REVIEW

The Promise of Millets in the Twenty-First Century: Emphasis on Breeding, Nutrition, Food Security and Sustainability

Tirthankar Bandyopadhyay[1] · Roshan Kumar Singh[1] · Palakurthi Ramesh[1] · Jyoti Maurya[1] · Manoj Prasad[1,2]

Abstract

Global population is expected to cross 11 billion by the turn of the century, which has put immense pressure on the existing agricultural systems worldwide. This is complicated by gradually decreasing productivity and acreage as a result of climate change in addition to ever-increasing input costs of resource hungry staple crops like rice, wheat, and maize. Unfortunately, the most affected by these events are those who have the least resources at their disposal to mitigate the issue, especially in countries of Asia and Sub-Saharan Africa. It is therefore pertinent to explore and adopt alternative and/or complementary crops that are easier to cultivate, climate change tolerant, less resource hungry, nutritionally richer for human consumption, and agriculturally sustainable. Millets are perfect cereal crops which meet all of these requirements and can realistically provide much-needed solutions to current global food and nutritional security challenges. In this review, we provide a bird's eye view of the relevance of millets in global agro-ecosystems in the context of their nutritional and agronomic attributes. Furthermore, we share perspectives on the major areas of crop improvement programs worldwide and discuss major challenges confronting the same. Finally, we discourse on the scope of millets for wider acceptability and highlight major points at the interface of genetic intervention–crop management post-harvest practices worth considering to potentially facilitate robust millet-based nutritional and food security.

Keywords Human nutrition · Hidden hunger · Food security · Climate change · Millets · Crop improvement

1 Introduction

Plants constitute a major part of human diet and act as chief source of proteins, carbohydrates, vitamins, and minerals for much of the developing world. On the other hand, plant nutrition is largely governed by the richness of the nourishing soil on which they grow, especially in terms of their mineral composition, which in turn impacts the nutritive value of edible plant parts. This is facilitated by other factors like their acquisition by the roots, type of their distribution to different plant tissues, and mobilization of nutrients to developing grains post-anthesis (for cereal crops), the efficiency of which is influenced by multiple abiotic and intrinsic genetic factors.

✉ Manoj Prasad
  manoj_prasad@nipgr.ac.in

1 National Institute of Plant Genome Research, Aruna Asaf Ali Marg, New Delhi 110067, India

2 Department of Plant Sciences, University of Hyderabad, Hyderabad 500046, Telangana, India

Insufficient availability of elemental micronutrients in the soil or within the (edible parts of the) plant is now considered to be the primary contributor towards the "hidden hunger" affecting more than 2 billion of global population (Ritchie et al. 2018; Graham et al. 2012). Such hunger is largely prevalent in populations with cereal-centric diets (like rice or wheat), since they are relatively poorly fortified with nutritionally important micronutrients (Nakandalage and Seneweera 2018; Von Grebmer et al. 2014; White and Broadley 2009). Furthermore, agronomically, rice and wheat cultivation is one of the largest consumers of NPK fertilizers among crops globally, thereby presenting a new challenge for agricultural sustainability, especially when they are prime targets of the climate change phenomenon (Ray et al. 2019) in the present decade. To make matters worse, population growth compounded by unplanned urbanization/industrialization policies in the recent decades in many countries has rendered the soil toxic resulting in alarming levels of cadmium and arsenic in plant foods (Clemens and Ma 2016; Zhao et al. 2010; Harvey et al. 2002), further complicating the road to complete human nutrition. In view of the same,

identification of crops having lower cost of cultivation with a higher sustainability quotient and climate change resilience is the need of the hour.

Millets are potentially relevant since they have all the attributes matching the above requirements. Millets are a group of C_4 cereal grasses within the grass subfamily *panicoideae* and include finger millet (*Eleusine coracana*), kodo millet (*Paspalum scrobiculatum*), proso millet (*Panicum miliaceum*), barnyard millet (*Echinochloa frumentacea*; *Echinochloa esculenta*), and little millet (*Panicum sumatrense*), among others. They are mainly grown in parts of Sub-Saharan Africa, Asia, as well as in Argentina and the USA (Dwivedi et al. 2012). India is one of the largest producers of millets in the world followed by China. In the present article, we provide major perspectives on the potential role of this crop in addressing nutritional food security as well as identify key areas of millet improvement for sustainable agriculture.

1.1 Nutritional Merits of Millets

Nutritionally, millets are equivalent or superior to major cereal grains including rice and wheat, especially in terms of protein, essential amino acids, vitamins, and mineral elements like iron, zinc, phosphorous, potassium, and calcium (Table 1) (Muthamilarasan and Prasad 2021; Hegde et al. 2005). Additionally, millet proteins are gluten free and possess many bioactive compounds, and they are rich in dietary fiber (Kumar et al. 2018), making it an ideal health food. While wheat and proso millet have comparable protein content in their seeds, the content of essential amino acids like isoleucine, thiamine, and leucine is significantly higher in the latter. Similarly, the lipid content in millets as a group is comparable to or higher than that in wheat and rice (Kumar et al. 2018). Furthermore, unlike most conventional food grains (like rice and wheat), millets have appreciably lower glycemic indices (Shukla and Srivastava 2014; Ugare et al. 2014), making it an ideal cereal of choice for the diabetic population. Epidemiological evidences indicate that millet-consuming populations have lower incidence of diabetes (Kim et al. 2011). For instance, studies have indicated the effectiveness of millets in augmenting glycemic control and reducing blood glucose (Geetha et al. 2020; Singh et al. 2020) as well as minimizing insulin resistance and reducing levels of glycosylated hemoglobin (HbA1c) (Geetha et al. 2020; Sobhana et al. 2020; Itagi et al. 2012; Thathola et al. 2011). Studies involving arabinose and xylose polysaccharides from finger millet have indicated that they can act as active prebiotics and have wound-dressing potential (Manisseri and Gudipati 2012; Mathanghi and Sudha 2012; Shobana and Malleshi 2007). In addition to being slowly digestible (and therefore low glycemic), resistant starch facilitates

production of bioactive metabolites like short-chain fatty acids (butyrate), widely known to be preventive against colon cancer (Ramesh et al. 2022; Annor et al. 2015; Englyst et al. 1992). Multiple studies in recent years have comprehensively documented the bioavailability and content of major macronutrients in millet grains and can be consulted for an in-depth account (Dhaka et al. 2021).

Minerals and vitamins constitute the micronutrients and play key roles in many physiologically important processes in human body like building of bones, formation of blood clots, signal transmission between neurons, maintaining heartbeat, acting as coenzymes, and metabolizing and synthesizing fats and proteins among many others (Soetan et al. 2010). The share of minerals in millet grain (1.7 to 4.3 g/100 g) is substantially higher than that in staple crops like wheat (1.5%) and rice (0.6%) (Kumar et al. 2018). Calcium (Ca) is an important mineral required for bone formation, growth, and prevention of osteoporosis. Finger millet has more than 8 times more Ca than wheat, while barnyard and pearl millets are rich sources of bioavailable iron, and their intake can help prevent anemia in pregnant women (Kumar et al. 2018). Foxtail millet has one of the highest zinc contents among crops, in addition to being rich in iron (Jaiswal et al. 2019). Millets are also rich sources of many beta-carotenes and B vitamins. A comparative account of micronutrient content between millet and other staple crops will provide a more detailed overview.

Phenolic compounds from millets have anti-mutagenic, anti-estrogenic, anti-inflammatory, antioxidant, and antiviral effects (Devi et al. 2014). In finger, foxtail, little, and proso millets, this is driven by high contents of carotenoid and tocopherols (Dykes and Rooney 2006). Phenolics cause partial inhibition of amylase and α-glucosidase which hydrolyze complex carbohydrates, thereby reducing the availability of postprandial glucose levels in the blood (Ofosu et al. 2020). A comprehensive account of phenolic profile of six millet types has been enumerated by Kumar et al. (2018). Furthermore, independent studies have confirmed hypolipidemic effects of millet seed extracts in rats (Sireesha et al. 2011; Lee et al. 2010). Bound polyphenols from the foxtail millet bran contain antitumor effect on human colorectal cancer HCT-116 cells (Shi et al. 2015). The polyphenol compounds were associated with the generation of reactive oxygen species (ROS) and activation of caspase-regulated apoptosis in the HCT-116 cells. Foxtail millet polyphenols are mainly consisting of caffeic acid, p-coumaric acid, ferulic acid, chlorogenic acid, syringic acid, and carotenoid (Dhaka et al. 2021). Comparatively higher antioxidant activity has been observed in the flour of germinated foxtail, kodo, and barnyard millets than in their raw flours (Sharma et al. 2016).

While millets are considered rich sources of many nutrients, they also contain some antinutritive compounds like polyphenols, phytic acid, and tannis which render a bitter taste to the

Table 1 Nutritional composition of main millets in comparison to major cereals (12% moisture; per 100-g edible portion) (Nakarani et al. 2021; Jaiswal et al. 2019; Muthamilarasan et al. 2016; Saleh et al. 2013; Englyst et al. 1992)

Nutrients	Finger millet	Pearl millet	Foxtail millet	Proso millet	Wheat	Rice (white, milled)	Rice (brown, medium grain)	Corn grain (white)	Sorghum	Oats	Barley
Proximate composition											
Moisture (g)	13.1	12.4	11.2	11.9	12.8	13.7	12.4	10.4	12.4	8.2	10.1
Energy (kcal)	336	361	331	341	346	345	362	365	329	389	352
Protein (g)	7.7	11.6	12.3	12.5	11.8	6.8	7.5	9.4	10.6	16.9	9.9
Fat (g)	1.5	5	4.3	1.1	1.5	0.5	2.7	4.7	3.5	6.9	1.2
Total dietary fiber (g)	11.5	11.3	2.4	–	12.5	4.1	3.4	7.3	6.7	10.6	15.6
Carbohydrate (g)	72.6	67.5	60.9	70.4	71.2	78.2	76.2	74.3	72.1	66.3	77.7
Minerals (g)	2.7	2.3	3.3	1.9	1.5	0.6	–	–	1.6	–	–
Minerals and trace elements											
Calcium (mg)	350	42	31	14	30	10	33	7	13	54	29
Iron (mg)	3.9	8	2.8	0.8	3.5	0.7	1.8	2.7	3.36	4.7	2.5
Magnesium (mg)	137	137	81	153	138	64	143	127	165	177	79
Phosphorus (mg)	283	296	290	206	298	160	264	210	222	523	221
Manganese (mg)	5.94	1.15	0.6	0.6	2.29	0.51	–	–	0.78	–	–
Molybdenum (mg)	0.102	0.069	0.7	–	0.051	0.05	–	–	0.039	–	–
Zinc (mg)	2.3	3.1	2.4	1.4	2.7	1.3	2.02	2.21	1.7	3.97	2.1
Sodium (mg)	11	10.9	4.6	8.2	17.1	–	4	35	2	2	9
Potassium (mg)	408	307	250	113	284	–	268	287	363	429	280
Vitamins											
Thiamine (mg)	0.42	0.33	0.59	0.2	0.45	0.06	0.41	0.39	0.33	0.76	0.19
Riboflavin (mg)	0.19	0.25	0.11	0.18	0.17	0.06	0.04	0.2	0.096	0.14	0.11
Niacin (mg)	1.1	2.3	3.2	2.3	5.5	1.9	4.3	3.6	3.7	0.96	4.6
Total folic acid (µg)	18.3	45.5	15	–	36.6	8	20	–	20	56	23
Vitamin E (mg)	22	–	–	–	–	–	–	–	0.5	–	0.02

derived food, thereby acting as a major factor affecting the larger acceptability of the crop by the farming community and consumers alike. These antinutrient contents are reported to chelate the essential multivalent cations in the human body after their intake (Pramitha et al. 2021). Interestingly, major food processing steps like decortication, milling, malting, fermentation, roasting, and grinding help reduce the antinutrient contents and enhance their alimentary properties (Hotz and Gibson 2007). Reducing the availability of these compounds in the crop is therefore a major target for crop improvement strategies.

Agronomically, millets exhibit exceptional tolerance to environmental stresses such as minimal soil fertility, drought, and higher temperature, making them even more suitable for climate-resilient agriculture (Singh et al. 2021). The monoculture system of staple crops like rice, wheat, and maize utilizes large amount of chemical fertilizers, causing deterioration of soil health and environmental pollutions. Mainstreaming millet cultivation together with these crops may contribute not only to the agriculture security, but also to ecosystem stability and enhanced income for farmers with smaller agriculture land. In view of the demonstrated nutritional, agronomic, and environmental benefits of millets, we provide our perspectives towards major initiatives currently underway to further improve the crop in terms of its grain-specific micro- and macronutrient attributes.

1.2 Genetic Improvement of Millets

Diversity of germplasm allows for variability which is important for sustainable agriculture. A limited and homogeneous genetic background of germplasm makes it more prone to crop failure from sudden onslaught of new pest and disease attacks as well as other vagaries of climate change. In this light, a total of 133,849 accessions of small millets have been conserved in genebanks, including 30,627 accessions from other species from the same genera (Vetriventhan et al. 2020). Furthermore, with greater realization of the nutritional and agronomic importance of millets, improving the crop in terms of many of its agronomic and nutritional attributes through conventional breeding and molecular genetic approaches has assumed great importance. Specifically, improving the yield, biomass, harvest index, tolerance to drought, and pathogen/pest attack in addition to improving the nutritional quotient of grain and fodder are major targets of crop improvement. In this context, high-throughput genomic resources can prove to be very helpful in identifying genomic loci/regions associated with such traits, thereby paving the way for their introgression to help develop better cultivars through conventional breeding and molecular genetic approaches. To this end, excellent core collections of genetically diverse foxtail (Upadhyaya et al. 2009), finger (Upadhyaya et al. 2011), and pearl millet (Upadhyaya et al. 2017) accessions have been established.

The pollination behavior of millets is varied and ranges from cleistogamy in kodo millet to partial outcrossing in small millets. Larger (seed size) millets like pearl millet are highly cross-pollinated and largely protogynous and result in the plants being highly heterozygous. The main breeding approaches are therefore those that target development of hybrids, synthetics, and composites. In the last few decades, hybrids have been commercially used to achieve considerable breakthrough in yield performance for sorghum and pearl millet. In both these crops, gene-cytoplasmic sterility-restorer platforms have provided a new direction to yield increase. On the other hand, small millets are largely self-fertilized, and hence, pure line selection has been the primary method for trait improvement of landraces. However, hybridization presents many advantages to combine desirable features and hot water, gametocide, and contact-based methods have been recently used with limited success in these crops. The discovery of male sterility in foxtail millet accessions in China provides new hope for significant trait enhancement of this crop (Zhang et al. 2021; Patil 2016). Overall, there is a strong need for standardization of hybridization and cross-pollination methods in small millets. A list of major traits targeted for nutritional improvement of sorghum and millets is provided in Table 2.

The iniadi germplasm of pearl millet native to Togo, Ghana, Burkina Faso, and Benin regions of west Africa has been extensively employed for improvement of the crop (Rai et al. 1999). With regard to small millets, especially finger millet, Indo-African crosses have been instrumental for breakthrough in yield performance in addition to improving traits related to blast tolerance, early vigor, panicle size, branching, finger number, and grain density (Patil 2016). Genotypes with higher protein content as well as efficient nitrogen responsiveness have also been identified (Bandyopadhyay et al. 2022). In kodo millet, three different cultivated complexes are recognized based on differences in raceme morphology, and hybridization between cultivated varieties and weedy races is common. The crop is known to be cleistogamous, but crosses have been largely made using few protogynous types. Interestingly, the absence of racial differentiation in the crop (despite more than 3000 years of known prevalence) is an important and interesting area of investigation with potential for some startling discoveries in genetics. Sorghum improvement programs have traditionally relied on five basic races (guinea kafir, bicolor, durra, caudatum, and their ten derived hybrid races) for identification of useful trait-related genes for major crop improvement programs globally (Patil 2016).

Conventional breeding approaches like pedigree selection, mass selection, pure line selection, and mutation breeding more amenable for self-pollinating crops have been applied to small millets. Most of the released varieties of small millets are derived from local cultivars or landraces, while hybridization

Table 2 Nutritional traits targeted for genetic improvement in Sorghum and millets

Crop	Desired trait	Number of genotypes/ mapping population	Genotyping platform	Approach used	References
	Seed protein content	635 Ethiopian sorghum accessions	Genotyping by sequencing	GWAS	Nida et al. 2021
	Grain quality traits	196 diverse sorghum inbred lines	Re-sequencing data	GWAS	Kimani et al. 2020
	Grain carotenoids	403 Sorghum accessions	SNP genotyping	GWAS	Cruet-Burgos et al. 2020
	Grain iron and zinc content	F_6 RIL population derived from cross 296B×PVK 801	DArTseq markers	QTL mapping	Kotla et al. 2019
	Grain quality traits	F4:5 generation of BTx642/BTxARG-1 and BTxARG-1/ P850029 and 390 diverse grain accessions	Genotyping by sequencing	QTL mapping and GWAS	Boyles et al. 2017
	Protein digestibility trait	F_2 segregants of P721Q×Tx623	Whole-genome sequencing	Bulked segregant analysis mapping	Massafaro et al. 2016
	Grain polyphenols	381 diverse lines	SNP genotyping	GWAS	Rhodes et al. 2014
	Grain quality traits	300 Sorghum accessions	SNP genotyping	GWAS	Sukumaran et al. 2012
Pearl millet	Starch traits	166 accessions	78 K SNP assay	GWAS	Yadav et al. 2012
	Grain iron and zinc content	F_6 RIL population derived from PPMI 683×PPMI 627	SSR genotyping	QTL mapping	Singh et al. 2021
	Nutritional traits	197 pearl millet inbred lines	76 K SNP assay	GWAS	Yadav et al. 2012
	Grain iron, zinc, and protein content	281 advanced inbred lines	DArT seq assay	GWAS	Pujar et al. 2019
	Grain iron and zinc content	RIL population derived from ICMS 8511-S1-17–2-1–1-B-P03×AIMP 92901-S1-183–2-2-B-08	DArT and SSR genotyping	QTL mapping	Kumar et al. 2018
	Grain iron and zinc content	130 diverse lines	SSR genotyping	GWAS	Anuradha et al. 2017
Finger millet	Grain calcium content	202 diverse global accessions	Genotyping by sequencing	GWAS	Sharma et al. 2016
	Seed protein content	113 diverse genotypes	Genotyping by sequencing	GWAS	Tiwari et al. 2020
	Grain calcium content	238 accessions	SSR genotyping	GWAS	Yadav et al. 2012
	Grain nutritional traits	190 genotypes	Genotyping by sequencing	GWAS	Puranik et al. 2020
Foxtail millet	Nutritional traits	93 diverse accessions	10 K SNP assay	GWAS	Jaiswal et al. 2019
Proso millet	Seed traits	88 varieties and landraces	RAD sequencing	GWAS	Boukail et al. 2021

and selection (pedigree selection) were used to a lesser extent (Santra et al. 2019; Report on Compendium of Released Varieties in Small Millets 2014). Interestingly, mutation breeding has shown promise in small millets (self-pollinated crops), given the limited success of the hybridization-based approach in creating variability. Early maturing and high-yielding mutant lines of finger and proso millets have been developed along with other useful traits (Bhave et al. 2016; Ambavane et al. 2014; Muduli and Misra 2007). Overall, these breeding strategies have been useful in developing cultivars with improved yield parameters as well as with durable tolerance to biotic and abiotic stresses.

Genome sequencing approach, on the other hand, provides a new knowledge base of coding and regulatory regions of the genome, which can be exploited for enhancing major agronomic attributes in crops. In practical terms, this will allow development of molecular markers, which in turn will enable a deeper and comprehensive understanding of the structure and diversity of the genetic variability of the traits in question, thereby helping develop molecular tools for genomic-assisted improvement of the crops. In this respect, genomes of finger, foxtail, barnyard, and proso millets have been sequenced, including the complete chloroplast genomes in the first three of them (Vetriventhan et al. 2020). Furthermore, with the advent of genome sequencing platforms, a cheaper and effective way of scanning the genetic variability came to forefront—genotyping by sequencing (GBS). The technology enables high-throughput and cost-effective way of identifying single nucleotide polymorphisms (SNPs) with significant implications towards understanding the genetic basis of trait variability as well as population structure and diversity and has been employed in millets in recent years (Johnson et al. 2019; Upadhyaya et al. 2016; Wallace et al. 2015). However, it is noteworthy that limitations of employing millet genome sequence information exist, given higher ploidy levels and higher incidence of repetitive DNA in their genome (Vetriventhan et al. 2020). Advances in third-generation sequencing technology along with staggering progress in data science and analysis platforms observed in the recent years provide us great hopes in overcoming this bottleneck in the near future. In a nutshell, genomics-based approaches have great potential in contributing towards enhancing genetic gains in millets.

Studies have been done in different sorghum accessions to improve grain quality traits by combining different genotyping platforms such as SNP genotyping, resequencing, genotyping by sequencing (GBS), quantitative trait locus (QTL) mapping, and genome-wide association study (GWAS) approaches (Diatta-Holgate et al. 2022; Kimani et al. 2020; Boyles et al. 2017; Sukumaran et al. 2012). GWAS analysis of 635 Ethiopian sorghum accessions suggested genetic variations at the loci-containing genes such as late embryogenesis abundant (LEA) and tannin biosynthesis genes responsible for grain mold resistance in sorghum (Nida et al. 2021). Quantification of grain carotenoid content in diverse sorghum genotypes using high-performance liquid chromatography (HPLC) and GWAS has identified the key genes responsible for variation in seed carotenoid content (Cruet-Burgos et al. 2020). Among the genes identified in the study, a putative ortholog of maize *zeaxanthin peroxidase* has been found responsible for carotenoid variation in sorghum (Cruet-Burgos et al. 2020). A similar study has been carried out to quantify grain phenols, polyphenols, and proanthocyanadins in 381 sorghum accessions through the near-infrared spectroscopy (NIRS) and GWAS to identify the genetic loci with associated traits (Rhodes et al. 2014). Interestingly, a sorghum mutant P721Q, with high lysine content, has

been found to be associated with enhanced protein digestibility as compared to other sorghum cultivars. This higher lysine content was observed because of reduction of kafirin storage proteins. Genomic sequence analysis of bulked segregants from a P721Q × BTx623 mapping population suggested that the highly digestible protein trait maps with the same cluster of kafirin genes containing high-lysine mutation (Massafaro et al. 2016).

Major traits, which are widely targeted for improvement, are the iron and zinc contents of the grain in a diverse population of pearl millet and sorghum to identify genetic loci controlling the traits (Singhal et al. 2021; Kotla et al. 2019; Pujar et al. 2019; Kumar et al. 2018). A total of 166 pearl millet accessions were evaluated for total starch (TS), rapidly and digestible starch (RDS and SDS), and resistant starch (RS) content, depending on available glucose percentage after digestion (Yadav et al. 2022). Most significant genetic variations of starch-related traits lead to the identification of donor accessions for pearl millet-breeding programs. Owing to the higher calcium content in finger millet, recent reports emphasize its importance as a nutritional trait. For example, a study by Sharma et al. (2022) involved a set of 202 finger millet accessions grown in two different environments in India which are subjected to grain calcium content assessment, which was ranging between 53 and 454 mg per 100 g of grain. This study led to identification of two putative homologs of *Setaria italica* genes, calmodulin-binding protein (CBP) and CBL-interacting protein kinase7 (CIPK7), through GBS and marker trait association, which might be regulating the grain calcium content. Furthermore, both genes were highly expressed in calcium-rich genotypes in comparison to medium- and low-calcium-containing genotypes (Sharma et al. 2016). In foxtail millet, a comprehensive assessment of 23 nutritional traits in 93 different accessions has identified the genetic variation responsible for varying phosphorus and potassium contents (Jaiswal et al. 2019). Major traits targeted for nutritional improvement of sorghum and millets are summarized in Table 2. Altogether, understanding the genetic regulation controlling nutritional traits in millets has enormous potential for wider application in breeding and biotechnical programs to further improve nutritional quality of millets as well as other cereal crop plants.

1.3 Major Challenges in Millet Improvement

Millet production, especially of the small millets, is inconsistent due to many factors. They are often grown in marginal lands, generally poor in nutrients and water retention, leading to variable productivity across different growing seasons. Farmers for these crops do not generally implement the modern crop management practices due to multiple socioeconomic considerations. They also

lack organized programs for production and supply of improved seed varieties. The main drawback of pearl millet consumption is their apparent lack of flavor and bitter taste (due to rancidity), making them a relatively less-popular choice than other staples. Additionally, the shelf life of pearl millet flour is shorter due to rapid rancidity (Goswami et al. 2020; Yadav et al. 2012). A collective effort in the area of production, marketing, and food processing is required to again reestablish millets in the central position of the global agri-economic sector (Fig. 1).

Genetic modification for targeted trait improvement is widely applied in major cereal crops. However, due to lack of good reference genome and their annotation and stable genetic transformation system due to recalcitrant to *in vitro* propagation of most of the millets, accessions have resulted in limited success of this technology in millets. *Agrobacterium*-mediated transformation methods are reported only for the foxtail, finger, and pearl millets (Sood et al. 2020; Singh and Prasad 2016; Ramineni et al. 2014; Ceasar et al. 2017). While many genomic and genomic interventions identified several candidate genes related to agronomic and defense-related traits, their functional genomic analysis using modern biotechnological platforms is currently a major bottleneck (Singh et al. 2021). Furthermore, the application of Clustered Regularly Interspaced Short Palindromic Repeat (CRISPR)/CRISPR-associated protein (Cas) has been extensively employed in many cereal crops with tangible benefits, the same is yet to be employed in millets, except for the foxtail millet (Yang et al. 2020). The application of targeted genome editing is required to be applied to other millets also. However, majority of the minor millet crops lack good reference genomes and their annotations, functional characterization of their genes, and genetic transformation system (Singh et al. 2022).

Fig. 1 Challenges and possible strategies to re-establish millets as major food for food and nutritional security

1.4 Scope and Future Prospects

Extreme climate fluctuations and hidden hunger are one of the major factors confronting global food and nutrition security in this era, and the salient features of unique stress adaptation and nutritive value make millets the ideal candidate for crop improvement strategies. Furthermore, due to their relative photo-insensitivity than other staple crops, shorter growing season, and low moisture demand, growing millets is economically more affordable to marginal farmers of Asia and Sub-Saharan Africa. Additionally, their longer storability and nutritional potential make them ideal candidates to act as "famine reserves." This assumes more significance, given the recent trends in climate change characterized by global warming, water shortages, and malnutrition, which has severely impacted most of the developing world wherein a millet-based food security system in these countries appears to be durable solution. However, the specific aspects of millet cultivation and post-harvest processes would require renewed focus and direction to achieve the goals of food and nutrition security. Despite the fact that millets are common to dryland farming systems, they are irrigation responsive. Hence, selecting genotypes with better water use efficiency (WUE) is important. Improvement of nutritive quality of millet stands to directly impact the health of consuming population, which are largely poor or marginal, thereby helping to improve a significant section of our societies.

With the employment and advancement of hybridization, heterosis, and genomic techniques accompanied by better crop management, millets can potentially register significantly more yields. Approaches encompassing genomic-assisted breeding and genetic engineering/biotechnology will help in identification of novel genes, alleles, and the underlying regulatory pathways influencing agronomic attributes of importance. Since most of the millet crops are polyploid (except for the pearl and foxtail millets) in nature, making segregation is challenging in them. However, they may display enhanced vigor and outperform their parental lines following hybridization. Generating and analyzing molecular markers can be complicated in polyploid species due to the high sequence homology between sub-genomes. Furthermore, advances in next-generation sequencing technologies will provide enough data and leads that will efficiently complement the comparative genomics approach for identification of novel ortholog gene targets for improving millets whose genome is not fully sequenced and/or annotated yet.

In view of the above observations, betterment of yield and nutritive potential of millets is poised to make a significant contribution towards addressing malnutrition globally in the twenty-first century. The existence of significant genetic variability in them allows for planned breeding work to be possible. In the present global situation, the demand for millets is going to significantly increase in the international markets, and,

hence, serious efforts must be made not only to develop varieties that cater for nutritional needs of the population but also to present them as champions of sustainable global food security.

Author Contribution TB and MP conceptualized and designed the outline of the manuscript. TB, RKS, and JM wrote the manuscript; PR prepared the tables. TB, RKS, and MP revised the manuscript. All authors read and approved the final manuscript.

Declarations

Conflict of Interest The authors declare no competing interests.

References

Ambavane AR, Sawardekar SV, Gokhale NB, Desai SAS, Sawant SS, Bhave SG, Devmore JP (2014) Studies on mutagenic effectiveness and efficiency of finger millet [*Eleucina coracana* (L.) Gaertn] in M1 generation and effect of gamma rays on its quantitative traits during M2 generation. Int J Agric Sci 10(2):603–607

Annor GA, Marcone M, Corredig M, Bertoft E, Seetharaman K (2015) Efects of the amount and type of fatty acids present in millets on their in vitro starch digestibility and expected glycemic index (eGI). J Cereal Sci 64:76–81

Anuradha N, Satyavathi CT, Bharadwaj C, Nepolean T, Sankar SM, Singh SP, Meena MC, Singhal T, Srivastava RK (2017) Deciphering genomic regions for high grain iron and zinc content using association mapping in pearl millet. Front Plant Sci 8:412. https://doi.org/10.3389/fpls.2017.00412

Bandyopadhyay T, Swarbreck SM, Jaiswal V, Maurya J, Gupta R, Bentley AR, Griffiths H, Prasad M (2022) GWAS identifies genetic loci underlying nitrogen responsiveness in the climate resilient C4 model *Setaria italica* (L.). J Adv Res. https://doi.org/10.1016/j.jare.2022.01.010

Bhave KG, Dalvi VV, Thaware BL, Mahadik SG, Kasture MC, Desai SS (2016) Mutagenesis in proso millet (*Panicum miliaceum* L.). Int J Sci Res 5:1635–1638

Boukail S, Macharia M, Miculan M, Masoni A, Calamai A, Palchetti E, Dell'Acqua M (2021) Genome wide association study of agronomic and seed traits in a world collection of proso millet (Panicum miliaceum L.). BMC Plant Biol 21(1):330

Boyles RE, Pfeiffer BK, Cooper EA, Rauh BL, Zielinski KJ, Myers MT, Brenton Z, Rooney WL, Kresovich S (2017) Genetic dissection of sorghum grain quality traits using diverse and segregating populations. Theor Appl Genet 130(4):697–716

Ceasar SA, Baker A, Ignacimuthu S (2017) Functional characterization of the PHT1 family transporters of foxtail millet with development of a novel Agrobacterium-mediated transformation procedure. Sci Rep 7(1):14064

Clemens S, Ma JF (2016) Toxic heavy metal and metalloid accumulation in crop plants and foods. Annu Rev Plant Biol 67(1):489–512. https://doi.org/10.1146/annurev-arplant-043015-112301

Cruet-Burgos C, Cox S, Ioerger BP, Perumal R, Hu Z, Herald TJ, Bean SR, Rhodes DH (2020) Advancing provitamin A biofortification in sorghum: genome-wide association studies of grain carotenoids in global germplasm. Plant Genome 13(1)

Devi PB, Vijayabharathi R, Sathyabama S, Malleshi NG, Priyadarisini VB (2014) Health benefits of finger millet (*Eleusine coracana* L.) polyphenols and dietary fiber: a review. J Food Sci Technol 51(6):1021–1040

Dhaka A, Singh RK, Muthamilarasan M, Prasad M (2021) Genetics and Genomics Interventions for Promoting Millets as Functional Foods. Curr Genomics 22:154–163

Diatta-Holgate E, Hugghis E, Weil C, Faye JM, Danquah A, Diatta C, Tongoona P, Danquah EY, Cisse N, Tuinstra MR (2022) Natural variability for protein digestibility and grain quality traits in a West African Sorghum Association Panel. J Cereal Sci 107:103504

Dwivedi S, Upadhyaya H, Senthivel S, Hash C, Fukunaga K, Diao X, Santra D, Baltensperger D, Prasad M (2012) Millets: genetic and genomic resources. In: Janick J (ed) Plant breeding reviews. Wiley-Blackwell, 35:247–347

Dykes L, Rooney LW (2006) Sorghum and millet phenols and antioxidants. J Cereal Sci 44(3):236–251

Englyst HN, Kingman SM, Cummings JH (1992) Classification and measurement of nutritionally important starch fractions. Eur J Clin Nutr 46:S33

Geetha K, Yankanchi GM, Hulamani S, Hiremath N (2020) Glycemic index of millet-based food mix and its effect on pre-diabetic subjects. J Food Sci Technol 57(7):2732–2738

Goswami S, Asrani P, Ansheef Ali TP et al (2020) Rancidity matrix: development of biochemical indicators for analysing the keeping quality of pearl millet flour. Food Anal Methods 13:2147–2164. https://doi.org/10.1007/s12161-020-01831-2

Graham, R. D., Knez, M., & Welch, R. M. (2012). Chapter one - how much nutritional iron deficiency in humans globally is due to an underlying zinc deficiency? (D. L. B. T.-A. in A. Sparks (Ed.); Vol. 115, pp. 1–40). Academic Press. https://doi.org/10.1016/B978-0-12-394276-0.00001-9

Harvey CF, Swartz CH, Badruzzaman ABM, Keon-Blute N, Yu W, Ali MA, Jay J, Beckie R, Niedan V, Brabander D, Oates PM, Ashfaque KN, Islam S, Hemond HF, Ahmed MF (2002) Arsenic mobility and groundwater extraction in Bangladesh. Science (New York, N.Y.) 298(5598):1602–1606. https://doi.org/10.1126/science.1076978

Hegde PS, Rajasekaran NS, Chandra TS (2005) Effects of the antioxidant properties of millet species on oxidative stress and glycemic status in alloxan-induced rats. Nutr Res 25(12):1109–1120. https://doi.org/10.1016/j.nutres.2005.09.020

Hotz C, Gibson RS (2007) Traditional food-processing and preparation practices to enhance the bioavailability of micronutrients in plant-based diets. J Nutr 137(4):1097–1100

Itagi S, Naik R, Bharati P, Sharma P (2012) Ready-made foxtail millet mix for diabetics. Int J Sci Nat 3(1):47–50

Jaiswal V, Bandyopadhyay T, Gahlaut V, Gupta S, Dhaka A, Ramchiary N, Prasad M (2019) Genome-wide association study (GWAS) delineates genomic loci for ten nutritional elements in foxtail millet (Setaria italica L.). J Cereal Sci 85:48–55

Johnson M, Deshpande S, Vetriventhan M, Upadhyaya HD, Wallace JG (2019) Genome-wide population structure analyses of three minor millets: kodo millet, little millet, and proso millet. Plant Genome 12(3):190021

Kim J-S, Hyun TK, Kim M-J (2011) The inhibitory effects of ethanol extracts from sorghum, foxtail millet and proso millet on α-glucosidase and α-amylase activities. Food Chem 124(4):1647–1651. https://doi.org/10.1016/j.foodchem.2010.08.020

Kimani W, Zhang LM, Wu XY, Hao HQ, Jing HC (2020) Genome-wide association study reveals that different pathways contribute to grain quality variation in sorghum (Sorghum bicolor). BMC Genomics 21(1):112. https://doi.org/10.1186/s12864-020-6538-8

Kotla A, Phuke R, Hariprasanna K et al (2019) Identification of QTLs and candidate genes for high grain Fe and Zn concentration in sorghum [Sorghum bicolor (L.)Moench]. J Cereal Sci 90:102850

Kumar A, Tomer V, Kaur A, Kumar V, Gupta K (2018) Millets: a solution to agrarian and nutritional challenges. Agric Food Secur 7(1):31. https://doi.org/10.1186/s40066-018-0183-3

Lee SH, Chung I-M, Cha Y-S, Park Y (2010) Millet consumption decreased serum concentration of triglyceride and C-reactive protein but not oxidative status in hyperlipidemic rats. Nutr Res 30(4):290–296

Manisseri C, Gudipati M (2012) Prebiotic activity of purified xylobiose obtained from ragi (Eleusine coracana, Indaf-15) Bran. Indian J Microbiol 52(2):251–257. https://doi.org/10.1007/s12088-011-0176-4

Massafaro M, Thompson A, Tuinstra M, Dilkes B, Weil CF (2016) Mapping the increased protein digestibility trait in the high-lysine sorghum mutant P721Q. Crop Sci 56:2647–2651

Mathanghi SK, Sudha K (2012) Functional and phytochemical properties of finger millet (*Eleusine coracana* L.) for health. Int J Pharm Chem Biol Sci 2(4):431–438

Muduli KC, Misra RC (2007) Efficacy of mutagenic treatments in producing useful mutants in finger millet (Eleusine coracana Gaertn.). Indian J Genet Plant Breed 67(03):232–237

Muthamilarasan M, Dhaka A, Yadav R, Prasad M (2016) Exploration of millet models for developing nutrient rich graminaceous crops. Plant Sci 242:89–97

Nakandalage N, Seneweera S (2018) Chapter 12 - micronutrients use efficiency of crop-plants under changing climate (M. A. Hossain, T. Kamiya, D. J. Burritt, L.-S. Phan Tran, & T. B. T.-P. M. U. E. Fujiwara (Eds.); pp. 209–224). Academic Press. https://doi.org/10.1016/B978-0-12-812104-7.00015-0

Nakarani UM, Singh D, Suthar KP, Karmakar N, Faldu P, Patil HE (2021) Nutritional and phytochemical profiling of nutracereal finger millet (Eleusine coracana L.) genotypes. Food Chem 341(Pt 2):128271

Nida H, Girma G, Mekonen M, Tirfessa A, Seyoum A, Bejiga T, Birhanu C, Dessalegn K, Senbetay T, Ayana G, Tesso T, Ejeta G, Mengiste T (2021) Genome-wide association analysis reveals seed protein loci as determinants of variations in grain mold resistance in sorghum. Theor Appl Genet 134(4):1167–1184

Ofosu FK, Elahi F, Daliri EB-M, Chelliah R, Ham HJ, Kim J-H, Han S-I, Hur JH, Oh D-H (2020) Phenolic profile, antioxidant, and antidiabetic potential exerted by millet grain varieties. Antioxidants (Basel, Switzerland) 9(3):254. https://doi.org/10.3390/antiox9030254

Patil JV (2016) Millets and sorghum: biology and genetic improvement. John Wiley & Sons, pp 1–431

Pramitha JL, Rana S, Aggarwal PR, Ravikesavan R, Joel AJ, Muthamilarasan M (2021) Chapter three – diverse role of phytic acid in plants and approaches to develop low-phytate grains to enhance bioavailability of micronutrients In: Kumar G DBT-A Ed., Academic Press, pp 89–120. https://doi.org/10.1016/bs.adgen.2020.11.003

Pujar M, Gangaprasad S, Govindaraj M, Gangurde SS, Kanatti A, Kudapa H (2019) Genome-wide association study uncovers genomic regions associated with grain iron, zinc and protein content in pearl millet. Sci Rep 10(1):19473. https://doi.org/10.1038/s41598-020-76230-y

Puranik S, Sahu PP, Beynon S, Srivastava RK, Sehgal D, Ojulong H, Yadav R (2020) Genome-wide association mapping and comparative genomics identifies genomic regions governing grain nutritional traits in finger millet (Eleusine coracana L. Gaertn.). Plants, People, Planet 2:649–662

Rai KN, Murty DS, Andrews DJ, Bramel-Cox PJ (1999) Genetic enhancement of pearl millet and sorghum for the semi-arid tropics of Asia and Africa. Genome 42(4):617–628. https://doi.org/10.1139/g99-040

Ramesh P, Singh RK, Panchal A, Prasad M (2022) 5M approach to decipher starch–lipid interaction in minor millets. Plant Cell Rep. https://doi.org/10.1007/s00299-022-02930-6

Ramineni R, Sadumpati V, Khareedu VR, Vudem DR (2014) Transgenic pearl millet male fertility restorer line (ICMP451) and hybrid (ICMH451) expressing Brassica juncea Nonexpressor of pathogenesis related genes 1 (BjNPR1) exhibit resistance to downy mildew disease. PLoS One 9(6):e90839. https://doi.org/10.1371/journal.pone.0090839

Ray DK, West PC, Clark M, Gerber JS, Prishchepov AV, Chatterjee S (2019) Climate change has likely already affected global food production. PLoS ONE 14(5):e0217148. https://doi.org/10.1371/journal.pone.0217148

Report on compendium of Released Varieties in Small Millets (2014) http://hdl.handle.net/10625/53730

Rhodes DH, Hoffmann L Jr, Rooney WL, Ramu P, Morris GP, Kresovich S (2014) Genome-wide association study of grain polyphenol concentrations in global sorghum [Sorghum bicolor (L.) Moench] germplasm. J Agric Food Chem 62(45):10916–10927. https://doi.org/10.1007/s42729-022-01070-w

Ritchie H, Reay DS, Higgins P (2018) Quantifying, projecting, and addressing India's hidden hunger. Front Sustain Food Syst 2:11 (https://www.frontiersin.org/article/10.3389/fsufs.2018.00011)

Saleh ASM, Zhang Q, Chen J, Shen Q (2013) Millet grains: nutritional quality, processing, and potential health benefits. Compr Rev Food Sci Food Saf 12(3):281–295. https://doi.org/10.1111/1541-4337.12012

Santra DK, Khound R, Das S (2019) Proso millet (Panicum miliaceum L.) breeding: progress, challenges, and opportunities. Advances in Plant Breeding Strategies: Cereals, 223–257

Sharma D, Tiwari A, Sood S, Meher PK, Kumar A (2022) Identification and validation of candidate genes for high calcium content in finger millet [Eleusine coracana (L.) Gaertn.] through genome-wide association study. J Cereal Sci. https://doi.org/10.1016/j.jcs.2022.103517

Sharma S, Saxena DC, Riar CS (2016) Nutritional, sensory, and in-vitro antioxidant characteristics of gluten-free cookies prepared from flour blends of minor millets. J Cereal Sci 72:153–161

Shi J, Shan S, Li Z, Li H, Li X, Li Z (2015) Bound polyphenol from foxtail millet bran induces apoptosis in HCT-116 cell through ROS generation. J Funct Foods 17:958–968

Shobana S, Malleshi NG (2007) Preparation and functional properties of decorticated finger millet (Eleusine coracana). J Food Eng 79(2):529–538

Shukla K, Srivastava S (2014) Evaluation of finger millet incorporated noodles for nutritive value and glycemic index. J Food Sci Technol 51(3):527–534. https://doi.org/10.1007/s13197-011-0530-x

Singh RK, Prasad M (2016) Advances in Agrobacterium tumefaciens-mediated genetic transformation of graminaceous crops. Protoplasma 253(3):691–707. https://doi.org/10.1007/s42729-022-01070-w

Singh RM, Fedacko J, Mojto V, Isaza A, Dewim M, Watanabe S (2020) Effects of millet-based functional foods-rich diet on coronary risk factors among subjects with diabetes mellitus: a single arm real world observation from hospital registry. MOJ Public Health 9(1):18–25

Singh RK, Muthamilarasan M, Prasad M (2021) Biotechnological approaches to dissect climate-resilient traits in millets and their application in crop improvement. J Biotechnol 327:64–73

Singh RK, Sreenivasulu N, Prasad M (2022) Potential of underutilized crops to introduce the nutritional diversity and achieve zero hunger. Funct Integr Genomics. https://doi.org/10.1007/s10142-022-00898-w

Singhal T, Satyavathi CT, Singh SP et al (2021) Multi-environment quantitative trait loci mapping for grain iron and zinc content

using bi-parental recombinant inbred line mapping population in pearl millet. Front Plant Sci 12:659789. https://doi.org/10.3389/fpls.2021.659789

Sireesha Y, Kasetti RB, Nabi SA, Swapna S, Apparao C (2011) Antihyperglycemic and hypolipidemic activities of Setaria italica seeds in STZ diabetic rats. Pathophysiology 18(2):159–164

Sobhana PP, Kandlakunta B, Nagaraju R, Thappatla D, Epparapalli S, Vemula SR, Gavaravarapu SRM, Korrapati D (2020) Human clinical trial to assess the effect of consumption of multigrain Indian bread on glycemic regulation in type 2 diabetic participants. J Food Biochem 44(11):e13465

Soetan KO, Olaiya CO, Oyewole OE (2010) The importance of mineral elements for humans, domestic animals, and plants—a review. Afr J Food Sci 4(5):200–222

Sood P, Singh RK, Prasad M (2020) An efficient Agrobacterium-mediated genetic transformation method for foxtail millet (Setaria italica L.). Plant Cell Rep 39(4):511–525

Sukumaran S, Xiang W, Bean SR, Pedersen JF, Kresovich S, Tuinstra MR, Tesso TT, Hamblin MT, Yu J (2012) Association mapping for grain quality in a diverse sorghum collection. The Plant Genome 5:3. https://doi.org/10.3835/plantgenome2012.07.0016

Thathola A, Srivastava S, Singh G (2011) Effect of foxtail millet (Setaria italica) supplementation on serum glucose, serum lipids, and glycosylated hemoglobin in type 2 diabetics. Diabetol Croat 40(1):23–29

Tiwari A, Sharma D, Sood S, Jaiswal JP, Pachauri SP, Ramteke PW, Kumar A (2020) Genome-wide association mapping for seed protein content in finger millet (Eleusine coracana) global collection through genotyping by sequencing. J Cereal Sci 91:102888

Ugare R, Chimmad B, Naik R, Bharati P, Itagi S (2014) Glycemic index and significance of barnyard millet (Echinochloa frumentacae) in type II diabetics. J Food Sci Technol 51(2):392–395. https://doi.org/10.1007/s13197-011-0516-8

Upadhyaya HD, Ramesh S, Sharma S, Singh SK, Varshney SK, Sarma NDRK, Ravishankar CR, Narasimhudu Y, Reddy VG, Sahrawat KL, Dhanalakshmi TN, Mgonja MA, Parzies HK, Gowda CLL, Singh S (2011) Genetic diversity for grain nutrients contents in a core collection of finger millet (Eleusine coracana (L.) Gaertn.) germplasm. Field Crops Res 121(1):42–52. https://doi.org/10.1016/j.fcr.2010.11.017

Upadhyaya HD, Pundir RPS, Gowda CLL, Reddy VG, Singh S (2009) Establishing a core collection of foxtail millet to enhance the utilization of germplasm of an underutilized crop. Plant Genet Resour 7(2):177–184

Upadhyaya HD, Reddy KN, Ahmed MI, Kumar V, Gumma MK, Ramachandran S (2017) Geographical distribution of traits and diversity in the world collection of pearl millet [Pennisetum glaucum (L.) R. Br., synonym: Cenchrus americanus (L.) Morrone] landraces conserved at the ICRISAT genebank. Genet Resour Crop Evol 64(6):1365–1381

Upadhyaya HD, Vetriventhan M, Dwivedi SL, Pattanashetti SK, Singh SK (2016) 8 - Proso, barnyard, little, and kodo millets (M Singh & H. D. B. T.-G. and G. R. for G. C. I. Upadhyaya (Eds.); pp. 321–343). Academic Press. https://doi.org/10.1016/B978-0-12-802000-5.00008-3

Vetriventhan M, Azevedo VCR, Upadhyaya HD, Nirmalakumari A, Kane-Potaka J, Anitha S, Ceasar SA, Muthamilarasan M, Bhat BV, Hariprasanna K, Bellundagi A, Cheruku D, Backiyalakshmi C, Santra D, Vanniarajan C, Tonapi VA (2020) Genetic and genomic resources, and breeding for accelerating improvement of small millets: current status and future interventions. Nucleus 63(3):217–239. https://doi.org/10.1007/s13237-020-00322-3

Von Grebmer K, Saltzman A, Birol E, Wiesman D, Prasai N, Yin S, Yohannes Y, Menon P, Thompson J, Sonntag A (2014) 2014 Global hunger index: the challenge of hidden hunger. Bonn, Washington, D.C., and Dublin: Welthungerhilfe, International Food Policy Research Institute, and Concern Worldwide. https://doi.org/10.2499/9780896299580

Wallace JG, Upadhyaya HD, Vetriventhan M, Buckler ES, Tom Hash C, Ramu P (2015) The genetic makeup of a global barnyard millet germplasm collection. Plant Genome 8(1) plantgenome2014.10.0067. https://doi.org/10.3835/plantgenome2014.10.0067

White PJ, Broadley MR (2009) Biofortification of crops with seven mineral elements often lacking in human diets – iron, zinc, copper, calcium, magnesium, selenium, and iodine. New Phytol 182(1):49–84. https://doi.org/10.1111/j.1469-8137.2008.02738.x

Yadav CB, Srivastava RK, Beynon S, Englyst K, Gangashetty PI, Yadav RS (2022) Genetic variability and genomewide marker association studies for starch traits contributing to low glycaemic index in pearl millet. Food Energy Secur 11:e341. https://doi.org/10.1002/fes3.341

Yadav DN, Anand T, Kaur J, Singh AK (2012) Improved storage stability of pearl millet flour through microwave treatment. Agricultural Research 1(4):399–404. https://doi.org/10.1007/s40003-012-0040-8

Yang Z, Zhang H, Li X, Shen H, Gao J, Hou S, Zhang B, Mayes S, Bennett M, Ma J, Wu C, Sui Y, Han Y, Wang X (2020) A mini foxtail millet with an Arabidopsis-like life cycle as a C4 model system. Nat Plants 6(9):1167–1178

Zhang W, Zhi H, Tang S, Zhang H, Sui Y, Jia G, … Diao X (2021) Identification of no pollen 1 provides a candidate gene for heterosis utilization in foxtail millet (Setaria italica L.). Crop J 9(6):1309–1319. https://doi.org/10.1016/j.cj.2021.03.018

Zhao F-J, McGrath SP, Meharg AA (2010) Arsenic as a food chain contaminant: mechanisms of plant uptake and metabolism and mitigation strategies. Annu Rev Plant Biol 61(1):535–559. https://doi.org/10.1146/annurev-arplant-042809-112152