



Genetic and genomic resources, and breeding for accelerating improvement of small millets: current status and future interventions

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Abstract

Current agricultural and food systems encourage research and development on major crops, neglecting regionally important minor crops. Small millets include a group of small-seeded cereal crops of the grass family *Poaceae*. This includes finger millet, foxtail millet, proso millet, barnyard millet, kodo millet, little millet, teff, fonio, job's tears, guinea millet, and browntop millet. Small millets are an excellent choice to supplement major staple foods for crop and dietary diversity because of their diverse adaptation on marginal lands, less water requirement, lesser susceptibility to stresses, and nutritional superiority compared to major cereal staples. Growing interest among consumers about healthy diets together with climate-resilient features of small millets underline the necessity of directing more research and development towards these crops. Except for finger millet and foxtail millet, and to some extent proso millet and teff, other small millets have received minimal research attention in terms of development of genetic and genomic resources and breeding for yield enhancement. Considerable breeding efforts were made in finger millet and foxtail millet in India and China, respectively, proso millet in the United States of America, and teff in Ethiopia. So far, five genomes, namely foxtail millet, finger millet, proso millet, teff, and Japanese barnyard millet, have been sequenced, and genome of foxtail millet is the smallest (423–510 Mb) while the largest one is finger millet (1.5 Gb). Recent advances in phenotyping and genomics technologies, together with available germplasm diversity, could be utilized in small millets improvement. This review provides a comprehensive insight into the importance of small millets, the global status of their germplasm, diversity, promising germplasm resources, and breeding approaches (conventional and genomic approaches) to accelerate climate-resilient and nutrient-dense small millets for sustainable agriculture, environment, and healthy food systems.

Keywords Small millets · Climate-resilience · Genomics · Breeding · Germplasm · Underutilized crops

Introduction

The global population is projected to reach 9.8 billion by 2050, will require a 60–70% increase in food production from the current level, posing a significant challenge to feed growing population. On the other hand, among the

major staple food crops, three cereals, rice [*Oryza sativa* L.], wheat [*Triticum aestivum* L.], and maize [*Zea mays* L.] provide > 60% of plant-based human energy intake, and this is greater in several countries in Asia [22, 177]. Although these major staple cereal grains make up a critical portion of many diets, they possess a lower concentration of mineral elements (micro and macro nutrients). The hidden hunger due to micronutrients deficiency affects about 2 billion people globally [16, 102, 142]. This is mainly because of our heavy reliance on only a few major food staples. Therefore, there is a need for a big transformation of current agriculture and food systems towards greater diversity (crops and diets) by promoting cultivation and consumption of traditionally and regionally important underutilized, climate-resilient

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and nutrient-dense crops for sustainable agriculture and healthy diets [177].

Small millets, also known as minor millets, are a group of small-seeded cereal crops of the grass family *Poaceae*. This includes finger millet (*Eleusine coracana* (L.) Gaertn.), foxtail millet (*Setaria italica* (L.) P. Beauv.), proso millet (*Panicum miliaceum* L.), barnyard millet (*Echinochloa crus-galli* (L.) P. Beauv. and *Echinochloa colona* (L.) Link), kodo millet (*Paspalum scrobiculatum* L.), little millet (*Panicum sumatrense* Roth. ex. Roem. & Schult.), teff (*Eragrostis tef* (Zucc.) Trotter], fonio (*Digitaria exilis* Stapf and *D. iburua* Stapf.), job's tears (*Coix lacryma-jobi* L.), guinea millet (*Brachiaria deflexa* (Schumach.) C.E.Hubb. ex Robyns, = *Urochloa deflexa* (Schumach.) H.Scholz), and browntop millet (*Brachiaria ramosa* (L.) Stapf. = *Urochloa ramosa* (L.) T.Q. Nguyen) (Table 1, Figure S-1). Small millets are known for their climate-resilient features, including their broader adaptation to diverse ecological conditions, lesser water requirement, lower occurrence of insect pests and diseases, and minimum vulnerability to environmental stresses [14, 49, 150]. Small millets are important crops of rainfed areas in semi-arid regions. Currently they are grown on a limited area representing a small portion of global millet production, because of the shift from traditional crops to cash crops. Some of these small millets are considered as weeds, particularly the wild forms (<http://tropical.theferns.info/>; <https://www.cabi.org/isc>); however, they are the crops of local importance that provide reliable yields on marginal lands, and contribute significantly to the food security.

Small millets grains are versatile that can easily be incorporated into existing rice or maize-based diets or as substitutes for rice in existing recipes. They also serve as major food components in various traditional foods and beverages, and are ingredients in a variety of multigrain and gluten-free cereal products. Millets are also consumed as fermented beverages making increased nutrients availability, including protein and mineral bioavailability, and digestibility, and reduces antinutritional factors [124]. Because of growing sedentary lifestyle and its associated health issues, consumers are seeking more nutrient-rich foods that are both tasty and healthy. Small millets fit the bill as a healthy food choice because they provide high energy, high dietary fibre, protein with balanced amino acid profile, many essential minerals, vitamins, antioxidants, and have a low glycemic index (GI) [32, 45, 83, 145]. Because of these features, they are called as 'Smart-Food Crops' and 'nutri-cereals'. The nutrient content of millets vary with variety and type. However, regardless of variety, finger millet grains contain exceptionally high calcium (> 350 mg per 100 g) followed by teff (159 mg per 100 g); proso millet, job's tears, foxtail millet and barnyard millet are rich in protein (> 10%); foxtail millet, little millet and job's tears are rich in fat (> 4.0%); barnyard millet, little millet, foxtail millet and fonio are rich in crude

fibre (6.7–13.6%), little and barnyard millets are rich in iron (9.3–18.6 mg per 100 g) compared to other major cereals such as rice, wheat and sorghum [21, 145]. Grain iron, zinc, calcium, protein and crude fiber contents among small millets are presented in Fig. 1. Small millets play a strategic role as a staple food for the poor, and lately, as a healthy food for those in urban areas, underline the necessity of directing more research and development towards these crops.

Origin, domestication and taxonomy

Small millets belong to nine different genera of the grass family *Poaceae*. Figure 2 shows the taxonomical classification of small millets, together with major cereals, and pseudo-cereals. Table 1 presents a list of small millets and their scientific name, chromosome number, place of domestication and distribution. Cultivated germplasm of finger millet, foxtail millet, proso millet, kodo millet, little millet, and barnyard millet can be subdivided into races, and sub-races, based on panicle morphology and shape (Table 1). No racial classification has been reported in other small millets. However, teff can be classified on the basis of seed color: ivory (white), qey (red/brown) and sergegna (mixed). In fonio, five morpho-types have been recognized namely gracilis, stricta, rustica, mixta, and densa on the basis of morphology [21]. In job's tears, three morphologically distinct forms have been reported, including one cultivated type, var. ma-yuen and two wild types, var. stenocarpa and var. monilifer [8]. Morphotypes or races are not known in guinea millet and browntop millet. The divergence of small millets is also seen in terms of their chromosome number and ploidy level which range from the diploid foxtail millet ($2n=2x=14$) to the hexaploid barnyard millet ($2n=6x=54$). All these small millets are originated and domesticated in Asia, and/or Africa, and distributed globally, either as food crop, or feed, and/or as weeds/grasses (Table 1).

Global status of small millets cultivation

The area, production and productivity of small millets are not well documented and mostly reported together as 'millets', unlike major crops. Foxtail millet is the second most produced millet after pearl millet and is an important food for human consumption in China, India, Korea, Japan, and Nepal [10, 45]. It is widely cultivated in Asia, Europe, North America, Australia, and North Africa for grains or forage. China ranks first in foxtail millet production (1.81 million (m) tons (t) from 0.72 m hectares (ha) during 2014). However, its area under cultivation has fallen drastically in the last 65 years, from 9.2 m ha in 1949 to 0.72 m ha in 2014, resulting in a decline in production from 7.79 m t to 1.81 m t,

Table 1 Small millets and their scientific name, chromosome number, racial classification, place of domestication and distribution

Crop name	Subspecies	Race	Subrace	Domestication	Distribution	References
Finger millet <i>Eleusine coracana</i> (L.) Gaertn. (2n=4x=36, AABB)	<i>coracana</i>	<i>elongata plana</i> <i>compacta vulgaris</i>	<i>laxa, reclusa and sparsa seriata, confundera, and grandigluma</i> No subraces <i>liliacea, stellata, incurvata, and digitata</i>	Ethiopia and Uganda	India, China, Nepal, Myanmar and Sri Lanka; Uganda, Kenya, Sudan, Eritrea, Zimbabwe, Zambia, Malawi, Madagascar Rwanda, Burundi	[36, 67, 68]
Foxtail millet <i>Setaria italica</i> (L.) P. Beauv. (2n=2x=18, AA)	–	<i>moharia maxima indica</i>	<i>aristata, fusiformis and glabra</i> <i>compacta, spongiosa and assamense</i> <i>erecta, glabra, nana and profusa</i>	China, Europe and Afghanistan-Lebanon	India, China, Nepal Afghanistan, Korea, Japan, Russia, USA, France	[42, 95, 144, 183, 189]
Proso millet <i>Panicum miliaceum</i> L. (2n=4x=36)	–	<i>miliaceum, patentissimum, contractum, compactum, and ovatum</i>	No subraces	China and Europe	India, China, Japan, Russia, Afghanistan, Iran, Iraq, Syria, Turkey, Mongolia, Romania, USA	[40, 71, 72, 108]
Little millet <i>Panicum sumatrense</i> Roth. ex Roem. & Schult. (2n=4x=36, AABB)	–	<i>nana robusta</i>	<i>laxa and erecta laxa and compacta</i>	India	India, Nepal, Pakistan, Sri Lanka, eastern Indonesia and western Myanmar	[37]
Japanese barnyard millet <i>Echinochloa crus-galli</i> (L.) P. Beauv. (2n=6x=54)	<i>crus-galli utilis</i>	<i>crus-galli utilis and intermedia</i>	No subraces No subraces	Japan	Korea, Japan, India	[39]
Indian Barnard millet <i>Echinochloa colona</i> (L.) Link)	<i>colona frumentacea</i>	No races <i>stolonifera, intermedia, robusta, laxa</i>	No subrace No subrace	India		
Kodo millet <i>Paspalum scrobiculatum</i> L. (2n=4x=40)	–	<i>regularis, irregularis and variabilis</i>	No subrace	India	India, as wild cereal in western Africa	[33, 38, 69]

Table 1 (continued)

Crop name	Subspecies	Race	Subrace	Domestication	Distribution	References
Teff <i>Eragrostis tef</i> (Zucc.) Trotter (2n=4x=40, AABB)	–	Not reported	Not reported	Ethiopia	Mainly in Ethiopia and to some extent the highlands of Eritrea, Kenya, South Africa, the United States, Canada, Australia, Europe and Yemen. It is also grown as forage grass in South Africa, Morocco, Australia, India and Pakistan	[172, 173]
Fonio White fonio: <i>Digitaria exilis</i> Stapf (2n=36) Black fonio: <i>Digitaria iburua</i> Stapf. (2n=36)	–	Not reported	Not reported	West Africa	White fonio is grown in Mali, Nigeria, Niger, Burkina Faso, Senegal and Guinea, Benin, Togo, Ghana, Côte d'Ivoire; Black fonio is grown as cereal in Nigeria, Togo, Benin, and Cameroon	[1, 11]
Job's tears <i>Coix lacryma-jobi</i> L. (2n=10,20,30)	–	Not reported	Not reported	Southern and eastern Asia	Northeast India, Southeast Asia, southern China	[103]
Guinea millet <i>Urochloa deflexa</i> (Schumacher.) H. Scholz (= <i>Brachiaria deflexa</i>) (2n=18, 36)	–	Not reported	Not reported	Semi-domesticated weed of African savanna	It is found from Cape Verde and Senegal eastern to Ethiopia, Eritrea, Somalia, South Africa; It also occurs in western Asia to Pakistan and India	[125]
Browntop millet <i>Urochloa ramosa</i> (L.) T.Q. Nguyen (= <i>Brachiaria ramosa</i> (L.) Stapf.) (2n=2x=18; 2n=4x=36, 72)	–	Not reported	Not reported	South East Asia	India, Bangladesh, Bhutan, Cambodia, Malawi, Myanmar, Nepal, Senegal, South Africa, Yemen and Zimbabwe	[34]

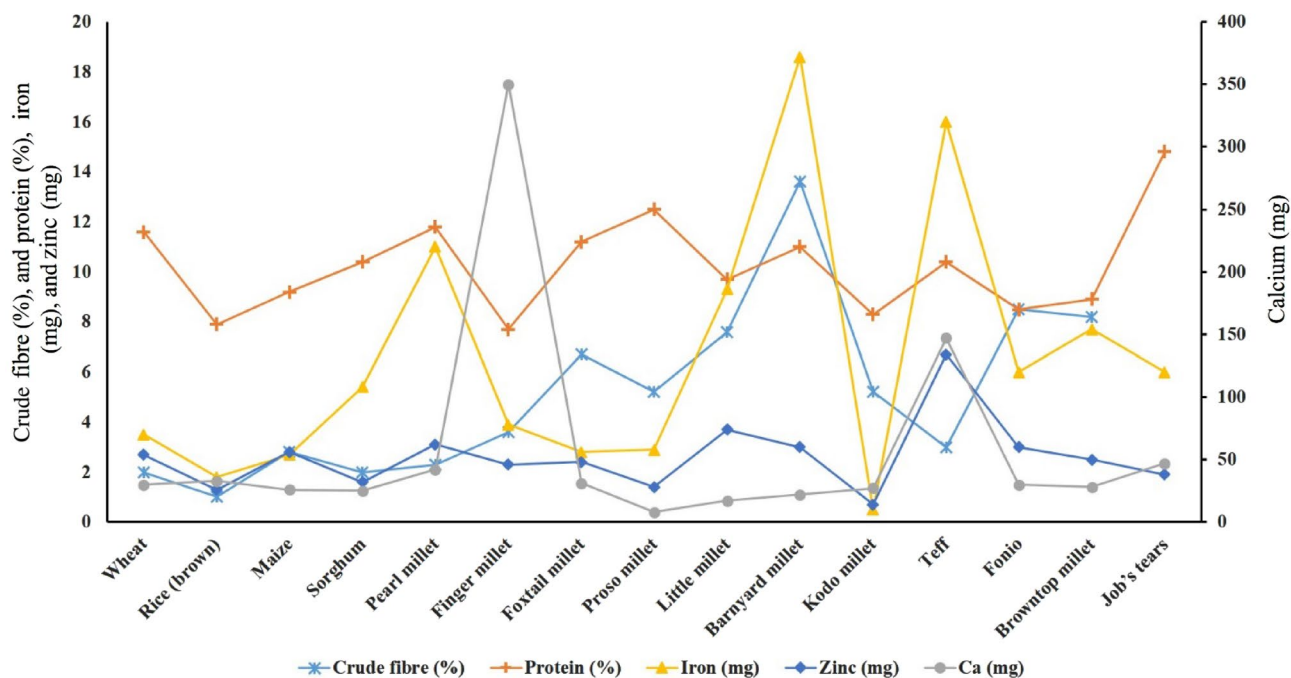


Fig. 1 Nutrient composition of small millets in comparison with major cereals (100 g edible part at 12% moisture) Source: [13, 46, 148, 185]; <http://krishikosh.egranth.ac.in/handle/1/5810027060>

respectively [43]. In India, foxtail millet was once an important crop in rainfed areas because of its drought tolerance. However, its area fell by more than half during the 1990s, mainly due to the introduction of more remunerative crops [63]. At present, in India it is cultivated on about 0.07 m ha with a production of 0.05 m t [18]. Finger millet is estimated to be cultivated on 4.0–4.5 m ha globally, with a production of about 4.5 m t [54]. The important finger millet growing countries in eastern and southern Africa are the sub-humid regions of Ethiopia, Kenya, Tanzania, Zambia, Malawi, Democratic Republic of the Congo, Uganda and Zimbabwe, while in South Asia, the crop is widely cultivated in India, Nepal, Bhutan and Sri Lanka [47]. Proso millet is grown in Asia, Australia, North America, Europe, and Africa, and used for feeding birds and livestock in developed countries, and for food in some parts of Asia [139]. Proso millet is cultivated on about 0.82 m ha in Russia, 0.32 m ha in China [43], 0.20 m ha in USA [60], 0.03 m ha in India [18] and 0.002 m ha in Korea [131]. The USA is among the top producer, and exports 15–20% of its annual production to over 70 countries [60]. Globally, fonio was cultivated on 0.96 m ha in 2017 with a production of 0.67 m t. It is largely cultivated in Guinea over an area of 0.67 m ha with a production of 0.51 m t, followed by Nigeria (0.19 m ha and 0.08 m tons). Among the other countries growing fonio are Mali, Burkina Faso, Ivory Coast, Niger, Senegal, Benin, and Guinea-Bissau (<http://www.fao.org/faostat/en/#data>, accessed on 20 March 2019).

Other minor or regionally important crops include barnyard millet, kodo millet, little millet, browntop millet, teff, and job's tears. Barnyard millet is an important crop in India, China, Japan and Korea, where it is being used for human consumption as well as fodder [163]. In India, barnyard millet is grown on 0.146 m ha with a production of 0.151 m t [18]. Kodo millet is grown in upland rice regions in India, Indonesia, Philippines, Thailand and Vietnam, and also in Bangladesh and Myanmar [64]. At present kodo millet (area 0.20 m ha and production 0.084 m t) and little millet (area 0.26 m ha and 0.12 m t) are mainly cultivated in India [18]. Teff is largely grown as a major cereal crop in Ethiopia, where it occupied 3.02 m ha in 2017, ranking first among all the cereals cultivated in the country [93]. Teff also spreading to other countries such as Australia, Cameroon, Canada, China, India, Netherlands, South Africa, the UK, Uganda and the USA. However, production statistics are not available [93]. Job's tears is grown mainly in southeast Asian countries, including China, Vietnam, Laos, Japan, and Korea. In China, it is widely distributed in nearly all the provinces except Qinghai and Tibet, and mainly grown in Guizhou, Yunnan, Guangxi, and Fujian. It is estimated to be cultivated over 0.07 m ha with a grain yield of 0.22 m t [43]. Browntop millet is grown mostly in southern India [19], and also grown in some parts of the USA as a fodder crop and bird feed.

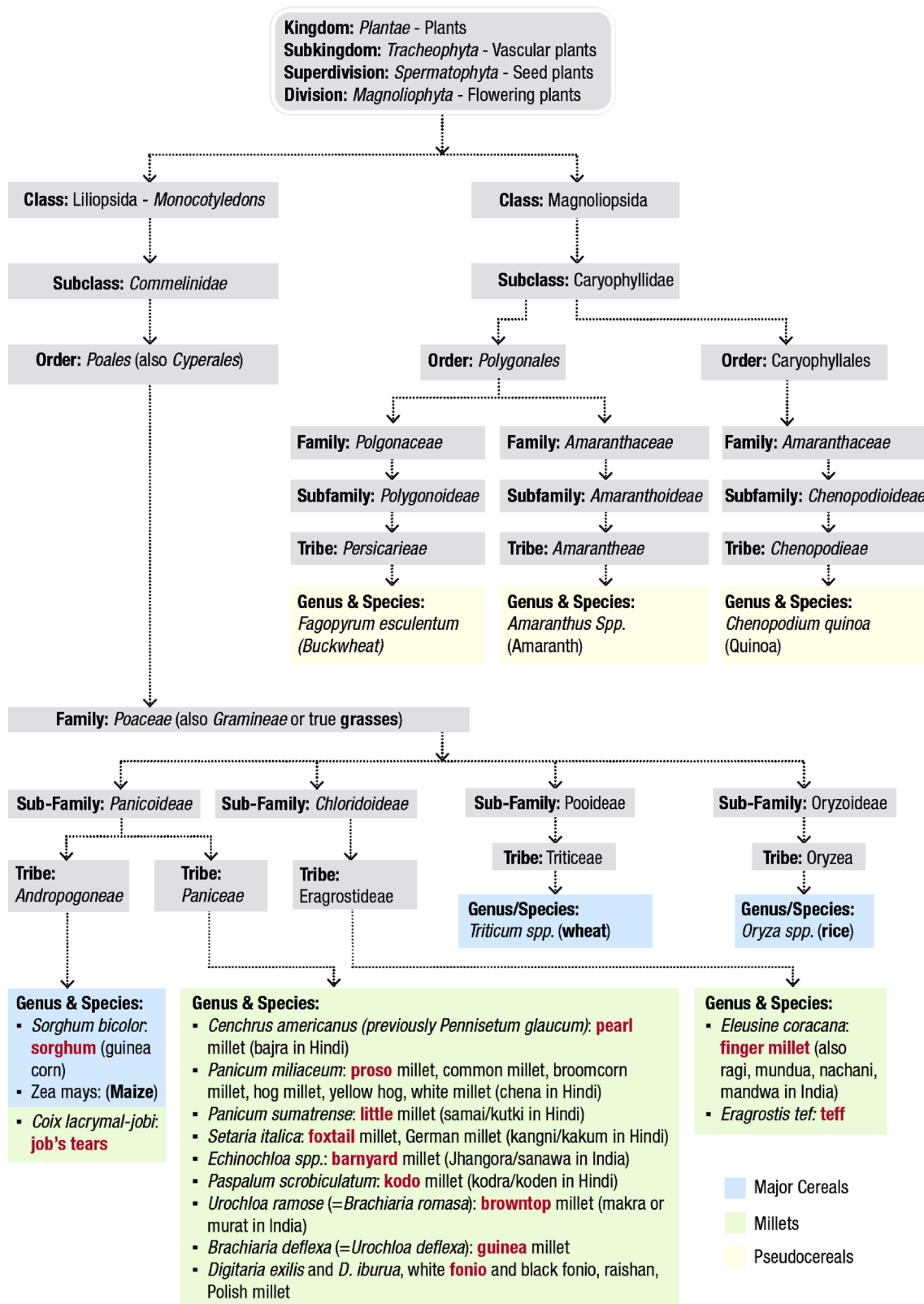


Fig. 2 Taxonomical classification of small millets and other major cereals and millets, and pseudo-cereals [Note: “Millet” is a common term to categorize small-seeded grasses that are often called dryland cereals. The grasses most commonly referred to as millets are: Major millet (pearl millet) and small millets (finger millet, foxtail millet, proso

millet, little millet, barnyard millet, kodo millet, browntop millet, fonio, teff and job’s tears, and guinea millet; and sometimes sorghum is categorized as a major millet - this is typically included in the common definition of millets in India but less so in other countries].

Germplasm resources

Global status of germplasm resources

Diversity in crop cultivars is important for sustainable agriculture. Germplasm provides the required variability for crop improvement. The narrow genetic base of cultivars leads to increased risk of vulnerability resulting in crop failure due to insect pests and disease epidemics or unpredictable climate effects. Globally, about 133,849 cultivated germplasm of small millets are conserved in genebanks, while other species of these genera include 30,627 accessions (Table 2). Region-wise, a majority of accessions are conserved in Asia (64.4%), followed by Africa (13.8%), and Europe (13.5%). These figures could vary slightly due to considerable portion of germplasm that could be duplicates within and/or between the genebanks. The major collections of foxtail millet germplasm are conserved in China, India, France, and Japan, while India and African countries such as Kenya, Ethiopia, Uganda, and Zambia have major finger millet collections. Similarly, the major collections of proso millet germplasm are in the Russia, China, Ukraine, and India; barnyard millet in Japan and

India; kodo millet in India and USA; and little millet in India [171, 175]. Major collections of teff, fonio and job's tears were conserved in Ethiopia, USA and Japan, respectively. The largest germplasm collection of small millets conserved by institute are: finger millet (9522), kodo millet (2180) and little millet (1253) at National Bureau of Plant Genetic Resources (NBPGR, India); foxtail millet at Institute of Crop Science, Chinese Academy of Agricultural Sciences (ICS-CAAS) (26,233); barnyard millet at Department of Genetic Resources I, National Institute of Agrobiological Sciences, Japan (3671); proso millet at N.I. Vavilov All-Russian Scientific Research Institute of Plant Industry (VIR) (8778); teff at Ethiopian Institute of Biodiversity, Ethiopia (5169); fonio at Laboratoire des Ressources Génétiques et Amélioration des Plantes Tropicales, ORSTOM, France (235); and job's tears at the Department of Genetic Resources I, National Institute of Agrobiological Sciences, Japan (151). Guinea millet accessions were present only at Centro Internacional de Agricultura Tropical (CIAT), Colombia (2) and International Livestock Research Institute (ILRI) Ethiopia (1), while 2087 accessions belong to the genus *Brachiaria* were conserved globally. Except for finger millet, foxtail

Table 2 Global status of cultivated, wild and weedy relatives of small millets germplasm conserved in genebanks

S. no	Crop name	Africa	Asia	United States of Americas	Europe	Oceania	Total
1	Finger millet (<i>Elusine coracana</i>)	6700	28,663	1456	36	18	36,873
	Other species of the genus <i>Elusine</i>	1628	256	20	40	22	1966
2	Foxtail millet (<i>Setaria italica</i>)	166	38,572	1145	4548	330	44,761
	Other species of the genus <i>Setaria</i>	976	209	341	372	9	1907
3	Barnyard millet (<i>Echinochloa colona</i> & <i>E. crus-galli</i>)	59	7444	316	53	51	7923
	Other species of the genus <i>Echinochloa</i>	248	371	71	8	9	707
4	Proso millet (<i>Panicum miliaceum</i>)	11	12,110	1147	15,812	228	29,308
5	Little millet (<i>Panicum sumatrense</i>)	7	2830	226	–	1	3064
	Other species of the genus <i>Panicum</i>	3853	9599	2161	677	142	16,432
6	Kodo millet (<i>Paspalum scrobiculatum</i>)	356	4043	354	14	13	4780
	Other species of the genus <i>Paspalum</i>	357	190	2812	41	524	3924
7	Teff (<i>Eragrostis tef</i>)	5046	402	373	41	20	5882
	Other species of the genus <i>Eragrostis</i>	1338	236	1281	253	77	3185
8	White Fonio (<i>Digitaria exilis</i>)	604	4	1	236	17	862
	Black fonio (<i>Digitaria iburua</i>)			1			1
	Other species of the genus <i>Digitaria</i>	712	542	798	56	367	2475
9	Job's tears (<i>Coix lacryma-jobi</i>)	3	288	26	40	4	361
	Other species of the genus <i>Coix</i>				2		2
10	Guinea millet (<i>Urochloa deflexa</i>)	1		2			3
11	Browntop millet (<i>Urochloa ramosa</i>)	1	29		1		31
	Other species of the genus <i>Urochloa</i>	675	73	1285	26	28	
Grand total		22,741	105,861	13,816	22,256	1860	164,447

Source: http://www.fao.org/views-archive/germplasm_query.htm?i_l=EN, accessed in 29 Aug 2018

millet and proso millet, germplasm conserved in genebanks globally are very low for other crops. This could be due to low research priority on those crops, and most landraces already been lost due to a shift from traditional crops and landraces to cash crops and improved varieties and hybrids. Therefore, collection and conservation of existing small millets' diversity is crucial before we lose them forever, particularly in fonio, job's tears, guinea millet, and browntop millet, where a very limited number of germplasm (< 1000) are conserved globally.

Germplasm diversity representative subsets

Germplasm diversity representative subsets such as core collection (~ 10% of the entire collection) and mini core collection (~ 1% of the entire collection and/or ~ 10% of core collection) are the ideal starting point for using germplasm in crop improvement. Such subsets are available in most small millets (Table 3). These diversity representative sets could be effectively evaluated in multiple locations and years to identify and utilize promising trait-specific germplasm resources in crop improvement. Similar efforts are required in other small millets where such sets are not available, and when the size of the collection is considerably large, for example, in teff.

Promising trait-specific germplasm resources

Small millets germplasm contains significant variation for morpho-agronomic, quality and stress tolerance traits, and promising germplasm sources have been reported in most crops. In finger millet core collection, 15 accessions each for grain Fe (37.66–65.23 mg kg⁻¹), Zn (22.46–25.33 mg kg⁻¹), Ca (3.86–4.89 g kg⁻¹) and protein (8.66–11.09%) contents were identified, and 24 of them were identified based on

their superiority over control cultivars for two or more grain nutrients [166]. In foxtail millet core collection, 21 diverse promising accessions each for early maturity, higher grain yield, and higher grain nutrients (protein 15.6–18.5%; Ca 171.2–288.7 mg kg⁻¹; Fe 58.2–68.0 mg kg⁻¹; and Zn 54.5–74.2 mg kg⁻¹) were identified [167]. In proso millet, germplasm for higher grain-yield (18 accessions), and greater seed weight (8 accessions) were reported [176]. For grain nutrients, 12 proso millet accessions were identified for Fe (63.3–73.2 mg kg⁻¹), 27 accessions for Zn (40.6–46.7 mg kg⁻¹), 56 accessions for Ca (185.5–241.2 mg kg⁻¹) and 27 for protein (16.1–19.1%), of which 28 were rich in two or more grain nutrients, including IPm 2069, IPm 2076 and IPm 2537 for high Fe, Zn, Ca, and protein content [176]. In kodo millet, promising trait specific accessions for early maturity (8 accessions), greater seed weight (10), high grain yield (15), and higher grain nutrients [Fe (8), Zn (14), Ca (6) and protein (7)] have been reported, of which 10 accessions (IPs 4, IPs 5, IPs 77, IPs 83, IPs 222, IPs 264, IPs 279, IPs 686, IPs 689, and IPs 814) were reported as promising for both agronomic and grain nutrient traits [177]. In little millet, 10 accessions for greater seed weight, 15 each for high grain yield and high biomass yield, and 30 for high grain nutrients have been identified, including 3 accessions for two or more nutrients (IPmr 449 for Fe, Zn, Ca and protein; IPmr 981 for Zn and protein; and IPmr 977 for Ca, and protein); and five accessions (IPmr 855, IPmr 974, IPmr 877, IPmr 897, and IPmr 767) that produced grain yield over 1500 kg ha⁻¹ (Vetriventhan, unpublished).

Blast in finger millet and foxtail millet; grain smut and sheath blight in little millet; head smut and blight in kodo millet; smut and leaf spot in barnyard millet; head smut, sheath blight and bacterial spot in proso millet; and rust in teff are important diseases. Germplasm sources for blast resistance in finger millet [12] and foxtail millet [155],

Table 3 Germplasm diversity representative subsets, core and mini core collections in small millets

Crop	Germplasm subsets	No. of accessions used	No. of traits	No. of accessions in subset	References
Finger millet	Core collection	5940	14	622	[164]
	Core collection	4511	27	551	[53]
	Core collection	1000	23	77	[61]
	Mini core collection	622	20	80	[168]
Foxtail millet	Core collection	1474	23	155	[165]
	Core collection	1478	23	156 and 78	[51]
	Mini core collection	155	21	35	[167]
Proso millet	Core collection	833	20	106	[169]
Barnyard millet	Core collection	736	21	89	[163]
	Core collection	729	24	50	[50]
Little millet	Core collection	460	20	56	[163]
	Core collection	895	21	55	[52]
Kodo millet	Core collection	656	20	75	[163]

salinity and drought tolerance in finger millet [87, 89] and foxtail millet [86, 88], have been reported. Ramakrishnan et al. [141] identified finger millet mini core accessions tolerant to low phosphorus stress; five (IE 5201, IE 2871, IE 7320, IE 2034, IE 3391) of them had high root and shoot length, root hair density, and root hair length. A limited number of resistant sources for major diseases, and to some extent, for pests in proso, barnyard, little and kodo millets have been reported [171, 175]. In teff, shoot fly is an important insect pests. Nigus [123] evaluated 49 teff germplasm, including 32 released varieties, 12 promising lines and local landraces for shoot fly resistance, and reported acc. 17 WJ as resistant (< 5% damage), 10 accessions as moderately resistant (6–10% damage), and others as susceptible (> 11% damage).

Small millets improvement

Production constraints and breeding targets

Table 4 shows breeding target traits for each of small millets. In general, yield and parameters contributing to yield are the most targeted traits in small millets improvement. Therefore, selection for yield per se has been the major basis for improving productivity, but genotype \times environment interactions highly influence these traits. Therefore, assessing yield stability across multiple environments and investigating physiological traits (such as harvest index, water use efficiency, etc.) associated with yield and adaptation are essential to target yield increase. Germplasm collections exhibit significant variation for various traits, including maturity duration [163–165, 169, 176, 177] that can be exploited to breed custom-made cultivars that fit into the different maturity groups: early, mid-late and late, depending on the location-specific requirements of soil, rainfall, temperature,

humidity, day-length and cropping patterns. Short-duration varieties would be suitable for double/intensive cropping regions and medium-to long-duration varieties for single cropping season areas.

Small millets have high nutritional potential, while their utilization is limited by the presence of antinutrients such as phytate, phenols, tannins, and enzyme inhibitors, and also a high amount of protease and amylase inhibitors that affect the digestibility of millets grains [178]. Most grain nutrients in small millets are generally higher than the major cereals, however, large variability exists in germplasm, including for grain nutrients [166, 167, 176, 177] and antinutrients [130, 178]. Exploiting existing variability present in germplasm and hybridization-derived variations can support in breeding nutrients-dense cultivars in higher-yielding background.

Small millets are well adapted to diverse climatic conditions and are less affected by major biotic and abiotic stresses. However, a few diseases and insect pests are causing considerable yield loss, and therefore, breeding for cultivars resistant to diseases and pests is important. Blast is a very prominent disease in finger millet; yield losses of up to 88% have been reported [119, 143]. Similarly, blast, rust and smut are the most severe diseases in foxtail millet [175]; sheath blight, bacterial spot and head smut in proso millet; grain and head smut and leaf spot diseases in barnyard millet, kodo millet and little millet [171], leaf rust in teff; and smut and leaf spot in job's tears. Proso millet, barnyard millet, little millet and kodo millet are mostly damaged by shoot fly, and finger millet and barnyard millet by stem borers [171].

Small millets are mostly grown as rainfed crops, and are considerably affected by drought due to the failure of monsoon. In addition to drought, lodging is major problem in all small millets, mainly due to their soft stalk, crop management and environmental factors [146, 171, 175]. There is no direct estimate of yield loss in small millets due to lodging,

Table 4 Targeted traits for improvement of small millets for increased yield, adaptation and quality

Crop	Trait focus
Finger millet	Blast resistance, drought and salinity tolerance, machine harvestable, non-lodging, and bold grain size
Foxtail millet	Blast and sheath blight resistance, non-lodging, bold grain size, and strong culm for mechanical harvesting
Proso millet	Shoot fly and smut resistance, non-shattering, and non-lodging
Little millet	Shoot fly resistance, non-lodging, and bold grain size
Kodo millet	Shoot fly, head smut and sheath blight resistance, non-lodging, nutrient-response and drought recovery
Barnyard millet	Grain smut, sheath blight and shoot fly resistance, bold grain size, and non-shattering
Teff	Drought tolerance and lodging resistance, desirable grain quality, non-shattering, and bold grain size
Fonio	Non-shattering, non-lodging, early maturity, and bold grain size
Job's tears	Non-lodging, smut and leaf spot resistance
Guinea millet	Non-lodging, non-shattering, and bold grain size
Browntop millet	Non-lodging, and non-shattering

but major cereals like rice and wheat have recorded up to 50% losses [161]. It occurs due to the bending of plants at maturity due to higher panicle weight, soft stalk and weak anchorage roots [162]. Lodging is genotype-dependent and influenced by the environment, therefore developing cultivars with improved lodging resistance is essential to minimize yield and quality losses. Another important trait for small millets is shattering [146]. Significant yield losses occur due to grain shattering in small millets, therefore shattering-resistant/tolerant small millets will be critical to prevent shattering-induced yield losses.

Special breeding traits to enhance the cultivation and consumption of small millets are developing machine harvestable cultivars, enhancing the nutritive value of grain and fodder to fetch high market value, developing cultivars suitable to make value-added products such as rice, flour, vermicelli, flakes, hot and cold extruded snacks, noodles and ready-to-cook mixtures, shade-tolerant genotypes for orchards and agro-forestry, quick growing genotypes for inter-cropping and genotypes suitable for rice-fallows.

Conventional breeding approaches

Various breeding methods such as pure line selection, pedigree selection, mass selection, and mutation breeding, which are applicable to self-pollinating crops are followed in small millets as well. Reports on small millets cultivars released over a period of time shown that a majority of them were released following selection from local landraces/cultivars, followed by pedigree selection (hybridization and selection). For example, in India, of the 248 varieties of six small millets (finger millet—121, foxtail millet—32, proso millet—24, kodo millet—33, barnyard millet—18 and little millet—20), about 65% were released following selection from landraces, about 30% through pedigree selection, and 5% through mutation breeding [3]. In the USA, 11 proso millet cultivars were released following selection from landraces and 8 following pedigree selection [146, 147].

Hybridization to create variability followed by selection in segregating population has been an important breeding method in small millets particularly in finger millet, foxtail millet and proso millet. In finger millet, 45% of the cultivars released in India were following hybridization and selection breeding method, while 22% in foxtail millet and 29% in proso millet [3]. However, small millets are not easily amenable to hybridization due to their floral morphology and anthesis behavior. Hybridization techniques available in small millets include contact method (panicles of selected plants are enclosed in a parchment bag before flowering to enhance the chances of natural cross-pollination) and controlled hybridization either by hand emasculation or hot water emasculation. Hot water treatment of inflorescence (3–4 days of emergence) at 52 °C for

5 min found effective in inducing male sterility in finger millet, while 48 °C for 4–5 min in barnyard millet [56]. Emasculation and crossing techniques have been reported in small millets [56, 96, 121, 158]. Understanding floral biology and pollination system helps in devising appropriate emasculation and crossing protocols [56]. However, the success rate of making the cross is generally very low, even for experienced hands, thereby limiting the number of genetic studies and yield improvement in small millets.

Exploitation of hybrid vigor is limited in small millets, due to difficulties in hybridization. Thus, developing male sterile lines would be a viable option to use heterosis, which is being successfully implemented in major crops for commercial hybrid seed production. So far, only one male sterile line has been reported in finger millet (INFM 95001), which has a GMS system developed from the source parental line IE 3318 (germplasm) through chemical mutation (EMS) [59]. In foxtail millet, several types of male sterile lines have been developed in China [180]. However, only partial genetic male sterile lines have been used successfully in hybrid seed production [42]. There are no reports on male-sterile lines in other small millets.

In general, mutation breeding has played a key role in self-pollinated crops where hybridization is very difficult to create variability. Mutation breeding has resulted in the release of 13 small millet cultivars (finger millet 8, kodo millet 3, and little millet 2) in India. The use of chemical hybridizing agents (CHAs) to induce male sterility in small millets needs to be explored. The usefulness of mutagen depends on its mutagenic effectiveness (mutations per unit dose of mutagen) and efficiency (mutation in relation to undesirable changes/damage like sterility, lethality, injury etc.) in order to recover a high frequency and spectrum of desirable mutations. In finger millet, 500 Gray (Gy) and 600 Gy were found effective in the developing early-maturing mutant lines with high yield and yield component characters [5], and Muduli et al. [113] reported that the treatments with 0.30% and 0.45% EMS, 0.03% nitroso guanidine (NG) and combination treatment of 300 Gy gamma ray + 0.30% EMS as more effective in inducing useful mutations. Bhavé et al. [20] irradiated local cultivar of proso millet using gamma rays and identified two early-maturing mutants from 40 krad and 50 krad doses, and two high-yielding mutants from 20 krad and 60 krad doses. In barnyard millet, 0.3% of EMS was identified as LD₅₀ value and 500 Gy and 600 Gy of gamma irradiation create good variability (IIMR, unpublished). In kodo millet, a dose of 0.4% EMS was reported as suitable for optimum recovery of viable mutants [79]. In teff, Desta et al. [41] used 0.2% of EMS for 8 h and reported significant variability in the mutant population and identified candidate mutant lines that showed Al-tolerance. Induced mutation techniques are also being used in teff to generate

variability for important traits such as lodging resistance given the lack of sufficient variability in the existing germplasm collection [9]. Animasaun et al. [6] reported that the most efficient treatment time in fonio for inducing variation was 0.1 M nitrous acid for 4 h of exposure of seeds.

Conventional breeding approaches have been successful in characterizing small millets germplasm and their use in developing and releasing several cultivars, including for resistance/tolerance to biotic and abiotic stresses. Genomics-assisted improvement by utilizing various omics approaches can potentially contribute to enhanced genetic gains in small millets improvement.

Genomic resources and genomics-assisted small millets improvement

Genome sequence

Genome sequencing provides direct access into the coding and non-coding regions of the genome that regulates growth, development and response to environmental stimuli. Also, the sequence data facilitates the development of genome-scale markers that provide a greater understanding of diversity, structure, evolution, mapping sequence variation associated with traits of interest, and in developing molecular tools to use in genomics-assisted crop improvement. Versatile sequencing platforms have not only eased

costs but also provide higher coverage, depth and reliability. In the case of small millets, genomes of foxtail millet, finger millet, proso millet, teff, and Japanese barnyard millet have been sequenced so far, and also complete chloroplast genome sequences of foxtail millet, proso millet, little millet and barnyard millet are available (Table 5). Foxtail millet has the smallest genome size (423–510 Mb) while finger millet has the largest one (1.5 Gb) followed by barnyard millet (*E. crus-galli*, 1.27 Gb). Foxtail millet was the first crop among millets to have its genome fully sequenced; it serves as a model for C₄ crop species because of its small diploid genome, short duration and self-pollinating nature. Despite the use of next-generation platforms, most of the millet genomes are in the draft sequence stage and require resequencing and reannotation efforts to fill the gaps, mis-annotations and chromosomal assignments. However, the draft sequence information is adequately informative for large-scale genotyping applications and gene mining. The ICRI-SAT in collaboration with Cornell University genotyped a diverse set of six small millets (finger millet, barnyard millet, foxtail millet, proso millet, kodo millet and little millet) through genotyping-by-sequencing (GBS) approach and identified genome-wide single nucleotide polymorphisms and assessed the population structure and diversity [81, 170, 179]. One of the bottlenecks in millets genome sequencing could be attributed to the ploidy levels and higher proportion of repetitive DNA. However, the emergence of third-generation sequencing systems coupled with high-throughput data

Table 5 Nuclear and chloroplast genome sequence resources of small millets

Crop	Scientific name	Genotype name	Genome size	No. of gene(s)	Sequence type	References
<i>Nuclear genome sequence</i>						
Foxtail millet	<i>Setaria italica</i>	Yugu1	510 Mb	24,000–29,000	Reference genome	[17]
	<i>S. italica</i>	Zhang gu	423 Mb	38,801	Draft genome	[194]
Finger millet	<i>Elusine coracana</i>	ML-365	1196 Mb	85,243	Draft genome	[70]
		PR202	1500 Mb	62,348	Draft genome	[65]
Proso millet	<i>Panicum miliaceum</i>	Landrace (Accession Number 00000390)	923 Mb	55,930	Draft genome	[196]
	<i>P. miliaceum</i>	Longmi4	887.8 Mb	63,671	Draft genome	[156]
Teff	<i>Eragrostis tef</i>	Tsedey (DZ-Cr-37)	672 Mb	28,113	Draft genome	[23]
Barnyard millet	<i>Echinochloa crus-galli</i>	STB08	1.27 Gb	108,771	Draft genome	[55]
<i>Chloroplast genome</i>						
Foxtail millet	<i>S. italica</i>	–	135,516 bp	111	–	[157]
Proso millet	<i>P. miliaceum</i>	–	139,929 bp	132	–	[25]
	<i>P. miliaceum</i>	–	139,826 bp	108	–	[122]
Little millet	<i>P. sumatrense</i>	Accession No. IT261894	139,384 bp	125	–	[151]
Barnyard millet	<i>Echinochloa esculenta</i> (= <i>E. crus-galli</i> ssp. <i>utilis</i>)	Accession No. IT230633	139,851 bp	111	–	[152]
	<i>E. crus-galli</i>	BTS02	139,800 bp	–	–	[190]
	<i>E. frumentacea</i>	CO(KV)2	139,593 bp	112	–	[133]

– Data not available or not applicable

analysis platforms are expected to resolve these bottlenecks in due course of time.

Gene mapping

Prior to the emergence of genome sequence approaches, genes and genomic regions regulating traits of interest were mapped in millets using low-throughput markers, including RAPD, RFLP, AFLP and SSRs. In foxtail millet, Wang et al. [184] were the first to construct an RFLP-based map to identify that chromosome 8 carries a gene that strongly affects gamete fertility. The RAPD and ISSR-based germplasm characterization was reported in finger millet by Gupta et al. [58]; however, the first genetic map spanning 721 cM on the A genome and 787 cM on the B genome was constructed by Dida et al. [44] using a combination of RFLP, AFLP and SSR markers. In addition, DNA markers (SSR, EST-SSR, ILP and microRNA-based molecular markers) developed using foxtail millet genome sequence information showed higher (> 85%) cross-genera transferability among other millets, including proso millet, barnyard millet, little millet and kodo millet, as well as non-millet species [90, 129, 186], and approximately 62% of switchgrass SSR markers were transferable to proso millet [139]. These higher percentage of cross-transferability demonstrate the potential of these markers in germplasm characterization, marker-trait association and marker-assisted breeding in other millets for which no genomic resources are available. In well researched crops like foxtail millet and finger millet, next-gen approaches, including GBS have been used to pinpoint quantitative trait nucleotides (QTNs) associated with traits of interest. Jia et al. [80] constructed a high-density haplotype map in foxtail millet using ~ 1 million SNPs and identified 512 loci associated with forty-seven agronomic traits. Following this, Jaiswal et al. [75, 76] identified SNPs associated with ten yield-contributing agronomic traits as well as micronutrients in foxtail millet. Sharma et al. [153] and Rajput et al. [140] in proso millet identified SNP markers associated with important agro-morphological traits.

In addition to mapping, direct identification of genes has been made possible through advancements in whole genome sequencing. The availability of genome sequences in public databases (like Phytozome, Gramene and GenBank) had enabled the identification of genes and gene families in sequenced genomes followed by their functional characterization [118]. Foxtail millet being the first millet to be sequenced had evidenced a large number of reports on identification and characterization of gene families, including *NAC* [134], *WD40* [111], *AP2/ERF* [91], *C₂H₂ zinc finger* [115], *MYB* [116], *DCL*, *AGO*, *RDR* [187], *WRKY* [114], *LecRLK* [195], *ADP-ribosylation factors* [117], *ATG* [101], heat shock proteins and

factors [160], *CDPK* [191] and *LIM genes* [188]. In the wild ancestor, *S. viridis*, [31] has identified and validated the phosphate transporter gene family.

Other omics approaches for gene discovery and crop improvement

Transcriptomics

Although genetics and genomics have made significant progress in studying millets, other omics approaches are relatively new to these crops, and not much of reports are available on the use of other omics tools to study the millets. Transcriptome-based gene expression profiling is a functional genomic approach for characterizing the candidate genes regulating various biological processes, and provides comprehensive information about expression pattern of genes and functional polymorphism [82]. In this aspect, foxtail millet transcriptome was the first to be released, where Zhang et al. [194] had sequenced the total RNA of root, stem, leaf and spike of the strain ‘Zhang gu’. Recently, Li et al. [99] had sequenced the transcriptome of foxtail millet during *Sclerospora graminicola* infection, and identified several candidate genes for further functional characterization. Notably, the study pinpointed an amidase encoding gene, *Seita.2G313400*, that showed 30-fold upregulation during the infection. In finger millet, Rahman et al. [136] analyzed the salinity responsive leaf transcriptome of contrasting finger millet genotypes and identified several differentially expressed genes in the tolerant genotype. Hittalmani et al. [70] had sequenced the transcriptome of finger millet variety ML-365 under well-watered and low moisture stress treatments. The study identified 12,893 unigenes specifically expressed in low moisture stress. Following this study, Akbar et al. [4] had performed RNA-seq of developing spikes to dissect the oxalic acid biosynthesis pathway in finger millet. The data concluded that ascorbate-tartrate pathway could be a predominant player in oxalic acid biosynthesis, and this could be useful in studying the nutrients-antinutrients interactions in this crop. Parvathi et al. [132] had analyzed the transcriptome dynamics in the leaf samples of finger millet exposed to drought stress. The study highlighted two candidate genes, *CIPK31* and *TAF6*, that could be studied further to delineate their roles in conferring drought tolerance. In proso millet, RNA-seq data was first reported by Yue et al. [193], which served as an excellent sequence resource for gene discovery and marker development in this crop. Few reports also available in other millets, including barnyard millet for drought tolerance, and Fe and Zn accumulation [77], submergence tolerance [120]; and in teff for waterlogging [24], to understand the

gene regulatory mechanisms in these crops. These studies underline the application of transcriptomics in identifying the gene repertoire underlying the traits-of-study, which can then be further characterized and used in crop improvement.

Proteomics and metabolomics

As transcript abundance and expression does not directly correlate with the protein/metabolome levels, and in order to study the post-translational modifications that proteins/metabolomes undergo to perform any given function, proteomics and metabolomics studies gain importance. For example, in finger millet, Singh et al. [159] characterized the calcium binding proteins (CaBPs) in grain filling stages using proteomics approach and reported that the higher synthesis of CaBP during later stages of grain filling might be responsible for the sequestration of calcium in endoplasmic reticulum of finger millet. In foxtail millet, Li et al. [98] investigated proteomic changes in the grains under drought stress and salinity, and identified 104 differently expressed proteins, while Veeranagamallaiah et al. [174] performed proteomic analysis of 7-days old salt-treated tolerant cv. 'Prasad' seedlings and identified 29 differentially expressed proteins involved in signal transduction, photosynthesis, metabolism and stress response. In metabolomics aspect, De Oliveira Dal'Molin [35] was the first to perform metabolic reconstruction and multiple omics mapping using transcriptome, proteome, and targeted metabolome data of foxtail millet. The study identified significant abundance of metabolites that play roles in C_4 metabolism, which underlines the potential of foxtail millet as a C_4 model. Similarly, Li et al. [100] studied the qualitative and quantitative differences in both the primary and secondary metabolites in six foxtail millet varieties using LC–MS analysis. The study not only defined the specific accumulation of metabolites, but also provided insights into metabolome engineering to develop trait-specific metabolites. Recently, Agtuca et al. [2] reported the metabolomic changes in the roots during colonization of endophytic bacteria in *S. viridis*, the wild progenitor of foxtail millet. The study highlighted how the endophytic plant growth-promoting bacteria modulates host metabolic pathways to enhance the growth, development and defense response of *S. viridis*. At this point-of-time, metabolomics has not been extended to other millets, and in light of these experiments reported in foxtail millet, it is expected to gain momentum in other related crops.

Genetic transformation of small millets

Agrobacterium-mediated system has been predominantly used in small millets transformation. However, compared to other major cereals like rice, genetic transformation

studies in millets are lagging [29]. Reports on optimization of transformation protocols and transgenic plants expressing functionally active transgenes in millets are of recent origin. Details on genetic transformation studies reported in small millets are presented in Table 6. There are substantial number of reports on finger millet and foxtail millet on genetic transformation. The first finger millet transformation study was reported by Gupta et al. [57], whose preliminary work used biolistic method to compare the efficiency of five gene promoters for the expression of *GUS* reporter gene. Later, several studies in finger millet focused on development of transgenics for leaf blast resistance [73, 92], drought and salinity tolerance [66], herbicide resistance [15], and improved zinc concentration [142]. In foxtail millet, *Agrobacterium*-mediated transformation was first reported by Liu et al. [106]. Later studies have focused on developing transgenic foxtail millet tolerant to drought and salinity [94, 97, 127, 181], and characterization of phosphate transport [26]. While only a few studies on the genetic transformation are available on barnyard millet, teff, and fonio and none are available on little millet, proso millet and kodo millet. There is one report each on barnyard millet, fonio and teff. In barnyard millet, an old report is available on biolistic transformation for testing the efficiency of various promoters in *GUS* expression [57]. Since then, no effort has been made to transform barnyard millet using *Agrobacterium*-mediated system. Teff was transformed by *Agrobacterium* with runner bean (*Phaseolus coccineus*) *gibberellin inactivation* (*PcGA2ox1*) gene [48] to study its function on growth. Embryogenic callus derived from immature embryos was used as explants for transformation. In vitro regeneration protocol was reported in proso millet [62], kodo millet [28, 84, 85], little millet [112], and barnyard millet [137, 138], that could enable transgenic work to be explored in order to introduce key genes to confer resistance against various stresses.

The availability of optimized protocols for genetic transformation has seen the application of transgene-based approach in a few small millets. However, this is yet to be standardized in several millets; until then, manipulating genes directly to overexpress, knock-out/down, or using CRISPR/Cas9 system will not be feasible. Genome editing systems like CRISPR/Cas9 have been frequently used in other major cereals like rice for functional genomics and crop improvement studies [30]. The use of CRISPR/Cas9 mutagenesis was reported in foxtail millet [104], where mutation of foxtail millet *PDS* gene by CRISPR/Cas9 system has been achieved through protoplast transfection. Several genes with roles in enhancing yield-contributing agronomic traits, disease resistance, stress tolerance, and other desirable factors were identified in small millets but await comprehensive functional characterization

Table 6 Details on genetic transformation studies reported in small millets

Name of the millet	Method of transformation	Name of the genotype(s) used	Type of explant used	Functional gene used	Frequency of transformation (%)	Application	References
Finger millet	<i>Agrobacterium</i> -mediated	PR 202	Embryogenic seed	–	44.4%	Optimization of transformation protocol	[154]
		GPU 45 and Co(Ra) 14	Shoot apex	–	3.8%	Optimization of transformation protocol	[27]
		GPU 45	Shoot apex	Rice <i>chitinase</i> (<i>chi11</i>) gene	3.5–3.9%	Leaf blast resistance	[73]
		GPU 28	Callus and embryogenic callus	<i>OsZIP1</i>	–	Improvement of seed Zn concentration	[142]
		Tropikanka and Yaroslav 8	Embryogenic callus	<i>HvTUB1</i> and <i>TUAm1</i>	1.5%	Resistance to herbicide	[15]
		GPU 28	Embryogenic callus	Bacterial <i>mtlD</i> gene	7.5%	Multiple stress resistance	[66]
		GPU 28	Callus and embryogenic callus	<i>PgNHX1</i> and <i>AVP1</i>	–	Salinity tolerance	[78]
		ML 181	Callus	<i>SbVPPase</i>	–	Salinity tolerance	[7]
	Biolistic	CO(Ra) 14, PR 202, Try 1 and Paiyur 2	Shoot apex	–	11.8%	Optimization of transformation protocol	[149]
		PR 202	Leaf sheath	–	–	Testing the efficiency of various promoters	[57]
		Local cultivar PGEC 2 and 19 accessions	Shoot apex	Antifungal protein (PIN) of prawn	–	Leaf blast resistance	[92]
		PGEC 2	Shoot tip-embryogenic callus	<i>PcSrp</i>	–	Salinity tolerance	[109]
		PR 202	Green nodular calli	–	–	Optimization of transformation protocol	[74]
Foxtail millet	<i>Agrobacterium</i> -mediated	–	Callus	–	6.6%	Optimization of transformation protocol	[106]
		cv. Jigu11	Callus	<i>Si401</i>	–	Regulation of anther development	[135]
		cv. Jigu11	Callus	<i>SBgLR</i>	90.72%	Optimization of transformation protocol	[182]
		Jigu11 and Yugu2	Callus	–	–	Optimization of transformation conditions	[192]
		cv. Jigu11	Callus	<i>SiLEA14</i>	–	Drought and salinity tolerance	[182]
		cv. Jigu11	Callus	<i>SiARDP</i>	–	Drought tolerance	[94]

Table 6 (continued)

Name of the millet	Method of transformation	Name of the genotype(s) used	Type of explant used	Functional gene used	Frequency of transformation (%)	Application	References
		cv. Jigu11	Callus	–	–	Characterization of seed specific promoter pF128	[128]
		cv. Jigu11	Callus	<i>SiLTP</i>	–	Drought and salinity tolerance	[127]
		Maxima	Shoot apex	<i>SiPHT1;1,2 and 3</i>	10%	Characterization of phosphate transport	[26]
		cv. Jigu11	Callus	<i>SiASRP4</i>	–	Drought and salinity tolerance	[97]
	Biolistic	var. 3661	Florets	<i>SiPf40</i>	–	Functional characterization of <i>SiPf4</i> gene	[105]
Barnyard millet	Biolistic method	VL 29	Callus	–	–	Testing the efficiency of various promoters	[57]
Teff	<i>Agrobacterium</i> -mediated	cv. DZ-01-196	Callus	<i>PcGA2ox</i>	–	Inducing semi-dwarfism	[48]
Fonio	<i>Agrobacterium</i> -mediated	Agyong and Churiwe	Callus	–	2.1–2.7%	Testing the efficiency of various promoters	[126]

SiPHT1, *Setaria italica* phosphate transporter 1; *SiLEA14*, *Setaria italica* late embryogenesis abundant 14; *SBgLR*, lysine-rich protein from potato; *SiLTP*, *Setaria italica* lipid transfer proteins; *mtID*, mannitol-1-phosphate dehydrogenase; *SbVPPase*, vacuolar H⁺-pyrophosphatase gene from *Sorghum bicolor*; *HvTUB1*, *Hordeum vulgare* β 1-tubulin; *TUAm1*, mutant α 1-tubulin; *PgNHX1*, *Pennisetum glaucum* sodium hydrogen exchanger1, *AVP1*, *Arabidopsis* vacuolar pyrophosphatase1; *OsZIP1*, *Oryza sativa* zinc-regulated iron-regulated like protein; *SiARDP*, Dehydration-responsive element binding protein; *SiASRP* Absciscic acid-, stress-, and ripening-induced proteins; *SiPf40*, *Setaria italica* ZIP-like gene; *PcGA2ox*, *Phaseolus coccineus* gibberellin inactivation gene; *PcSrp*, *Porteresia coarctata* serine-rich-protein

using genomics tools. However, the lack of an efficient transformation system is a bottleneck, which if resolved, could lead to functional studies on individual genes in small millets enabling a study of their roles in related crops like rice, wheat and sorghum using transgene-based approaches.

Global status of small millets improvement

In India, seven small millets (finger millet, foxtail millet, proso millet, barnyard millet, kodo millet, little millet, and browntop millet) are being cultivated. The All India Coordinated Research Project on Small Millets (AICRP-Small Millets) carries out this research in India, through a network of 14 centers located in State Agricultural Universities, ICAR institutes and 21 voluntary centers. Crop improvement through AICRP-Small Millets resulted in the development of high yielding varieties with resistance to blast disease, quality fodder, early and medium maturity and white seed

in finger millet; resistance to head smut in kodo millet and resistance to shoot fly in proso millet and little millet. So far, a total of 248 varieties of these small millets have been released in India (AICSMIP, 2014; <http://www.aicrpsm.res.in/>). Among the cultivars released in India, selection from eight ICRISAT germplasm accessions were released as cultivars (Table 7). Currently, recombination breeding has been the approach used, especially in finger millet, resulting in the development of diverse and high grain yielding cultivars in India. It has also been used in foxtail millet, proso millet and barnyard millet. Finger millet varieties yield up to 5–6 t ha⁻¹, and cultivars of other small millets yield up to 2.5–3 t ha⁻¹ under optimum management conditions.

In African, particularly in eastern and southern Africa, finger millet is an important food crop. However, systematic breeding efforts are very limited. A majority of the cultivars grown in Africa are either landraces or direct introductions. The ICRISAT-HOPE project in collaboration with the Department of Research and Development (DRD), Tanzania, released cultivars such as P 224 and U 15 in Tanzania, and

the same cultivars were also released in Kenya and Uganda (<http://hope.icrisat.org/new-varieties-promise-an-increase-in-tanzanias-finger-millet-production/>). Selection from three ICRISAT's finger millet accessions were released as cultivars in Zambia (2) and Kenya (1) (Table 7). Teff is an important crop in Ethiopia in terms of area, production and consumption. Teff breeding in Ethiopia is coordinated by Debre Zeit Agricultural Research Center (DAZRC) of the Ethiopian Agricultural Research Institute (EIAR). About 42 teff varieties have been released in Ethiopia largely through direct selection from landraces and intraspecific hybridization of lines selected from the germplasm with yields of 1.4–3.6 t ha⁻¹ [110].

In China, foxtail millet and proso millet are the most widely grown small millets. Cultivars released in the 1950s and 1960s were largely with simple grain yield comparisons among landraces, while hybridization-based pedigree selection gained popularity after the 1970s. About 870 cultivars have been released since 1950. Heterosis breeding in foxtail millet began in the 1960s with the development of male sterile lines by various approaches to develop hybrid cultivars. For example, a high yielding hybrid cultivar Zhangzagu 5 was released by Zhangjiakou Academy of Agricultural Sciences, Hebei Province, China, and yielded 12,159 kg/ha versus conventional cultivars whose yields ranged from 4500 to 6000 kg/ha in 2007 [107]. The development of herbicide-resistant foxtail millet cultivars has made the exploitation of heterosis a reality through the use of herbicide-resistant

varieties as restorer lines [43]. Proso millet is a relatively minor crop compared to foxtail millet in China. Pure line selection and hybridization-based pedigree selection are the main methods of proso millet breeding. So far, there is no efficient method for emasculating this plant; so only a few cultivars have been developed through hybridization-based breeding and progress in proso millet breeding is rather slow. About 162 cultivars have been released since the 1950s, and among which the most popular ones currently grown in China include Yumi 2, Ningmi 14, Longmi 10, Neimi 5, Jinshu 8 and Longshu 23 [43]. Job's tears is also grown on limited acreage in China, and cultivars grown were mostly landraces with an average yield of about 3.21 t ha⁻¹. Only a few institutes in Guizhou and Yunnan provinces are having breeding programs dedicated to this crop [43].

In the United States, proso millet and foxtail millet are most widely grown millets. Grains of these crops are largely used for birdfeed and in cattle-fattening rations. A focused breeding program to improve proso millet productivity started in 1965 under the alternative crops breeding program at Panhandle Research and Extension Centre (PHREC). This led to the release of several cultivars such as Sunup, Dawn, Cerise, Rise, Early bird, Hutsman, Sunrise, Horizon, and Plateau, which resulted in significant improvement in proso millet productivity. In the USA, 18 cultivars of proso millet are available to growers, 10 of which are landraces while remaining 8 are developed through hybridization [60, 146, 147]. Foxtail millet is cultivated as a catch crop, especially

Table 7 List of varieties released in small millets through selection from ICRISAT germplasm

Crop/accession number	Country of origin	Country of release	Release name	Year released
<i>Barnyard millet</i>				
IEc 542	Japan	India	PRJ 1	2003
<i>Finger millet</i>				
IE 723		India	BM 1	1985
IE 2947	Malawi	Zambia	FMV 287	1987
IE 4115	Uganda	Kenya	KAK-WIMBI 2	2016
IE 2929	Malawi	Zambia	Lima	1987
IE 1010	Unknown	Uganda	NAROMIL 1	2018
IE 882		Uganda	NAROMIL 2	2018
IE 2440	Kenya	Uganda	NAROMIL 5	2018
IE 524		India	VL 101	1978
<i>Foxtail millet</i>				
ISe 377	India	India	Chitra	1982
ISe 279	India	India	SIC 3 (K 548-79)	1985
<i>Kodo millet</i>				
IPs 19	India	India	GK 1	1977
IPs 115	India	India	PSC 1	1986
IPs 85	India	India	TNAU 86	2012
<i>Proso millet</i>				
IPm 2769	Ukraine	India	DHP 2769	2018

for fodder and pet food for caged and wild birds. Nearly all foxtail millet cultivars grown in the USA are the result of selections from landraces. Several advanced lines that are resistant to wheat streak mosaic virus have been developed through hybridization [13].

Promotion of small millets for better nutrition

Cultivation and consumption of small millets can be promoted by (1) supporting production and improving productivity (through research and developments to enhance yield and nutritional qualities, cultivation as pure crops as well as intercrop with other main crops, cultivation as fail-safe crops – late sowing when monsoon fails, particularly early-maturing cultivars that yield considerably even under constrained environments); (2) providing on-farm support and linking farmers to value chains; (3) undertaking campaigns to build consumer awareness; (4) ensuring products in demand are available and accessible; (5) supporting processors, food service, health/medical and industrial sectors to incorporate millets (for example, development of modern ready-to-eat and ready-to-cook products, post-harvest processing technology development, nutrition investigation, methods for extending shelf life, etc.); and (6) policy support (including small millets and value-added products in the public distribution systems, minimum support price and mid-day meal/school feeding schemes, etc.). The global Smart Food initiative, led by Africa and Asia with an executive council composed of FARA, CORAF, FANRPAN, APAARI and ICRISAT; and in India, the National Food Security Mission of the Government a Sub-mission on Nutri-cereals, are the great initiatives for millets promotion, consumption, demand creation, post-harvest value-addition and ultimately doubling farm level economy. In India, the year 2018 was celebrated as the National Year of Millets, and the FAO has endorsed India's proposal to declare 2023 as the International Year of Millets, to be submitted to the UN General Assembly, that show the significance of millets in a global prospective.

Future challenges and prospects

Small millets have the potential to serve as an alternate/supplement to major cereal staples because of their ability to be used/cooked in similar ways, diverse adaptation to adverse conditions and nutritional qualities. Small millets can fit very well into multiple cropping systems both under irrigated and rainfed conditions. Their storability under normal storage conditions has made them 'famine reserves'. They can provide nutritious grains as well as valuable fodder

in a short span of time. A very low number of germplasm and inadequate information on genetic diversity limits their effective utilization in crop improvement programs. Therefore, prioritizing germplasm collection is key to identifying trait specific resources, genes and alleles, which can be utilized in small millets breeding programs. So far, small millets varieties have been developed mainly through conventional breeding methods. The yield barrier in small millets can be broken by a male sterility system and exploiting heterosis, and genomics-assisted crop improvement, together with better crop management and mechanization. Genomics-assisted breeding will facilitate the identification of novel alleles and genes with superior agronomic performance and resistance to biotic and abiotic stresses to accelerate small millets improvement. Biotechnology techniques such as tissue culture and genetic engineering reported in related crops could potentially support small millets improvement. The rapid development of sequencing technologies can generate millions of sequence reads at a low cost and in a short time irrespective of whether there is prior sequence information or not. Next generation sequencing techniques enable the molecular characterization of an entire set of small millets germplasm. These techniques could be used in crops such as little millet, kodo millet, and job's tears where genome decoding has not yet been done. Similarly, comparative genomics facilitates the exploration of orthologous genes of important traits in less studied crops with available genome sequence information from rice and foxtail millet. The emergence of genome editing techniques allows the modification of the genome of small millets to enhance production and stress tolerance. In addition to conventional breeding and genomics-assisted improvement, a comprehensive and coordinated transdisciplinary collaboration across the agronomy, biomedical, food science and technology areas is required in order to shift the status of small millets out of 'minor and underutilized' crops' group. Additionally, public-private partnerships, public awareness, farmers' engagement across the countries who are interested in small millets research and promotion will be needed to incorporate small millets-based food products as an important source of nutrients in diets. Given the changing climate scenario and prevailing hidden hunger, greater research and developmental focus on small millets (and other traditionally important crops) is the key to achieve food, feed and nutrition security.

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