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Oñate Narciso, Joan; Nyström, Laura

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The genetic diversity and nutritional quality of proso millet (*Panicum miliaceum*) and its Philippine ecotype, the ancient grain “kabog millet”: A review

Joan Oñate Narciso^{*}, Laura Nyström^{**}

Laboratory of Food Biochemistry, Department of Health Sciences and Technology, Institute of Food, Nutrition and Health, ETH Zürich, Schmelzbergstrasse 9, CH-8092, Zurich, Switzerland

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ABSTRACT

Background: Climate change and biodiversity loss will push us to revolutionise and transform our existing food systems to feed the global population and provide sustainable nutrition. Alternative crops such as proso millet present a viable option to diversify our diet and contribute to food security. Proso millet (*Panicum miliaceum* L.) is nutritious but is not a widely popular food grain in developed countries. This review provides existing relevant information on the genetic diversity and nutritional properties of proso millet. This paper also presents additional current information on the “kabog millet”, an ancient grain from Cebu, Philippines, considered an ecotype of proso millet. The nutritional profiles of these ancient grains should be emphasised because farmers tend to abandon cultivation of these ancient grains in the absence of nutritional data. By understanding the nutritional profile of “kabog millet” and other ancient grains, the local diets could be redesigned to incorporate these crops for a more complete and balanced nutrition.

Main conclusions: Proso millet offers a resilient, nutritious crop in the face of climate change. Nutritional analyses of proso millet varieties and other minor crops are tools to encourage farmers and growers to cultivate them and for consumers to integrate these crops in the diet. Without nutritional studies, many minor crops will be overlooked and will soon be forgotten. The inclusion and consumption of ancient grains like “kabog millet” as staple food can help address the challenge of food insecurity by providing more balanced diets, and biodiversity loss by encouraging cultivation of overlooked and often forgotten plant varieties.

1. Introduction

The term “millets” is used to describe a broad family of annual cereals that consists of pearl millet (*Pennisetum glaucum* L.), finger millet (*Eleusine coracana*), proso millet (*Panicum miliaceum* L.), kodo millet (*Paspalum scrobiculatum*), foxtail millet (*Setaria italica*), barnyard millet (*Echinochloa crus-galli*, *Echinochloa esculenta*, *Echinochloa frumentacea*), little millet (*Panicum sumatrense* (*P. miliare*)), fonio (*Digitaria iburua*), and teff (*Eragrostis tef*) [1]. Millets are usually cultivated and grown in dry areas of temperate, subtropical, and tropical regions [1]. Millets that originated from Africa are finger millet, pearl millet, fonio, and teff, whereas foxtail millet, proso millet, little millet, barnyard millet, and kodo millet originated from Asia [2]. Foxtail millet and proso millet are known to be the oldest of the cultivated millets in Asia, even older than

rice, which originated around 9000 years ago in the Yangtze Valley [3]. The earliest evidence for domesticated proso millet and foxtail millet dates back to 10,000 years ago in northern China [4–6]. Finger millet and pearl millet are endemic African cereals. Archaeologically, they indicated two different growth environments: pearl millet was first domesticated in the West African savannah, and finger millet was domesticated in the East African highlands [2,7]. They later spread to Asia, for example, to India [8]. Finger millet is the oldest recorded African cereal [7]. The first stages of food globalisation came around the period from the late third millennium BC to the start of the first millennium AD [9]. During this period, a significant number of important crops from China, India, Africa, and West Asia crossed Central Asia into Europe. Millets from East Asia probably reached Europe via the “Inner Asian Mountain Corridor”, as first proposed by Ref. [10]. This route

* Corresponding author.

** Corresponding author.

E-mail addresses: joan.narciso@hest.ethz.ch (J.O. Narciso), laura.nystroem@hest.ethz.ch (L. Nyström).

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culminated in the “Silk Road” by the end of the first millennium BC [11]. Millet found its way to Europe, and wheat and barley came to Asia [12]. During the Middle Ages, millet was one of the main “poor man’s cereals” or “inferior” grains of Europe [175]. During the 19th century, wheat, rice, maize, rye, and potato produced higher yields than millet in Europe [175]. This is one of the factors which might have led to the decline in millet production. Millet, unlike wheat, does not have gluten, which is required for making good-raised bread. In addition, millets have stronger taste than wheat and rice, which have a bland and mild taste [175]. Consumers ultimately preferred other cereals with milder taste over millets, which are nutritionally superior but have stronger taste.

In Africa, the most widely grown millets are pearl millet, finger millet, teff, and fonio, with roughly 80% of the total land area for millets production devoted to pearl millet, followed by finger millet, teff, and fonio [13]. [14] reported that in 2018, 31.0 million tonnes of millets were produced globally in 33.5 million hectares of land. About half of this area is in Africa and in Asia, roughly 1% in Europe and in North America. The top 10 countries in terms of acreage are the African countries of Niger, Nigeria, Sudan, Mali, Burkina Faso, Chad, Ethiopia, and Senegal, India, and mainland China in Asia. In 2016, India was first in terms of acreage with 28%, followed by Niger, Nigeria, Sudan, Mali and Burkina Faso, Chad, China, and Senegal, and Pakistan [15]. In terms of production amongst African countries, the largest producer is Niger, followed by Sudan, Nigeria, Mali, Burkina Faso, Ethiopia, Chad, and Senegal. In 2019, in terms of area and production, India ranks first with 8.4 million ha and 10.2 million tonnes, respectively [16]. Millets cultivated in the Americas, Europe, and Oceania are usually put into animal feed and non-food uses [14]. A summary of the millets, including their botanical names, chromosome number, and global grain production in tonnes, is presented in Table 1. A map of their predicted origins of domestication is also shown (Supplementary Fig. 1).

This review aims to provide an overview of proso millet (*Panicum miliaceum* L.), one of the minor millets, its genetic diversity, the genomic tools currently available for breeding programmes, and its nutritional profiles. In addition, “kabog millet” from Cebu, the Philippines is

Table 1
Millets and their properties.

Common names	Botanical names	Chromosome number	World grain production (tonnes)
Pearl millet (bulrush millet)	<i>Pennisetum glaucum</i> (<i>P. americanum</i> , <i>P. typhoides</i>)	2n = 14	~15 million
Foxtail millet (Italian/German/ Hungarian/ Siberian millet)	<i>Setaria italica</i>	2n = 18	~5 million
Proso millet (common/hog/ broomcorn/ Russian millet)	<i>Panicum miliaceum</i>	2n = 36 or 72	~4 million
Finger millet	<i>Eleusine coracana</i>	2n = 36	<4 million
Fonio (black fonio)	<i>Digitaria iburua</i>	2n = 54	< <3 million
White fonio (acha, hungry rice)	<i>Digitaria exilis</i>		<3 million
Barnyard millet, (barnyard grass)	<i>Echinochloa crus-galli</i>	2n = 36 to 72	<3 million
Japanese barnyard millet	<i>Echinochloa esculenta</i>	2n = 54	
Indian barnyard millet	<i>Echinochloa frumentacea</i>	2n = 36,54,56	<3 million
Teff	<i>Eragrostis tef</i>	2n = 40	<3 million
Little millet	<i>Panicum sumatrense</i> (<i>P. miliare</i>)	2n = 36	<3 million
Kodo millet (creeping paspalum, dronkgras)	<i>Paspalum scrobiculatum</i>	2n = 40	<3 million

Adapted from Ref. [125].

introduced as a forgotten ancient grain, considered as an ecotype of proso millet, with its morpho-agronomic and nutritional properties. It is hoped that besides the morpho-agronomic characteristics of many minor crops, their nutritional value should also be studied and emphasised, since in the absence of nutritional data, consumers will not be motivated to integrate these crops as staple foods and farmers will ultimately be discouraged to grow them for lack of a market to trade their crops. Many of these ancient minor crops also hold cultural significance, and sensitivity towards the indigenous communities who traditionally cultivate them must be considered.

2. Proso millet

Proso millet (*Panicum miliaceum* L.) is a cereal crop commonly referred to broomcorn, yellow hog, hershey, white millet, common millet and hog millet [17]. It belongs to the order *Poales* and the family *Gramineae* [18]. Proso, barnyard, little, and kodo millets are under-researched and underutilised in terms of production, promotion, and research and development.

2.1. Proso millet is an easy-to-grow crop

Proso millet is still widely considered as a self-pollinated crop despite the possibility of natural cross-pollination [19]. Proso millet seeds exhibit a variety of colours, from white, cream, yellow, orange, red, black, to brown (Supplementary Fig. 2), and are generally smaller than pearl millet seeds [19]. It is a short-season crop, thriving between 6 and 12 weeks, and has low water demand [20]. Proso millet requires an annual average precipitation of only less than 600 mm [21]. It needs an average daytime temperature above 17 °C during vegetation to thrive [21]. Proso millet also needs little nitrogen fertiliser and is quite resistant to diseases [22]. It can survive at altitudes of up to 3500 m; is highly adaptable to plateau conditions, and can be cultivated in areas further north in latitude than other millets [17,23]. Proso millet is a C₄ crop and can efficiently fix carbon under drought conditions, high temperatures, and limited nitrogen and carbon dioxide [24].

2.2. Proso millet is grown worldwide

Extensive cultivation areas for proso millet are present in East Asia (China), South Asia (India and Nepal), Eastern Europe (Ukraine and Belarus), Africa, Russia, Middle East, Turkey, and Romania [25]. Proso millet spread to North America through German-Russian immigrants who arrived in North America in 1875. The immigrants cultivated proso millet along the eastern Atlantic coast [24]. The areas in the states of Colorado, Nebraska, and South Dakota in the Central Great Plains of North America are the main producers of proso millet [26]. In western Nebraska, commonly cultivated proso millet varieties are Horizon, Sunrise, Huntsman, Earlybird, Sunup, Dawn, and 172-2-9 [27], with Dawn being the parent of most cultivars released in Nebraska [28]. These varieties have been selected for cream/white seeds (Supplementary Fig. 2), and many studies on the characteristics of proso millet were performed using these varieties. The genetic base of the cultivars widely cultivated in the United States is narrow due to the limited number of varieties used as parents during breeding [29]. Proso millet is used in these states as a rotational crop after sunflower (*Helianthus annuus* L.) and maize (*Zea mays* L.) [26]. Farmers take advantage of the short growing season of proso millet by harvesting it prior to sowing winter crops such as winter wheat, which is the base crop in dryland cropping system [30]. Globally, there are very limited information on the statistics and trading of proso millet because they are lumped together with other millets in official data.

2.3. Proso millet is classified into different races

There are five races of cultivated proso millet based on their panicle

traits namely, *miliaceum*, *patentissimum*, *contractum*, *compactum*, and *ovatum* [31,32]. The characteristics of the different races are presented in Fig. 1. Race *miliaceum* has large, open inflorescences and sub-erect branches, whilst race *patentissimum* has slender and diffused panicle branches. Races *contractum*, *compactum*, and *ovatum* have compact inflorescences [32,33]. Proso millet has a chromosome number of $2n = 36$ with basic chromosome number of $x = 9$ (see Table 1) [34]. [35] suggested that proso millet may have allotetraploid origins with *Panicum capillare* (or a close relative) as a maternal ancestor and the other genome coming from *Panicum repens* based on its nuclear and chloroplast genomes. Further studies of other Old World *Panicum* species are still needed.

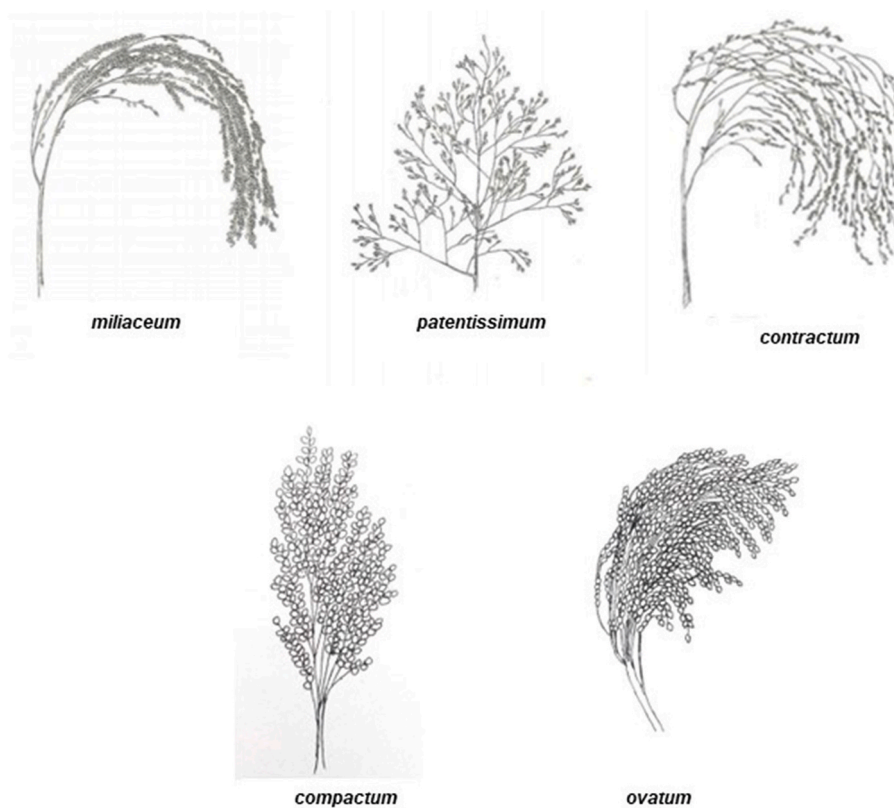
Traditional landraces and wild species are vital sources of genetic variation, which is a significant factor in crop improvement. The loss of genetic diversity can be attributed to non-usage of the traditional landraces in favour of modern high-yielding cultivars [36]. In addition, traditional landraces of proso millet are grown mainly under subsistence farming, which also results in genetic erosion. Until the start of the twentieth century, proso millet was a highly significant crop in China, but recently higher-yielding varieties of other crops (such as rice, maize, wheat) have replaced proso millet and led to a significant decline in its cultivation [37].

2.4. Proso millet germplasm collections exhibit wide species variation

There are more than 29,000 germplasm collections of proso millet conserved worldwide. The major genebanks of proso millet germplasms are listed in Table 2. China, India, Russia, and Ukraine have the key collections [38]. Recent reviews and research studies published on the characterisation and identification of germplasm accessions for stress tolerances, both abiotic and biotic, and agronomic and nutritional traits were reported [20,24,30,34,53].

2.4.1. Germplasm evaluation for traits

The identification, classification, and the evaluation of genetic relationship through crop characterisation at macro or micro level are the foundation for future millet researches and crop improvement [39]. The Institute for the Semi-Arid Tropics (ICRISAT) in India has one of the extensive germplasm collections of proso millet (Table 2). ICRISAT embarked on the characterisation of their proso millet germplasm collections based on flowering, plant height and panicle exertion [33]. Most Syrian accessions are early flowering varieties, whilst those from India are late flowering varieties [33]. Accessions with dwarf plant height were recorded from Mexico whilst Sri Lanka have tall plant accessions [33]. Accessions from Australia and China have good panicle exertion, whilst the former USSR have the shorter panicle exertion accessions [33]. Elite accessions of proso millet were identified based on agronomic properties, disease resistance, and nutritional content from



Races *miliaceum*, *patentissimum*, and *contractum* adapted Ref [163]

Races *compactum* and *ovatum* handdrawn by Joan Oñate Narciso based on photographs (Ref [167] with copyright clearance; Ref [34]).

Fig. 1. Different races of proso millet based on panicle (inflorescence) shape.

Table 2
Major genebanks conserving germplasm of proso millet worldwide.

Country	Institute	Germplasm accessions		
		Cultivated	Wild	Total
Australia	Australian Tropical Crops and Forages Genetic Resources Centre	228		228
Bangladesh	Plant Genetic Resources Centre, BARI	198		198
Bulgaria	Institute for Plant Genetic Resources "K. Malkov"	489		489
China	Institute of Crop Science, Chinese Academy of Agricultural Sciences	8451		8451
Czech Republic	Genebank Department, Division of Genetics and Plant Breeding, Research Institute of Crop Production	171		171
Germany	Genebank, Leibniz Institute of Plant Genetics and Crop Plant Research	165	1	166
Hungary	Institute for Agrobotany	243	1	244
India	AICRP on Small Millets	920	4	920
	International Crop Research Institute for the Semi-Arid Tropics (ICRISAT)	849		849
Japan	National Bureau of Plant Genetic Resources	994		998
	Department of Genetic Resources I, National Institute of Agrobiological Sciences	516		516
Mexico	Estación de Iguala, Instituto Nacional de Investigaciones Agrícolas	400		400
Poland	Botanical Garden of Plant Breeding and Acclimatization Institute	354		354
	Plant Breeding and Acclimatization Institute	359		359
Russia	N.I. Vavilov All-Russian Scientific Research Institute of Plant Industry	8778		8778
Ukraine	Institute of Plant Production n.a. V. Y. Yurjev of UAAS	1046	1	1046
	Ustymivka Experimental Station of Plant Production	3975		3976
USA	North Central Regional Plant Introduction Station, USDA-ARS,	717	4	721

Adapted from Ref. [38].

the germplasm collections at the National Centre for Crop Germplasm Conservation in China [40].

[41] performed a comprehensive analysis of 386 proso millet core collections to evaluate different parameters at various growth stages such as leaf filling, maturation and after harvest. They found that the biggest contributors to the principal components were plant height, diameter of main stem, plant tiller number, leaf area of top3 leaves, and 1000-seed weight [41]. They also observed that more than half of the accessions have yellow and red hull colours, which agreed with the statistical analyses of 8515 proso millet genotypes [41]. Panicle type and inflorescence colour distributions also agreed with a previous study [42]. The high variation coefficients reflect the proso millet genetic diversity and the abundant variation found in core germplasms [43].

Plant height, diameter of main stem, top3 leaves area, and 1000-seed weight are traits associated with growing periods – usually long-growing-period genotypes are stronger and have high yields [41]. However, for extremely long growing period, the yield decreases [41]. A possible explanation is that cultivars with long growth periods result in low grain filling due to lower light and decreasing temperature [44]. Breeders can take advantage of these phenotypes by modestly extending the growing period to increase yields.

2.4.2. Genomic and genetic resources for proso millet breeding

The previous unavailability of genetic markers made the molecular characterisation of proso millet particularly challenging. Consequently, DNA markers from other related species were initially used to help

genetically characterise proso millet. For example, reference genome sequences of foxtail millet were available [45,46]. By using expressed sequence tag-simple sequence repeat (EST-SSR), the genome of foxtail millet showed a high degree of cross-genera amplification with eight millet (barnyard millet, finger millet, kodo millet, little millet, pearl millet, proso millet, switchgrass, guinea grass) and four non-millet (sorghum, wheat, rice, and maize) species [47]. Cross-genera amplification at an average of ~85% between foxtail millet and the eight millet was noted using intron length polymorphic (ILP) markers [48], an average of ~89% using microsatellite markers [49], and an average of ~67% using microRNA-based molecular markers [50]. The genomic data of switchgrass were used to develop simple sequence repeat (SSR) markers for proso millet. It has been shown that 62% of the switchgrass SSR markers were transferable to proso millet [51].

2.5. DNA markers for proso millet are available and well-established

Through time, DNA markers of proso millet were established. Traditional DNA markers that were used successfully in determining the genetic diversity of proso millet were Amplified Fragment Length Polymorphism (AFLP) [52]; SSR [29,53–55]; Random Amplified Polymorphic DNA (RAPD) [56]; and Inter Simple Sequence Repeat (ISSR) [57,58]. In the case of RAPD, one interesting application was the determination of intraspecific and interspecific variations amongst *Panicum* species. The wild ancestor of *Panicum sumatrense* is believed to be *Panicum psilopodium* [59,60]. The maternal progenitor of *Panicum miliaceum* is suggested to be *Panicum capillare* [35]. This lack of close association amongst the species suggests that they were domesticated from distantly related species and have no significant interspecific cross breeding [56]. The polymorphism observed in RAPD markers amongst cultivars of proso millet demonstrates the effectiveness of RAPD markers in determining intraspecific variation [56].

2.6. Chloroplast genome markers provide robust genetic phylogeny

A more robust alternative to traditional markers previously mentioned is the chloroplast genome markers. Chloroplast genomes show less variation within species but exhibit substantial variation between higher plant species [61]; hence, they offer excellent markers to study evolution and phylogeny. Salih and coworkers (2017) analysed complete chloroplast genomes from apomictic *Taraxacum* (Asteraceae), and they found that some parts of the chloroplast genomes of these species are evolving at a slower rate, and it is necessary to use appropriate chloroplast genome markers to form accurate conclusions on phylogeny. In addition, Salih and coworkers (2017) mentioned an interesting observation that chloroplast genomes evolve at more slowly than nuclear markers, which may have an impact on the phylogenetic studies of apomictic species.

Following on [61]; a significant advancement in proso millet genetic and genomic studies occurred with the recent publication of the complete chloroplast genome sequence of proso millet [62]. The chloroplast genome sequence helps identify more DNA markers that can be used as a barcode for examining the phylo-geography, genetic diversity, and evolution of proso millet [63]. In a recent work, Cao and coworkers (2021) performed *de novo* and reference-guided assembly of whole chloroplast genomes from five proso millet cultivars. They then analysed the phylogenetic relationships amongst these five proso millet cultivars and other closely related *Panicum* species (*P. sumatrense*, *P. virgatum*), comparing them with outgroups such as maize (*Zea mays*) and sorghum (*Sorghum bicolor*). The proso millet cultivars grouped together, whilst the other *Panicum* species also clustered together [63]. Cao and coworkers (2021) managed to show that chloroplast genomes are effective in differentiating the phylogeny of closely related *Panicum* species, and this can be applied to other genera as well. These works will facilitate the breeding programs not only for proso millet but also for other cereals. Proso millet is a C4 crop, which can serve as a model plant to

examine C4 physiology and morphology including extreme stress tolerance.

2.7. Modern genetic approaches for phylogeny analyses are developed

More modern approaches were developed for phylogeny analyses, such as next-generation sequencing (NGS) of whole genomes and RNA sequencing (RNA-Seq) for SNPs and quantitative trait loci (QTLs) gene expression. In addition, the nuclear genome sequence of proso millet has been published [64]. The development of these modern approaches and the availability of the complete nuclear genome sequence of proso millet greatly facilitate genotyping analyses of this crop. Under NGS, genotyping by sequencing (GBS) has been used extensively in crop improvement programmes because this approach leads to wide usage of molecular markers, despite the disadvantages of the intrinsic error rate of the sequencing process and low depth of sequencing associated with it [65]. However, GBS still helps in the identification and genotyping of many SNPs. Once the desired SNPs have been identified, they can be linked with traits through genome-wide association mapping and/or QTL mapping (Sahu et al., 2021). The information obtained from this stage can be used in marker-assisted breeding for gene introgression (Sahu et al., 2021). Related to GBS is restriction site associated DNA (RAD) sequencing. RAD-Seq and GBS both use restriction enzymes to divide the genome into DNA fragments, which are then sequenced on NGS platforms [66]. The main difference between the two techniques is that GBS library preparation requires less DNA and is accomplished in fewer steps than RAD-Seq [67]. RAD-Seq also requires a size selection step for the DNA fragments, which is not necessary in GBS [67]. If the reference genomes are not available, RAD-Seq is the preferred method for biological diversity applications. However, it is not suitable for routine use in plant breeding because RAD-Seq requires large amount of high-quality DNA during the size selection step and high DNA preparation costs [66]. If the whole genomic sequence of a crop is available, an NGS approach called whole genome resequencing (WGR) can be used to genetically characterise a plant. In WGR, the genome of a novel specimen is sequenced and matched with that of the reference individual to detect polymorphisms, insertions-deletions, and gene conversions, amongst others [68].

RNA-Seq is another approach under NGS. RNA-Seq requires cDNA from total transcripts, usually from protein-coding regions in the genome, then applies direct sequencing on them [69]. It has proven to be an essential device for wide-ranging profiling of QTL gene expression. Candidate genes associated with a desired phenotype can be identified by comparing the expression profiles of a mutant plant with the parent plant through NGS assisted expression profiling or comparative RNA-Seq analyses [68]. RNA-Seq analysis can also be combined with QTL analysis (also known as expression QTLs or eQTLs) [70,71]. Together, they enable the expression of complex traits [72,73].

A recently developed technique, called Hyb-Seq [74], combines target enrichment of low-copy nuclear genes and genome skimming [75] with low coverage shotgun sequencing to assemble high-copy (e.g., organellar) genomic targets. This Hyb-Seq approach generates a probe set that specifically targets genomic regions which give phylogenetic information on different plant genera or families [76]. Hyb-Seq is considered better over other approaches like transcriptome sequencing (RNA-Seq). One of the reasons is that Hyb-Seq is that Hyb-Seq only requires small amounts of relatively degraded DNA, whilst other approaches require living, flash-frozen, or especially-preserved tissue for RNA extraction [74]. RNA-Seq is also subject to large amounts of missing loci across samples and is not effective in capturing rapidly evolving noncoding regions [74]. Hyb-Seq focusses on orthologous targets which reduces the amount of missing data compared to RNA-Seq and RAD-Seq [74]. Until whole genome sequencing of plant samples becomes affordable and practical, Hyb-Seq will find its niche as a quick and efficient method of generating genome-scale datasets for phylogenetic studies.

2.7.1. Genetic diversity of proso millet – examples from Asia and Europe

Genetic variations of 42 varieties of proso millet, which are conserved in the National Agriculture Genetic Resource Centre in Japan and are cultivate in the western part of Himalayas, were assessed by Ref. [77]. Seven quantitative and nine qualitative traits were analysed. High variation was noted in quantitative traits like days to heading and maturity, plant height, panicle length, panicle exertion, flag leaf length and grain yield [77]. Variation was low for the qualitative traits of leaf sheath colour, flag leaf angle, grain shape, and grain colour [77]. The declining diversity of proso millet, specifically in Western Himalayas of Nepal may be due to farming preferences, including market demand for the crop, farmer interest in growing the crop, available suitable area for crop cultivation, and the choice of easily manageable variety [78,79]. Farmers prefer varieties that are higher yielding, easy to dehusk, early to mature and flower, great tasting, and have high biomass [33]. In addition, early flowering varieties are preferred by farmers in the high mountainous region of Western Himalayas of Nepal due to the early start of cold weather and which is now becoming more susceptible to drought due to climate change [77].

From the Central Himalayan Region of India, sixteen representative accessions of proso millet were collected (Triveda et al., 2015). They showed high level of diversity in leaf length and width, plant height, days to 50% flowering, days to 80% maturity, and 1000-seed weight [80]. The collected accessions were also evaluated for biochemical parameters, such as chlorophyll, carotenoids, lipid peroxidation, cellular hydrogen peroxide, activity of nitrate reductase, lipoxygenase, catalase, peroxidase, and superoxide dismutase [80]. These biochemical parameters can predict whether the plant will survive in high altitudes and severe climate conditions [80]. Survival of proso millet varieties in extreme agro-climatic conditions of the Central Himalayan Region can be attributed to the considerable variability in plant height, leaf uprightiness and crop maturity [80]. The days to 50% flowering and days to 80% maturity are critical key adaptive traits, which ensure flower setting at the ideal time for pollination, seed development, and dispersal [81]. Farmers have traditionally bred proso millet with different flowering time to increase yield and broaden its geographical range [81].

The exact centre of millet domestication in China is still disputed. The presence of early millet sites in Dadiwan in the Loess Plateau and Xinle and Xinglonggou in northeast China, far from the Yellow River valley, does not seem to support the view of a north Chinese agricultural origin for proso millet and foxtail millet that is centred around the central Yellow River valley [82]. However, it can also mean that a different location is the focus of proso millet domestication or there are multiple foci within China [83–85]. Based on comparisons of landrace genetic diversity between regions in China, Hu et al. [54] inferred a centre of proso millet domestication in the Loess Plateau. The level of landrace genetic diversity from the Loess Plateau was not significantly higher than those from other regions of China. Sufficient precise geographical information is needed to enable analyses of phylogeography or genetic diversity of many accessions from China [82].

[82] analysed 16 microsatellite loci to explore the genetic diversity amongst landraces from across Europe and Asia and to assess the phylogeographic structure in the Old World proso millet by dividing the accessions into “western” and “eastern”. They proposed a geographical boundary in northwestern China. Many “western” landraces were found also in northeastern China [82]. Considering chronological data, Eastern Europe is a more likely second, non-Chinese centre of domestication than Central Asia [82]. However, this theory cannot be substantiated with the available data from early Neolithic Ukraine, which do not show significant millet consumption [86].

Studies on Slovenian landraces based on a set of 11 SSR markers [55] and a later genotyping of six genotypes [87] has demonstrated an overall low heterozygosity amongst Slovenian landraces of proso millet. This is most likely caused by short geographical distance and similar pedo-climatic conditions [87]. Most of the landraces had “contractum” or arched branches, and with regard to compactness of the inflorescences,

two land races had intermediate compactness (*contractum*), three with open inflorescences (*miliaceum*), and two had compact inflorescences (*glosum*) [87]. Grain colours of these landraces exhibited differences, with white, yellowish brown, and reddish brown [87]. The Slovenian landraces need to be characterised since they could be a good source of genetic diversity for developing proso millet varieties [87].

3. “Kabog millet” – an ecotype of proso millet from the Philippines ?

3.1. Cultivation and cultivars

There are very limited information about “kabog millet”, an ecotype of proso millet. It comes in darker and lighter brown varieties [39]. The use of “kabog millet” as a staple cereal food in Cebu, located in central Visayas of the Philippines, precedes the coming of the Spanish colonisers into the Philippines. “Kabog millet” has become very rare because farmers have shifted to growing and cultivating high-yielding crops such as rice [39]. Tuburan, Catmon, and Sogod in Cebu are the only municipalities that grow native millets [39]. The three millet types “kabog pakdas”, “kabog pilit” and “dawa” grown in Cebu have been comparatively characterised, classified, and identified based on their morphology (structure) and agronomic traits (growth and yield performance) by Ref. [39]. Based on morphology and the agronomic traits, the three millet cultivars were classified as *Panicum miliaceum* convar. *patentissimum*, *Panicum miliaceum* convar. *compactum*, and *Setaria italica*, respectively (Table 3).

3.2. Morpho-agronomic traits of “kabog millet”

The study done by Ref. [39] is one of the limited research that characterised the “kabog millet” cultivars grown namely, “kabog pakdas”, “kabog pilit”, and “dawa” in Cebu. Morphological analyses were focused on five major plant parts, leaf, culm, panicle, flower, and seed. The summary of the morphological characterisation and agronomic traits (mean values) such as plant height, grains per panicle, 1000-seed weight, and grain yield (kg/ha) is shown in Table 3. The three cultivars have distinct panicle shape: “kabog pakdas” has open and semi-erect panicles; “kabog pilit” has compact and drooping panicles; and “dawa” has very compact and drooping panicles (Fig. 2). “Kabog pakdas” and “kabog pilit” have high shattering abilities whilst “dawa” has low shattering ability. “Kabog pilit” had the highest grain yield, whilst “kabog pakdas” had the lowest grain yield. “Kabog pakdas” seeds are light-coloured and bigger than “kabog pilit” seeds, whilst “kabog pilit” seeds are yellower (Fig. 2). The former is used as bird seed, whilst “kabog pilit” is the cultivar usually referred to by the term “kabog millet” by the farmers and people in Cebu, and the one used for making the traditional Cebuano dish called “budbud kabog”. In terms of number of days from sowing to emergence, “kabog pakdas” had the shortest period to emergence at 5 days, whilst “dawa” had the longest period at 10.8 days [39]. Genetic characterisation of “kabog millet” is needed to confirm the classification obtained from morpho-agronomic traits. Genotyping analyses to classify “kabog millet” and determine its

phylogeny with respect to other proso millet varieties are currently ongoing. Recently, a study on the morpho-agronomic traits and variability in phenotypic traits of global proso millet germplasm was published, which is hoped to aid proso millet improvement programmes [34].

3.2.1. Genotypes can affect nutritional profiles of proso millet

The nutritional profiles of proso millet can be affected by the genotypes. For example, it is possible that some proso millet genotypes could be resistant to processing-induced changes in phenolic acid and carotenoid content than other genotypes. Starch properties can also be potentially modified by changing starch synthesis in proso millet varieties by techniques such as TILLING, as in the case of an Italian traditional durum wheat Svevo cv. to increase the amylose content from 25% to 55% [88]. Amylose content is a factor in determining future food applications of proso millet (Section 4.7). By screening proso millet accessions for interesting phenotypes and grain properties, components of proso millet flour can be improved for specific food products.

4. Nutritional quality of proso millet and kabog millet

Proso millet has nutritional and health benefits and its incorporation in the daily food diet may overcome nutrient deficiencies. However, there remain few studies assessing the grain nutritional content of proso millet based on genetic variations [20]. Proso millet is rich in protein, phytochemicals, vitamins, minerals, micronutrients including iron, zinc, copper and manganese, and other non-nutritive compounds that provide protection to the plant [89–91]. Proso millet has high protein content (11.6%), which is within the range with that of wheat (8–15%) [92], although proso millet has higher content of leucine, isoleucine, and methionine [90,93].

4.1. Starch

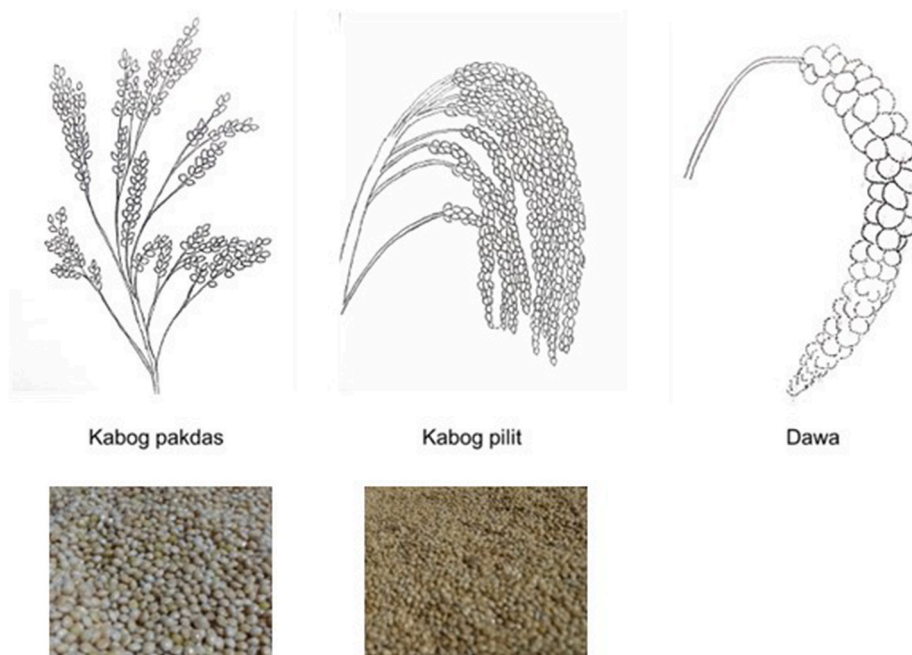
Starch made up 52% out of the total carbohydrate content of 68.2% in proso millet grains [94–97]. In native proso millet varieties cultivated in South Korea, starch content ranged from 84.4% to 85.7% [98]. On the other hand dehulled kabog millet grains contained 60%–63% total starch [99]. In comparison, whole wheat grain flour has around 58–62% starch [25,100], whilst white rice, brown rice, red rice, and black rice have ~82%, ~76%, ~72%, and ~73% starch, respectively [99]. On the other hand, starch comprises 72–73% of maize kernel [101].

Amylopectin and amylose constitute starch, but it is the amylopectin that is widely accepted as playing a role in starch crystallinity [102]. In waxy proso millet, amylopectin comprises 99–100% of the total starch. In non-waxy proso millet, amylopectin makes up around 96–97% of the total starch [96,103]. In the common types of proso millet, the total starch was found to be 61.4–72.8% amylopectin [96,104,105]. The native proso millet varieties cultivated in South Korea had amylopectin content ranging from 78.5% to 98.8% [98], whereas dehulled kabog millet had amylopectin content ranging from 80.9% to 89.3% [99]. The different results in starch content and the ratio of amylose to amylopectin can be attributed to the different extraction methods, grain

Table 3
Classification of the millet cultivars grown in Cebu based on morpho-agronomic traits^a.

Cultivar/Species	Number of days			Plant height (cm)	Panicle			Weight of 1000 seeds (g)	Grain yield (kg/ha)
	Sowing to emergence	Emergence to anthesis	Anthesis to maturity		Length (cm)	Weight (g)	Grains/panicle		
Kabog pakdas <i>P. miliaceum</i> convar. <i>patentissimum</i>	5.0	33.2	24.0	47.5	22.38	3.02	708	7.64	810.35
Kabog pilit <i>P. miliaceum</i> convar. <i>compactum</i>	7.8	52.9	32.1	98.9	41.75	7.23	1483	3.07	1332.03
Dawa <i>S. italica</i>	10.8	55.2	21.8	159.8	32.63	6.08	3232	1.10	824.41

^a Adapted from Ref. [39].



Handdrawn by Joan Oñate Narciso from photographs by Ref [39].
 “Kabog millet” seed photographs taken by Rosaflor Estenzo.

Fig. 2. Panicle morphology of the three millet cultivars grown in Cebu, “kabog pakdas”, “kabog pilit”, and “dawa” and seed colour of “kabog pakdas” and “kabog pilit”. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

processing (dehulling and milling), varietal differences and growing conditions.

4.2. Resistant starch

[106] defined resistant starch (RS) as a portion of starch that is highly resistant to α -amylase hydrolysis, and which could reach the colon to be fermented by microbiota. Depending on their digestive rates, there are three main types of RS according to Ref. [107]: physically enclosed starch (type 1), ungelatinised granules (type 2) and retrograded amylose (type 3) [107]. RS can act similarly to dietary fibre, resulting in positive health effects [108]. Proso millet with 17.2% (w/w, dry mass, dm) amylose had 0.4% w/w dm RS – much higher than in rice (0.2% w/w dm) [109], and durum wheat [88,110]. No previous study has been performed on the RS level in kabog millet.

Autoclaving and cooling of native starch in proso millet could lead to an increase of the RS content to 15.5% [111]. RS in native and treated millet type starches are determined by the total amylose content [111]. The *in vivo* digestibility of native RS of millets and rice (*Oryza sativa*) were evaluated in rats by Ref. [109]. They found that proso millet had 50% digestibility which was significantly higher compared to other millets but still lower than the rice which had 59% [109]. In addition, they observed that compared to a rice diet, the blood glucose, serum cholesterol, and serum triglyceride levels were reduced in rats fed with the native starch of proso millet and treated starch [109].

4.3. Dietary fibre

The American Association of Cereal Chemists (2001) defined dietary fibre (DF) as “the edible parts of plant or analogous carbohydrates that are resistant to digestion and absorption in the human small intestine with complete or partial fermentation in the large intestine”. This

definition includes polysaccharides, oligosaccharides, lignin, and associated plant substances [112]. High DF consumption has been associated with many metabolic, cardiovascular, and colonic health benefits [113]. Because of these benefits, integrating more DF into the diet is advisable. In the case of proso millet, DF content ranges between 8.9 and 12.5% [114]. On the other hand, whole grain “kabog millet” contains 14–15% DF, whilst dehulled “kabog millet” has around 4% DF [99]. Proso millet also contains hemicellulose, which is mainly made up of glucose, arabinose, uronic acid, and xylose, and is considered DF [103]. In comparison, wheat flour has roughly 12% DF and maize has around 13% DF [25]. White rice, brown rice, red rice, and black rice contain around 1%, 4%, 6%, and 5% DF, respectively [99].

4.4. Protein

Proso millet and other millets crops are gluten-free, which makes it ideal for people with gluten-intolerance and coeliac disease [115]. There are four groups of proteins in grains based on their solubility: (1) albumins (soluble in distilled water and dilute buffers at neutral pH); (2) globulins (soluble in salt solutions but insoluble in distilled water); (3) glutelins (soluble in dilute acid or alkali solutions); and (4) prolamins (soluble in aqueous alcohols of 70–90%) [116]. Prolamin, the main protein fraction in proso millet, constitutes 25.1–36.9% of total protein [103,117]; and is composed of a major band (24 kDa) and two minor bands (14 and 17 kDa) when run under SDS-PAGE [118]. In the case of kabog millet, the total protein content ranges from 12 to 13% in whole kabog millet and dehulled kabog millet [99]. In comparison, wheat flour and maize flour have roughly 14% and 12% total protein, respectively [25]. This is comparable in kabog millet. Meanwhile, black rice has roughly 8% total protein [99]. So far, no detailed analyses of the different protein fractions have been performed on kabog millet; however, an SDS-PAGE of total protein extracts from kabog millet and wheat

flour confirms the absence of gluten fractions in kabog millet (Supplementary Fig. 3).

4.5. Amino acid composition and protein quality

The essential amino acid composition of a protein defines its quality. The amino acid composition of proso millet and whole kabog millet grains is presented in Table 4 [18,99]. It shows that amongst the essential amino acids, whole kabog millet contains relatively low histidine (His), methionine (Met), and phenylalanine (Phe) compared to other proso millet varieties [93,119]. In comparison, a study on six most-yielding varieties of wheat collected from the Agricultural Research Institute in Tarnab, Iran showed that wheat proteins from these varieties are deficient in Lys, Trp, Thr, Met, and His [120]. On the other hand, maize protein is deficient in Lys and Trp and has fair amounts of sulfur-containing amino acids, Met and Cys [101]. The essential amino acids Lys, Val, and Ile are higher in rice [99].

Proso millet is primarily low in one of the essential amino acids, Lys [103] due to the low content of lysine-rich albumin-globulin and glutelin fractions [103]. The *in vitro* digestibility of raw and cooked proso millet flour following the multi-enzyme protocol of [121] was found to have an average of 71.3% and 88.6%, respectively [119]. On the other hand [122], reported a true digestibility of 95%–99.3% using rats fed with dehulled millet diets. The enzymatic method, therefore, could lead to under-estimates.

To evaluate the protein quality, several methods have been proposed. The “protein digestibility–corrected amino acid score (PDCAAS)” is one of the methods and was developed by the FAO/WHO to evaluate the protein quality based on human amino acid requirements [123]. The limiting amino acid score (that is, the ratio of the first-limiting amino acid in a gram of target food protein to that in a reference protein or requirement value) is multiplied by the protein digestibility [124]. The essential amino acid requirements of preschool-aged children is the basis of this scoring pattern [125] and is calculated using the following formula [125]:

$$PDCAAS (\%) = \frac{\text{mg of limiting amino acid in 1 g of test protein}}{\text{mg of same amino acid in 1 g of reference protein}} \times \text{faecal true digestibility (100 \%)} \times 100$$

A PDCAAS of 1 means that the entire minimal requirements for indispensable amino acid intake would be met if the amount of the test protein eaten was equivalent to the estimated average requirement for protein. For high-quality proteins that have a PDCAAS greater than 1.0, the PDCAAS scores are truncated to 1.0 [126]. For kabog millet flour, both whole and dehulled, the PDCAAS values ranged from 0.25 to 0.30 (Supplementary Table 1).

Digestible indispensable amino acid score (DIAAS), a more recent protein quality score uses the true ileal protein digestibility rather than the faecal protein digestibility [127]. DIAAS is based on the comparison between the content of all digestible essential amino acids present in a protein to that of a reference protein, which has an amino acid profile similar with the requirement by a 0.5–3 years old child [127]. The DIAAS is calculated as follows:

$$DIAAS = 100 \times \frac{\text{mg of digestible dietary indispensable amino acid in 1 g dietary protein}}{\text{mg of the same dietary indispensable amino acid in 1 g reference protein}}$$

The indispensable amino acid in the DIAAS equation is the amino acid that has the lowest reference ratio [127]. The DIAAS values of

cooked cereals and pseudocereals are 42 for brown rice, 37 for polished rice, 68 for buckwheat, 43 for oats, 7 for proso millet, 10 for foxtail millet, and 20 for wholewheat [128]. Except for buckwheat, which is limiting in sulfur-containing amino acids, the other cereals are limiting in lysine. The DIAAS scores of whole milk is 114 while that of hard-boiled eggs, and chicken breast had 113, and 108, respectively [129].

4.6. Phenolic acids

Phenolic acids are hydroxylated derivatives of benzoic and cinnamic acids. They act as antioxidants and prevent damage of cells due to free-radical oxidation reactions [130]. In proso millet, they can be found in the endosperm and primarily in the bran can [131–133]. Hydroxycinnamic acids are more common than hydroxybenzoic acids in proso millets [134], with ferulic and chlorogenic acids being the most abundant in three proso millet cultivars [134]. The predominant phenolic acids in proso millet grits are ferulic acid and *p*-coumaric acids, ferulic acid dehydromers, and soluble chlorogenic acid [135]. [136] noted that proso millet had the least total phenolic content amongst kodo, finger, foxtail, proso, pearl, and little millets), (both bound and soluble: ~9.4 μmol ferulic acid equivalent/g defatted meal), whereas kodo millet had the highest total phenolic content, with ~114 μmol ferulic acid equivalent/g defatted meal for both bound and soluble phenolic acids. In whole kabog millet, phenolic acid levels are in the range of 1500–1600 μg/g sample, with *p*-coumaric acid and ferulic acids being the most abundant in whole grain kabog millet [99]. Whole grain kabog millet also contains vanillic acid (~60–70 μg/g sample) and cinnamic acid (~35 μg/g sample) [99]. In comparison with pigmented maize varieties grown in the Philippines, *p*-coumaric (~44–96 μg/g sample), ferulic (~2–5 μg/g sample), and gallic (~10–26 μg/g sample) acids were the major phenolic acids identified [137]. Ferulic acid can also be found in finger millet, existing as a bound form with arabinoxylans. This water-soluble feruloyl arabinoxylans are called feraxans, one of the major components of soluble fibre in finger millet [138]. It has been

shown to be a potent antioxidant [138].

In a study on antioxidant activity of frequently consumed cereals and beans in Korea, Choi et al. [139] found that proso millet had significantly lower antioxidant activities and had lower total phenolic contents than red sorghum (25 × lower) and black rice (10 × lower) in terms of mg gallic acid equivalent (GAE). However, the GAE values for proso millet were comparable with those of white rice, brown rice, mungbean, foxtail millet, barley, and adlay [139]. In another study by Ref. [136]; foxtail millet had higher antioxidative activity in terms of Trolox equivalent antioxidant capacity (TEAC) and reducing power in both bound and soluble phenolic acid extracts than that of proso millet. In a recent study on kabog millet, the TEAC values of whole kabog millet total phenolic acid extracts were comparable to those of black rice, whilst the TEAC values of dehulled kabog millet were significantly lower, indicating that dehulling can remove important antioxidants found in the bran [99]. In addition, phenolic acids have different antioxidant activities depending on whether they are found in free, esterified, glycosylated, and/or non-glycosylated forms [140,141].

4.7. Commercial food applications of proso millet and “kabog millet”

Proso millet can be used in many food applications. Food applications can depend on the properties and amylose content of the proso

Table 4
Maximum values and minimum values for crude protein and amino acids.

Essential	Minimum ^{a,b,f}	Maximum ^{a,b,f}	Whole Kabog millet ^c
Lysine (Lys)	1.60	3.48	1.58–1.81
Histidine (His)	2.30	3.94	1.81–1.90
Threonine (Thr)	3.70	4.50	3.07–3.16
Valine (Val)	4.69	7.30	6.37–6.79
Methionine (Met)	3.40	4.30	0.88–0.95
Isoleucine (Ile)	4.22	5.81	4.64–4.70
Leucine (Leu)	12.52	14.70	14.08–14.26
Tryptophan (Trp)	n.a.	n.a.	n.a.
Phenylalanine (Phe)	5.62	6.82	4.25–4.26
Non-essential	Minimum ^{a,b,f}	Maximum ^{a,b,f}	Whole Kabog millet ^c
Arginine (Arg)	4.00	4.30	2.97–3.33
Aspartic acid (Asp)	6.60	12.00	5.26–5.27
Serine (Ser)	4.43	7.90	7.27–7.54
Glutamic acid (Glu)	21.94	25.40	16.88–16.98
Proline (Pro)	7.60	7.90	7.92–8.08
Cysteine (Cys)	0.90	1.10	n.a.
Glycine (Gly)	2.80	4.73	4.09–4.38
Alanine (Ala)	9.68	12.40	14.67–15.54
Tyrosine (Tyr)	4.30	4.70	2.57–2.75
Crude Protein	12.12 ^d	16.30 ^d	12.00–12.10 ^e

n.a. Not analysed.

^a Amino acid data is expressed in g/100 g protein.

^b [93,119].

^c [99].

^d Protein content is expressed in % of dry matter; Total N was analysed by micro-Kjeldahl.

^e Total N was analysed by Dumas procedure and the conversion factor is 6.25.

^f Adapted from Ref. [18].

millet starch. Less amylose ($\leq 10\%$) means a lower peak temperature during pasting [142]. Higher amylose starches exhibit higher cold paste viscosity [143]. Wax starch breaks down more than non-waxy starch. Waxy starches also retrograded more slowly during pasting, indicating greater stability [144]. Waxy millets are therefore good raw materials for beverages due to their low retrogradation [145]. Based also on these properties, the cultivar Earlybird, a low-amylose proso millet, is suggested for breadmaking, whilst cultivars Sunrise and Sunup, for example, are good for gluten-free pasta because of their higher cold paste viscosity [142].

As mentioned, proso millet can be incorporated into wheat-based breads. Addition of enzymes such as xylanase and transglutaminase can improve bread properties by increasing the specific volume [146]. Using transglutaminase alone, a cross-linking enzyme, results in a very dense undesirable crumb [147]. In gluten-free breads containing proso millet flour, adding non-gluten proteins like pea, rice, and whey, and the enzyme transglutaminase can increase the volume and decrease the hardness and bitterness of the breads [148]. Proso millet can also be incorporated into pasta. Varieties with high amylose and carotenoid content are more suitable for this application [149]. Incorporation of xanthan gum and guar gum made the dough more structured and reduced the disintegration after cooking [150]. Proso millet pasta was more yellow than wheat pasta after cooking due to higher lutein and zeaxanthin in proso millet [150].

The undesirable bitterness of proso millet remains an obstacle to its widespread consumption. It is unclear which constituents contribute most to its bitterness because even in food products made of proso millet that have low tannins exhibit a degree of bitterness. Different processing strategies such as sprouting or fermentation can be used and assessed to reduce bitterness [151].

5. Conclusion

Diversification of our diet is a means to ensure food security by providing sufficient and balanced nutrition in a rapidly changing world and helps prevent the extinction of many plant food species. Proso millet, under which “kabog millet” is classified, requires less water and

fertilisers, can withstand drought stress, and is a short-season crop, making it suitable for cultivation in areas that are at risk to the effects of climate change, famine, and malnutrition. To prevent extinction of ancient grain species, nutritional studies on these crops should be performed and emphasised for consumers to start integrating these crops into their diets. In the absence of nutritional profile analyses, farmers abandon growing these crops for lack of a market and means to trade and advertise them. “Kabog millet” was on the brink of extinction because consumers did not know how nutritious “kabog millet” is, and hence, there was limited market for its consumption and cultivation. Consumption of these crops helps small-scale and medium-scale farmers with their livelihoods by providing them a source of income and encourages them to preserve landraces with highly nutritious and desirable morpho-agronomic qualities that might otherwise have gone forgotten and extinct.

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Declaration of competing interest

The Authors declare no conflict of interest.

Data availability

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Appendix A. Supplementary data

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References

- [1] FAO, Millet: Post-harvest Operations, 2001. <http://www.fao.org/3/av009e/av009e.pdf> (23 Mar 2021).
- [2] D.Q. Fuller, Millets: origins and development, in: C. Smith (Ed.), *Encyclopedia of Global Archaeology*, Springer New York, New York, NY, 2014, pp. 4945–4948.
- [3] R.M. Gutaker, S.C. Groen, E.S. Bellis, et al., Genomic history and ecology of the geographic spread of rice, *Nature Plants* 6 (2020) 492–502.
- [4] H. Lu, J. Zhang, K-b Liu, et al., Earliest domestication of common millet *Panicum miliaceum* in East Asia extended to 10,000 years ago, *Proc. Natl. Acad. Sci. USA* 106 (2009) 7367–7372.
- [5] Z. Zhao, New archaeobotanic data for the study of the origins of agriculture in China, *Curr. Anthropol.* 52 (2011) S295–S306.
- [6] X. Diao, G. Jia, Origin and domestication of foxtail millet, in: A. Doust, X. Diao (Eds.), *Genetics and Genomics of Setaria*, Springer International Publishing, Cham, 2017, pp. 61–72.
- [7] J.M.J. de Wet, Domestication of african cereals, *Afr. Econ. Hist.* (1977) 15–32.
- [8] R.P. Joshi, A.K. Jain, N. Malhotra, M. Kumari, Chapter 4 - origin, domestication, and spread, in: S. Mohar, S. Sood (Eds.), *Woodhead Publishing Series in Food Science, Technology and Nutrition, Millets and Pseudo Cereals*, Woodhead Publishing, 2021, pp. 33–38, <https://doi.org/10.1016/B978-0-12-820089-6.00004-5>.

- [9] C.J. Stevens, C. Murphy, R. Roberts, L. Lucas, F. Silva, D.Q. Fuller, Between China and South Asia: a Middle Asian corridor of crop dispersal and agricultural innovation in the bronze age, *Holocene* 26 (2016) 1541–1555.
- [10] M. Frachetti, Multiregional emergence of mobile pastoralism and nonuniform institutional complexity across Eurasia, *Curr. Anthropol.* 53 (2012) 2–38.
- [11] N.F. Miller, R.N. Spengler, M. Frachetti, Millet cultivation across Eurasia: origins, spread, and the influence of seasonal climate, *Holocene* 26 (2016) 1566–1575.
- [12] R. Spengler, M. Frachetti, P. Doumani, et al., Early agriculture and crop transmission among Bronze Age mobile pastoralists of Central Eurasia, *Proc. Royal Soc. B* 281 (2014), <https://doi.org/10.1098/rspb.2013.3382>, 20133382-20133382.
- [13] A. Obilana, Overview: importance of millets in Africa, *World* 38 (2003) 28–45. <http://www.afripro.org.uk/papers/paper02Obilana.pdf> (23 Mar 2021).
- [14] Faostat. <http://www.fao.org/faostat/en/#home>, 2020. (Accessed 23 March 2021).
- [15] I.K. Das, S. Rakshit, Chapter 1 - millets, their importance, and production constraints, in: I.K. Das, P.G. Padmaja (Eds.), *Biotic Stress Resistance in Millets*, Academic Press, 2016, pp. 3–19.
- [16] Faostat. <http://www.fao.org/faostat/en/#home>, 2021. (Accessed 24 September 2021).
- [17] D. Baltensperger, Foxtail and proso millet, in: J. Janick (Ed.), *Progress in New Crops*, ASHS Press, Alexandria, 1996, pp. 182–190.
- [18] E. Arendt, E. Zannini, Millet, in: E. Arendt, E. Zannini (Eds.), *Cereal Grains for the Food and Beverage Industries*, first ed., Woodhead Publishing Limited: Sawston, Cambridge, UK, 2013, pp. 312–350.
- [19] D. Baltensperger, Progress with proso, pearl and other millets, in: J. Janick, A. Whipkey (Eds.), *Trends in New Crops and New Uses*, ASHS Press, Alexandria, 2002, pp. 100–103.
- [20] M. Vetriventhan, H.D. Upadhyaya, Diversity and trait-specific sources for productivity and nutritional traits in the global proso millet (*Panicum miliaceum* L.) germplasm collection, *Crop J.* 6 (2018) 451–463.
- [21] R. Hoffmann-Bahnsen, Alte Kulturpflanze neu entdeckt—Perspektiven und Möglichkeiten der Wiederinkulturation von Rispenhirse (*Panicum miliaceum*) im ökologischen Landbau. On-farm-Erhaltung genetischer Ressourcen von Getreide und Ölpflanzen, 2004, pp. 91–100.
- [22] C. Humphrys, Raps und Hirse im biologischen anbau (Rape and millet in organic farming), in: *Biolandbau (Organic Farming) Congress*, 2005.
- [23] S. Matz, Millet, wild rice, adlay, and rice grass, in: *Cereal Science*, Avi Press, Westport, CT, 1986, pp. 225–229.
- [24] C. Habiaryemye, J.B. Matanguihai, J. D’Alpoim Guedes, et al., Proso millet (*Panicum miliaceum* L.) and its potential for cultivation in the Pacific Northwest, U.S.: a review, *Front. Plant Sci.* 7 (2017), 1961–1961.
- [25] S. Das, R. Khound, M. Santra, D.K. Santra, Beyond bird feed: proso millet for human health and environment, *Agriculture* 9 (2019) 64.
- [26] D.J. Lyon, P.A. Burgener, K.L. DeBoer, et al., Proso Millet in the Great Plains, University of Nebraska Extension Service, Lincoln, NB, 2008.
- [27] D.K. Santra, Proso Millet Varieties for Western Nebraska, University of Nebraska-Lincoln, Lincoln, NE, 2013.
- [28] D. Lyon, P. Burgener, K. DeBoer, Producing and Marketing Proso Millet in the Great Plains, 2008. <https://digitalcommons.unl.edu/cgi/viewcontent.cgi?referer=https://www.ecosia.org/&httpsredir=1&article=1702&context=extensionhist>. (Accessed 23 March 2021).
- [29] S. Rajput, D. Santra, Evaluation of genetic diversity of proso millet germplasm available in the United States using simple-sequence repeat markers, *Crop Sci.* 56 (2016) 2401–2409.
- [30] D.C. Nielsen, M.F. Vigil, Water use and environmental parameters influence proso millet yield, *Field Crop. Res.* 212 (2017) 34–44.
- [31] M. Zarnkow, M. Keßler, W. Back, E.K. Arendt, M. Gastl, Optimisation of the mashing procedure for 100% malted proso millet (*Panicum miliaceum* L.) as a raw material for gluten-free beverages and beers, *J. Inst. Brew.* 116 (2010) 141–150.
- [32] J.M.J. de Wet, Origin, evolution and systematics of minor cereals, in: A. Seetharam, K.W. Riley, G. Harinarayana (Eds.), *Small Millets in Global Agriculture*, Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi, India, 1986, pp. 19–30.
- [33] V. Reddy, H. Upadhyaya, C.L.L. Gowda, Morphological characterization of world’s proso millet germplasm, *J. SAT Agric. Res.* 3 (2007) 4pp.
- [34] M. Vetriventhan, V.C.R. Azevedo, H.D. Upadhyaya, D. Naresh, Variability in the global proso millet (*Panicum miliaceum* L.) germplasm collection conserved at the ICRIAT genebank, *Agriculture* 9 (2019) 112, <https://doi.org/10.3390/agriculture9050112>.
- [35] H.V. Hunt, F. Badakshi, O. Romanova, C.J. Howe, M.K. Jones, J.S.P. Heslop-Harrison, Reticulate evolution in *Panicum* (Poaceae): the origin of tetraploid broomcorn millet, *P. miliaceum*, *J. Exp. Bot.* 65 (2014) 3165–3175.
- [36] M. Vetriventhan, H.D. Upadhyaya, S.L. Dwivedi, S.K. Pattanashetti, S.K. Singh, Finger and foxtail millets, in: M. Singh, H.D. Upadhyaya (Eds.), *Genetic and Genomic Resources for Grain Cereals Improvement*, Academic Press, San Diego, 2016, pp. 291–319.
- [37] A. Bonjean, Origin and historical diffusion in China of major native and alien cereals, in: H. Zhonghu, A.P.A. Bonjean (Eds.), *Cereals in China*, CIMMYT: Texcoco, Mexico, 2010, pp. 1–14.
- [38] H.D. Upadhyaya, M. Vetriventhan, S.L. Dwivedi, S.K. Pattanashetti, S.K. Singh, 8 - proso, barnyard, little, and kodo millets, in: M. Singh, H.D. Upadhyaya (Eds.), *Genetic and Genomic Resources for Grain Cereals Improvement*, Academic Press, San Diego, 2016, pp. 321–343.
- [39] S. Borbon, *In Situ* Characterization of Millet Cultivars Grown in Cebu, Philippines: Crop Improvement Proposals, PhD Thesis, Cebu Technological University, Cebu, Philippines, 2011.
- [40] L. Wang, X. Wang, Q. Wen, B. Wu, L. Cao, Identification of salt tolerance in Chinese proso millet germplasm, *Plant Genetic Resource.* 8 (2007) 426–429.
- [41] D.-Z. Zhang, R.B. Panhwar, J.-J. Liu, et al., Morphological diversity and correlation analysis of phenotypes and quality traits of proso millet (*Panicum miliaceum* L.) core collections, *J. Integr. Agric.* 18 (2019) 958–969.
- [42] L. Wang, X.Y. Wang, Q. Wen, B. Wu, Research and utilization of Proso millet germplasm resource in China, *Plant Genetic Resource.* 6 (2005), 474–471.
- [43] H.D. Upadhyaya, S. Sharma, C. Laxmipathi Gowda, V. Reddy, S. Sube, Developing proso millet (*Panicum miliaceum* L.) core collection using geographic and morpho-agronomic data, *Crop Pasture Sci.* 62 (2011) 383–389.
- [44] X. Yuan, Y. Zhang, Y. Su, et al., The relationship between growth period and traits of stem and panicle in foxtail millet, *J. Shanxi Agric. Univ. (Soc. Sci. Ed.)* 36 (2016) 391–394.
- [45] J.L. Bennetzen, J. Schmutz, H. Wang, et al., Reference genome sequence of the model plant *Setaria*, *Nat. Biotechnol.* 30 (2012) 555–561.
- [46] G. Zhang, X. Liu, Z. Quan, et al., Genome sequence of foxtail millet (*Setaria italica*) provides insights into grass evolution and biofuel potential, *Nat. Biotechnol.* 30 (2012) 549–554.
- [47] K. Kumari, M. Muthamilarasan, G. Misra, et al., Development of eSSR-markers in *Setaria italica* and their applicability in studying genetic diversity, cross-transferability and comparative mapping in millet and non-millet species, *PLoS One* 8 (2013), <https://doi.org/10.1371/journal.pone.0067742> e67742-e67742.
- [48] M. Muthamilarasan, B. Venkata Suresh, G. Pandey, K. Kumari, S.K. Parida, M. Prasad, Development of 5123 intron-length polymorphic markers for large-scale genotyping applications in foxtail millet, *DNA Res.* 21 (2014) 41–52.
- [49] G. Pandey, G. Misra, K. Kumari, Genome-wide development and use of microsatellite markers for large-scale genotyping applications in foxtail millet [*Setaria italica* (L.)], *DNA Res.* 20 (2013) 197–207.
- [50] C.B. Yadav, M. Muthamilarasan, G. Pandey, Y. Khan, M. Prasad, Development of novel microRNA-based genetic markers in foxtail millet for genotyping applications in related grass species, *Mol. Breed.* 34 (2014) 2219–2224.
- [51] S. Rajput, T. Plyler-Harveson, D. Santra, Development and characterization of SSR markers in proso millet based on switchgrass genomics, *Am. J. Plant Sci.* 5 (2014) 175–186.
- [52] D. Karam, P. Westra, S. Nissen, S. Ward, J. Figueiredo, Genetic diversity among proso millet (*Panicum miliaceum*) biotypes assessed by AFLP technique, *Planta Daninha* 22 (2004) 167–174.
- [53] M. Liu, Y. Xu, J. He, S. Zhang, Y. Wang, P. Lu, Genetic diversity and population structure of broomcorn millet (*Panicum miliaceum* L.) cultivars and landraces in China based on microsatellite markers, *Int. J. Mol. Sci.* 17 (2016), 370–370.
- [54] X. Hu, J. Wang, P. Lu, H. Zhang, Assessment of genetic diversity in broomcorn millet (*Panicum miliaceum* L.) using SSR markers, *J. Genet. Genom.* 36 (2009) 491–500.
- [55] Y.-I. Cho, J.-W. Chung, G.-A. Lee, et al., Development and characterization of twenty-five new polymorphic microsatellite markers in proso millet (*Panicum miliaceum* L.), *Gene. Genomics* 32 (2010) 267–273.
- [56] H.K. M’Ribu, K.W. Hilu, Detection of interspecific and intraspecific variation in *Panicum* millets through random amplified polymorphic DNA, *Theor. Appl. Genetic.* 88 (1994) 412–416.
- [57] R. Lágler, G. Gyulai, M. Humphreys, et al., Morphological and molecular analysis of common millet (*P. miliaceum*) cultivars compared to an aDNA sample from the 15th century (Hungary), *Euphytica* 146 (2005) 77–85.
- [58] M. Parani, K. Rajesh, M. Lakshmi, L. Parducci, A.E. Szmíd, A. Parida, Species identification in seven small millet species using polymerase chain reaction - restriction fragment length polymorphism of trnS-psbC gene region, *Genome* 44 (2001) 495–499.
- [59] J.M.J. de Wet, K.E. Prasada Rao, D.E. Brink, Systematics and domestication of *Panicum sumatrense* (graminae), *J. Agric. Tradit. Bot. Appl.* (1983) 159–168.
- [60] S. Hiremath, G. Patil, S. Salimath, Genome homology and origin of *Panicum sumatrense* (Gramineae), *Cytologia* 55 (1990) 315–319.
- [61] R.H.M. Salih, Majeský L, T. Schwarzacher, R. Gornall, P. Heslop-Harrison, Complete chloroplast genomes from apomictic *Taraxacum* (Asteraceae): identity and variation between three microspecies, *PLoS One* 12 (2) (2017), e0168008, <https://doi.org/10.1371/journal.pone.0168008>.
- [62] X. Nie, X. Zhao, S. Wang, et al., Complete chloroplast genome sequence of broomcorn millet (*Panicum miliaceum* L.) and comparative analysis with other panicoidae species, *Agronomy* 8 (2018) 159.
- [63] X. Cao, S. Litu, Z. Mu, Z. Qiao, Characterisation and comparative analysis of the whole chloroplast genomes of five common millet (*Panicum miliaceum*), *Mitochondrial DNA Part B, Resources* 6 (3) (2021) 738–744, <https://doi.org/10.1080/23802359.2020.1866452>.
- [64] C. Zou, L. Li, D. Miki, et al., The genome of broomcorn millet, *Nat. Commun.* 10 (2019) 436, <https://doi.org/10.1038/s41467-019-08409-5>.
- [65] K.L. Nguyen, A. Grondin, B. Courtois, P. Gante, Next-generation sequencing accelerates crop gene discovery, *Trends Plant Sci.* 24 (3) (2019) 263–274, <https://doi.org/10.1016/j.tplants.2018.11.008>.
- [66] D.P. Wickland, G. Battu, K.A. Hudson, B.W. Diers, M.E. Hudson, A comparison of genotyping-by-sequencing analysis methods on low-coverage crop datasets shows advantages of a new workflow, GB-eaSy, *BMC Bioinf.* 18 (1) (2017) 586, <https://doi.org/10.1186/s12859-017-2000-6>.
- [67] R.J. Elshire, J.C. Glaubitz, Q. Sun, et al., A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species, *PLoS One* 6 (5) (2011), e19379, <https://doi.org/10.1371/journal.pone.0019379>.

- [68] P.K. Sahu, R. Sao, S. Mondal, et al., Next generation sequencing based forward genetic approaches for identification and mapping of causal mutations in crop plants: a comprehensive review, *Plants* 9 (2021) 1355, <https://doi.org/10.3390/plants9101355>.
- [69] E.S. Lander, L.M. Linton, B. Birren, et al., Initial sequencing and analysis of the human genome, *Nature* 409 (2001) 860–921, <https://doi.org/10.1038/35057062>.
- [70] B. Derakhshani, H. Jafary, B. Maleki Zanjani, K. Hasanpur, K. Mishina, et al., Combined QTL mapping and RNA-Seq profiling reveals candidate genes associated with cadmium tolerance in barley, *PLoS One* 15 (4) (2020), e0230820, <https://doi.org/10.1371/journal.pone.0230820>.
- [71] S. Wang, M. Cao, X. Ma, et al., Integrated RNA sequencing and QTL mapping to identify candidate genes from *Oryza rufipogon* associated with salt tolerance at the seedling stage, *Front. Plant Sci.* 8 (2017) 1427, <https://doi.org/10.3389/fpls.2017.01427>.
- [72] J. Majewski, T. Pastinen, The study of eQTL variations by RNA-seq: from SNPs to phenotypes, *Trends Genet.* 27 (2) (2011) 72–79, <https://doi.org/10.1016/j.tig.2010.10.006>.
- [73] H.J. Westra, L. Franke, From genome to function by studying eQTLs, *Biochim. Biophys. Acta* 1842 (10) (2014) 1896–1902, <https://doi.org/10.1016/j.bbdis.2014.04.024>.
- [74] K. Weitmier, S.C. Straub, R.C. Cronn, M. Fishbein, R. Schmickl, A. McDonnell, A. Liston, Hyb-Seq: combining target enrichment and genome skimming for plant phylogenomics, *Appl. Plant Sci.* 2 (9) (2014), <https://doi.org/10.3732/apps.1400042>.
- [75] S.C. Straub, M. Parks, K. Weitmier, M. Fishbein, R.C. Cronn, A. Liston, Navigating the tip of the genomic iceberg: next-generation sequencing for plant systematics, *Am. J. Bot.* 99 (2) (2012) 349–364, <https://doi.org/10.3732/ajb.1100335>.
- [76] X. Yu, D. Yang, C. Guo, L. Gao, Plant phylogenomics based on genome-partitioning strategies: progress and prospects, *Plant Divers.* 40 (4) (2018) 158–164, <https://doi.org/10.1016/j.pld.2018.06.005>.
- [77] K.H. Ghimire, B.K. Joshi, R. Dhakal, B.R. Sthapit, Diversity in proso millet (*Panicum miliaceum* L.) landraces collected from Himalayan mountains of Nepal, *Genet. Resour. Crop Evol.* 65 (2018) 503–512.
- [78] A. Parajuli, A. Subedi, A.R. Adhikari, S.R. Sthapit, B.K. Joshi, D. Gauchan, B. Bhandari, Baseline Survey Report: IV. Chhipra, Humla. Integrating Traditional Crop Genetic Diversity into Technology: Using a Biodiversity Portfolio Approach to Buffer against Unpredictable Environmental Change in the Nepal Himalayas, LI-BIRD, NARC and Bioiversity International, Pokhara, Nepal, 2016, pp. 1–44.
- [79] E. Palikhey, S. Sthapit, S. Gautam, et al., Integrating traditional crop genetic diversity into technology: using a biodiversity portfolio approach to buffer against unpredictable environmental change in Nepal Himalayas, in: Baseline Survey Report, DoA Swiss Agency for Development and Cooperation SDC, 2019.
- [80] A.K. Trivedi, L. Arya, M. Verma, S.K. Verma, R.K. Tyagi, A. Hemantaranjan, Genetic variability in proso millet [*Panicum miliaceum*] germplasm of Central Himalayan Region based on morpho-physiological traits and molecular markers, *Acta Physiol. Plant.* 37 (2015) 23, <https://doi.org/10.1007/s11738-014-1770-y>.
- [81] J. Cockram, H. Jones, F.J. Leigh, et al., Control of flowering time in temperate cereals: genes, domestication, and sustainable productivity, *J. Exp. Bot.* 58 (2007) 1231–1244.
- [82] H.V. Hunt, M.G. Campana, M.C. Lawes, et al., Genetic diversity and phylogeography of broomcorn millet (*Panicum miliaceum* L.) across Eurasia, *Mol. Ecol.* 20 (2011) 4756–4771.
- [83] G.W. Crawford, Plant domestication in East Asia, in: J. Habu, P.V. Lape, J. W. Olsen (Eds.), *Handbook of East and Southeast Asian Archaeology*, Springer New York, New York, NY, 2017, pp. 421–435.
- [84] G. Shelach, The earliest neolithic cultures of northeast China: recent discoveries and new perspectives on the beginning of agriculture, *J. World PreHistory* 14 (2000) 363–413.
- [85] X. Liu, H. Hunt, M.K. Jones, River valleys and foothills: changing archaeological perceptions of North China's earliest farms, *Antiquity* 83 (2008) 82–95.
- [86] M.C. Lillie, M. Richards, Stable isotope analysis and dental evidence of diet at the mesolithic–neolithic transition in Ukraine, *J. Archaeol. Sci.* 27 (2000) 965–972.
- [87] M. Flajsman, N. Stajner, D. Acko, Genetic diversity and agronomic performance of Slovenian landraces of proso millet (*Panicum miliaceum* L.), *Turk. J. Bot.* 43 (2019) 185–195.
- [88] G. Romano, L. Del Coco, F. Milano, M. Durante, S. Palombieri, F. Sestili, A. Visioni, A. Jilal, F.P. Fanizzi, B. Laddomada, Phytochemical profiling and untargeted metabolite fingerprinting of the MEDWHEALTH wheat, barley and lentil wholemeal flours, *Foods* 11 (24) (2022) 4070, <https://doi.org/10.3390/foods11244070>.
- [89] B. Rao, M. Nagasampige, M. Ravikiran, Evaluation of nutraceutical properties of selected small millets, *J. Pharm. BioAllied Sci.* 3 (2011) 277–279.
- [90] A.S.M. Saleh, Q. Zhang, J. Chen, Q. Shen, Millet grains: nutritional quality, processing, and potential health benefits, *Compr. Rev. Food Sci. Food Saf.* 12 (2013) 281–295.
- [91] S.S. Gomashe, Proso millet, *Panicum miliaceum* (L.): genetic improvement and research needs, in: J.V. Patil (Ed.), *Millets and Sorghum: Biology and Genetic Improvement*, John Wiley & Sons, Chichester, UK, 2017, pp. 150–169.
- [92] P.R. Shewry, Wheat, *J. Exp. Bot.* 60 (6) (2009) 1537–1553, <https://doi.org/10.1093/jxb/erp058>.
- [93] J. Kalinova, J. Moudry, Content and quality of protein in proso millet (*Panicum miliaceum* L.) varieties, *Plant Foods Hum. Nutr.* 61 (2006) 43.
- [94] P. Casey, K. Lorenz, Millet: functional and nutritional properties, *Baker's Dig.* (1977) 45–51.
- [95] J.H. Hulse, E.M. Laing, O.E. Pearson, *Sorghum and the Millets: Their Composition and Nutritive Value*, Academic Press, London; New York, 1980.
- [96] G.A. Yañez, C.E. Walker, Effect of tempering parameters on extraction and ash of proso millet flours, and partial characterization of proso starch, *Cereal Chem.* 63 (1986) 164–167.
- [97] K.P. Parameswaran, S. Sadasivam, Changes in the carbohydrates and nitrogenous components during germination of proso millet, *Panicum miliaceum*, *Plant Foods Hum. Nutr.* 45 (1994) 97–102.
- [98] S.K. Kim, H.J. Choi, D.K. Kang, H. Kim, Starch properties of native proso millet (*Panicum miliaceum* L.), *Agron. Res.* 10 (2012) 311–318.
- [99] J.O. Narciso, L. Nyström, Breathing new life to ancient crops: promoting the ancient philippine grain “kabog millet” as an alternative to rice, *Foods* 9 (2020) 1727.
- [100] H. Wieser, P. Koehler, K.A. Scherf, Chapter 6 - nutritional value of wheat, in: H. Wieser, P. Koehler, K.A. Scherf (Eds.), *Wheat - an Exceptional Crop*, Woodhead Publishing, 2020, pp. 133–148, <https://doi.org/10.1016/B978-0-12-821715-3.00006-X>.
- [101] FAO. <https://www.fao.org/3/t0395e/t0395e00.htm#Contents>, 1992. (Accessed 18 December 2022).
- [102] D.J. Gallant, B. Bouchet, P.M. Baldwin, Microscopy of starch: evidence of a new level of granule organization, *Carbohydr. Polym.* 32 (1997) 177–191.
- [103] S. Serna-Saldivar, L.W. Rooney, Structure and chemistry of sorghum and millets, in: D.A.V. Dendy (Ed.), *Sorghum and Millets: Chemistry and Technology*, American Association of Cereal Chemists, 1995, pp. 69–124.
- [104] Y. Tomita, Y. Sugimoto, S. Sakamoto, H. Fuwa, Some properties of starches of grain amaranths and several millets, *J. Nutr. Sci. Vitaminol.* 27 (1981) 471–484.
- [105] G.A. Yañez, C.E. Walker, L.A. Nelson, Some chemical and physical properties of proso millet (*Panicum miliaceum*) starch, *J. Cereal. Sci.* 13 (1991) 299–305.
- [106] H.N. Englyst, J.H. Cummings, Digestion of the polysaccharides of some cereal foods in the human small intestine, *Am. J. Clin. Nutr.* 42 (5) (1985) 778–787, <https://doi.org/10.1093/ajcn/42.5.778>. PMID: 2998174.
- [107] H.N. Englyst, S. Kingman, J. Cummings, Classification and measurement of nutritionally important starch fractions, *Eur. J. Clin. Nutr.* 46 (1992) S33–S50.
- [108] P. Raigond, R. Ezekiel, B. Raigond, Resistant starch in food: a review, *J. Sci. Food Agric.* 95 (2015) 1968–1978.
- [109] S.K. Kumari, B. Thayumanavan, Comparative study of resistant starch from minor millets on intestinal responses, blood glucose, serum cholesterol and triglycerides in rats, *J. Sci. Food Agric.* 75 (1997) 296–302.
- [110] G. Artavia, C. Cortés-Herrera, F. Granados-Chinchilla, Total and resistant starch from foodstuff for animal and human consumption in Costa Rica, *Curr. Res. Food Sci.* 3 (2020) 275–283, <https://doi.org/10.1016/j.crf.2020.11.001>.
- [111] M.-Z. Zheng, Y. Xiao, S. Yang, et al., Effects of heat–moisture, autoclaving, and microwave treatments on physicochemical properties of proso millet starch, *Food Sci. Nutr.* 8 (2020) 735–743, <https://doi.org/10.1002/fsn.31295>.
- [112] American Association of Cereal, Chemists report. <https://www.cerealsgrains.org/initiatives/definitions/Documents/DietaryFiber/DFDef.pdf>, 2001. (Accessed 24 September 2021).
- [113] T.M. Barber, S. Kabisch, A.F.H. Pfeiffer, M.O. Weickert, The health benefits of dietary fibre, *Nutrients* 12 (10) (2020) 3209, <https://doi.org/10.3390/nu12103209>.
- [114] D. Ferriola, M. Stone, Sweetener effects on flaked millet breakfast cereals, *J. Food Sci.* 63 (1998) 726–729.
- [115] S. Rai, A. Kaur, C.S. Chopra, Gluten-free products for celiac susceptible people, *Front. Nutr.* 5 (2018) 116, <https://doi.org/10.3389/fnut.2018.00116>.
- [116] K.J. Bradford, Seeds: physiology of development and germination, *Seed Sci. Res.* 5 (1995) 127–128.
- [117] R.W. Jones, A.C. Beckwith, U. Khoo, G.E. Inglett, Protein composition of proso millet, *J. Agric. Food Chem.* 18 (1970) 37–39.
- [118] K. Kohama, T. Nagasawa, N. Nishizawa, Polypeptide compositions and NH₂-terminal amino acid sequences of proteins in foxtail and proso millets, *Biosci., Biotechnol., Biochem.* 63 (11) (1999) 1921–1926, <https://doi.org/10.1271/bbb.63.1921>.
- [119] G. Ravindran, Seed protein of millets: amino acid composition, proteinase inhibitors and in-vitro protein digestibility, *Food Chem.* 44 (1992) 13–17.
- [120] M. Khan, E. Ali, S. Ali, W.M. Khan, M.A. Sajad, F. Hussain, Assessment of essential amino acids in wheat proteins: a case study, *J. Biodivers. Environ. Sci. (JBES)* 4 (6) (2014) 185–189.
- [121] H.W. Hsu, D.L. Vavak, L.D. Satterlee, G.A. Miller, A multienzyme technique for estimating protein digestibility, *J. Food Sci.* 42 (1977) 1269–1273.
- [122] P. Geervani, B.O. Eggum, Nutrient composition and protein quality of minor millets, *Plant Foods Hum. Nutr.* 39 (1989) 201–208.
- [123] FAO. http://www.fao.org/input/download/report/513/al89_40e.pdf, 1989. (Accessed 4 October 2021).
- [124] FAO. <http://www.fao.org/ag/humannutrition/35978-02317b979a686a57aa4593304ffc17f06.pdf>, 2011. (Accessed 24 September 2021).
- [125] G. Schaafsma, The protein digestibility–corrected amino acid score, *J. Nutr.* 130 (2000) 1865S–1867S.
- [126] R.R. Wolfe, S.M. Rutherford, I.-Y. Kim, P.J. Moughan, Protein quality as determined by the Digestible Indispensable Amino Acid Score: evaluation of factors underlying the calculation, *Nutr. Rev.* 74 (2016) 584–599.
- [127] I. Joye, Protein digestibility of cereal products, *Foods* 8 (2019) 199.
- [128] F. Han, F. Han, Y. Wang, et al., Digestible indispensable amino acid scores of nine cooked cereal grains, *Br. J. Nutr.* 121 (2019) 30–41.
- [129] C.P.F. Marinangeli, J.D. House, Potential impact of the digestible indispensable amino acid score as a measure of protein quality on dietary regulations and health, *Nutr. Rev.* 75 (2017) 658–667.

- [130] N. Kumar, N. Goel, Phenolic acids: natural versatile molecules with promising therapeutic applications, *Biotechnol. Rep.* 24 (2019), e00370, <https://doi.org/10.1016/j.btre.2019.e00370>.
- [131] D.H. Hahn, L.W. Rooney, Effect of genotype on tannins and phenols of sorghum, *Cereal Chem.* 63 (1986) 4–8.
- [132] C.M. McDonough, L.W. Rooney, C.F. Earp, Structural characteristics of *Eleusine corocana* (finger millet) using scanning electron and fluorescence microscopy, *Food Microstruct.* 5 (1986) 247–256.
- [133] P. Mattila, J.-M. Pihlava, J. Hellström, Contents of phenolic acids, alkyl- and alkenylresorcinols, and avenanthramides in commercial grain products, *J. Agric. Food Chem.* 53 (2005) 8290–8295.
- [134] L. Zhang, R. Liu, W. Niu, Phytochemical and antiproliferative activity of proso millet, *PLoS One* 9 (2014), e104058, <https://doi.org/10.1371/journal.pone.0104058>.
- [135] J. Kalinová, Nutritionally important components of proso millet (*Panicum miliaceum* L.), *Food, Global Sci. Book.* 1 (1) (2007) 91–100.
- [136] A. Chandrasekara, F. Shahidi, Content of insoluble bound phenolics in millets and their contribution to antioxidant capacity, *J. Agric. Food Chem.* 58 (2010) 6706–6714.
- [137] J.A.M.A. Libron, D.E.M. Cardona, J.M.C. Mateo, A.K.M. Beltran, A.P.P. Túaño, T. P. Laude, Nutritional properties and phenolic acid profile of selected Philippine pigmented maize with high antioxidant activity, *J. Food Compos. Anal.* 101 (2021), 103954, <https://doi.org/10.1016/j.jfca.2021.103954>.
- [138] R.S. Rao, G. Muralikrishna, Water soluble feruloyl arabinoxylans from rice and ragi: changes upon malting and their consequence on antioxidant activity, *Phytochemistry* 67 (1) (2006) 91–99, <https://doi.org/10.1016/j.phytochem.2005.09.036>.
- [139] Y. Choi, H.-S. Jeong, J. Lee, Antioxidant activity of methanolic extracts from some grains consumed in Korea, *Food Chem.* 103 (2007) 130–138.
- [140] C.A. Rice-Evans, N.J. Miller, G. Paganga, Structure-antioxidant activity relationships of flavonoids and phenolic acids, *Free Radic. Biol. Med.* 20 (7) (1996) 933–956, [https://doi.org/10.1016/0891-5849\(95\)02227-9](https://doi.org/10.1016/0891-5849(95)02227-9).
- [141] J. Chalas, C. Claise, M. Edeas, C. Messaoudi, L. Vergnes, A. Abella, A. Lindenbaum, Effect of ethyl esterification of phenolic acids on low-density lipoprotein oxidation, *Biomed. Pharmacother.* 55 (1) (2001) 54–60, [https://doi.org/10.1016/S0753-3322\(00\)00011-1](https://doi.org/10.1016/S0753-3322(00)00011-1).
- [142] C. Tyl, A. Marti, J. Hayek, J. Anderson, B.P. Ismail, Effect of growing location and variety on nutritional and functional properties of proso millet (*Panicum miliaceum*) grown as a double crop, *Cereal Chem.* 95 (2018) 288–301, <https://doi.org/10.1002/cche.10028>.
- [143] K. Li, T. Zhang, S. Narayanamoorthy, C. Jin, Z. Sui, Z. Li, S. Li, K. Wu, G. Liu, H. Corke, Diversity analysis of starch physicochemical properties in 95 proso millet (*Panicum miliaceum* L.) accessions, *Food Chem.* 324 (2020), 126863, <https://doi.org/10.1016/j.foodchem.2020.126863>.
- [144] Q. Yang, W. Zhang, J. Li, X. Gong, B. Feng, Physicochemical properties of starches in proso (Non-Waxy and waxy) and foxtail millets (Non-Waxy and waxy), *Molecules* 24 (9) (2019) 1743, <https://doi.org/10.3390/molecules24091743>.
- [145] G. Chao, J. Gao, R. Liu, L. Wang, C. Li, Y. Wang, Y. Qu, B. Feng, Starch physicochemical properties of waxy proso millet (*Panicum miliaceum* L.), *Starch Staerke* 66 (2014) 1005–1012.
- [146] R. Schoenlechner, M. Szatmari, A. Bagdi, S. Tömösközi, Optimisation of bread quality produced from wheat and proso millet (*Panicum miliaceum* L.) by adding emulsifiers, transglutaminase and xylanase, *LWT-Food Sci. Technol.* 51 (2013) 361–366, <https://doi.org/10.1016/j.lwt.2012.10.020>.
- [147] P.A. Caballero, M. Gómez, C.M. Rosell, Improvement of dough rheology, bread quality and bread shelf-life by enzymes combination, *J. Food Eng.* 81 (1) (2007) 42–53, <https://doi.org/10.1016/j.jfoodeng.2006.10.007>.
- [148] J. Tomić, A. Torbica, M. Belović, Effect of non-gluten proteins and transglutaminase on dough rheological properties and quality of bread based on millet (*Panicum miliaceum*) flour, *LWT-Food Sci. Technol.* 118 (2020), 108852, <https://doi.org/10.1016/j.lwt.2019.108852>.
- [149] A. Marti, M.A. Pagani, What can play the role of gluten in gluten free pasta? *Trends Food Sci. Technol.* 31 (1) (2013) 63–71, <https://doi.org/10.1016/j.tifs.2013.03.001>.
- [150] H.M. Romero, D. Santra, D. Rose, Y. Zhang, Dough rheological properties and texture of gluten-free pasta based on proso millet flour, *J. Cereal. Sci.* 74 (2017) 238–243, <https://doi.org/10.1016/j.jcs.2017.02.014>.
- [151] A. Marti, C. Tyl, Capitalizing on a double crop: recent advances in proso millet's transition to a food crop, *Compr. Rev. Food Sci. Food Saf.* 20 (1) (2021) 819–839, <https://doi.org/10.1111/1541-4337.12681>.
- [175] E. Anderson, J.H. Martin, World production and consumption of millet and sorghum, *Econ. Bot.* 3 (1949) 265–288.