

Review

# Role of Genome Sequences of Major and Minor Millets in Strengthening Food and Nutritional Security for Future Generations

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**Abstract:** Millets are small-seeded cereals belonging to the family Poaceae. They are considered to be climate-resilient and future nutritional food cereals for humans. Millets are resistant to biotic and abiotic stressors compared to other major cereals and thrive in low-quality soils with little maintenance and less rainfall. The importance of millets is still not well known to many people due to the lack of popularity and cultivation in semi-arid tropics of Asia and Africa. The United Nations has declared 2023 as the International Year of Millets (IYM 2023) to promote millet cultivation and popularize their health benefits globally. A few years ago, the application of molecular biology was in its infancy in millets due to the unavailability of genome sequences. Genome sequences are available for most of the millets on NCBI and Phytozome databases. In this review, we discuss the details of genome sequences for millets, candidate genes identified from the native genome of millets. The current status of quantitative trait loci and genome-wide association studies in millets are also discussed. The utilization of millet genome sequences in functional genomics research and translating the information for crop improvement will help millet and non-millet cereals survive harsh environments in the future. Such efforts will help strengthen food security and reduce malnutrition worldwide in 2050.

**Keywords:** food security; genes; genome sequences; genome-wide association studies (GWASs); millets; quantitative trait loci (QTL)



**Citation:** Maharajan, T.; Krishna, T.P.A.; Krishnakumar, N.M.; Vetriventhan, M.; Kudapa, H.; Ceasar, S.A. Role of Genome Sequences of Major and Minor Millets in Strengthening Food and Nutritional Security for Future Generations.

*Agriculture* **2024**, *14*, 670.

<https://doi.org/10.3390/agriculture14050670>

Academic Editor: Rodomiro Ortiz

Received: 26 March 2024

Revised: 22 April 2024

Accepted: 22 April 2024

Published: 25 April 2024

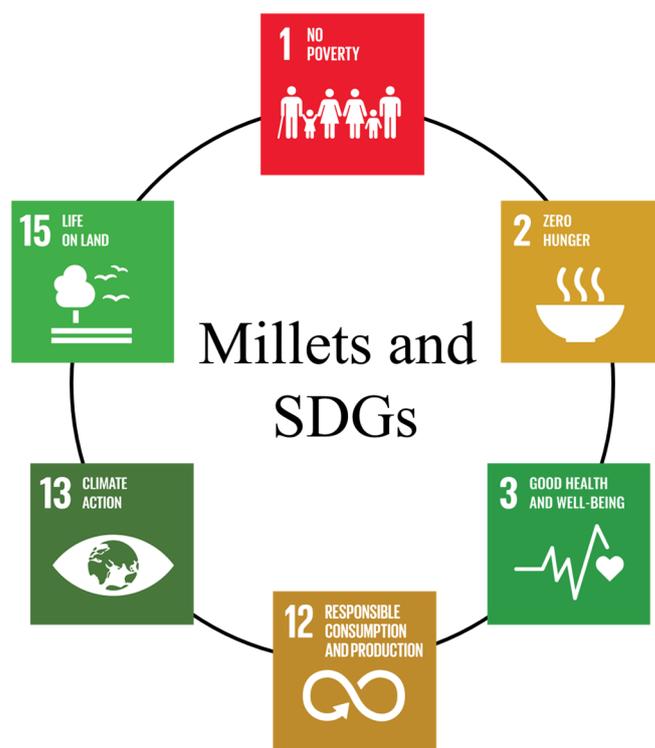


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## 1. Introduction

Millets are a group of small-seeded cereal crops grown largely on marginal dry lands or with limited access to irrigation. There are several millet species cultivated worldwide, such as sorghum (*Sorghum bicolor*), pearl millet (*Cenchrus americanus*), finger millet (*Eleusine coracana*), foxtail millet (*Setaria italica*), proso millet (*Panicum miliaceum*), little millet (*Panicum sumatrense*), kodo millet (*Paspalum scrobiculatum*), barnyard millet (*Echinochloa esculenta*), brown top millet (*Urochloa ramosa*), tef (*Eragrostis tef*), fonio millet (*Digitaria exilis*), job's tear (*Coix lacryma-jobi*), guinea millet (*Brachiaria deflexa*), raishan (*Digitaria cruciate*), etc. Millets are generally called gluten-free and are highly nutritious and contain higher protein, minerals, vitamins, and fiber compared to major cereal crops, rice (*Oryza sativa*), wheat (*Triticum aestivum*), and maize (*Zea mays*) [1]. Millets can grow with less water than most other major cereals and are well suited to drought-like conditions [2]. Millets' production traditionally does not depend on artificial fertilizers, and most are unaffected by storage

pests [3]. In addition, millets have natural biodiversity that makes them suitable for cultivation in various agro-climatic conditions [4]. They have a short lifecycle and can be grown between main cropping seasons and enrich the soil with their micronutrients [5]. The affordability of millets also makes it the “poor man’s food grain” [6]. The world is now looking at millets for their enormous potential. In addition to the cultivation advantages of millets, they are highly nutritious and climate-resilient. Because of this, mainstream society is beginning to understand and appreciate the long-term benefits of millets. Millets are a nutritional powerhouse, and they are now referred to as “Nutri-Cereals” [7]. They are rich in protein, fiber, key vitamins, and mineral sources. About 80% of millets have long been an important part of a nourishing diet [8]. Millets are high in fiber, which aids digestion and prevents constipation [9]. They are also gluten-free and suitable for celiac patients [10]. They contain antioxidants, which help to protect our cells from free radicals [11]. Calcium is necessary for bone health, blood vessel and muscular contractions, and proper nerve function. Finger millet contains more calcium (162–487 mg/100 g) than milk (124 mg/100 mL) and other cereals (10 mg/100 g of rice, 21.40/100 g of maize, 33 mg/100 g of wheat and 21.40 mg/100 g of sorghum), which supports boosting the calcium level in the human body [12]. The highest iron content (>11 mg/100 g) is found in pearl millet and has the potential to treat anemia [13]. It is also high in zinc (>3 mg/100 g) and folic acid, making it ideal for pregnant women [14]. Pearl millet contains twice (9–21 g/100 g) as much protein as milk (3.4 g/100 mL) [15]. Kodo millet has three times the fiber (10.2 g/100 mg) of wheat (2.5 gm/100 mg) and maize (2.0 g/100 g) and ten times the fiber of rice (1 gm/100 g) [1]. Hence, millets are considered the world’s next superfood. Millets have the potential to help achieve many sustainable development goals (SDGs) (Figure 1) [3].



**Figure 1.** Role of millets in achieving the United Nations Sustainable Development Goals.

Understanding the need to promote millets’ diversity, nutritional, and ecological benefits, the United Nations has declared the year 2023 as the International Year of Millets (IYM 2023), following a proposal by the Government of India. The main intention of the IYM 2023 is to increase millet production and consumption with four strategies to improve millets’ cultivation: (1) promoting sustainable production, (2) enhanced nutrition,

(3) wider acceptance, and (4) increased consumption. However, millets' research is still in its infancy with limited genomic resources. Some research laboratories have released draft/annotated genome sequences for some millets. In this review, we have discussed the availability of genome sequences for major (sorghum and pearl millet) and seven minor millets (finger millet, barnyard millet, foxtail millet, proso millet, teff, fonio, and job's tear) and the way forward to utilize millets' genome sequences and genomics resources for crop improvement. We have discussed genome-wide association studies (GWASs) in millets and summarized the identified candidate genes and the current status of millets' molecular breeding. Finally, the role of millet genome sequences to achieve food availability in 2050 is discussed. This review will raise awareness for millet researchers to utilize millets' genomes for their future experiments through various molecular tools. Identifying and characterizing more candidate genes from millets will help improve millet and non-millet cereals for biotic/abiotic stresses and nutritional traits.

## 2. Nutritional Profile and Health Benefits of Millets

Millets are nutritionally excellent because their grains are rich in proteins, minerals, flavonoids, polyphenols, and vitamins; therefore, they may offer multiple health benefits. About 80% of millet grains have long been an important part of the nutritious diet. Many research/review articles have already discussed the nutritional importance and health benefits of millets [16–18]. Millets are now considered “God's own cereal” due to their rich nutritional profile. Consuming millets in our daily diet raises the levels of proteins (especially adiponectin) that help protect against cardiovascular diseases [19]. Millets also contain a higher amount of vitamin B3/niacin, which helps lower certain risk factors of heart diseases such as high cholesterol and triglycerides and is effective in lowering oxidative stress [20]. Millet grains contain the lowest carbohydrate content compared to other cereals (especially rice) and so are highly recommended for people with type 2 diabetes [21]. Oxidative stress can cause various chronic diseases (neurodegenerative disorders, arthritis, and diabetes) [22]. A high-fat diet is also a risk factor for the development of dementia because it increases oxidative stress in the brain [23]. Millets are a good source of antioxidants, which can help support the body's ability to fight oxidative stress, a factor in illness and aging [24]. Hence, consuming millets could decrease the risk of chronic diseases [24]. Millets are rich in phytochemicals (polyphenols, lignans, phytosterols, phyto-oestrogens, phytocyanins) that help protect people from age-related degenerative diseases like diabetes, cancer, etc. [25]. Each millet has some unique nutritional properties that help improve human health. For example, a sufficient amount of calcium is essential for bone health, blood vessel and muscular contractions, and to ensure proper nerve function [12]. Finger millet has a higher calcium content than all other millets, cereals, and milk [17] and hence is one of the best grain sources to improve/maintain proper calcium levels in humans [26]. Proso millet contains high lecithin which supports the neural health system [27]. Kodo millet contains a high amount of potassium (>120 mg/100 g), which helps reduce abdominal cramps during the menstrual cycle [28,29]. Including pearl millet in our daily diet is an effective way to prevent iron deficiency anemia as its grains are rich in iron [13]. Overall, the consumption of millets reduces the risk of heart disease, protects from diabetes, improves the digestive system, lowers the risk of cancer, detoxifies the body, increases immunity in respiratory health, increases energy levels and improves muscular and neural systems, and is protective against several degenerative diseases.

## 3. Germplasm Resources of Millets

Germplasm resources are an essential strategic resource for continued progress in crop improvement for global food security and nutrition. Many millet researchers have already discussed the genetic resource of millets in various review articles [30,31]. The recent report on a global millets' conservation strategy indicates that more than 479,000 germplasms of sorghum and millets are conserved globally [32]. Millet germplasms are majorly conserved in Asian and African countries such as India, China, Japan, Kenya, Ethiopia, Uganda, and

Zambia. It is noteworthy that developed countries such as the US, Canada, France, Russia, and Italy also conserve millet germplasms [31]. The International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Hyderabad, Telangana, India, conserves the largest collection of millets (about 80,000 accessions of eight millets) which includes sorghum (42,869 accessions), pearl millet (25,537 accessions), finger millet (7513 accessions), foxtail millet (1542 accessions), barnyard millet (749 accessions), kodo millet (665 accessions), little millet (473 accessions), and proso millet (849 accessions) (<https://genebank.icrisat.org/>; accessed on 6 March 2024). The ICARI-National Bureau of Plant Genetic Resources Institute (ICAR-NBPGRI), New Delhi, India, conserves over 58,000 accessions of millet including sorghum (25,669), pearl millet (8699), finger millet (11,667), foxtail millet (4685), proso millet (1055), barnyard millet (2010), kodo millet (2404), little millet (2226), and brown top millet (44). (<http://genebank.nbpgri.ernet.in/SeedBank/Default.aspx>; accessed on 6 March 2024). The United States Department of Agriculture (USDA-ARS) gene bank conserved five millets' germplasms (such as 1452 finger millet, 1314 pearl millet, 300 kodo millet, 212 little millet, and 719 proso millet) (<https://www.ars.usda.gov/southeast-area/griffin-ga/pgrcu/>; accessed on 6 March 2024). Over the past 15 years, the conservation of millets' germplasm resources has become an important part of national and international research programs. However, the number of germplasms available for small millets particularly little millet, kodo millet, barnyard millet, brown top millet, and other minor millets is very low [31], because researchers have not yet prioritized those millets and most traditional genotypes have already disappeared due to the dominance of other cash crops. Hence, the collection and conservation of existing small millets are crucial before we lose them forever, which may help to support millets' improvement globally.

#### 4. Evolution of Millets

Millets are believed to be the oldest ancient domesticated crop. There is evidence that millets were cultivated in Asia and Africa over 5000 to 10,000 years ago [33]. Archaeobotanical evidence has proved that foxtail millet and proso millet were first domesticated in China ~10,500 calendar years before the present (cal. BP) [34]. Pearl millet has its origin in Africa, and the earliest evidence of its cultivation is reported from northeast Mali (4500 cal. BP) [35,36]. Kodo millet originated in India, and its domestication took place about 3000 years ago [28,37]. Little millet was domesticated in several sites across India around 6400 cal. BP [38]. Hence, millets are not new to the world; they have always been a part of our staple foods since ancient times. Due to the ability of millets to grow on marginal lands with low external inputs such as water, fertilizer, pesticides, etc., farmers are trying to revive its cultivation and bring it back to the market.

#### 5. Ploidy Level of Millets

The genome size, ploidy level, and chromosome number are of great importance for studying the evolution of millets and the development of the breeding program [39]. In addition, the knowledge of a plant's genome size and ploidy status can provide clues about the mechanisms responsible for decreases or increases in the genomic content along the evolutionary pathway [39]. The genome size and ploidy levels varied extensively among the millets. The ploidy level and chromosome number of each millet are provided in Table 1. Among the millets, pearl millet, kodo millet, and finger millet have the largest genome sizes. The genome size for little millet has not yet been estimated. Foxtail millet is a member of the subfamily Panicoideae and the tribe Paniceae, with chromosome numbers of  $2n = 2x = 18$  [40,41]. It is recognized as a diploid but is closely related to many tetraploid and higher ploidy level species. Finger millet is an allotetraploid ( $2n = 4x = 36$ ) that belongs to the Chloridoideae subfamily [42–44]. Barnyard millet is a hexaploid ( $2n = 6x = 54$ ), and it belongs to the subfamily Panicoideae [45]. Three millets such as proso millet, kodo millet, and little millet are tetraploid, and their chromosome range is 36–40 [46,47] (Table 1).

**Table 1.** Details on ploidy level and genome size of millets based on available reports.

Name of the Millets	Scientific Name	Chromosome Number	Genome Size (Mb)	Ploidy Level	Reference
Sorghum	<i>Sorghum bicolor</i>	2x = 2x = 20	730	Diploid	[48]
Pearl millet	<i>Cenchrus americanus</i>	2n = 2x = 14	~1700	Diploid	[49]
Finger millet	<i>Eleusine coracana</i>	2n = 4x = 36	1593	Allotetraploid	[42–44]
Foxtail millet	<i>Setaria italica</i>	2n = 2x = 18	~515	Diploid	[40,41]
Proso millet	<i>Panicum miliaceum</i>	2n = 4x = 36	~900	Tetraploid	[46]
Kodo millet	<i>Paspalum scrobiculatum</i>	2n = 4x = 40	~1900	Tetraploid	[47]
Little millet	<i>Panicum sumatrense</i>	2n = 4x = 36	Unknown	Tetraploid	[47,50]
Japanese Barnyard millet	<i>Echinochloa crus-galli</i>	2n = 6x = 54	~1270	Hexaploid	[45]
Teff	<i>Eragrostis tef</i>	2n = 4x = 40	672	Tetraploid	[51]
Fonio	<i>Digitaria exilis</i>	2n = 4x = 36	716	Tetraploid	[52]
Job's tears	<i>Coix lacryma-jobi</i>	2n = 20	1280	Diploid	[53,54]

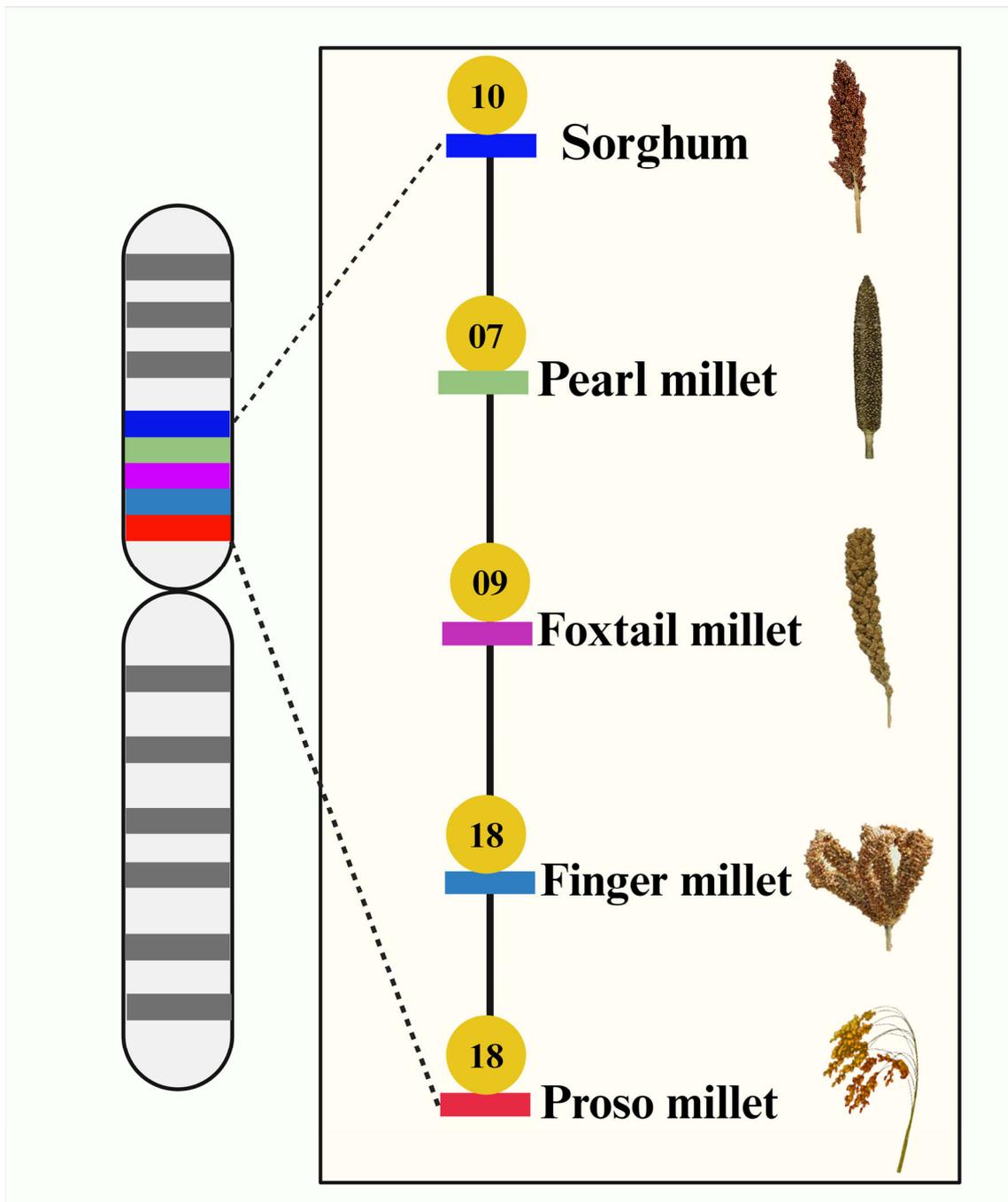
## 6. Genome Sequences of Millets

The field of millet genomics has grown rapidly in the past 10 years. Millet researchers have developed genome sequences for major and minor millets except two minor millets (little millet and kodo millet). Notably, five millet genome sequences were assembled at the chromosome level (Figure 2). In addition, the quality of sorghum, foxtail millet, and finger millet genome assemblies is much improved now compared to what it was a few years ago (<https://phytozome-next.jgi.doe.gov/>; accessed on 8 March 2024). The genomic resources of millets will enable millet researchers to identify candidate genes related to biotic/abiotic stresses and nutritional and other agronomically important traits and develop various DNA markers to conduct genetic mapping studies, which will increase millet production in the near future. In this section, we have listed out the availability of draft and annotated genomes of major and minor millets.

### 6.1. Major Millets

#### 6.1.1. Sorghum

The first sorghum genome was released in 2009 at the chromosome level using the BTx623 genotype [48]. The assembled genome size was ~730 Mb with 229 scaffolds and 10 chromosomes. From the genome, they have identified more than 70,000 simple sequence repeat (SSR) markers and >34,000 annotated genes. Likewise, around 35,490 genes were identified from the genome sequence of the Rio genotype (Table 2). A total of 21 genome assemblies are currently available at NCBI, and many high-quality improved annotated genome sequences are available at the Phytozome database. The current version 5.1 is available in the Phytozome database ([https://phytozome-next.jgi.doe.gov/info/Sbicolor\\_v5\\_1](https://phytozome-next.jgi.doe.gov/info/Sbicolor_v5_1); accessed on 8 March 2024). After releasing the genome sequences of sorghum, several studies related to GWASs, transcriptomes, functional genomics, and molecular breeding have been extensively conducted. Sorghum has entered an exciting and fruitful era due to the abundant availability of genetic, genomic, and breeding resources for millet researchers. Hence, the genomic resources of sorghum can serve as a reference genome for all other millet species.



**Figure 2.** Genome assembly of millets at chromosome level. Sorghum, pearl millet, finger millet, foxtail millet, and proso millet genomes were assembled at chromosome level. Number of chromosomes in assembled genomes is indicated by golden circle for each millet.

**Table 2.** Summary of available millet genome assemblies.

Name of the Millet	Genotype Name	Sequenced Genome Size	Number of Scaffolds	Scaffold N50 (Mb)	Number of Genes Identified	Bio-Sample ID	Gen-Bank Assembly Accession
Sorghum	BTx623	~730 Mb *	867	68.7	34,118	SAMN02953738	GCA_000003195
	Hongyingzi	724.4 Mb *	10	70.9	-	SAMN38071627	GCA_033546955
	Huandiaonuo	726.9 Mb *	10	70.7	-	SAMN38071628	GCA_033546955
	Rio	729.4 Mb *	3830	0.39	35,490	SAMN05444726	GCA_015952705
	TX2783	721.4 Mb #	13	66.1	-	SAMEA6819231	GCA_903166285
	TX436	722.1 Mb #	13	68.1	-	SAMEA6819238	GCA_903166325
	Leoti	687.3 Mb #	10	68	-	SAMEA111279259	GCA_947241725
	Rio	817.2 Mb #	622	76.7	-	SAMEA111279266	GCA_947241735
	Tx430	666.2 Mb #	308	32.2	-	SAMN09228096	GCA_003482435
	Chinese Amber	789.4 Mb #	588	78.7	-	SAMEA111279257	GCA_947241645
	655,972	792.7 Mb #	835	73.8	-	SAMEA111279265	GCA_947241635
	506,069	795.5 Mb #	957	75.3	-	SAMEA111279263	GCA_947241665
	297,155	767.9 Mb #	826	74.9	-	SAMEA111279261	GCA_947241675
	229,841	757.5 Mb #	923	72.6	-	SAMEA111279260	GCA_947241625
	329,311	789.8 Mb #	1761	74.8	-	SAMEA111279262	GCA_947241655
	Grassl	717.4 Mb #	648	70.2	-	SAMEA111279258	GCA_947241715
	BTx623	374.3 Mb #	2657	0.2	-	SAMN12341013	GCA_008000285
510757	768.2 Mb #	1800	74.3	-	SAMEA111279264	GCA_947241685	
Pearl millet	Tift 23D2B1-P1-P5	1.8 Gb *	52,033	240.6	40,658	SAMN04124419	GCA_002174835
	Tift 23D2B1-P1-P5	1.8 Gb *	7	259.2	-	SAMEA112192700	GCA_947561735
	PI537069	1.9 Gb *	98	266.8	-	SAMN20372178	GCA_020739565
	PI526529	2 Gb *	839	287	-	SAMN20372180	GCA_020739535
	Tifleaf 3	2 Gb *	69	279.2	-	SAMN20372183	GCA_020739585
	PI343841	2 Gb *	912	263.7	-	SAMN28616536	GCA_027745475
	PI521612	1.9 Gb *	331	278.5	-	SAMN20372179	GCA_020739525
	PI587025	1.9 Gb *	4064	257.5	-	SAMN20372182	GCA_021560375.1
	PI186338	2 Gb *	139	284.6	-	SAMN28616529	GCA_027789755
PI583800	1.9 Gb *	138	261.4	-	SAMN20372181	GCA_020739575	
Foxtail millet	Yugu1	405.7 Mb *	327	47.3	>34,584	SAMN02981383	GCA_000263155
	Zhang gu	~423 Mb *	2689	1.0	>38,801	SAMN04534922	GCA_001652605
Finger millet	KNE 796-S	1.12 Gb *	1058	12.1	73,012	SAMN35346668	GCA_032690845
	PR202	1.5 Gb #	1196	23.9	62,348	SAMD00076255	GCA_021604985
	ML365	1.19 Gb #	525,759	23.7	85,243	SAMN04849255	GCA_002180455

Table 2. Cont.

Name of the Millet	Genotype Name	Sequenced Genome Size	Number of Scaffolds	Scaffold N50 (Mb)	Number of Genes Identified	Bio-Sample ID	Gen-Bank Assembly Accession
Proso millet	Pm_0390	923 Mb *	1305	46.7	61,631	SAMN08389585	GCA_003046395
	jinshu7	862 Mb *			-	SAMN30451036	GCA_026771285
	BC332	856.2 Mb *	580	48.5	-	SAMN13925972	GCA_032594955
	BC475	870.7 Mb *	843	48.1	-	SAMN13926115	GCA_032595135
	Longmi4	846 Mb *	441	48.2	-	SAMN08335224	GCA_002895445
	BC477	877.2 Mb *	1031	48.2	-	SAMN13926117	GCA_032595115
	BC494	863.2 Mb *	722	48.1	-	SAMN13926134	GCA_032595125
	BC404	870.4 Mb *	813	48.1	-	SAMN13926044	GCA_032595235
	BC498	869.9 Mb *	753	48.2	-	SAMN13926138	GCA_032595105
	BC328	867.1 Mb *	799	48.2	-	SAMN13925968	GCA_032595055
	BC27	907.3 Mb *	1520	45	-	SAMN13925667	GCA_032594635
	BC426	882.1 Mb *	1166	48.3	-	SAMN13926066	GCA_032595225
	BC398	896.4 Mb *	1451	48.1	-	SAMN13926038	GCA_032595255
	BC382	861 Mb *	799	48.4	-	SAMN13926022	GCA_032594965
	BC418	867.8 Mb *	874	48.2	-	SAMN13926058	GCA_032595215
	BC407	874.9 Mb *	1052	48.2	-	SAMN13926047	GCA_032595245
	BC434	872.2 Mb *	994	48.5	-	SAMN13926074	GCA_032595155
	BC362	870 Mb *	1068	48	-	SAMN13926002	GCA_032594995
	BC311	890.6 Mb *	1408	48.1	-	SAMN13925951	GCA_032594875
	BC264	892.1 Mb *	1166	48.4	-	SAMN13925904	GCA_032594675
	BC350	867.7 Mb *	945	48.1	-	SAMN13925990	GCA_032594985
	BC360	860.2 Mb *	594	48.2	-	SAMN13926000	GCA_032594975
	BC292	891 Mb *	1075	48.3	-	SAMN13925932	GCA_032594685
	BC315	891.8 Mb *	1343	48.4	-	SAMN13925955	GCA_032594835
	BC310	872.1 Mb *	970	48.1	-	SAMN13925950	GCA_032594855
	BC136	867.8 Mb *	889	48.1	-	SAMN13925776	GCA_032594655
	BC235	871.9 Mb *	934	48.2	-	SAMN13925875	GCA_032594705
	BC217	872.5 Mb *	1137	49.3	-	SAMN13925857	GCA_032594775
	BC170	875.8 Mb *	929	48.1	-	SAMN13925810	GCA_032594555
	BC48	878.1 Mb *	1260	48.2	-	SAMN13925688	GCA_032594585
	BC188	861.7 Mb *	752	47.9	-	SAMN13925828	GCA_032594795
	BC204	871 Mb *	935	49.2	-	SAMN13925844	GCA_032594715
BC244	890.4 Mb *	1443	47.8	-	SAMN13925884	GCA_032594695	
BC100	864.3 Mb *	883	47.8	-	SAMN13925740	GCA_032594575	
BC40	860.4 Mb *	846	48.6	-	SAMN13925680	GCA_032594595	
Barnyard Grass	STB08	1.27 Gb #	19,699	1.8	108,771	SAMN03246123	GCA_025118225
	-	1.5 Gb #	4534	1.8	-	SAMEA104207156	GCA_900205405

\* Assembly at chromosome level; # assembly at scaffold level.

### 6.1.2. Pearl Millet

Pearl millet is a cross-pollinated crop with a genome size of ~1.7 Gb. Its genome was partially assembled and published in 2017 using the inbred Tift 23D2B1-P1-P5 genotype of pearl millet [49]. They used whole-genome shotgun and bacterial artificial chromosome (BAC) sequencing techniques to assemble the genome for the Tift 23D2B1-P1-P5 genotype. After stringent filtering and correction steps, 1.49 Tb of sequence data was assembled into 1.58 Gb of contigs and 1.82 Gb of scaffolds. Finally, they generated a genome sequence around 1.76 Gb for the Tift 23D2B1-P1-P5 genotype, indicating that ~90% of the pearl millet genome was assembled. A total of 1.22 Gb repeat elements was predicted from the Tift 23D2B1-P1-P5 genome assembly which indicates that 77.2% of the assembled genome is repetitive. From the genome, a total of 27,893 genes were annotated, and 10,686 genes were unannotated. They also identified transfer RNA (tRNA) (909), ribosomal RNA (rRNA) (235), messenger RNA (mRNA) (183), and small nuclear RNA (snRNA) (752) genes from the genome. Apart from this, 88,256 SSRs were also identified in the pearl millet genome using a microsatellite program, which can be used for future genetics and breeding applications. Based on their resequencing data, they also predicted 29,542,173 single-nucleotide polymorphisms (SNPs) by PMiGAP lines. Among these, 450,000 high-quality SNPs were identified based on principal component analysis which would be helpful for advancing molecular breeding studies on pearl millet. Apart from this genome assembly, a total of nine partial genome assemblies were developed by Sichuan Agricultural University using various cultivars (Table 2). They also generated a partial genome assembly for pearl millet at the chromosome level, and the generated genome size is between 1.9 and 2.0 Gb. There is no doubt the available draft genome of pearl millet will provide a resource for the millet research community to understand trait variation and accelerate the genetic improvement of pearl millet.

## 6.2. Minor Millets

### 6.2.1. Foxtail Millet

Among the minor millets, the genome sequence was first released for foxtail millet. It is a diploid cereal with a comparatively smaller genome (~515 Mb) than other minor millets. Two institutes (US Department of Energy Joint Genome Institute, Berkeley, CA, USA and Beijing Genomics Institute, Beijing, China) have released completely annotated genome sequences for two different foxtail millet cultivars [40,41]. Zhang et al. (2012) developed a draft genome (~423 Mb) for the Zhang gu genotype of foxtail millet [41]. The scaffold N50 was 1.0 Mb, and 90% of the scaffolds were 380 Mb. They predicted 542,322 SNPs from the annotated genome of foxtail millet. The Zhang gu genome comprised >46% of transposable elements (both retroelements and DNA transposons), indicating that the genome contains many repetitive genes. They identified 38,801 genes by integrated annotation pipeline methods, and the average length of annotated genes was 2522 bp. In addition, they also identified 1367 pseudogenes in the genome. Several noncoding RNA genes were also detected from the Zhang gu genome assembly. The second high-quality reference genome sequence for foxtail millet was generated for the Yugu1 cultivar [40]. The Yugu1 assembly contains 405.7 Mb of the sequence in nine chromosomes and an additional 4.2 Mb in 327 scaffolds that are unanchored by the genetic map, with an estimated genome coverage of ~80%. Like the Zhang gu genome, the Yugu1 genome also composed of 40% of transposable elements. The Yugu1 genome contained 24,000 to 29,000 protein-encoding genes. Genome sequences for both cultivars are available in the NCBI database (Table 2). Apart from this, a completely annotated genome sequence of foxtail millet (version 2.2) is also currently available at the Phytozome database. The version 2.2 assemblies were constructed by Program to Assemble Spliced Alignments (PASA) from ~1.28 million foxtail millet expressed sequence tag (EST) reads sequenced at the Joint Genome Institute (JGI) against the 8.3X. Each locus of the current version of the foxtail millet genome was determined by BLASTX alignments of proteins from sorghum, rice, *Arabidopsis thaliana*, and grapevine (*Vitis vinifera*) genomes. Homology-based predictors FGENESH+ and GenomeS-

can were used to predict models of each gene. Therefore, foxtail millet could serve as an ideal surrogate genome for the future research and development of switchgrass and related biofuel crops.

### 6.2.2. Finger Millet

Two draft assemblies and one completely annotated genome assembly are currently available for finger millet. In 2017, the first draft genome assembly was released for an Indian cultivar (ML-365) using Illumina and sequencing by oligonucleotide ligation and detection (SOLiD) sequencing technologies [42]. Around 45 Gb of paired-end and 21 Gb of mate-pair data by Illumina and SOLiD sequencing technologies were generated and further used to assemble the ML-365 genome, followed by gap closure which gave a consensus genome size of 1196 Mb, representing 82.31% of the estimated finger millet genome. About 85,243 genes (78,647 non-transposable elements related and 6596 transposable elements related genes) were predicted based on the de novo method of gene prediction using Augustus. Of the 85,243 genes, 52,541 genes contained the Pfam domain, and these genes were distributed in 3254 gene families. Also, most of the identified genes were involved in ATP binding activities and zinc ion and nucleic acid binding. Furthermore, 2866 drought-responsive genes, 1766 disease-resistance genes, 330 calcium transport and accumulation-related genes, and 146 C4 photosynthetic pathways were captured in the genome. Apart from this, a total of 114,083 SSRs were detected from which di- (66,805), tri- (40,578), tetra- (2179), penta- (3010), and hexa- (1511) repeats were identified. The identified SSR markers from this genome assembly can be further used in diverse studies, linkage map construction, association mapping, the quantitative trait loci (QTL) mapping of agronomically important traits, and marker-assisted breeding programs. This is the first breakthrough report on the finger millet genome. In the next year, Hatakeyama et al. (2018) generated draft genome sequences for another Indian cultivar (PR-202) using Illumina MiSeq [43]. They estimated a genome around 1.5 Gb by the flow cytometry method. The total number of scaffolds was 1897 with an N50 length > 2.6 Mb. The N50 of PR-202 was higher than ML-365 which may allow for an RNAseq analysis of each homeolog separately and resequencing analyses. Overall, 62,348 genes were predicted from the PR-202 genome assembly. Among these, 57,066 genes were annotated and submitted to NCBI. In addition, a total of 1440 universal single-copy genes were identified. Of these, 606 genes were found to be single-copy genes, and 783 genes were duplicate genes.

The complete annotated genome sequence (version 1.0 assembly) was recently generated by Prof. Devos' group of University of Georgia, USA for the Kenyan finger millet cultivar (KNE 796) using mapping, error correction, and a de novo assembly tool (MECAT) assembler [44]. The assembled size of the KNE 796 genome is 1129.7 Mb. Overall, the assembled KNE 796 genome comprised 1058 scaffolds, with a contig N50 of 12.1 Mb, and the average length of scaffolds was 2275 bp. The assembled genome contained 18 chromosomes and 1.11 billion bases (Gb). About 48,836 high-confidence and 24,176 low-confidence genes were distributed across the annotated finger millet genome. The annotated genome is a great opening to identify and validate the genes and understand the genetic basis of finger millet. The annotated genome will help mine and characterize calcium and other nutrients' transporter and regulatory genes for further research (for example, identifying genes involved in grain nutrient filling). The development of finger millet against blast and other diseases by conventional breeding methods is hampered by limited genetic variability. Hence, generating blast disease-resistant finger millet using antifungal protein-encoding genes would be useful. The annotated genome sequence of finger millet could pave the way to identify genes associated with blast and other diseases. Undoubtedly, the annotated genome sequence of finger millet will be a great resource to accelerate food security and nutrient fortification in less developed countries of Asia and Africa.

### 6.2.3. Proso Millet

The normal genome size of proso millet is ~900 Mb. It is an allotetraploid cereal with a chromosome number of  $2n = 4x = 36$ . A total of 35 draft genome assemblies for proso millet have been developed and submitted to NCBI (Table 2). Of these, 34 partial genome assemblies were developed by the Chinese Academy of Sciences, and the single genome assembly was developed by Shanghai Center for Plant Stress Biology. Interestingly, all the partial genome sequences were assembled at the chromosome level (Table 2). Unfortunately, no candidate genes and markers were predicted for 34 genome assemblies developed by the Chinese Academy of Sciences. However, the partial genome assembly developed by Shanghai Center for Plant Stress Biology predicted many candidate genes and markers from their genome [46]. The assembled partial genome of the Pm\_0390 genotype was 923 Mb. They predicted 221,787 SNPs and 112,158 SSR markers from the Pm\_0390 genotype's partial genome. All the identified markers were composed of di- and tri-nucleotide motifs with an average length of ~22 bp. This resource can serve for developing SSR- and SNP-based genetic markers for proso millet. They also predicted 55,930 protein-coding genes, 339 micro RNAs (miRNAs), 1420 tRNAs, 1640 rRNAs, and 2302 snRNAs from the genome. Compared to the other millets, proso millet has a higher number of partial genome assemblies. All currently available partial genome sequences are valuable resources for small millet breeders and will provide a foundation for studying the exceptional stress tolerance.

### 6.2.4. Barnyard Millet

A species-specific genome sequence for barnyard millet has yet to be developed; however, the partial genome has been developed for barnyard grass related to barnyard millet. The draft genome for barnyard grass was developed by Zhejiang University, China [45]. They developed two partial genome sequences for barnyard grass at the scaffold level. Around 108,771 protein-coding genes were predicted from the partial genome. In addition to protein-coding genes, 785 miRNAs, 2306 tRNAs, 1890 rRNAs, and 3378 snRNAs were identified in the barnyard grass genome. They predicted several gene families associated with detoxification such as cytochrome P450 monooxygenase genes (917), glutathione S-transferase genes (277), and many differentially expressed genes (4945) from the draft genome of barnyard grass. Apart from this, 4945 differentially expressed genes (2534 up-regulated and 2411 down-regulated) were identified. Two partial genome assemblies are currently available for barnyard grass at NCBI (Table 2). This genome sequence provides new insights into the adaptive molecular mechanisms for barnyard millet survival.

### 6.2.5. Other Minor Millets

Genome sequences are now available for some other minor millets. For example, the draft genome sequence for *tef* was released in 2014 by the University of Bern, Switzerland [51]. The draft genome of *tef* is currently available at the NCBI (Accession: GCA\_000970635.1) and Ensembl Plants ([https://plants.ensembl.org/Eragrostis\\_tef/Info/Index](https://plants.ensembl.org/Eragrostis_tef/Info/Index); accessed on 8 March 2024) databases. The estimated draft genome of *tef* is about 672 Mb, which clearly indicates that the *tef* genome is almost 87% sequenced. A total of 49,600 SSR markers and 38,000 transcripts were found in the draft genome of *tef*. The draft genome sequence of *tef* is more reliable for developing molecular markers and identifying candidate genes related to abiotic stress tolerance. In addition, the *tef* draft genome will pave the way for conducting GWASs and GBS for *tef* improvement.

The genomic resources for fonio millet were released in 2020 at the chromosome level using the CM05836 cultivar [52]. From the fonio genome, they predicted 59,844 protein-coding genes with an average length of 2.5 kb. In addition, they also identified 11,046,501 high-quality SNPs, and they were all evenly distributed across the 18 chromosomes. In the same study, two genes, such as *grain size 5 (GS5)* and *shattering 1 (Sh1)*, were identified to play an important role in regulating the grain size of fonio and conserving the seed shattering of fonio, respectively. The draft genome of job's tear was developed for the Korean cultivar (Johyun) by de novo assembly [53,54]. Around 3362 scaffolds were generated, with a total

length of 1.28 Gb [53]. A total of 3988 differentially expressed genes (1470 up-regulated and 2518 down-regulated) related to seeds and other tissues were identified in the draft genome of job's tear. In addition, a total of 317 transcription factors (including basic region/leucine zipper motif (bZIP), MYB, NAC, basic helix–loop–helix (bHLH), and ethylene response factor (ERF)) were identified as related to seed development. All identified genes and transcription factors will support the development of high-quality seeds of job's tear and other millets through molecular breeding and other biotechnological approaches. Apart from this, 76 genes (including 57 *cupin* superfamily genes, 18 *coixin* genes, and one *glutelin* gene) associated with seed storage proteins and 13 genes involved in the biosynthesis of benzoxazinoids were also identified from the job's draft genome. The chloroplast genome sequence is now available for little millet [50]. The developed chloroplast genome sequence length was 139,384 bp, and the genome contained 91 protein-coding genes, 4 rRNA genes, and 30 tRNA genes. This chloroplast genome of little millet may provide valuable information for this cereal, which will help to initiate further molecular experiments for improving this crop. The sequencing of millet genomes made it possible to assess intraspecific polymorphism, identify key genes influencing the formation of significant features, and develop molecular markers of economically valuable traits, and this has become the basis for the genomics-assisted breeding for crop improvement. An adequate review of the molecular breeding and functional genomics of sorghum has already been published. Hence, hereafter, this review only focusses on discussing molecular breeding and functional genomics for pearl millet and other minor millets only.

## 7. Pan-Genomic and Telomere-to-Telomere Genome Resources of Major and Minor Millets

The available genomic resources for millets have been developed from a single germplasm line/genotype of millets, which provides genetic information on a single genotype. Pan-genome studies will enable the simultaneous generation of genome resources for different cultivars, landraces, and wild species [55]. This will allow researchers to search for novel genes and alleles that may have been inadvertently lost in domesticated crops during the historical process of crop breeding or extensive plant breeding. Pan-genomic resources are currently available for two major (sorghum and pearl millet) and two minor (foxtail millet and proso millet) millets. A pan-genome analysis of 13 genetically diverse genotypes of sorghum revealed extensive hidden genomic variations between cultivated and wild species [56]. For example, a pan-genome was generated for 13 genotypes of sorghum to explore the genetic variations between the cultivated and wild species. The developed pan-genome consists of core genes (58.8%), shell genes (37.9%), private genes (3.3%), and cloud genes (0.4%). Among these, core genes are found to be involved in RNA processing, reproductive system development, leaf development, seed development, cell differentiation, and chloroplast organization in sorghum [56]. They also identified 19,359 and 147,899 presence and absence variants, respectively, associated with sorghum domestications and grain color variation. In another study, the pan-genome of 176 genotypes of sorghum identified 18,898 variable genes associated with various stresses, 1788 drought-responsive genes, and 2.0 million SNPs [57]. Similarly, a pan-genome assembly of eleven pearl millet genotypes identified structural variations in endoplasmic reticulum-related genes associated with heat stress [58]. A total of 39,143 gene families, including 46.60–52.08% of core genes, 39.75–49.94% of dispensable genes, and 0.73–8.73% of private genes, were obtained from the developed pan-genome of pearl millet. Additionally, 744,364 structural variations associated with heat-related genes were identified, including 306,679 presence variations, 315,905 absence variations, 2177 inversions, 91,852 copy number variations, and 27,751 translocations [58]. In minor millets, a pan-genome sequence has been generated for foxtail millet using 110 genotypes (35 wild, 40 landraces, and 35 modern cultivated) [59]. The developed pan-genome of foxtail millet contains 73,528 gene families, of which 23.8%, 42.9%, 29.4%, and 3.9% are core, softcore, dispensable, and individual genes, respectively. In addition, 14,283 gene families involved in RNA capping, light response, and specific metabolic processes were identified from the pan-genome of foxtail millet [59]. It is interesting to note that these gene families are not already present in the available Yugu1 refer-

ence genome. In the same study, approximately 202,884 non-redundant structural variations (107,151 insertions, 76,915 deletions, 18,455 translocations, and 363 inversions) and 158,906 presence and absence variations associated with foxtail millet domestication and improvement were detected in the pan-genome of foxtail millet. Thirty-two proso millet high-quality pan-genomes contained 27,727 core, 8288 softcore, 24,494 dispensable, and 5533 private gene families [60]. From the developed pan-genome assemblies, 207,033 structural variations and 50,515 presence or absence variants (26,195 deletions and 24,320 insertions) related to 43 domestications and 31 agronomic traits of proso millet were identified. The developed millet pan-genome represents an important resource for millet improvement and gene discovery. Novel genes identified in the pan-genomes of millets can be reintroduced into high-yielding millets by implementing traditional plant breeding, genetic selection, and transgenic approaches. Apart from the pan-genome, the telomere-to-telomere genome has been developed for HYZ-T2T genotypes of sorghum to identify structural genes, transcription factors, and transporters involved in the biosynthetic pathways of tannins in sorghum [61]. These millet pan-genomic resources will be useful for achieving the SDGs in developing countries by accelerating the genetic gain in arid and semi-arid ecologies.

### 8. QTL Associated with Various Traits in Major and Minor Millets

In general, molecular markers help to identify QTL associated with several traits in plants. In millets, several QTL related to various agro-morphological, biochemical, and yield-related traits were identified. Several SSR, SNP, and Diversity Arrays Technology (DArT) markers were widely used to identify QTL in millets. Blast diseases cause severe yield constraints of millets in many millet-producing regions. Three QTL associated with leaf blast disease were identified in 305 recombinant inbred lines (RILs) of foxtail millet using more than 30K SSR markers [62]. Rust disease caused by the fungus (*Puccinia substriata*) is one of the most important yield constraints of pearl millet worldwide, leading to grain yield losses of up to 76% and major losses in fodder yield and quality [63]. A total of 256 DArT and 70 SSR markers were used for the identification of a novel QTL for pearl millet rust disease using 168 RILs [63]. Like rust disease, downy mildew caused by *Sclerospora graminicola* is the most destructive disease of pearl millet [64]. A total of five QTL associated with resistance to pearl millet downy mildew disease were identified in 187 RILs using 88 SSR markers [65]. The identification of disease resistance QTL will be useful in cultivar development and the study of the genetic control of disease resistance in millets. Compared to the other millets, the contents of iron and zinc are higher in pearl millet. More than 18 QTL associated with pearl millet grain iron and zinc content were identified using SSR and DArT markers [66,67]. After further validation of these QTL, they can be used for the development of high grain iron and zinc pearl millet through marker-assisted breeding programs. Soil nutrient deficiency is one of the abiotic constraints on millet production and yield. Compared to other major cereals, QTL associated with improving nutrients' use and acquisition efficiencies have not been identified much in millets. Recently, more than 50 QTL associated with various agro-morphological, phosphorus contents in shoot and roots and biomass traits were identified in 100 RILs of finger millet using 101 SSR markers under low- and high-phosphate conditions [68]. The same group also identified eight QTL for root- and shoot-related traits under the same low- and high-phosphate conditions using 87 SSR markers in finger millet through association mapping [69]. Apart from this, 11 QTL related to shoot-, root-, and biochemical-related traits were identified in finger millet grown under drought stress [70]. Many QTL for various agro-morphological, yield, biomass, growth, and other related traits were detected in finger millet, pearl millet, foxtail millet, and proso millet by various researchers (Table 3). All the identified QTL set a foundation for fine mapping, the identification of candidate genes, the elaboration of molecular mechanisms, and use in millet breeding programs through marker-assisted selection. No QTL have been identified yet in millet under salinity, cold, heat, or other abiotic stress conditions. The availability of the genomic sequence of millets would accelerate the development of markers to assist genotypic classification and breeding practices. Previously, researchers used EST array molecular markers for the identification of QTL in many millets. These are low-throughput molecular markers that limit the efficiency and accuracy of QTL mapping. Also, it is very expensive and time-consuming. The genome sequence of millets

will allow millet researchers to rapidly identify millions of markers (SSR, SNP, EST-SSR, DArT, etc.), which will enable the generation of large-scale genotypic data for linkage mapping analysis. Apart from this, using molecular markers developed from genome sequences to detect QTL will increase the efficiency and accuracy of QTL which can definitely be used for the millet breeding program. The genome sequence will also allow for the identification of candidate genes associated with QTL and is useful for conducting gene expression and functional characterization studies.

**Table 3.** Summary of QTL associated with various traits in major and minor millets.

Name of the Millets	Number of RILs	Number and Types of Markers Used	Number of QTL Identified	Targeting Traits	References
Pearl millet	106	95 SSR, 2 STS, and 208 DArT	44	FT, PH, PL, and GW	[71]
	168	256 DArT and 70 SSR	1	Rust disease	[63]
	317	235 DArT and 33 SSR	23	FL, PH, PL, and TGW	[72]
	188	96 SSCP-SNP, 96 SSR, 96 EST-SSR, and 43 STS	18	PL, PD, and GS	[73]
	187	88 SSR	5	Downy mildew disease	[65]
	317	258 DArT and 63 SSR	19	Grain iron and zinc content	[66]
	210	372 SSR	22	Grain iron and zinc content	[67]
	149	95 RFLP, SSR, TRAP, and EST-SSR	24	Dry stover yield and GY	[74]
	172	26 SSR and 20 RFLP	24	Downy mildew disease	[75]
Foxtail millet		50 RFLP and 29 SSR	3	GY	[76]
	305	35,065 SNP	3	Leaf blast	[62]
	164	1047 SNP	47	SW, PW, GW, and TGW	[77]
	333	3744 SNP	26	PH	[78]
	543	48,790 SNP	57	PH, PL, PD, PNL, FID, SID, PW, GW, and TGW	[79]
	215	20,748 SNP	39	Hull color traits	[80]
	439	33,579 SNP	59	HD, PL, TN, PW, PD, FLL, FLD, PH, SD, SNN, code number, CGN, TGW, and NL	[81]
	164	2297 bin and 74 SSR	221	SL, SD, SNN, PDL, TN, FLL, FLW, PL, PD, SDY, GN, bristle length, SW, PW, GW, and TGW	[82]
	124	9968 SNP	11	PH, PDL, PD, FID, SID, and TID	[83]
400	43,001 SNP	5	Anther and hull color	[84]	
Finger millet	100	101 SSR	92	SDW, RDW, ShL, RHL, RHD, and SPC and RPC	[68]
	-	87 SSR	15	Leaf blast, PH, TN, NPT, NF, RL, and GY	[85]
	-	87 SSR	8	RDW, SDW, and RL	[69]
	-	87 SSR	11	RL, RDW, and biochemical traits	[70]
	151	5422 SNP	8	DF, PH, PN, LBS, and PBI	[86]
190	46 SSR	2	DF, FLW, and PH	[87]	
Proso millet	93	833 SNP	18	HD, PH, PDL, lodging, PL, grain shattering, TGW, and GPP	[88]

Abbreviations: CGN, Code Grain Number; Dart, Diversity Arrays Technology; DF, Days to 50% Flowering; EST-SSR, Expressed Sequence Tag-Derived Simple Sequence Repeat; FID, First Internode Diameter; FLL, Flag Leaf Length; FLW, Flag Leaf Width; FT, Flowering Time; GN, Grain Number; GPP, Grains Per Panicle; GS, Grain Size; GW, Grain Weight; GY, Grain Yield; HD, Heading Date; LBS, Leaf Blast Severity; NF, Number of Fingers; NL, Neck Length; NPT, Number of Productive Tillers; PBI, Panicle Blast Incidence; PD, Panicle Diameter; PDL, Peduncle Length; PH, Plant Height; PL, Panicle Length; PN, Panicle Number; PNL, Panicle Neck Length; PW, Panicle Weight; RDW, Root Dry Weight; RFLP, Restriction Fragment Length Polymorphism; RHD, Root Hair Density; RHL, Root Hair Length; RIL, Recombinant Inbred Line; RL, Root Length; RPC, Root Phosphorus Content; SD, Stem Diameter; SDW, Shoot Dry Weight; SDY, Spikelet Density; ShL, Shoot Length; SID, Second Internode Diameter; SL, Stem Length; SNN, Stem Node Number; SNP, Single-Nucleotide Polymorphism; SPC, Shoot Phosphorus Content; SSR, Simple Sequence Repeat; STS, Sequence-Tagged Site; SW, Straw Weight; TGW, Thousand Grain Weight; TID, Third Internode Diameter; TN, Tiller Number; and TRAP, Target Region Amplified Polymorphism.

## 9. Genome-Wide Association Studies (GWASs) in Millets

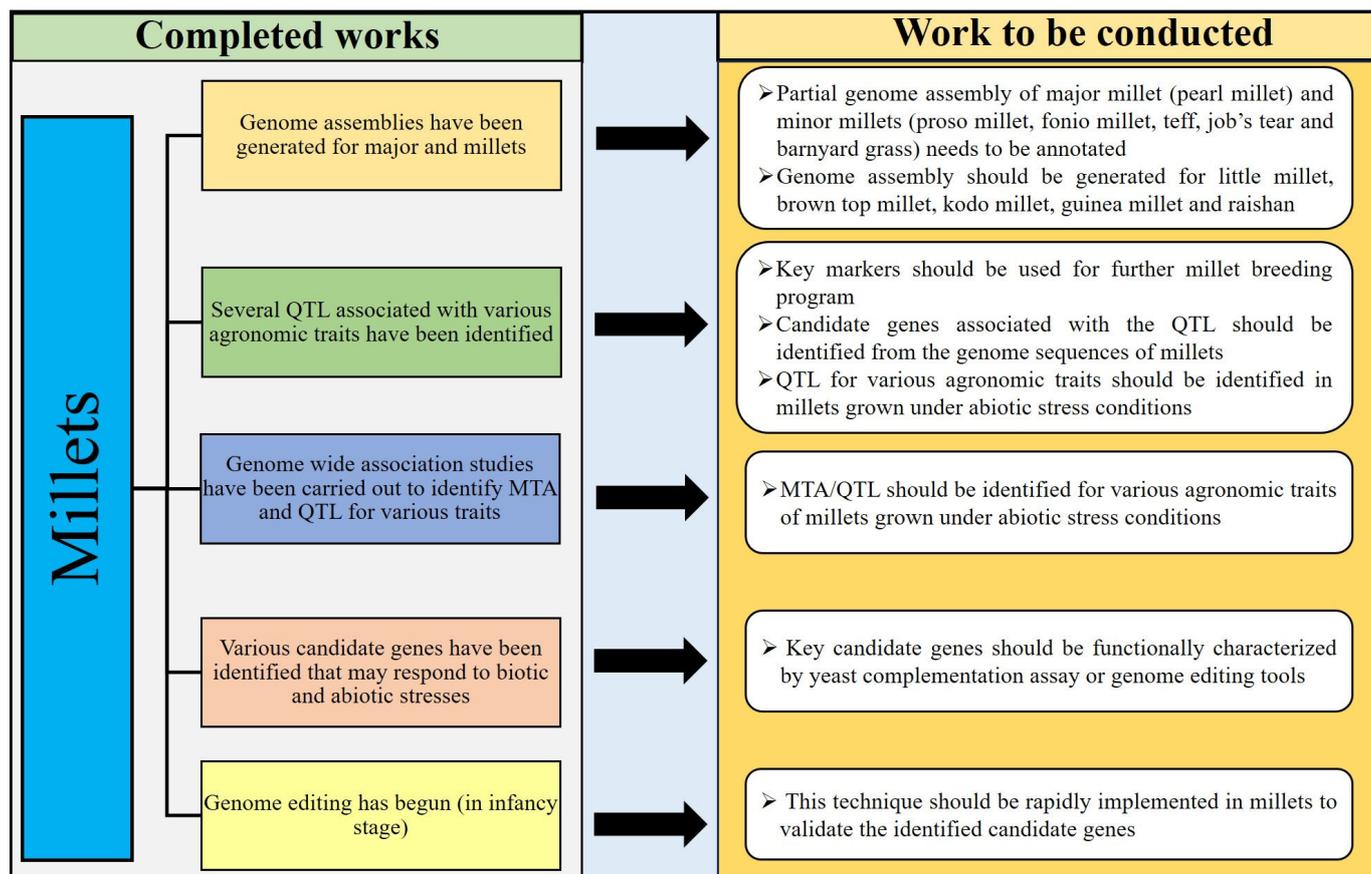
QTL mapping based on linkage analysis provides high power to detect QTL for a trait of interest. It has a very low mapping resolution because of the few recombination events that it takes into consideration which would ultimately lead to long linkage blocks. High-throughput genotyping technologies such as genotyping-by-sequencing (GBS) and genome-wide association studies (GWASs) help to generate high-quality genome-wide genetic markers, which enable the detection of marker–trait associations (MTAs) or QTL for crop improvement. A total of 706,646 SNP markers were developed from 407 foxtail millet genotypes by GWASs [89], and the developed SNP markers were used to identify 87 QTL associated with various panicle-related traits in foxtail millet (Table 4). GWASs were also used to identify 81 MTAs for several agronomic, plant growth, and yield-related traits by 10,000 high-quality SNPs in 142 foxtail millet genotypes [90]. The same group used GWASs to identify 74 MTAs associated with ten nutritional elements using the same 10,000 SNPs in 93 foxtail millet accessions [91]. In pearl millet, a total of 87,748 DArT markers were developed from 281 cultivars by GWASs. Among these, 58,719 high-quality SNPs were used to identify 78 MTAs for iron, zinc, and protein content [92]. A total of 392 pearl millet cultivars were used to develop 21,633 SNPs by GWASs, and the developed SNPs helped to identify 18 QTL for flowering time, plant height, tillering, and biomass [93]. In another study, 1132 MTAs for six starch-related traits were identified in 166 genotypes of pearl millet by GWASs using 78,000 SNPs [94]. In proso millet, 13 MTAs for agronomic and seed-related traits were identified by 2412 high-quality SNPs developed through GWASs [95]. A total of 190 genotypes of finger millet were used to generate 169,365 SNPs by a combination of GBS and a GWAS, which were used to identify several MTAs for iron, zinc, calcium, magnesium, potassium, and sodium and protein contents [96]. Apart from the above-mentioned studies, several QTL and MTAs were identified for many traits using both GWAS and GBS techniques in millets (Table 4). To date, there is no information regarding GWASs and GBS for little millet, brown top millet, tef, fonio millet, barnyard millet, and kodo millet. A GWAS should be carried out to identify QTL and MTAs for various traits in millets under biotic and abiotic stress conditions (Figure 3), which will help to develop a new cultivar via breeding programs. The identified QTL and MTAs by GWASs and GBS might be used for millet breeding programs. The genome assembly enables the scanning of SNP markers developed by GWASs across the complete set of DNA or genomes. It helps to find genetic variations associated with any particular traits. Once the new genetic traits are identified, researchers can use the traits for a further millet breeding program. Such studies are particularly important to find genetic variations that contribute to common complex diseases and environmental stresses.

**Table 4.** Identification of QTL/MTAs by genome-wide association studies (GWASs) in major and minor millets.

Name of the Millet	Number of Genotype	Number of SNPs	Number of QTL/MTA Identified	Targeting Traits	Reference
Sorghum	300	79,132	14	Stalk rot diseases in grain	[97]
	390	268,830	108	Yield per panicle, grain number per panicle, and 1000-grain weight	[98]
	315	136,285	101	Plant height, panicle length, panicle exertion, stem circumference, tiller number, internode number, flowering time, leaf angle, and seed number	[99]
	300	265,487	42	Shoot and root weight, shoot and root length, chlorophyll contents, and anthocyanin content in shoot under cold and heat stress	[100]
	374	265,487	14	Leaf firing and leaf blotching under heat stress	[101]
	194	44,515	21	Final emergence percentage, seedling survival, and seedling vigor under cold stress	[102]
	245	85,585	42	Crude protein, neutral detergent fiber, acid detergent fiber, hemicellulose, and cellulose contents	[103]

Table 4. Cont.

Name of the Millet	Number of Genotype	Number of SNPs	Number of QTL/MTA Identified	Targeting Traits	Reference
Sorghum	212	268,289	2	Low seed deterioration and emergence rate	[104]
	1425	72,190	102	Plant height, presence or absence of awns, glume cover, pericarp color, panicle compactness and shape, panicle exertion, smut resistance, and male sterility	[105]
	634	260,000	70	Amylose and amylopectin contents in grain	[106]
	2000	142,567	81	Seed size	[107]
	403	341,514	52	Grain carotenoids ( $\beta$ -Carotene and Zeaxanthin)	[108]
	242	6,094,317	19	Panicle length and width, panicle compactness, and peduncle recurving	[109]
	219	73,730	>80	Plant height, flowering time, forage biomass, grain weight, and water use efficiency under drought stress	[110]
	245	85,585	338	Plant height, tiller number, stem diameter, and fresh weight per plant	[111]
	96	192,040	40	Heading date, plant height, dry yield, and phenolic compounds	[112]
	354	6186	79	Plant height and drought-tolerance indices	[113]
	162	193,727	100	Seed area size, length, width, length-to-width ratio, perimeter, circularity, distance between intersection of length and width, center of gravity, and seed darkness and brightness	[114]
Pearl millet	392	21,663	18	Biomass, flowering time, plant height, and tillering	[93]
	281	58,719	78	Iron, zinc, and protein content	[92]
	197	76,000	897	Starch-, lipid-, antioxidant-, vitamin-, sucrose-, and flavone-related traits	[115]
	222	67,000	218	Antioxidant biosynthesis	[116]
	166	78,000	1132	Readily digested starch, slowly digested starch, resistant starch, total starch, and available starch	[94]
Foxtail millet	916	2,584,083	512	Morphology characteristics, yield components, growth time, disease resistance, and coloration	[117]
	104	30,000	67	Eleven nutritional-related traits	[118]
	407	706,646	87	Panicle length, main panicle diameter, panicle weight per panicle, grain weight per panicle, and thousand-grain weight	[89]
	827	161,562	257	Top second leaf width, main stem width, panicle diameter of main stem, panicle length of main stem, per plant grain weight, and main stem panicle weight	[119]
	107	72,181	53	Plant height, stem diameter, leaf length, leaf width, chlorophyll SPD value, spike length, spike weight, spike diameter, grain length, grain width, and grain length/width ratio	[120]
	93	10,000	74	Grain nutritional elements such as potassium, nickel, calcium, boron, magnesium, phosphorus, sulfur, zinc manganese, and iron	[91]
	142	10,000	81	Flag leaf length, flag leaf width, peduncle length, panicle length, tiller maturity, grain yield, and thousand-grain weight and plant height	[90]
Finger millet	190	169,365	418	Grain nutrition traits (calcium, iron, sodium, potassium, magnesium, zinc) and protein content	[96]
	113	23,000	109	Basal tiller number, culm thickness, days to 50% flowering, days to 50% maturity, ear length, ear width, flag leaf blade length, flag leaf blade width, fingers per head, grain yield, length of longest finger, plant height, peduncle length, and width of longest finger	[121]
	113	2977	40	Seed protein content, grain yield, and days to maturity	[122]
Proso millet	88	494,200,000	13	Plant height, leaf number, seed length, seed width, seed perimeter, seed length-to-width ratio, and seed color	[95]



**Figure 3.** Schematic diagram of resources developed and future scope of research on millets.

### 10. Identification and Characterization of Candidate Genes from Native Genome Sequences of Millets

In earlier studies when the genome sequences of millets were not generated, researchers used the sequences of closely related cereals to design primers and characterize the genes in millets for various biotic and abiotic stress conditions. The availability of millet genome sequences has paved the way for the identification and functional characterization of several candidate genes related to biotic, abiotic, and other stresses in many millets (Table 5). Interestingly, several candidate genes related to major environmental stresses (drought, salinity, and heat) have been identified from the annotated genome sequences of foxtail millet, which will certainly help identify the key candidate genes for further characterization studies in the future. In foxtail millet, the expression pattern of 187 basic helix–loop–helix (bHLH) genes was analyzed under several abiotic and phytohormone treatments [123] (Table 5). A total of 52 soluble-N-ethylmaleimide-sensitive-factor accessory-protein receptor (SNARE) [124], 35 DNA binding with one finger (Dof) [125], and 103 WRKY genes [126] were particularly responsive to drought stress in foxtail millet. Twelve phosphate transporter 1 (PHT1) family genes were identified specifically for foxtail millet, which help improve phosphorus uptake, translocation, and remobilization under low-phosphate stress [127]. Further, the identified key *PHT1* genes were functionally characterized by yeast complementation assay [128]. The identified 29 high-affinity potassium (HAK) transporters can increase the potassium concentration in foxtail millet tissues and enhance foxtail millet growth and yield under potassium-deficiency soil [129]. Twelve natural resistance-associated macrophage proteins (NRAMPs) were developed from the foxtail millet genome support to alleviate cadmium and other heavy metals in millet tissues and grains [130]. In finger millet, 12 *PHT1* and 6 zinc-regulated, iron-regulated transporter-like protein (ZIP) family transporters were detected, and their expression pattern was analyzed under an individual or combined deficiency of phosphorous and zinc conditions [131].

This study revealed the expression pattern of *PHT1* and *ZIP* family transporters under a differential supply of phosphate and zinc. Apart from this report, 116 nucleotide-binding site–leucine-rich repeat (NBLRR) genes were identified from the native genome of finger millet, and they were analyzed in blast disease-infected finger millet [132]. Blast disease is one of the major biotic constraints on finger growth and yield. The identified *NBLRR* genes may contribute to alleviating the understanding of blast disease in finger millet. Eight classical drought-responsive genes were also identified from the annotated genome of finger millet, and they were analyzed in drought-tolerant and drought-sensitive genotypes [133]. More than 250 *MYB* genes were identified from the pearl millet genome responding to cold, high temperature, osmotic stress, drought, salinity, abscisic acid, salicylic acid, and methyl jasmonate [134,135] (Table 5). To date, only 180 *NAC* genes have been identified from the proso millet genome associated with drought stress [136]. There are more than 30 draft gene assemblies for proso millet, but it is regrettable that research progress is very poor compared to other millets. It is good to note that more than 1000 candidate genes have been identified and their expression pattern analyzed in various tissues of millets related to drought and salinity stress. We feel that many key genes associated with drought, salinity, and other stresses have been identified in foxtail millet. This clearly represents that foxtail millet can serve as a model millet for other minor millets such as brown top millet, fonio millet, little millet, green foxtail, tef, and other cereals. However, functional genomics research in millets is still in its infancy. In recent years, the genome editing tool CRISPR/Cas has gained popularity among plant science researchers to study the function of genes and generate stress-resistant and nutrient-rich plants. The CRISPR/Cas9 system has been widely applied in diverse plants, including millets [137]. This tool has been successfully implemented in sorghum, tef, and foxtail millet. The knockout of the *SEMIDWARF-1* gene in tef through the CRISPR/Cas9 system enabled the development of lodging-resistant varieties (dwarf plants) of tef [138]. Induced site-directed mutations in the *kafirin* genes of sorghum by CRISPR/Cas9 improved protein digestibility and vitreous endosperm [139,140]. Herbicide-tolerant foxtail millet was developed by targeting two genes (*acetolactate synthase* (*SiALS*) and *acetylcoenzyme A carboxylase* (*SiACC*)) through CRISPR base editors (cytosine and adenosine base editors) [141]. The knockout of two *carotenoid cleavage dioxygenase* genes (*SbCCD8a* and *SbCCD8b*) reduced orobanchol production and parasite weed (in particular *Striga*) germination in sorghum [142]. Hence, a further functional characterization of key genes from already available reports through genome editing approaches will help to enhance millet growth, which will support improving food availability in 2050.

**Table 5.** Details of candidate genes identified from native genome sequences of millets.

Name of the Millet	Name of the Genes	Name and Total Number of Genes Identified	Treatments	Reference
Pearl millet	<i>MYB</i>	208 ( <i>PgMYB1–PgMYB208</i> )	Cold, high temperature, osmotic stress, drought, and salinity	[134]
	<i>MYB</i>	279 ( <i>PgMYB1–PgMYB279</i> )	Dehydration and salinity stress, abscisic acid, salicylic acid, and methyl jasmonate	[135]
	<i>WRKY</i>	97 ( <i>PgWRKY1–PgWRKY97</i> )	Dehydration and salinity stress	[143]
	<i>SBP</i>	18 ( <i>PgSBP1–PgSBP18</i> )	Drought, salinity, and abscisic acid	[144]
	<i>NAC</i>	151 ( <i>PgNAC1–PgNAC151</i> )	Drought and salinity stress	[145]
Foxtail millet	<i>BZR</i>	7 ( <i>SiBZR1 to SiBZR7</i> )	Abscisic acid and salinity stress	[146]
	<i>MADS-box</i>	89 ( <i>SiMADS1–SiMADS89</i> )	Acid, alkali, salt, drought, flooding, dark, heat and cold stresses	[147]
	<i>bHLH</i>	187 ( <i>SibHLH1–SibHLH187</i> )	Acid, alkali, drought, salinity, heat, cold, flooding, and darkness conditions	[123]
	<i>nsLTP</i>	45 ( <i>SinsLTP1–SinsLTP45</i> )	Drought, salt, and cold stress	[148]
	<i>SOD</i>	8 ( <i>SiSOD1–SiSOD8</i> )	Drought and salinity	[149]
	<i>GATA</i>	28 ( <i>SiGATA1–SiGATA28</i> )	Acid, alkali, salinity, drought, dark, flooding, heat, and cold	[150]
	<i>SAUR</i>	72 ( <i>SiSAUR1–SiSAUR72</i> )	Drought, salinity, abscisic acid, salicylic acid and gibberellic acid	[151]
<i>SNARE</i>	52 ( <i>SiSNARE1–SiSNARE52</i> )	Drought stress	[124]	

Table 5. Cont.

Name of the Millet	Name of the Genes	Name and Total Number of Genes Identified	Treatments	Reference
Foftail millet	<i>SPL</i>	18 ( <i>SiSPL1</i> to <i>SiSPL18</i> )	Acid, alkali, salinity, drought, flooding, dark, heat, and cold	[152]
	<i>GST</i>	73 ( <i>SiGST1</i> – <i>SiGST73</i> )	Osmotic, salinity, cold stress, and abscisic acid	[153]
	<i>CLE</i>	41 ( <i>SiCLE1</i> – <i>SiCLE41</i> )	Gibberellic acid treatment	[154]
	<i>Dof</i>	35 ( <i>SiDof1</i> – <i>SiDof35</i> )	Drought stress	[125]
	<i>LecRLK</i>	113 ( <i>SiLecRLK1</i> – <i>SiLecRLK113</i> )	Drought and high temperature	[155]
	<i>CCT</i>	19 ( <i>SiCCT1</i> – <i>SiCCT19</i> )	Abscisic acid, drought, and salinity	[156]
	<i>MAPK</i>	16 ( <i>SiMAPK1</i> – <i>SiMAPK16</i> )	Abscisic acid, gibberellic acid, jasmonic acid, drought, salinity, cold, and heat	[157]
	<i>MKK</i>	11 ( <i>SiMKK1</i> – <i>SiMKK11</i> )	Abscisic acid, Gibberellic acid, jasmonic acid, drought, salinity, cold, and heat	[157]
	<i>MAPK</i>	93	Cold, salinity, and drought and abscisic acid and jasmonic acid	[158]
	<i>CDPK</i>	29 ( <i>SiCDPK1</i> – <i>SiCDPK29</i> )	Drought and abscisic acid	[159]
	<i>CYP450</i>	331	Drought, salinity, abscisic acid, low-temperature, and herbicide treatments	[160]
	<i>AP2/ERF</i>	171 ( <i>SiAP2/ERF1</i> – <i>SiAP2/ERF171</i> )	Dehydration and salinity stress	[161]
	<i>ATG</i>	37	Drought, salt and cold, and nitrogen and carbon starvation	[162]
	<i>NF-Y</i>	39 (10 <i>NF-YA</i> , 13 <i>NF-YB</i> , and 13 <i>NF-YC</i> )	Drought, salinity, osmotic, and oxidative stress	[163]
	<i>HAK</i>	7 ( <i>SiHKT1</i> – <i>SiHKT7</i> )	Salt stress	[164]
	<i>MYB</i>	209 ( <i>SiMYB1</i> – <i>SiMYB209</i> )	Salinity, dehydration, abscisic methyl jasmonate, and salicylic acid	[165]
	<i>LBD</i>	33 ( <i>SiLBD1</i> – <i>SiLBD33</i> )	Drought, salinity, and abscisic acid	[166]
	<i>TRX</i>	35 ( <i>SiTRX1</i> – <i>SiTRX35</i> )	Drought and salinity stress	[167]
	<i>HAT</i>	24 ( <i>SiHAT1</i> – <i>SiHAT24</i> )	Nitrate and phosphate deficiency, salinity, and drought	[168]
	<i>HD-Zip</i>	47 ( <i>SiHD-ZIP1</i> – <i>SiHD-ZIP47</i> )	Dehydration, salinity, and abscisic acid	[169]
	<i>GSK</i>	8 ( <i>SiGSK21</i> , 23, 24, 11, 12, 13, 31 and 41)	Dehydration, salt, and oxidative stress	[170]
	<i>NPF</i>	92	Low-nitrate stress	[171]
	<i>PTI1</i>	12 ( <i>SiPTI1-1</i> to <i>SiPTI1-12</i> )	Salinity stress	[172]
	<i>DIR</i>	38 ( <i>SiDIR1</i> – <i>SiDIR38</i> )	Salinity, drought, and higher concentrations of calcium and cadmium stress	[173]
	<i>SPCP</i>	10	Cold, heat, salinity, drought, and various phytohormones	[174]
	<i>AAT</i>	94	Drought and salinity	[175]
	<i>LOX</i>	13 ( <i>SiLOX1</i> – <i>SiLOX13</i> )	Salt and drought	[176]
	<i>REM</i>	21 ( <i>SiREM1</i> – <i>SiREM21</i> )	Abscisic acid, gibberellic acid, methyl jasmonate, drought, and salinity	[177]
	<i>WRKY</i>	103 ( <i>SiWRKY1</i> – <i>SiWRKY103</i> )	Drought stress	[126]
	<i>PHT1</i>	12 ( <i>SiPHT1;1</i> – <i>SiPHT1;12</i> )	Phosphate stress	[127]
	<i>NRAMP</i>	12 ( <i>SiNRAMP1</i> – <i>SiNRAMP12</i> )	Cadmium stress	[130]
	<i>HAK</i>	29 ( <i>SiHAK1</i> – <i>SiHAK29</i> )	Potassium deficiency and salt stress	[129]
	<i>NRT1 and NRT2</i>	3 <i>NRT1</i> ( <i>NRT1;1</i> , <i>1;11</i> and <i>1;12</i> ) and 1 <i>NRT2</i> ( <i>SiNRT2;1</i> )	Low N stress	[178]
<i>BOR</i>	1 ( <i>SiBOR1</i> )	Boron stress	[179]	
<i>ZIP</i>	7 ( <i>SiZIP1</i> – <i>SiZIP7</i> )	Drought stress	[180]	
Finger millet	<i>PHT1</i>	12 ( <i>EcPHT1;1</i> – <i>EcPHT1;12</i> )	Phosphate and zinc stress	[131]
	<i>ZIP</i>	6 ( <i>EcZIP1</i> – <i>EcZIP6</i> )	Phosphate and zinc stress	[131]
	<i>ckx</i>	20 ( <i>EcCKK1</i> – <i>EcCKK10</i> )	Various biotic and abiotic stress	[181]
	<i>NBLRR</i>	116 ( <i>EcNBLRR1</i> – <i>EcNBLRR116</i> )	Blast disease Magnaporthe grisea infection	[132]
Proso millet	<i>NAC</i>	180 ( <i>PmNAC1</i> – <i>PmNAC180</i> )	Drought stress	[136]

Abbreviations: AAT, Amino acid transporter; AP2/ERF, APETALA2/ethylene-responsive element binding factor; ATG, Autophagy-associated gene; BHLH, Basic helix-loop-helix (bHLH); BOR, Boron transporter; BZR, Brassinazole Resistant; CDPK, Calcium-dependent protein kinase; CLE, Clavata3/embryo-surrounding region; cck, Cytokinin oxidase/dehydrogenase; CYP450, Cytochrome P450 monooxygenase; Dof, DNA binding with one finger; DIR, Dirigent; HAT, Histone acetyltransferase; GSK, Glycogen synthase kinase; GST, Glutathione S-transferase; HAK, High-affinity potassium transporter; HD-Zip, Homeodomain leucine zipper; LBD, Lateral organ boundaries domain; LecRLK, Lectin receptor-like kinase; LOX, Lipoxygenase; MAPK, Mitogen-activated protein kinase; NF-Y, Nuclear Factor Y; NPF, Peptide transporter; NBLRR, Nucleotide-binding site-leucine-rich repeat; NRAMP, Natural resistance-associated macrophage protein; NsLTP, Non-specific lipid transfer protein; PHT1; Phosphate transporter 1; PTI1, Pto-interacting 1; REM, Remorin; SAUR, Small auxin-up RNA; SBP, SQUAMOSA promoter binding protein-like proteins; SNARE, Soluble-N-ethylmaleimide-sensitive-factor accessory-protein receptor; SOD, Superoxide dismutase; SPL, Squamosa promoter binding-like; Shaker potassium channel protein (SPCP); TRX, Thioredoxins; and ZIP, Zinc-regulated, iron-regulated transporter-like protein.

### 11. Will Genome Sequences of Millets Help Improve Food and Nutritional Security by 2050?

The world needs to produce more food to feed a rapidly growing world population, which is expected to reach 8.5 billion by 2030 and 9.7 billion by 2050 [182]. In addition, climate change, water scarcity, poor soil quality, and plant diseases are reducing the current availability of foods in many places worldwide. More than 50,000 plant species are

available for human consumption, but less than 20 of them provide most of the world's food supply [183]. Among them, three major cereals (rice, wheat, and maize) account for most of the calories consumed by humans every day. We cannot assume that these three major cereals will feed more than 9 billion people in 2050. Also, it is difficult to cultivate these three cereals in the future's toughest environments. Millets are one of the oldest food grains known to humans, dating back to 3500 BC. Millets are capable of growing in drought conditions, under irrigated conditions, and very low rainfall conditions and have a low water footprint [184]. Millets do not require much fertilizer or pesticides to grow, so they are a highly profitable grain for small farmers on a limited budget [3]. Millets, with their extraordinary adaptability and resilience, have proven themselves a powerful tool in the fight against global food security [185]. They are not just cereals; they are the embodiment of substances for billions of people, especially in regions where harsh climates and resources limitations pose formidable challenges to agriculture. The story of millets does not stop at feeding the world's growing population. It extends to a profound commitment to environmental sustainability. The current annotated and draft genome sequences of major and minor millets have revolutionized the field of genomics and created significant molecular insights. Genome sequencing will help to develop millets with improved yield and nutritional values and superior resistance to various environmental stresses. Genome sequences play an important role in characterizing essential genes within a millet genotype by a variety of approaches including structural and functional analyses, linkage mapping, and gene editing. All these techniques have facilitated the genetic improvement of plants by understanding complex trait structures. The use of genome sequences in molecular breeding programs can effectively increase millet grain yield and productivity. In addition, genome sequences will help to optimize the utilization of genetic assets in different genotypes of millets. More than 30 thousand millet cultivars are globally available [31]. There is no doubt that millet genetic resources will play an important role for food security and sustainable agriculture. In a world grappling with climate change and its associated woes, the resilience of millets offers a glimmer of hope, demonstrating how a small yet mighty grain can contribute to soil health and reduce the ecological footprint of agriculture.

## 12. Conclusions and Future Perspectives

The availability of millet genomes facilitates the breeding and selection of millets, which are essential to support ongoing and future food security. However, researchers are trying to completely annotate the already available partial genome sequences of pearl millet, fonio millet, tef, job's tear, proso millet, and barnyard millet (Figure 3). The complete annotation of pearl millet, fonio millet, tef, job's tear, proso millet, and barnyard millet genome sequences will enable the rapid identification of the key genes that determine highly important traits in millets. Identifying markers and candidate genes from the available genome sequences would help millet improve against biotic and abiotic stresses. Also, this will allow for more efficient millet breeding by facilitating the selection of important traits. Genome sequences are not yet available for brown top millet, little millet, and kodo millet. Developing millet genome sequences for these three millets will support the improvement of these three millets. Genome editing is a famous tool in biotechnology to dissect the role of any candidate genes in any plants. Such novel techniques should be implemented in millets to dissect the already identified key genes related to biotic and abiotic stresses. The need for a rapid genetic improvement of millets is made more urgent by climate change, which demands new genotypes adapted to new and harsh environments. Maintaining millet genetic resources in seed banks and the conservation of the wild millet genotypes provide the genetic resources that are required for sustainable food production. More attention should be given to the collection and conservation of little millet, brown top millet, tef, fonio millet, job's tear, kodo millet, proso millet, and barnyard millet, because most of the traditional germplasm of those millets have already disappeared from the world. Improving the nutritional contents of each millet through nutritional transporter

gene manipulation may help enhance the nutritional availability in seeds of millets. In addition, several differentially expressed genes and molecular markers have already been identified for major and minor millets through transcriptomic resources. Hence, millet researchers can try to use the transcriptomic resources of millets for identifying candidate genes and developing molecular markers for those millets without complete annotated genome sequences.

**Author Contributions:** Conceptualization, T.M. and S.A.C.; table and image creation, T.M.; writing—original draft preparation, T.M. and T.P.A.K.; writing—review and editing, T.M., T.P.A.K. and N.M.K.; project administration, S.A.C. review, writing, and editing during revision, H.K. and M.V. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research was funded by Rajagiri College of Social Sciences under Seed Money for Faculty Minor Research.

**Acknowledgments:** We would like to acknowledge the Rajagiri College of Social Sciences (RCSS) for providing internet access, software, and system facilities for writing the manuscript.

**Conflicts of Interest:** The authors declare no conflict of interest.

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