Harnessing genetic resources and progress in plant genomics for fonio (Digitaria spp.) improvement

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RESEARCH ARTICLE

Harnessing genetic resources and progress in plant genomics for fonio (*Digitaria* spp.) improvement

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Abstract Fonio plays an important role in food security and in income generation, in drought prone areas of West Africa. This review aimed at highlighting fonio production constraints, breeding objectives and available genetic resources for fonio improvement. Lack of institutional support to research, lack of improved seeds, parasitic weed infestation, grain shattering, lodging and toilsome of the post-harvest handling are the major constraints limiting fonio production. These factors lead to negligence of the crop notwithstanding its high nutritional and market values. Breeding programs on fonio should first focus on solving these problems to improve overall yield. We explored the potential of mutation breeding, somaclonal variation, somatic hybridization, molecular markers, comparative genomics, individualized targeting induced local lesions in genomes (iTILLING), genotype by sequencing and genomic selection to develop improved fonio varieties. Determination of ploidy level, wide collection and

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characterization of fonio genetic resources, definition of core reference set collection, and exploitation of heterosis are some key research areas that would be of great interest in fonio improvement. However, this can only be achieved with adequate funding and institutional support.

Keywords Breeding · *Digitaria* spp. · Genetic resources · Genomics · Gramineae · Neglected and underutilized crop

Introduction

By 2050, world's population is expected to reach 9 billion (Nelson et al. 2010; Godfray et al. 2012). This will result in an exceedingly increased demand for food, which is estimated to reach 100–110% in 2050 compared to its level in 2005 (Tilman et al. 2011). However, crop production has been negatively affected by climate change (Nelson et al. 2010), competition for agricultural land and energy and water for irrigation (Khan et al. 2006; Ronald 2011). These phenomena will have severe negative effects on food security (FAO 2016). In addition, high risks of malnutrition arising from hidden hunger due to low diet food consumption might become significant (Kennedy et al. 2003; Bouis and Welch 2010; Ngozi 2013). With the current production model based on few crops species, it may be challenging to meet the global food demand. Sustainable intensification and diversification of agricultural and food systems through promotion of neglected crops species is being encouraged (Kahane et al. 2013; Padulosi et al. 2013; Massawe et al. 2016). One of such crops is fonio, which has high agricultural, nutritional and commercial values.

Fonio is one of the oldest domesticated cereals in West Africa dating back as far as c. 2400 BC (Larson et al. 2014). The earliest evidence of its cultivation dated to c. 1000 and 400 BC in Mali (Takezawa and Cisse 2004). It belongs to the Gramineae family, the subfamily Panicoideae and the genus *Digitaria*. Two major known cultivated fonio species are the white fonio; *Digitaria exilis* (Kippist) Stapf and the black fonio *Digitaria iburua* Stapf (Hilu et al. 1997; Adoukonou-Sagbadja et al. 2006). The closest grass genera to *Digitaria* are *Cenchrus* and *Setaria* (Fig. 1). Fonio plays a critical role in food security and income generation in marginal areas in West Africa. It is still referred to as either an old crop or women's crop (Vodouhè et al. 2007; Vall et al. 2011; Small 2015).

Fonio has several end products and consumption forms (e.g., porridge, couscous, and paste for human consumption) (Vodouhè et al. 2007). It has gained interest in food industry (formulation of bread, cookies, sour dough, drinks, non-fermented steamed and granulated dumpling products) resulting in increased demand and market value of the crop (Jideani and Jideani 2011). High traditional and customary values are attached to fonio, which is reserved for chieftaincies, royalties, special traditional occasions and ancestral worship (Adoukonou-Sagbadja et al. 2006; Blench 2012). The straw serves as good livestock feed (Clottey et al. 2006; Vodouhè et al. 2007). *D. exilis* and *D. iburua* contain on average per 100 g of edible grains about 8% protein, 75% carbohydrate and 6.8% dietary fiber (Table 1) (Brink 2006a). Due to its higher content of essential amino acids, methionine and cysteine compared to wheat, rye, barley, rice sorghum and maize, it is referred to as the most nutritious cereal grain (Table 1) (Vodouhè et al. 2007; Koroch et al. 2013; Ballogou et al. 2014). The grains are gluten-free and suitable for curing coeliac disease (Taylor et al. 2006) and its consumption is beneficial for lactating women and diabetic patients (Vodouhè et al. 2007).

Investing in neglected crops has been considered as cost-ineffective regarding their local production and less interest in international trade. However, owing to fonio importance, there have been several calls for breeding for improved fonio varieties, and conservation and uses of its genetic resources (Barnaud et al. 2013). Additionally, calls for improved cultural practices, processing and marketability have been reported (Gigou et al. 2009; Koreissi-Dembélé et al. 2013; Ballogou et al. 2014). There has been recent research on fonio improvement and related cereal species that need to be discussed to orient future research on the crop.

In this review, we addressed the following questions: (1) what factors constrain fonio's production? (2) what has been done to improve fonio? (3) what could be the objectives of fonio breeding programs? (4) what genomic resources and breeding techniques are available for use to achieve these objectives?

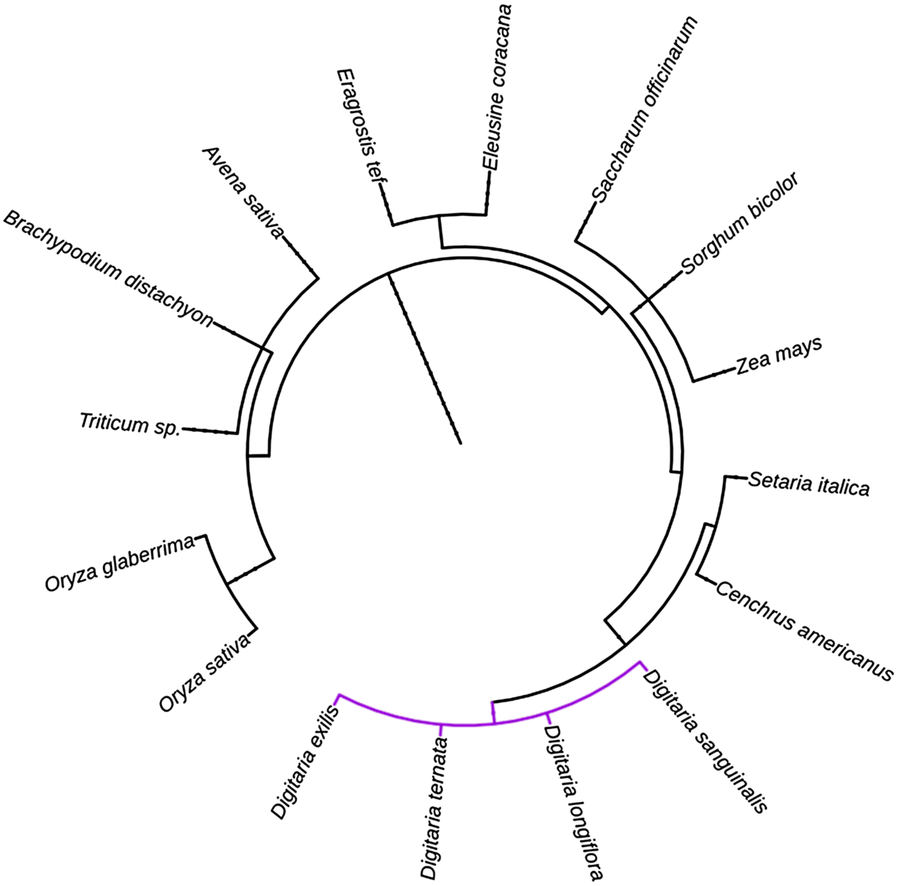


Fig. 1 Phylogenetic tree showing relationship among three fonio species and other grasses. The tree was generated using phyloT (http://phylot.biobyte.de) and visualized with (iTOL) v3 (Letunic and Bork 2016) based on the NCBI taxonomy. *D. iburua* is not in the NCBI database and it could be included in the tree

Table 1 Nutritional content per 100 g of *fonio* and other cereal crops. *Source*: Badu-Apraku and Fakorede (2006), Balole and Legwaila (2006), Brink (2006a, b), Vodouhè and Achigan Dako (2006)

Species	Protein (g)	Carbohydrate (g)	Dietary fiber	Tryptophan (mg)	Methionine (mg)	Phenylalanine (mg)	Threonine (mg)	Valine (mg)	Leucine (mg)
D. exilis	7.1	74.4	7.4	111	441	402	315	457	772
D. iburua	8.9	75.6	6.2	215	355	803	389	614	1395
Rice	6.7	81.3	3.8	87	140	330	230	390	560
Sorghum	11.3	74.6	–	124	169	546	346	561	1491
Maize	9.4	74.3	7.3	67	197	463	354	477	1155
Wheat	15.4	68	12.2	195	230	724	433	679	1038

Methodology

Literature search was conducted in various databases including Google Scholar, Web of Science, Scopus, PubMed Central and JSTOR. No date coverage was specified during the search. In each of the database, key words related to the defined questions were used to conduct the literature search. Fonio diversity, fonio germplasm were used to collect literature on fonio diversity and germplasm. Fonio production system, fonio cultivation, fonio post-harvest and fonio seed system were used to get published and unpublished (reports) works on fonio production systems, post-harvest handling and challenges. Literature on available genomic resources was obtained using key words including New Generation Sequencing, TILLING and plant breeding, Genotyping by sequencing: application in plant breeding, Genomic selection, mutagenesis and plant breeding, micro-propagation and plant breeding and genomic resources and neglected crops and genomic tools and cereals breeding. Papers' title and/or abstract were screened and selected based on their relevance to the questions being investigated. Additionally, the reference lists or bibliographies of the selected papers were checked manually for articles of interest. The selected papers were subjected to critical analysis.

Results and discussion

Fonio production

Fonio is cultivated across West African Savannah from Lake Chad to Senegal where it serves several millions of indigenous people as a staple and strategic crop for food security during lean periods (Barnaud and Billot 2011; Vall et al. 2011). Guinea is reported to be the top producer of all fonio growing countries with a cultivation area of about 459,563 ha and a production of 479,985 t in 2014, accounting for about 75% of the total fonio production (FAOSTAT 2017). West African farmers cultivate more than 550,000 ha of land area per annum (FAOSTAT 2017). Fonio production objective varied across growing areas. In semi-arid areas of Burkina-Faso, Guinea and Mali, fonio is mainly grown to supplement food shortage during lean periods while in sub-humid regions of these countries, fonio is mainly grown for crop diversification (Vall et al. 2011). The wide ecological adaptability of fonio gives it high potential as promising crop in future to provide food security, not only in West Africa where it is currently being cultivated, but also in other parts of Africa where its cereal counterparts thrive (Small 2015).

Challenges in fonio production system and post-harvest

Fonio farmers lack good agronomic practices and improved varieties, which are needed to reach the yield plateau. Farmers' access to improved varieties and good-quality seed is of great importance to increase productivity and production (Louwaars and de Boef 2012). However, as in other minor crops, there is no formal seed system in fonio (Ahmed et al. 2009; Ayenan and Ezin 2016). Designing of sustainable seed systems that are rooted in and led by the community and can enable production and timely delivery of good quality seeds to farmers is deemed important.

A low and relatively constant yield of 0.2–0.9 t ha^{-1} has been reported across fonio growing areas (Adoukonou-Sagbadja et al. 2006; Dachi and Gana 2008; Adoukonou-sagbadja 2010). Even though the crop is known to thrive well in marginal areas, prolonged or terminal drought stress have also been reported as important emerging constraint to fonio production especially in semi-arid zones, characterized by unpredictable, irregular and shorter (2–3 months) rainy season (Dansi et al. 2010).

In Benin, farmers reported some parasites including "insects' larvae", which consumed limbs during drought period and insects called "fonio mosquitoes" which feed on spikelet (Adoukonou-sagbadja 2010). Susceptibility of fonio to the fungi *Phyllachora sphearosperma* and *Helminthosporium* spp. as well as to rust caused by *Puccinia cahuensis* were also reported (Adoukonou-sagbadja 2010). This underlines the need for further study on the identification, incidence and severity of these pests in order to design adequate management strategies. Weeds also contribute to some extent to the yield gap as fonio plants are low weed competitors (Adoukonou-Sagbadja et al. 2006). Striga aspera and Striga hermonthica are reported as the most important fonio parasitic weeds in West Africa (Hillocks et al. 1996; Gigou et al. 2009). Other production challenges include shattering and lodging. It has been estimated that shattering causes up to 30% of grain loss in fonio (Vodouhè et al. 2007). While the production constraints are very important and efforts must focus on improving all productions aspects, there are aspects such as post-harvest challenges which should not be overlooked if fonio production is to be promoted.

Fonio grains are small in size (1000 grains weigh on average 0.44 g); their handling and processing (threshing, winnowing, dehulling, whitening) are hard and toilsome task in absence of appropriate technologies. These challenges have been for long and still being some of the reasons behind the neglected status of this crop (Ballogou et al. 2014). However, progress has been made across some of the fonio growing areas (Mali, Burkina-Faso, Guinea) with the designing of machines to reduce the tiresomeness of post-harvest operations (Marouzé et al. 2008). According to the authors, this has led to an increasing economic potential of the crop. There is still, however, a gap to be filled at both national and regional levels as far as the availability and the affordability of the threshing machines are concerned.

Potential breeding objectives in fonio

Actors (farmers, processors, consumers, etc.) in the value chains of a particular crop have specific traits of interest and needs upon which they select their preferred varieties. In regards to the preferred traits in a specific fonio variety, Dansi et al. (2010) reported eight preference criteria namely extra early-maturity, large grain size, culinary characteristics, ease of processing, productivity, ease of harvesting, grain size, storability and drought tolerance (Fig. 2). These criteria must guide the implementation of fonio breeding programs.

Breeding for delayed shattering

Breeding fonio for resistance to uncontrolled seed shattering is deemed important (Fig. 2). Loss of shattering habit was a major event in domestication process of cereals (Konishi et al. 2006; Lin et al. 2012). Seed shattering in fonio is believed to be both environmentally and developmentally controlled (Patterson et al. 2016). Using comparative genomics, the ortholog of the gene qSH1, a shattering gene in rice and members of the Agamous-related family of genes such as JOINTLESS 1–3, SH2, and SH3, the free-threshing locus Q of wheat, as well as the Arabidopsis abscission-associated gene NEVERSHED (Patterson et al. 2016) were identified in fonio. In several cultivated cereals, loss of shattering was caused by few mutations at major QTLs controlling the trait. Thus, SNP mutation at *qSH1* locus in *Oryza sativa* (Konishi et al. 2006), three mutations in *Shattering1* (*Sh1*) locus in Sorghum (Lin et al. 2012) and SNP mutation at *GL4* locus in *Oryza glaberrima* (Steud.) (Wu et al. 2017) were responsible for loss of shattering in these crops. These mutations led to loss-of-function of genes underlying seed shattering. Further research to map QTLs controlling seed shattering in fonio and understanding of the molecular and physiological basis of this trait are important to enable breeders to select most appropriate methods to develop resistant varieties to uncontrolled seed shattering. When few major QTLs underlie grain shattering in fonio like in other cereals, use of mutation breeding could be efficient in developing non-shattering varieties that

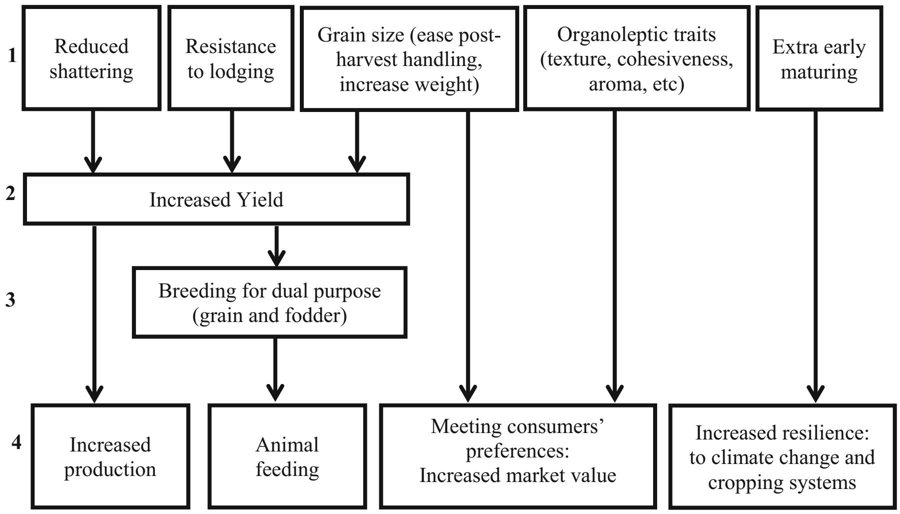


Fig. 2 From breeding objectives to outcomes for farmers and consumers (1, 2 and 3 = breeding objectives; 4 = outcomes for farmers and consumers)

would result in overall grain yield improvement. This approach was successfully used to develop non-shattering forage rice variety (Kato et al. 2006).

Breeding for resistance to lodging

Lodging poses limitations to fonio yield but till date, no breeding effort has tackled this issue (Fig. 2). Wide germplasm screening for both cultivated and wild relatives could help to identify materials resistant to lodging which could be used to develop improved varieties with stronger culms and/or with dwarfism genes. Additionally, two alternative options, involving Gibberellic Acid (GA) biosynthesis pathways which has been extensively used in other cereal crops (rice and wheat), could potentially be exploited to develop lodging resistant fonio varieties (Peng et al. 1999; Sasaki et al. 2002; Asano et al. 2009; Okuno et al. 2014). The first option is the creation of GA deficient mutants to generate dwarf lines which will be further evaluated for agronomic performance. The second option, which is now being explored in rice breeding, targets not only the breeding for resistance to lodging but also the production of high biomass by creating mutants with over-production of GA. This strategy enables formation of larger culm diameters and/or lignin accumulation resulting in improving the breaking-type lodging resistance (Okuno et al. 2014).

Breeding for larger grain size

Grain size is one of the two determinants of grain weight which is a major component of yield, for most cereal crops (Brocklehurst 1977). In fonio, small grain size has been, for long, a key limiting factor for its processing and low grain-yield. Although to date, no breeding effort has really addressed this challenge, the significant progress made in other cereals like rice and wheat could be advantageous. The use of comparative genomics is a potential avenue for breeding for large grain size in fonio. Two genes OsGS5 and OsGW2 were identified in rice as grain size and weight regulators; while OsGS5 encodes for large grain size by increasing the number of cells generated during cell division (Li et al. 2011), OsGW2 affects negatively the grain size and weight (Song et al. 2007). The homologous genes of OsGS5 and OsGW2 could therefore be cloned and mapped on fonio genome through comparative genomics as it was done in wheat for the genes TaGS5-3A (Ma et al. 2016) and TaGW2 (Su et al. 2011) and in maize for the genes ZmGW2-CHR4 and ZmGW2-CHR5 (Li et al. 2010). Functional genomics will then come in handy, to determine if these homologs have similar function in fonio as in rice, wheat and maize. Finally, through genetic engineering, a significant increase in fonio grain size could be achieved through the development of GW2-underexpressing lines. Indeed, increased grain size and weight have been obtained by Song et al. (2007) in rice after creating an antisense mutation that results in a truncation of 310 amino acids and by Hong et al. (2014) in wheat after transforming a TaGW2-RNA interference cassette in the variety Shi4185 with small grain.

Breeding for high-yielding varieties

Developing farmers' preferred and high yielding varieties is of utmost importance to upgrade the status of the crop. Although some phenotypic evaluations for high-yielding genotypes have been recently conducted, no major breeding efforts were made for the genetic improvement of fonio's productivity. However, from the multi-locational participatory variety selection implemented in Mali, seven landraces were identified as earlier-maturing and higher yielding than the local checks with the landrace "Fini of Samakou Dansira-1" which had a stable yield of 1.4 t ha^{-1} (Sanogo and Hash 2014). This indicates that significant improvement could be made through the collection and evaluation of germplasm at regional level. Besides, grain yield being a quantitative trait, function of several yield component traits, breeding for resistance to shattering and lodging and increased grain size result into an improvement of both fonio's production and productivity (Fig. 2).

Fonio's straw is good livestock feed for both monogastric (Clottey et al. 2006) and ruminant animals (Vodouhè et al. 2007). Breeding varieties with high biomass yield can be useful for animal feed especially in semi-arid zones characterized by unpredictable rainfall leading to low availability of fodder and pastures. Furthermore, fonio is well appreciated in some sub-Sahara African countries which are at high risk of micronutrient deficiency, thus an improvement of fonio for high density micronutrient characteristics will help to address the food security and nutrition challenges in this area.

Germplasm and conservation problematic: an incomplete and unstandardized collection

Plant breeders heavily rely on genetic variability without which little or no progress can be achieved. Readily available and well characterized germplasm collections are important for breeders. *D. exilis* has a wide distribution from Senegal to Lake Chad while *D. iburua* is mainly encountered in Nigeria, Benin and Togo (Adoukonou-sagbadja et al. 2004; Blench 2012). Based on this geographical distribution, important efforts have been made to collect accessions of *D. exilis*. The first regional mission of fonio genetic resources collection was undertaken by Clément and Leblanc (1984) in six countries (Benin, Niger, Togo, Mali, Burkina-Faso, Guinea) where they collected 641 accessions of *D. exilis* which are maintained by IRD (Institut de Recherche pour le Développement) in Montpellier (Clément and Leblanc 1984). Germplasm collection missions are also conducted at national level (e.g. Mali, Guinea, Nigeria and Benin) for genetic diversity studies and nutritional characterization. Duplicates of some of these fonio accessions are kept in international genebanks to limit the risk of their loss.

There is no collection of wild fonio and black fonio at regional level; and this may limit the extent of exploiting the secondary and tertiary gene pool of fonio (Olodo 2016). For *D. exilis*, it is essential to extend collection efforts in other countries where presence of fonio is reported in the literature [such as Gambia, Côte d'Ivoire, Guinea Bissau (FAOSTAT 2017), Sierra Leone (National Research Council 1996), Dominican Republic (Morales-payán et al. 2002)] (Fig. 3). It is worth noting that while fonio germplasm might have been collected and kept in national genebanks in some of these countries, to the best of our knowledge there is no record of their existence. This emphasizes the importance of keeping duplicates of genetic resources in international genebanks not only to ease access to these materials to potential users but also to avoid their loss. Threat on genetic erosion is reported in some growing areas (e.g. Togo) (Adoukonou-sagbadja et al. 2004), hence indicating the importance of developing strategies to conserve its diversity. We propose a gap analysis

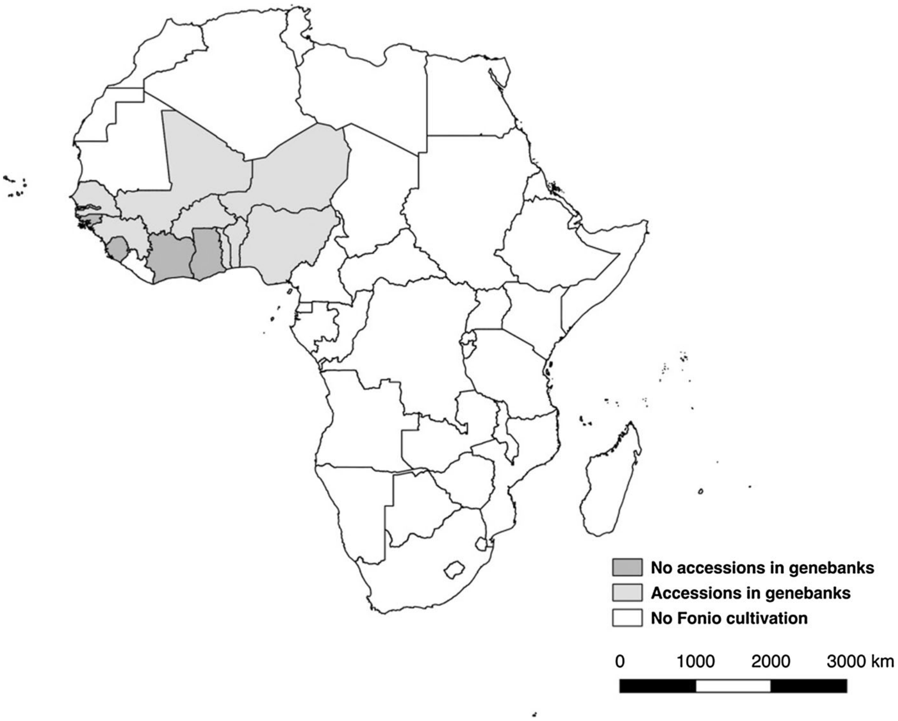


Fig. 3 Distribution of *Digitaria* spp. crops in West Africa with countries where from accessions kept in genebanks (U.S. National Plant Germplasm System and *Centre de Ressources Biologiques Tropicales de Montpellier* (CRB-T)) were reported or not. *Source*: Adapted from Blench (2012)

(Michael et al. 1993) to identify the areas where accessions are not collected or are under-represented in genebanks. This will require collaboration among various institutions involved in maintaining fonio germplasm. Doing so can help gather basic information (geographical coordinate, species, date of collection, number of available accessions) on fonio germplasm. After a wide collection, morphological, molecular and nutritional characterization of the germplasm should be carried out to develop a core reference set and make efficient use of the genetic resources (Glaszmann et al. 2010). That will enhance germplasm exchange and help breeders in selection of desired materials for their breeding programs.

Genetic diversity and available genomic resources

The analysis of nuclear DNA contents using flow cytometric confirmed the close relationship between the cultivated fonio *D. exilis* and *D. iburua* and the wild species *Digitaria longiflora* (Retz.) Pers. and *Digitaria ternata* (A. Rich.) Stapf (Adoukonou-Sagbadja et al. 2007) as reported earlier by Hilu et al. (1997). *D. longiflora* has been reported to have interesting agronomic traits, including erect habit, strong and resistant to lodging; long panicle with high number of grains and large seeds (Dansi et al. 2010). Morphological characterization of 67 white fonio accessions collected in Niger showed high variability in both qualitative (color of the grains and stems) and quantitative traits (yield, dry biomass, internode length and growth cycle) (Saidou et al. 2014).

Few genetic diversity studies have been done on fonio based on molecular markers. Hilu et al. (1997) and Kuta et al. (2003) assessed the genetic diversity in 10 fonio accessions collected from Togo and Nigeria, respectively. Adoukonou-Sagbadja et al. (2007) used Amplified Fragment Length Polymorphisms (AFLPs) to assess the genetic diversity among 122 accessions of *D. exilis* and *D. iburua* collected from Benin, Burkina Faso, Guinea, Mali and Togo. The AFLPs markers clearly separated *D. exilis* from *D. iburua*. Low genetic diversity was found in *D. iburua* while *D. exilis* showed moderate genetic diversity. A set of 38 nuclear microsatellite markers (SSR) were developed of which 21 exhibited polymorphism across a range of 36 accessions of *D. exilis* collected from Benin, Burkina Faso, Togo, Guinea and Mali (Barnaud et al. 2012). Transferability of these SSR markers to *D. iburua* and the wild relatives (*D. longiflora* and *D. ternata*) can be assessed for more comprehensive diversity analysis. Phylogenetic studies in fonio in order to establish domestication and distribution are also made possible with these markers.

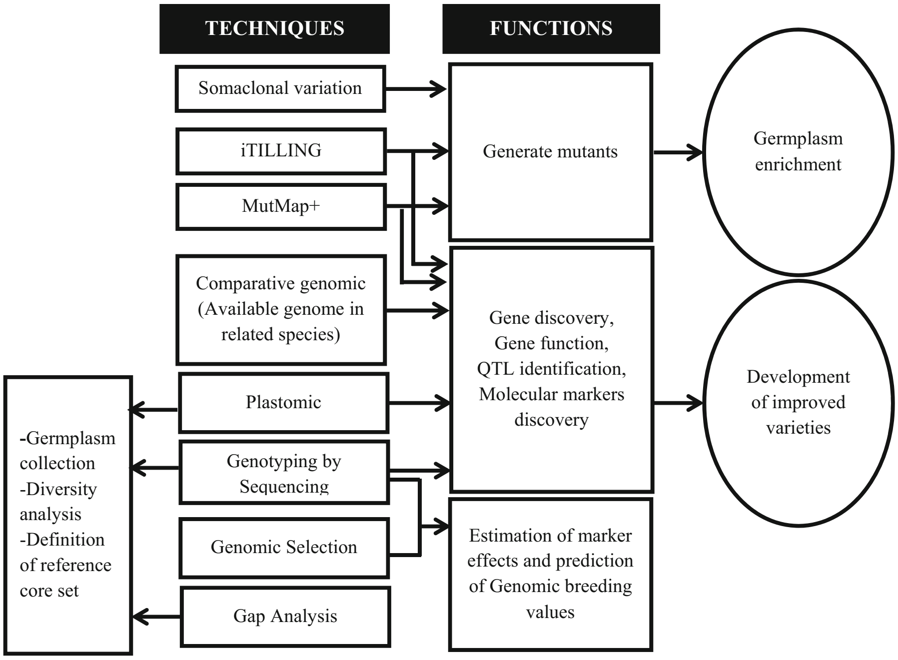
Fonio reproductive system

Fonio mating system was believed to be inbreeding or apomictic (Adoukonou-sagbadja et al. 2010). Recent evidence using micro-satellite markers revealed that the crop is predominantly self-fertilized with an outcrossing that could be up to 1.7% (Barnaud et al. 2017). Further investigation could address the potential to exploit heterosis in fonio to develop hybrid varieties. However, up to now no successful experience in artificial hybridization has been reported. Traditional hybridization is very-difficult in fonio as hand emasculation is often unsuccessful due to the extraordinarily miniature nature of its floral organs (Vodouhè and Achigan Dako 2006). Research avenues in somatic hybridization can be explored. This technique circumvents sexual reproduction and helps overcome crossing barriers (Jansky 2006). Thus, intra and interspecies crossings can be envisioned in fonio. Nevertheless, this will require the development of protoplast fusion, hybrid cell selection and hybrid regeneration methods.

Available genomic resources and breeding techniques for fonio

Next-generation sequencing (NGS) provides researchers with cost effective and faster methods for generating large quantities of sequence data (Mardis 2008; Varshney et al. 2009; Egan et al. 2012). Interestingly, genome synteny and the increasing availability of Plant Genome Databases (Phytozome, Ensembl Plants, PlantGDB Genome Browser, National Center for Biotechnology Information, etc.) have made possible comparative genomics. Thus, genomic resources developed in other well studied cereals with available genome sequences could be exploited in fonio (Barnaud et al. 2013; Saha et al. 2016). Increasing availability of genome sequence in cereals including *Zea mays* L., *Triticum aestivum* L., *Oryza sativa* L., *Sorghum bicolor* (L.) Moench, *Setaria italica* (L.) P. Beauv. could therefore be harnessed for

Fig. 4 Integrated tools and techniques for fonio improvement



gene discovery, mapping of molecular markers, and gene annotation in fonio.

Rapid decrease in costs of DNA sequencing combined with advances in bioinformatics allowed the use of genotyping-by-sequencing (GBS), DNA sequencing (RAD-seq) and Diversity Arrays Technology (DArT) for SNP discovery and genetic analysis even in non-model crops (Elshire et al. 2011; Saha et al. 2016). These genomic tools have a wide range of applications, including but not limited to genetic diversity study, molecular markers discovery, genome mapping, whole genome sequencing and gene discovery (Varshney et al. 2009; He et al. 2014). In fonio, GBS can be used to mine SNPs for population structure and diversity studies and to identify marker-trait associations (Fig. 4).

Molecular marker-based genetic linkage maps or genome-wide association studies (GWAS) important for detection of quantitative trait loci (QTLs) agronomic traits (yield, grain size, resistance to lodging and shattering, etc.) are yet to be carried out in fonio. Association of molecular markers to QTLs related to traits of interest could be established through comparative genomics approach (Saha et al. 2016). This would pave way for the use of marker-assisted selection (MAS) in breeding for improved fonio cultivars.

Recent progress in genomic and breeding methods could help to circumvent the limited knowledge on fonio's genome, leading to significant genetic gain (Fig. 4). Genomic Selection (GS) is becoming popular in plant breeding programs and relies extensively on the use of molecular markers. Most of the variation due to minor QTL is captured in the statistical prediction model (Meuwissen et al. 2001). In the absence of data on genome sequence and genetic maps in fonio, using GS with SNP mined from genotyping by sequencing tags could yield quick results in traits improvement.

Research on fonio plastome seems to gain interest in recent studies, namely identification of chloroplast SNP (Scarcelli et al. 2011) and a snapshot of transcriptome fonio *Niatia* seedling (Sarah et al. 2017). In addition, a cost-effective protocol has been developed to sequence complete chloroplast genome for several individuals at a single MiSeq run and this protocol has been validated with success in fonio (Mariac et al. 2014). The availability of complete chloroplast genome sequence is an opportunity for pre-breeding research (phylogenetic, domestication and genetic variability) in fonio (Mariac et al. 2014; Daniell et al. 2016). Chloroplast genome has already been used in phylogenetic studies of commercially important crops (e.g.: rice, cotton) and has helped in efficient use and conservation of genetic resource (Daniell et al. 2016).

Generating mutants can be a powerful approach to enrich diversity in fonio, carrying out basic research on gene function and subsequently identify materials which can be advanced and released as varieties. Tools are now available to plant biologists to identify with precision individuals carrying mutation of interest. Targeting Induced Local Lesions IN Genomes (TILLING) was initially developed in Arabidopsis to screen genes for mutations using a PCR-based assay (McCallum et al. 2000). This approach has been widely adopted in many other plants species (Bush and Krysan 2010). Modifications have been made on TILLING leading to new procedures such as individualized TILLING (iTILLING), making mutation-screening more practicable with reduced investment (Bush and Krysan 2010). Applying iTILLING does not require M2 seeds to be catalogued; they can be harvested in bulk from M1 population, hence, considerable time is saved (Bush and Krysan 2010). The iTILLING procedure would then be suitable for fonio because of its tiny seeds (Patterson et al. 2016).

Another approach for identifying mutation is MutMap+, initially developed and applied on rice to detect causal mutations by comparing SNP frequencies of bulked DNA of chemically-induced mutant and wild-type progeny of M3 generation derived from selfing an M2 heterozygous individual (Fekih et al. 2013). Because it does not require artificial crossing, which is a challenge in fonio, MutMap+ has been identified as a potential technique for gene isolation and identification of genes controlling important agronomic traits (Fekih et al. 2013).

Tissue culture harbors interesting perspectives for fonio improvement (Kuta et al. 2003). A protocol for fonio tissue culture has been established (Ntui et al. 2010) and can be exploited to generate somaclonal variation (Larkin and Scowcroft 1981). Somaclonal variation has been reported to be very successful in crops with limited genetic systems (e.g., apomicts, vegetative reproducers) and/or narrow genetic bases like fonio (Krishna et al. 2016). It was exploited to develop a mutant SE7 with reduced plant height and increased grain yield in finger millet (Baer et al. 2007), suggesting its potential use in fonio to enrich diversity and develop improved variety.

Combination of mutagenesis with micro-propagation could help in fonio improvement (Kuta et al. 2003). The former would increase the frequency of induced mutation while the latter would help to recover somaclones with desirable traits (Afrasiab and Iqbal 2010). However, technical challenges related to selection of stable mutants should be addressed through training of laboratory technicians and establishment/equipment of tissues culture facilities. In this regards, the assistance of the International Atomic Energy Agency (IAEA) in Vienna (Austria) can be requested in materials irradiation and other technical issues in mutation breeding. Use of chemical mutagens can be explored as well.

Institutional support for fonio research

Because of scarce resources devoted to fonio research, we advocate that a research hub should be created for fonio in West Africa. This approach will help to efficiently use available resources by avoiding duplication. The hub can be hosted by one of the national research institutes where basic research on the crop as well as varieties development will be done to cope with biotic and abiotic stresses and meet consumers' preferences. In this regards, noticeable advance in collaboration among national research institutes in West Africa and international research centers have been made (Vodouhe et al. 1998; Barnaud and Billot 2011). For example, through these collaborations, protocols have been defined in order to standardize collection of fonio genetic resources (see Arcad Project, https://www.arcad-project.org/). Such a regional approach has been identified as a key to the success in pigeonpea breeding in Eastern and South Africa (Kaoneka et al. 2016). Implement this approach to valorize fonio will require, as in other neglected crops, public funding (Stamp et al. 2012).

Conclusion

Fonio has potential that can be tapped into as a nutritious food security and commercial crop. However, low yield (grain and biomass), poor agronomic practices, lack of improved varieties, difficulty in post-harvest handling and processing are some of the factors that still hinder the exploitation of this potential. Herein, research avenues for fonio's improvement through determination of ploidy level especially in the wild relatives, wide collection and characterization of fonio's genetic resources, definition of reference core collection and setting up of breeding programs to tackle these constraints are explored. Our evaluation showed that there are available techniques and genomic resources that can be leveraged on to collect, conserve and develop improved fonio varieties. In addition, strengthening multi-stakeholder approaches and collaboration to advance fonio research through public funding might play crucial roles at closing these research-call gaps in fonio. In this review, we clearly presented what has been done so far with regard to fonio improvement, the way forward. The information provided is valuable for scientists interested in fonio research and offers a good roadmap for sustainably harnessing genetic resources and research capacities to boost fonio production and utilization.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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