MVD Database (<https://mvd.iaea.org>))

Crop	Variety	Country	Year of release
Finger millet	FMM 165	Zambia	2009
	FMM 175		
Foxtail millet	Lugu 7	China	1987
Japanese barnyard millet	Yumesakiyo	Japan	2013
Job's tears	Hatomusume	Japan	1993
	Hato-hikari		1996
	Hato-yutaka		2007

Mutation breeding approaches

Induced mutagenesis

Induced mutagenesis is one of the breeding strategies used

to create novel variations. This method also helps in mining new alleles, that do not persist among the existing genetic resources (Roychowdhury and Tah 2013). Induced mutagenesis is accomplished by exposing the seeds to either radiations or chemicals (Mba et al. 2007). Optimum dose of the mutagen (LD_{50}) is analysed using probit analysis which would produce viable mutants with minimum plant damage. The effectiveness and efficiency of the mutagens is estimated using the viable or chlorophyll mutants obtained. Then, mutants with desirable characteristics are selected from the subsequent segregating populations, improved mutants are then released as varieties. The procedure for developing cultivars using mutation breeding is given in Fig. 2.

Physical mutagenesis

Physical mutagenesis employs radiations emitted from radioactive or nuclear sources to damage the chromosome, leading to deletion of DNA fragments and production of

Table 3 Small millet mutant varieties released in India

Crop	Mutant variety	Pedigree	Year of release	Salient features	References
Finger millet	OUAT 2 (Surva)	Mutant of Co 9	1999	White seeded, long duration, moderately resistant to neck, finger blast and sheath blight	Millets report (2014)
	BM 9-1 (Bhairabi)	Mutant of Budha Mandia	1999	Light brown, early duration, non-lodging, moderately resistant to blast and stem borer	
	B11-1 (Rushikulya)	Mutant of Budha Mandia	1996	Moderately resistant to blast and brown spot, tolerant to stem borer and drought of 15-18 days, non-lodging, rich in protein	
	Nilachal (B-4-10-56)	Mutant of IE 642	1985	Light brown, medium sized grains, photo-sensitive, long duration	
	Dibya Sinha	Mutant of AKP-7	1971	Semi-dwarf, moderately blast resistant	
	Co 3	Mutant of Co 1	1942	Dwarf, Drought tolerant	
	Hagari 1 (Farm Ragi)	Mutant of Giddha Aryam	1941	Profuse tillering, long duration	
Foxtail millet	PS4	Mutant of SiA326	2020	High yield, wider adaptability, profuse tillering	Seetharam (2020)
Kodo millet	KMV-543	Mutant of Co 3	2019	High yielding	Cheruku et al. (2023)
	Jawahar Kodo 137	Mutant of RK 390	2018	High yielding and drought tolerant	
	Chhattisgarh Kodo 2	Mutant of Co 3	2014	Drought tolerant, early maturing (95–100 days) with non-shattering grains	Prabhakar et al. (2017)
	RK 390-25	Mutant of RK 390	2012	Moderately resistant to head smut, high yielding, non-shattering, non-lodging	Millets report (2014)
Little millet	JK 13	Mutant of JK 76	2007	Head smut resistance, high yielding	
	GV 2	Mutant of Gujarat Vari 1	2016	Clean white, bold seeds, resistant to pest and diseases	Millets report (2014)
	OLM 20 (Sabara)	Mutant of SS	2003	Drought tolerant, early duration	
	OLM 36 (Kolab)	8-1	2001	Resistant to brown spot, sheath blight, long duration, high yield	

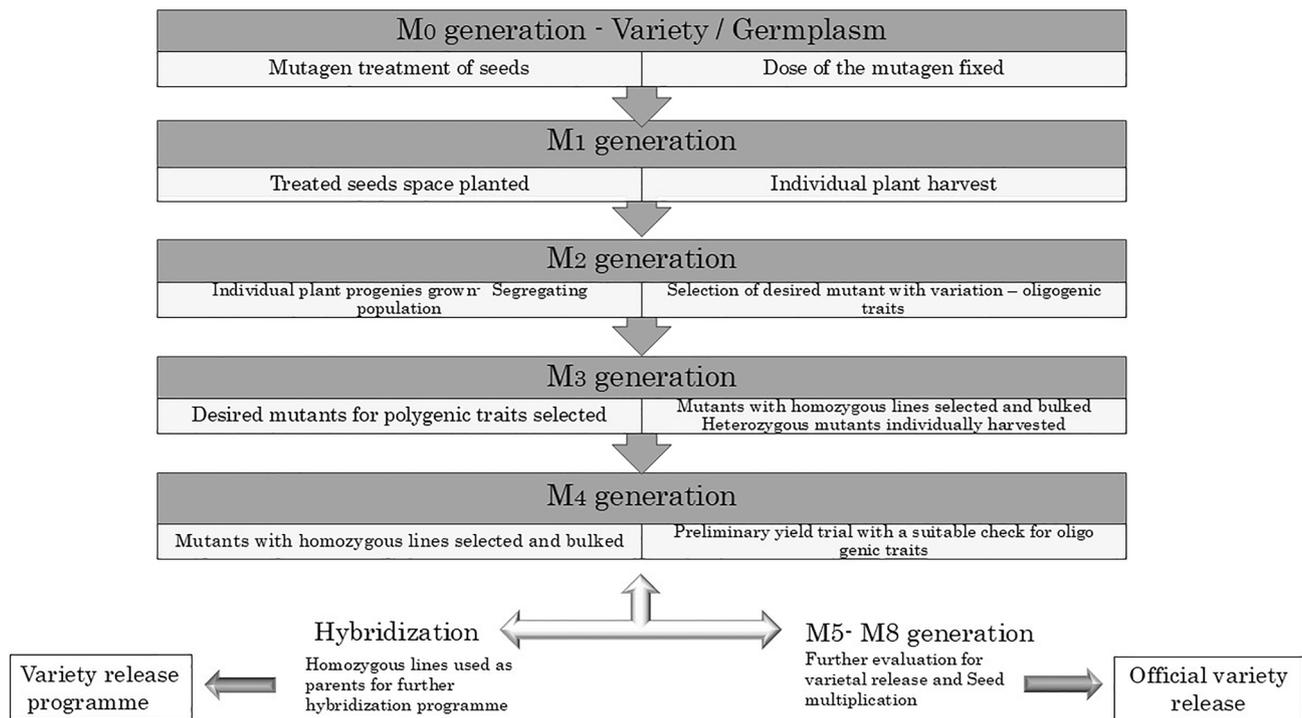


Fig. 2 Steps involved in conventional mutation breeding approach

knockout mutants (Naito et al. 2005). Physical mutagens play vital role in mutation breeding since 1920s. Physical mutagens can be either ionizing or non-ionizing radiations. Ionizing radiations are classified as particulate and non-particulate radiations. Ionizing, particulate radiations include α rays, β rays, fast and thermal neutrons. Ionizing, non-particulate radiations include X-rays, γ rays, and ion beams. X-rays originate from accelerating electrons. Gamma rays are emitted from the radioactive sources, either Cobalt-60 or Caesium-137 (Nor A'azizam et al. 2024). Gamma rays are better than X-rays, because of their shorter wavelength and greater energy emission. Alpha rays are not effective for inducing mutation due to their poor penetration power. Beta particles are emitted from nucleus of an atom and efficient for inducing mutations (Spencer-Lopes et al. 2018). UV rays are non-ionizing radiations which has poor penetrating power and wavelength of 100-400 nm. It forms DNA dimers and cause base deamination, thus leading to DNA damage. Mutagens, X-rays and Gamma rays have been used in small millets so far (Table 4). The most common physical mutagen which was applied to develop mutant lines in small millets is gamma rays. Gamma rays of doses ranging from 100 to 1000 Gy were employed in small millet genotypes for obtaining mutants with desirable yield contributing traits including high yield, early maturity, lodging resistance, abiotic stress tolerance, and biotic stress resistance (Table 4). The optimum doses for obtaining early maturity and high

yield in finger millet were observed as 500 Gy (Ambavane et al. 2015) and 600 Gy (Sellapillaibanumathy et al. 2022). In foxtail millet, gamma rays of 100 to 400 Gy in MU-1 and MU-2 were applied and genotypes with improved ear features were obtained (Gupta and Yashvir 1976). The optimum dose of gamma rays for obtaining non-lodging and photosynthetically efficient kodo millet mutants was reported as 300 Gy (Jency et al. 2016). Similarly, LD₅₀ gamma ray doses of 418 Gy (Francis et al. 2022a) and 200 Gy (Kate et al. 2018) were found effective for obtaining high yielding mutant lines in proso millet. In fonio millet, the effective doses of gamma rays were reported between 180 and 228 Gy (Nura et al. 2019) for obtaining high yielding mutants and 150 Gy gamma ray radiation was effective to develop *Curvularia* resistant fonio mutants (Mandinatou et al. 2024).

Chemical mutagenesis

Induced mutagenesis uses chemicals of different groups, in addition to physical mutagens to create novel variations. Chemical mutagens can be classified as alkylating agents, base analogues, deaminizing agents, and acridine dyes. The group alkylating agents include EMS (Ethyl Methyl Sulphonate), MMS (Methyl Methyl Sulphate), DMS (Dimethyl Sulphate), and DES (Diethyl Sulphate). Base analogues include the members, 5-bromo uracil, 5-choloro uracil, and 2-amino purine. De-aminizing agents include mustard gas,

Table 4 Physical and chemical mutation studies carried out in small millets

Crop	Variety	Mutagen	Concentrations/Doses	LD ₅₀	Purpose	References
Finger millet	Co 13	EMS	20, 30, 40 and 50 mM	30 mM	NA	Aviya and Mullainathan (2018)
		DES	20, 30, 40, 50, 60 mM	40 mM		
	Dapoli Dapoli Safed	Gamma rays	300, 400, 500, 600, 700 Gy	500 Gy	High yield and early maturity	Ambavane et al. (2015)
		GPU 28, GPU 67 MR6	Gamma rays	400, 500 and 600 Gy	-	High yield and yield attributes
	TRY 1	EMS	0.15%, 0.30%, 0.45%, 0.60% and 0.75%	-	Early maturity	Eswari et al. (2014)
	PYR 2	Gamma rays	100, 200, 300, 400, 500, 600 and 700 Gy	600 Gy	High yield and yield attributes	Sellapillaibanumathy et al. (2022)
	GPU 28 KMR 204	Gamma rays	300,400,500 Gy 300,400 Gy	-	Male sterility	Vasisth et al. (2022)
		VR 708 GPU 26	Gamma rays EMS	150, 300 and 450 Gy 0.15, 0.30 and 0.45%	-	High yield
			Nitroso guanidine	0.015, 0.030 and 0.045%		
			Combination of 300 Gy gamma rays with 0.30% EMS, 300 Gy gamma rays with 0.030% NG			
Foxtail millet	MU-1 MU-2	Gamma rays EMS DES	10 krad to 40 krad 0.1%—6 h, 12 h, 18 h, 24 h 0.1%—6 h, 12 h, 18 h, 24 h	-	Ear characters- Ear shape, spikelet and bristles	Gupta and Yashvir (1976)
	Kodo millet	Co3	Gamma rays EMS	100 Gy to 500 Gy 0.2%, 0.3%, 0.4% and 0.5%	300 Gy 0.42%	
Proso millet		ATL 1 CKMV1	Gamma rays	300 to 700 Gy	500 Gy 400 Gy	NA
	ATL 1	Gamma rays EMS	100 Gy to 1000 Gy 10 to 100 mM	418 Gy 41 mM	High yield	Francis et al. (2022a) Francis et al. (2022b)
Barnyard millet	Vari. No 10	Gamma ray	20 krad to 70 krad	20 krad	Yield attributes	Kate et al. (2018)
	Co 13	EMS DES	10 mM to 50 mM 10 mM to 50 mM	30 mM 40 mM	Yield attributes	Priyadharshini and Mullainathan (2021)
		Yarkoye 6 Shortandinskoye 7 K-10343 K-3742 Saratovskoe 6	Sodium azide	0.1 to 0.4%	0.1%	
	Local cultivar	Gamma rays	-	40 krad and 50 krad 20 krad and 60 krad	Early maturity High yield	Bhave et al. 2016
	Co (Kv) 2	Gamma rays EMS	500 Gy to 1000 Gy 30 mM to 100 mM	800 Gy 70 mM	Earliness	Ramesh et al. (2019)
MDU 1		EMS Sodium azide	5, 10 to 60 mM	16.19 mM 14.14 mM	Earliness	

Table 4 (continued)

Crop	Variety	Mutagen	Concentrations/Doses	LD ₅₀	Purpose	References
Little millet	CO (Samai) 4	EMS	5,10,15,20,25,30,35,40,45 and 50 krad	20 krad	NA	Ramkumar and Dhanavel (2021)
			5, 10, 15,20,25,30,35,40,45 and 50 mM	30 mM		
Teff	Tsedey (DZ-Cr-37)	EMS	1%, 1.5%	-	TILLING for semi-dwarf genes	Zhu et al. (2012)
			0.2%	-	Semi-dwarf, drought tolerant	Jost et al. (2015)
			0.2%	-	Aluminium tolerance	Desta et al. (2017)
Fonio millet	CVF 109 CVF 234 Solosso	Gamma rays	150 Gy	-	Resistance to <i>Curvalaria</i>	Mandinatou et al. (2024)
	Genotype from National cereal research institute, Nigeria	Nitrous acid	0.1 M for 2 h, 4 h,6 h and 8 h	0.1 M for 4 h	Yield	Animasaun et al. (2014)
	Dinat, Jakah Jiw 1, Jiw 2, Nkpowas	Colchicine	0.1,0.5,1.0,2.0 mM	0.1 mM	Growth and	Nura et al. (2017)
		Gamma rays	100 to 500 Gy	180 Gy to 228 Gy	Yield attributes	Nura et al. (2019)

sodium azide, and phenol thiourea. Acridine dyes include acridine orange, proflavine, etc. These chemicals result in single nucleotide polymorphism by creating point mutations, in contrast to the major deletions and chromosomal aberrations created by physical mutagens. Chemical mutagens such as EMS, DES, Sodium azide and colchicine have been used in small millets for obtaining mutants with desired traits like improved yield, early maturity, tolerance to abiotic stresses, and resistance to biotic stresses (Table 4). In finger millet, EMS, DES and nitrosoguanidine were employed to obtain high yield and early maturity and the concentrations 30 mM and 40 mM EMS were found effective (Aviya and Mullainathan 2018). EMS concentration of 0.42% was found effective in obtaining lodging resistant and photosynthetically efficient kodo millet mutants (Jency et al. 2017). In teff, 1% and 1.5% of EMS concentrations were employed in TILLING approach to mine the alleles responsible for semi-dwarfness (Zhu et al. 2012). 0.2% EMS was found effective in developing semi-dwarf, drought tolerant mutant lines (Jost et al. 2015) and high aluminium tolerant mutants (Desta et al. 2017). In fonio millet, two different chemicals such as nitrous acid and colchicine were used and the effective doses for these chemicals were found to be 0.1 M (Nura et al. 2017) and 0.1 mM (Nura et al. 2019) for obtaining mutant lines with improved yield attributes and yield.

Mutation in forward genetics

Gene mapping in useful mutants using NGS

The groundbreaking discovery of DNA sequencing by Sanger et al. (1977) marked the beginning of the genomics era. Travelling back to an era before the advent of genome sequencing, the gene sequences of the closely related family members of small millets like rice, sorghum, and pearl millet were used to design primers and for genetic characterization of the small millets (Maharajan et al. 2024). As a result of automation and improvement in current DNA sequencing technology, high-quality genomic data have been developed now, thereby reducing the time and expense needed for whole genome sequencing (Pettersson et al. 2009; Zhang et al. 2012). Genome sequencing has been successfully reported in finger millet (Hittalmani et al. 2017; Hatakeyama et al. 2018), foxtail millet (Benetzen et al. 2012; Zhang et al. 2012), broom corn millet (Zou et al. 2019), barnyard millet (Guo et al. 2017), teff (Cannarozzi et al. 2014), fonio (Abrouk et al. 2020), and job's tears (Kang et al. 2020; Li et al. 2021). Employing the sequencing techniques in genome and transcriptome of the wild type and the mutant with desired variation, the SNPs and InDels occurred due to induced mutagenesis can be identified and the functional SNPs responsible for the studied traits can be sorted. Chojuromochi (CH), a gamma ray waxy mutant of Japanese Barnyard millet Noghie, along

with Karumaizairai-Shiro, was used to sequence the regions governing the grain amylose content. Sequencing through genome walking identified the gene governing the trait along with flanking regions, which helped in developing molecular markers. Three homeologous waxy genes, *EeWX1*, *EeWX2*, and *EeWX3* were identified. Mutation led to single base deletion, resulting in pre-mature termination codon in *EeWX1* giving waxy trait (Ishikawa et al. 2013). EMS mutant of foxtail millet (*siago1b*) helped in sorting out the functions of the important slicer protein AGO1 (Argonaute1) of argonaute protein family in normal growth and development. Map-based cloning showed the transversion C-A and 7 bp deletion in C terminus of *siago1b* gene in the mutant. This C terminus is essential motif for interaction between SiAGO1b and SIHYL1. Further, RNA seq and protein interaction studies of the wild type and mutant, detected 1598 differentially expressed genes showing the role of *SiAGO1b* in various processes of plant growth and development and its role in drought tolerance (Liu et al. 2016). Proso millet ATL1 was subjected to gamma ray treatment to obtain high yielding mutants. Two contrasting mutants, one with high yield, lax panicle and another with low yield, dense panicle was chosen. They were genotyped by sequencing, which led to the identification of a total of 25,901 single nucleotide polymorphisms (SNPs) in the wild type, while 30,335 and 31,488 variants were observed in the ATL_hy and ATL_ly mutants, respectively. Among these, 84 impactful SNPs were identified in the high yielding mutant (ATL_hy), compared to 171 in the low-yielding mutant (ATL_ly). Two significant SNPs in ATL_hy and one in ATL_ly were linked to the gene coding for E3 ubiquitin-protein ligase UPL7. Functional analysis revealed that two SNPs in ATL_ly were involved in the starch production pathway, specifically linked to the starch synthase enzyme. This information can support the discovery of genes associated with diverse biochemical pathways in proso millet and for development of molecular markers (Francis et al. 2023). EMS mutant of Yi Xuan Da Hong Mei broom corn millet cultivar (*YX-yl*) was used to study the gene responsible for chlorophyll synthesis. Yellow mutant showed malformation in chloroplast with low number of grana and undistinguished membranes. Reduction in photosynthetic efficiency, plant height and yield were observed in the yellow mutant. Transcriptome analysis of wild type, and mutant revealed that these chlorophyll related genes function in chloroplast membrane, thylakoid, matrix, and work for chlorophyll biosynthesis and redox-based enzyme regulation (Wang et al. 2022). Kodo millet Co3 variety was subjected to gamma ray and EMS treatment for developing photosynthetically efficient and non-lodging mutants. Mutants with variation for leaf anatomy and culm thickness were selected for expression studies. Gene expression analysis for pyruvate phosphate dikinase (PPDK), Nicotinamide Adenine Dinucleotide Phosphate Hydrogen (NADPH), and

NADP-dependent malate dehydrogenase (NADP-MDH) were carried out in photosynthetically efficient and less efficient mutants. The findings revealed that PPDK expression in efficient mutant increased by 30 times, NADP-ME2 showed a ~onefold increase, and NADP-MDH10 also exhibited high expression levels. These results indicate that kodo millet utilizes an NADP-malic enzyme subtype C₄ photosynthesis system. For the lodging trait, expression profiling in lodging and non-lodging mutants using the genes *GA2ox6* and *Rht-B*, showed that the lodging mutant had high expression level of Gibberellic acid pathway and mutation in these genes, produced the non-lodging mutant (Jency et al. 2020).

MutMap-based approaches

Conventional gene mapping methods till date identify the QTLs at large genomic intervals, thereby restrict discerning the promising candidate genes responsible for the desired trait. Traditional methods consume more time, labour, and are low throughput in nature (Manchikatla et al. 2021). Next generation sequencing technology allows a quicker insight of the genetics of complex traits in cereals (Thudi et al. 2021). For crops with narrow genetic base owing to its floral biology and pollination behaviour, mutation would be a good alternate for creating novel variations by overcoming the existing barriers. Abe et al. (2012) first demonstrated the mapping of variation in genes created using mutation and identification of the changes in mutant nucleotide and its function, which is resolved using whole genome resequencing. Thus, the mapping process is hastened through different approaches involving induced mutations and sequencing like MutMap (Abe et al. 2012), MutMap+ (Fekih et al. 2013), MutMap-Gap (Takagi et al. 2013), SHOREMap (Schneeberger et al. 2009), NGM (Austin et al. 2011), MUTCHROMSEQ, and MUTRENSEQ. These mapping approaches are used for mapping genes governed by monogenic inheritance, particularly the recessive genes. Mutant obtained through induced mutagenesis, contrasting to the wild type for the desired type is selected from M₂. Then the selected recessive M₂ mutant is crossed to the wild type. F₁ plants are selfed to obtain F₂ population, in which the mutant and wild type are bulked with each represented by 20–30 plants. The pooled DNA of both the bulks are further encountered for whole genome sequencing. The parental reference genome is then compared with that of the mutant and the causal SNPs are found out. Unlinked SNPs and linked ones are differentiated using segregation ratio of 1:0 and 1:1 mutant: wild type. The SNP index, ratio of number of reads corresponding to the mutant SNP to the number of reads of the corresponding SNP must be 1 or close for a SNP to be linked with mutants. MutMap+ is a modified approach of MutMap, where the mutants and the wild type homozygous plants are bulked in M₃ generation and set for sequencing as that of MutMap.

Effective artificial crossing techniques have not yet been developed for a number of crop species, because of reduced floral size and emasculation challenges, where MutMap+ is positioned to be useful for the enhancement of orphan crops (Soumya and Sankar 2024). MutMap – Gap identifies the candidate genome region with SNP index1 and the sequence gap between the mutant and wild type. Sequence reads from a wild type plant with the mutant's parental background are used to gather the sequence reads that did not align to the reference genome. Then, sequence reads that have mapped close to the candidate area are combined with the unmapped reads to build scaffolds in de novo assembly. Sequence reads from the bulk DNA of mutant F₂ progeny are used to compute the SNP index. Lastly, the causative mutation was found by searching the SNP index of one scaffold (Yano et al. 2017). MUTCHROMSEQ is a technique suitable for polyploid crops, where the flow cytometry is used to isolate the chromosome with mutation and subjected to sequence alignment with respect to reference and the mutant sequence is identified (Sanchez-Martin et al. 2016). MUTRENSAQ, a novel technique which utilizes mutation, exome capture and gene cloning to identify the genes in which mutation occurred (Steuernagel et al. 2016). The SHOREMap differs from MutMap in crossing mutant to a divergent accession and in number of individuals bulked for resequencing. Here, the distant crossing produces more natural polymorphism allowing precise allele frequency estimation and limit the causal SNP locus. NGM (Next Generation Mapping) is a modified SHOREMap where the number of mutants bulked is little than the latter and it uses Linkage Disequilibrium (LD) to identify the genomic region.

Till date, MutMap and its modified approaches have been successfully experimented in foxtail millet, thereby opening the scope for its application in other small millets. A mutant library created by employing the chemical mutagen EMS in Yugu 1 foxtail millet led to the identification of several genes responsible for different yield attributes in *Setaria italica* (L.) P. Beauv. Dwarf mutant of Yugu 1 foxtail millet (*Sidwarf2*) which is a somoclonal variant identified from callus-based regeneration. Mapping population (F₂) was developed by crossing the wild type and the mutant one. The gene responsible for dwarfness (*D2*) was mapped on chromosome 3 with genomic region of 52.7 kb. Further, the role of the candidate gene, cytochrome P450 in governing the trait was identified (Xue et al. 2016). Yellow-green mutant *siygl1* isolated from 0.5% EMS treatment of Yugu1 foxtail millet led to the identification of gene responsible for photosynthesis. The mapping population was developed by crossing the *siygl1* mutant and SSR41 foxtail millet. The gene *SiYGL1* is recessive and encodes magnesium chelatase D subunit (CHLD) playing an important role in regulating a subset of genes involved in photosynthesis, thylakoid development

and chloroplast signalling (Li et al. 2016). *Loose panicle 1* (*lp1*) mutant obtained from the above M₂ population was used to identify the gene responsible for the panicle traits. Map-based cloning and high throughput sequencing of mRNA revealed that the gene governed the traits like lax pattern of panicle, semi-dwarf stature, and large seed size. This gene governs the panicle length and is responsible for decreased primary branches (Xiang et al. 2017). Foxtail millet dwarf mutant (*Sidwarf3*) in M₂ generation was isolated and crossed with wild type and the segregants were subjected to SNP index analysis and mapping. The gene *D3* for dwarfness was mapped on chromosome 8 and further annotation yielded 20 candidate genes. This further provides genetic information for developing lodging resistant foxtail millet genotypes (Fan et al. 2017). A stripe leaf foxtail mutant *Sist12* helped in sorting out the gene responsible for DNA replication, chloroplast biogenesis, cell cycle, and found to involve in C₄ cycle of photosynthesis. The gene was found orthologous (*OsDCD*) to that of rice. Point mutation from G to A in the fifth intron of the gene *Sist12* was found (Tang et al. 2019). The gene responsible for the panicle colour was mapped on chromosome 4 of *Setaria italica*. The results showed that the identified *WPI* worked for phytoene synthase and it was eight bp deletion in the loci, which lead to the pre-mature termination (Sun et al. 2019). EMS mutant *simads34* of the foxtail millet cultivar SSR41 was used to identify the recessive gene responsible for the inflorescence architecture and, thereby the yield. The single point mutation G- to A- was identified in the fifth intron of *SiMADS34* gene, which is expressed in the heading and panicle development stages (Hussin et al. 2021). *DROOPY LEAF1* (*DPY1*), an EMS mutant of Yugu 1 foxtail millet was used to find out the responsible gene. *DPY1*, an LRR receptor-like kinase, plays a pivotal role in regulating leaf droopiness by modulating brassinosteroid (BR) signalling. *DPY1* interacts and competes for SiBAK1, reducing the interaction between SiBRI1 and SiBAK1, SiBRI1 phosphorylation, and downstream BR signalling. Notably, plants with elevated *DPY1* expression display more erect leaves, sturdier stems, and larger panicles, suggesting its potential utility for improving crop productivity (Zhao et al. 2020). Function of the gene *SiNPI* was identified using male sterile EMS mutant '*sinpl*' of Yugu 1 through MutMap approach. The gene encoded a putative glucose-methanol-choline oxidoreductase, expressed in the panicle and found localized in the endoplasmic reticulum (Zhang et al. 2021). Male sterile mutant of Yugu1, the *sinog1* (no grain 1) was obtained through EMS mutagenesis and the causal gene was mapped from 32.44 to 34.29 Mb on chromosome 5. In this 1.85 Mb interval, 203 genes were identified with sequence variations involved in floret development (Zhang et al. 2024). *N*-nitroso-*N*-methyl urea mutagenesis of

A10.1 foxtail millet seeds yielded sparse panicle mutants which brought about the gene *SvAUX1* responsible for the inflorescence development and positive geotropism of the root. This gene was found orthologous to the maize gene *ZmAUX1* (Huang et al. 2017). Another function of the gene *AUX1* in lateral root development has been identified using the mutant *Siaux1-1* and *Siaux1-2* obtained from EMS mutant library of Yugu 1 foxtail millet. The promoter Hap-2412TT was identified as an allele for the gene *SiAUX1* and found to involve in the organization of root architecture in *Setaria italica*. RNA sequencing revealed the role of *AUX1* in seedling development (Tang et al. 2022). EMS mutant of A10.1 foxtail millet which had malformed C₄ Kranz anatomy and bleaching phenotype at heading stage, was crossed with wild type, a mapping population (F₂) was developed and the gene responsible for chloroplast development (*SvSTL1*) was identified. This gene encodes the ribonucleotide reductases (RNR) essential for DNA synthesis and chloroplast development (Li et al. 2022). In teff, gene for lodging resistance was identified using semi-dwarf EMS mutant, Kegne of DZ-Cr-37 (Tsedey). The α -tubulin gene was reported to be linked to lodging resistance (Jost et al. 2015). QTLs responsible for plant height was identified in broom corn millet using the mapping population obtained by crossing the wild type Longmi12 and the EMS dwarf mutant Zhang778. Mapping population (F_{2,3}) was developed and further BSA-Seq identified the QTL (*PH1.1*) conferring plant height and was fine mapped to 109 kb genomic region with 15 genes. The candidate genes for *PH1.1* might include *longmi011482* and *longmi011489* and *longmi011496* were found on chromosome 1 (Liu et al. 2022). Thus, the genotypes obtained through induced mutagenesis and the sequencing technique together help in the identification of functional genes governing traits of breeder's interest, which would be further used in developing functional molecular markers, beneficial for crop improvement.

Mutation in reverse genetics

Targeting Induced Local Lesions IN Genome (TILLING)

The process of identifying and characterizing the gene that causes the mutant trait is known as forward genetics. First, the phenotypic trait is noticed and then the genes or loci that cause the mutation are mapped. Conversely, reverse genetics examines the phenotype after a known gene is disrupted. TILLING is a feasible reverse genetic approach which uses conventional mutation and next-generation sequencing for the discovery of mutated SNPs and for elucidating its function. It was first developed in *Arabidopsis thaliana* by

McCallum et al (2000) during late 90's, as an alternate to insertional mutagenesis (Barman and Sil 2020). TILLING process involves the steps: (1) Creating mutant population using EMS treatment; (2) Pooling of mutant DNA from M₂ generation; (3) Detection of heteroduplexes formed between the mutant and wild type DNA; (4) Cleavage of heteroduplex DNA using CEL1 endonuclease; (5) Then, the DNA fragments are separated and detected through Li-Cor genotypers or other specific genotypers; and (6) The identified fragments are then sequenced and the concerned mutation sequences are identified. The fosmid library of teff USDA genotype PI524434 was subjected to sequencing and identification of the presence of homeologous *Sorghum* semi-dwarfing gene (*dw3*) in teff. Then, the teff cultivar DZ-Cr-37 was subjected to EMS treatment and on TILLING, two candidate genes for semi-dwarfing trait homeologous to *dw3* of *Sorghum bicolor* and *rht1* from wheat were sequenced and 120 candidate mutations were identified through 454 sequencing. Six independent mutations were then validated using Sanger sequencing within which two were found in *dw3* homeologues. These identified SNPs can be used in breeding programme to improve dwarf, non-lodging teff cultivars (Zhu et al. 2012). Teff TILLING project has been successfully implemented by the Teff Biotechnology Project, hosted by the Institute of Plant Sciences, University of Bern at Switzerland to develop non-lodging cultivar. Through this project, 10,000 M₁ and 6000 M₂ teff mutants were generated using EMS treatment to create point mutations. The population has been screened for two genes, namely *HTD1* (*HIGH TILLERING DWARF1*) (Zou et al. 2006) and *DWARF4* (Sakamoto et al. 2006). Two copies of each gene were found in teff and they were homologous to the each other in exonic region and vary in their intronic region (Esfeld et al. 2009). EcoTILLING is a modified TILLING approach, where the allelic variation prevailing among the natural population is identified in the place of induced mutations. It was first implemented in *Arabidopsis thaliana* by Comai et al. (2004). Another latest approach of TILLING, known as the iTILLING (individualized TILLING) was developed by Bush and Krysan (2010) in *Arabidopsis thaliana*. In conventional TILLING, the M₂ plants are grown and DNA is isolated and pooled. Here, the seeds collected from M₁ plants are bulked and one/two M₂ plants are raised on agar plugs in 96 well spin plates. The DNA is isolated from tissues directly following Ice Cap technique and the subsequent steps as in TILLING are followed. TILLING has advanced from proof-of-concept to production by launching publicly accessible services for barley, lotus, maize, and *Arabidopsis*. Pilot-scale studies on a number of additional plant species, including wheat, have been finished (Till et al. 2007). Gene expression studies using TILLING and EcoTILLING have received little attention (Wambi et al. 2021) and are still in the lane to explore in small millets other than teff.

Conclusion and prospects

Small millets are well known for their unrelenting nature to severe environments and are regarded as climate-resilient crops. They are proudly known as the nutri-cereals for their dense amount of nutrients such as protein, minerals, and vitamins in their grains. These potential crops frame the futuristic choice for sustainable agriculture and for combating malnutrition. Germplasm availability, assessment, and utilization in small millets are limited compared to other major crops like rice, wheat, sorghum, and pearl millet. This in turn minimizes the exploration of naturally available variation. So far, the majority of small millet varieties have been released by conventional breeding methods like pure line selection of local landraces/germplasm while floral biology and anthesis behaviour of small millets hinders the use of recombination breeding/heterosis breeding in crop improvement. Mutation breeding has been an excellent approach for creating variation in small millets and would be a suitable method for small millets improvement. However, varieties developed in small millets using mutagenesis are quite a few. Mutation breeding could help in developing small millet cultivars with novel variations conventionally, which can serve as a valuable genetic resource. Though, research in small millets for various climate resilient, nutritional traits have geared up, the use of high throughput mutation-based techniques in allele mining like TILLING and EcoTILLING, MutMap variations are still behind the eight ball. Next generation sequencing enables the characterization of the mutants at molecular level, decoding the role of genes in exhibiting useful phenotypes. Different approaches mentioned in the literature regarding gene mapping and its functional characterization are confined mostly to foxtail millet, which would also be implied in other nutri-cereals. Comparative genomics would help in mining out the orthologous genes of beneficial traits in other millets for available genome sequences of their family members. Some of the promising small millets including brown top millet, guinea millet, and job's tears remain underexplored, which on further investigations would leverage the potential of these millets in climate resilience. The germplasm resources owing to these crops are meagre which insists the need for their germplasm collection and conservation. Meanwhile, mutation would be an exhortation to the breeders to create variation and its exploitation in crop improvement. Thus, mutation helps in developing new improved cultivars, and in gene mapping through both forward and reverse genetic techniques. Genes mapped using forward and reverse genetics further help in genomic selection and marker-assisted selections, which would all come together to aid in improved cultivar development for food, feed and nutritional security.

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Declarations

Competing interests The authors declare that they have no competing interests.

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