15. From Shade to Light: Fonio, an African Orphan Crop, Towards Renewed Challenges

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Highlights box

- Fonio (*Digitaria exilis* Stapf) is a promising crop under a large range of environmental conditions
- Recent advances in genomic resource availability open up the road for more effective plant breeding
- Targeting these domestication genes would represent a first important step towards a significant improvement of fonio
- Needs for a coordinated transdisciplinary collaboration across research disciplines involving actors beyond research
- Fonio, a key crop in advancing agricultural development beyond the Green Revolution model

Abstract

The FAO recently estimated that demand for food will increase by 70% by 2050. The challenge will not only be on increasing the food supply but also on improving its nutritional value under an accelerating rate of environmental and social changes. One solution would be the wider use of underutilized crops to diversify alimentation and develop sustainable and low-input agriculture. Are orphan crops commodities for the future, and how can they be promoted? In this regard, fonio (*Digitaria exilis* Stapf) appears to be a promising crop. It is an indigenous staple cereal from Western Africa playing a crucial role in food security. Additionally, it is a model crop in important up-to-date concepts such as resilience, agroecology, population health, climatic changes, poverty reduction, and women's empowerment. Nevertheless, fonio has received limited attention from mainstream research compared to other dryland cereals, such as pearl millet and sorghum. Increasingly available genomic resources promise to promote advanced breeding strategies in fonio. This paper presents the past, present, and future of fonio research. We argue the need for interdisciplinarity and multistakeholder research approaches for increasing fonio production, conservation, and sustainable uses.

Keywords: Fonio, Neglected and Underutilized Species (NUS), Sustainable agriculture, Food and nutritional security, Breeding strategies, Resilience

Introduction

The FAO recently estimated that demand for food should be increased by 70% by 2050. The challenge will not only be on increasing the food supply but also on improving its nutritional value and alleviating poverty under environmentally sustainable production systems. Agricultural productivity is expected to decrease in the near future because of climate change, groundwater depletion, and land degradation. This decrease will particularly impact Sub-Saharan Africa (SSA), one of the most food-insecure regions globally (FAO et al., 2019). The agricultural sector in SSA is dominated by smallholder farmers (AGRA, 2016) and employs more than half of the population. SSA agriculture is characterized by almost exclusively rainfed crops (Lowder et al., 2016). In a context of multiple social and environmental constraints of varying intensity over time, increasing attention is being paid to agrobiodiversity to enhance resilience and adaptation of farming systems (Guarino & Lobell, 2011; Padulosi et al., 2011; Pironon et al., 2019). Beyond productivity, agrobiodiversity is also an asset supporting numerous ecosystem services (including associated biodiversity pest and disease control, etc.), flow regulation (including water quality, regulation of biogeochemical cycles, etc.), soil fertility, and sociocultural services (Altieri, 1999; Beilloin et al., 2021).

More than 7,000 species have been used throughout human history as agricultural or horticultural crops. However, food safety and nutrition worldwide now rely primarily on 12 species of cereals and 23 species of vegetables (Altieri, 1999) with wheat, rice, and maize alone providing more than 50% of the plant energy consumed by humans (FAOStat, 2010). Agricultural research has mainly concentrated on these few promoted species, but the vast majority of cultivated species have been neglected. Suitable for a large variety of agro-ecosystems, neglected crops have recently regained interest for their utility to unlock marginal lands for agriculture. Despite the call for increased use of underutilized crops, by the International Center for Underutilized Crops (ICUC) and the Global Facilitation Unit for Underutilized Species (GFU), to diversify alimentation and develop sustainable agriculture, those crops remain a largely untapped reservoir of agrobiodiversity. We will focus here on a neglected cereal from West Africa, fonio.

1. Is Fonio a Crop for the Future?

In addition to the well-known cereals such as sorghum and pearl millet, Africa exhibits several small millets, notably fonio. The term *fonio* encompasses two species (*Digitaria exilis* Stapf – white fonio and *Digitaria iburua* Stapf – black fonio) that are genetically differentiated (Figure 1). These cereals are indigenous staple crops from Western Africa with great potential for agriculture in marginal environments. However, black fonio covers only a slight disjunct geographical area in Benin and Nigeria, so we will focus on the widespread white fonio, *Digitaria exilis* (Figures 2 and 3a-b).

In a region stretching from Senegal to the Cameroon-Nigeria border, fonio is cultivated under a large range of environmental conditions, from the tropical seacoast in Sierra Leone to arid climate in the Sahel zone and high-altitude grasslands, such as the Jos Plateau (Figure 3a and 3b).

Figure 1

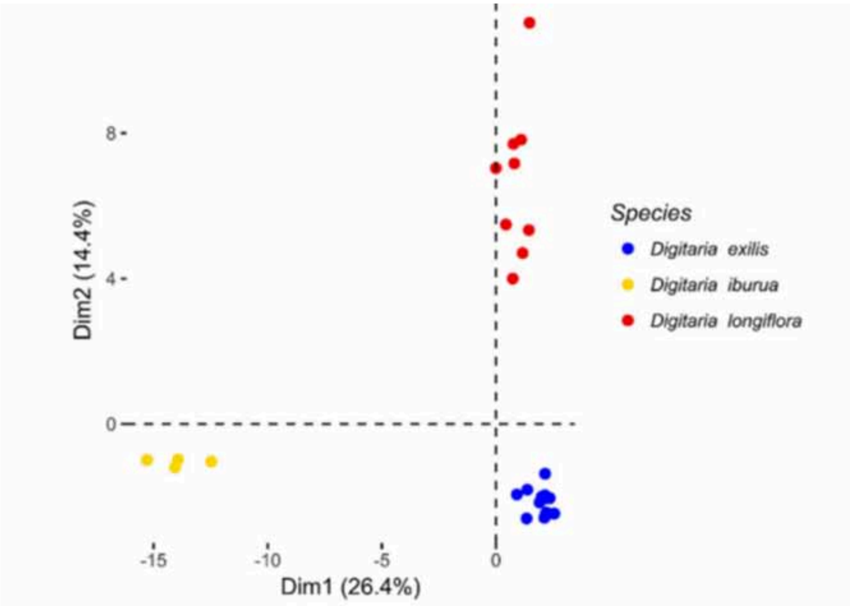

Figure 1 – Principal Component Analysis of the Pattern of Genetic Diversity among Digitaria Species- Digitaria Exilis (white fonio) Digitaria Uburua (black fonio) & Digitaria Longiflora (wild progenitors of white fonio)

Figure 2

Figure 2 – Digitaria Exilis, White Fonio, Plant

Figure 3a

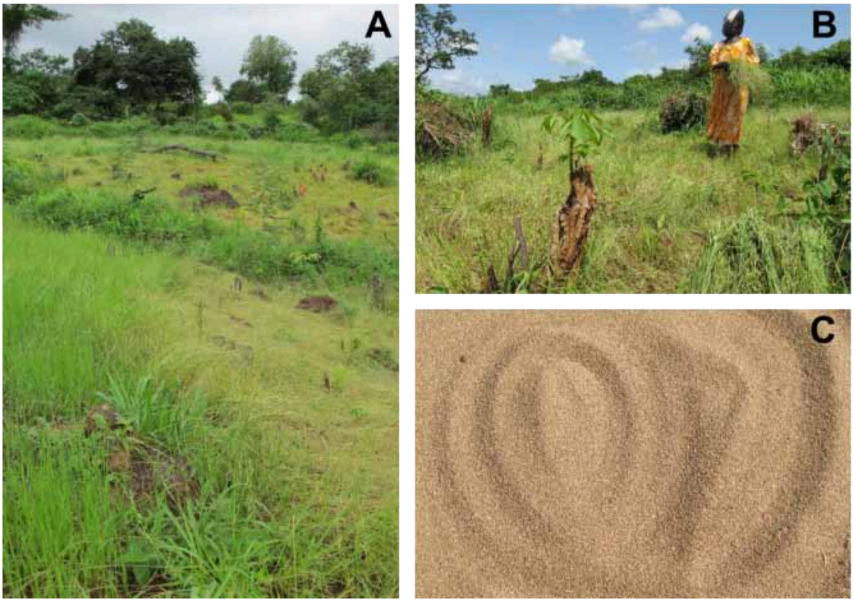

Figure 3a – Fonio, Digitaria exilis, an indigenous staple crop from Western Africa. A – Fonio fields growing short cycle and long cycle landraces; B – Fonio harvest; C – Fonio grains

Figure 3b

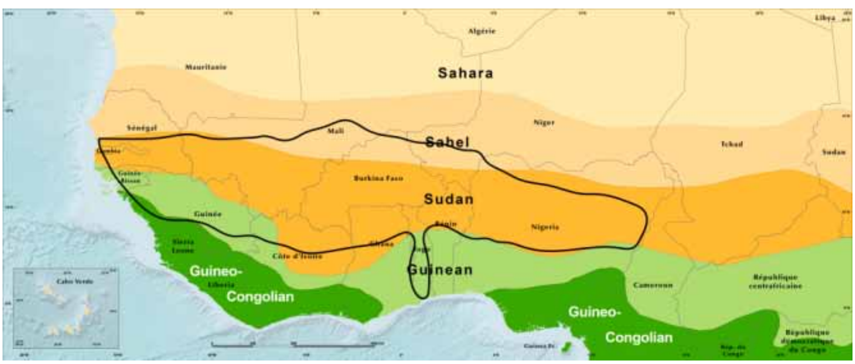

Figure 3b – Geographic distribution of fonio in the bioclimatic regions of West Africa (CILSS, 2016)

This level of adaptation is particularly relevant in the climate uncertainty context. Because of the historical and contemporary shifts toward high-yielding grain crops, its distribution has been disjunct and reduced to relic (Blench, 2016). Fonio, which is both drought-tolerant and does not depend on external inputs, becomes a key crop to plant. The two main producers are Guinea (530 Kt, 76% of the overall production, FAO 2019 production data) and Nigeria (83 Kt, 12%), making a significant comeback in several producing countries. Providing reliable yields on marginal lands, fonio contributes significantly to food and nutritional security, both at local and regional levels. Owing to its fast-maturing landraces, fonio is a key crop during food shortages (Vall et al., 2011). Such crop is crucial in Africa, where hunger is rising in almost all African subregions, with 20 percent of the population undernourished (Fao et al., 2019). Fonio has several nutritional properties compared to other staple cereal grains, thanks to its high levels of sulfur amino acid methionine and cystine, which enable it to provide all 20 amino acids (Jideani & Jideani, 2011). Additionally, it is regarded as a valuable source of income, especially for women and small-scale farmers, as shown by increasing urban market opportunities (FONIO, a project financed by the Common Fund for Commodities and supervised by FAO, http://fonio.cirad.fr/). The price of a kilo of fonio could be 1.5 to 2 times higher than a kilo of rice (Vodouhe et al., 2007): $120/Mt on the global market in 2018 in Guinea (FAOSTAT). Besides, there are large opportunities for value chain development (e.g., Senegal is importing almost half of its consumption with large opportunities for development in other countries, FAOSTAT). Furthermore, its cultivation requires few land works and is adapted to low fertile soils (Vodouhe et al., 2007). In addition, fonio is often grown on acidic soils with high aluminium content in monocultural systems after a fallow period (Gigou et al., 2009). Finally, fonio benefits from cultural embedding as it plays a key role in ritual systems in many African societies across West Africa, even where it is no longer the dominant crop in an agricultural system (Adoukonou-Sagbadja et al., 2006; Ballogou et al., 2014; Blench, 2016; Diop et al., 2018).

Despite the promising nature of fonio to ensure food security and income increase for farmers, it has received limited attention from mainstream research in terms of the development of genomic and breeding resources. Investing in research on fonio will help realize the full potential of this crop. This chapter provides comprehensive insight into the global status of its germplasm, diversity, promising genomic resources, and breeding challenges.

Fonio Genomic Resources to Foster Sustainable Agriculture Transition

Increasingly available genomic resources promise to advance research, trait discovery, and breeding in fonio to complement basic agronomical achievements aimed at improving fonio cultivation.

1. Unlocking Genomic Resources

Fonio, an underutilized crop, does not benefit from the same scientific knowledge and genomic resources as model crop species, but this is changing rapidly. Over the last two decades, many studies on genetic diversity have increased understanding of its biology and diversity, showing that fonio is a tetraploid species (2n = 4x = 36) (Adoukonou-Sagbadja, Schubert et al., 2007) with a high degree of selfing (Barnaud et al., 2017). Later studies mainly provided information about the distribution of its phenotypic and genetic diversity on a local and regional scale (Adoukonou-Sagbadja et al., 2007; Barnaud et al., 2012; Dansi et al., 2010; Hilu et al., 1997; Ibrahim Bio Yerima et al., 2020; Koreissi-Dembélé et al., 2013; Kuta et al., 2005 ; Kwon-Ndung & Ochigbo, 2004; Olodo et al., 2019). The development of novel DNA sequencing technologies have provided the most significant change over the last decade, 'moving from genotyping to genome typing' (Luikart et al., 2003). While these technical advances were mainly deployed in major crops, they can now be transferred directly to underutilized crops. The decrease in costs of next-generation sequencing technologies, combined with better expertise leading to automatic analysis of increasing data, directly benefited underutilized crops. The generation of high-quality genomic resources has accelerated basic and applied research, trait discovery, and breeding of major cereal crops such as rice, maize, sorghum, and wheat. Fonio now benefits from high-quality genomic resources that improve production. In fact, the size of the genome was estimated to be 893 Mb (Abrouk et al., 2020). New recently generated resources include a chloroplast genome (Scarcelli et al., 2011), transcriptomes (Sarah et al., 2017), a chromosome-scale genome reference assembly (Abrouk et al., 2020; Wang et al., 2021), and genome resequencing of 183 wild individuals and cultivated varieties (Abrouk et al., 2020).

These genomic resources allow for a comprehensive assessment of fonio evolution history and its pattern of genetic diversity. Detailed knowledge of the patterns of genetic diversity is essential in the identification of the relevant genetic resources needed to develop breeding programs. Using the deep re-sequencing of 157 white fonio landraces (Figure 4) highlighted the strong impact of geographic, climatic, and anthropogenic factors on shaping the diversity of fonio (Abrouk et al., 2020). These advances in genomic resource availability open the road for more effective plant breeding. The discussion on the fonio breeding product profile was initiated with the value chain actors.

Figure 4

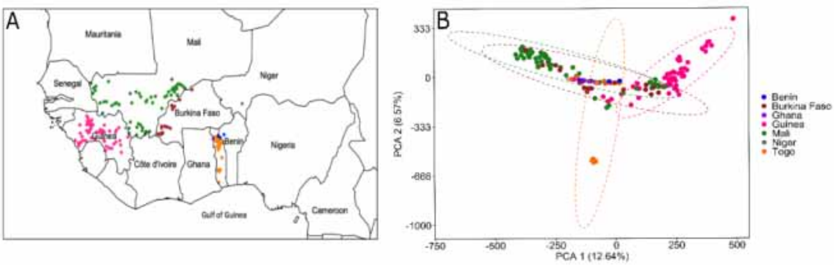

Figure 4 – Genomic Diversity of Fonio Landraces in West Africa

2. Challenges and Prospects of Fonio Breeding Strategies

The agronomical research on fonio enhanced cultivation practices and post-harvest technologies. Recent progress was made in fonio cultivation practices, including the optimal planting period, soil types, optimal sowing density, and fertilization rates (Gigou et al., 2009; Gueye et al., 2015; Ndor & Dauda, 2016). Advances are also noted in post-harvest technologies, which have long hampered the development of fonio cultivation, now increasing its economic potential (FONIO, http://fonio.cirad.fr/). However, no improvement program based solely on the hybridization of complementary progenies has been conducted on fonio because of the technical difficulty in manipulating extremely tiny floral organs. However, in recent years, mass selection strategy, based on homogenization, has been conducted on traditional heterogeneous populations of fonio to screen for homogeneous and best genotypes for several qualitative (raceme color, etc.) and quantitative (size, earliness, yield, etc.) traits (Kanlindogbè et al., 2020). Existing research has only focused on screening local diversity, targeting some high-yield varieties proposed to certification, such as the Senegalese varieties CFS52 called Fofana, CVF 477 called Fonio bi, and Niata in Senegal (Fofana et al., 2017; Kanfany et al., 2018).

Given recent advances in our understanding of genetic diversity and availability of genomic tools (Abrouk et al., 2020; Ibrahim Bio Yerima et al., 2021a; Sarah et al., 2017; Scarcelli et al., 2011), fonio now has the potential to be dramatically improved for yield with selective breeding (Ibrahim Bio Yerima et al., 2021b). Compared to other cereals, fonio still shows many unfavorable 'wild' traits, such as seed shattering, small seeds, and lack of apical dominance that could be targeted for breeding (Kanlindogbe et al., 2020). Knowledge of fonio's domestication and evolutionary history provides key elements for defining a genetic improvement strategy. A detailed analysis of the genetic diversity revealed that most 'domestication' genes identified in major cereals had not experienced a strong selection during fonio domestication (Abrouk et al., 2020). Targeting these genes would represent the first important step towards a significant improvement of fonio. For instance, identifying natural mutants, mutagenesis, or genome editing of the seed-shattering DeSh1-9B locus on chromosome 9B could rapidly result in a fonio cultivar with abolished seed shattering (Abrouk et al., 2020).

Beyond the traits associated with domestication, fonio adaptation to various agro-climatic conditions is important to the exploration of the underlying genetics associated with these adaptations. However, these approaches rely on the availability of genetic resources, and as with many other minor crops, germplasm available in national or international Genbank are scarce. For fonio, a very limited number of accessions (<2000) are conserved globally. At the instigation of the FAO, IRD (Institut de Recherche pour le Développement) and IPGRI (International Plant Genetic Resources Institute) collected more than 600 *D. exilis* accessions from Benin, Burkina Faso, Mali, Guinea, Niger, and Togo between 1977 and 1988. Over the last decade, a collective effort by the authors of this chapter, involving national and international institutions, has been made to collect accessions of *D. exilis* in Benin (54 accessions), Guinea (415 accessions), Nigeria (221 accessions), Niger (247 accessions), and Senegal (175 accessions). These collections relied on a common survey protocol to collect landraces and associated traditional ecological knowledge. These collections are stored in national gene banks and at ARCAD (Crop biodiversity research and resource center) in Montpellier, France. National collections are also available for some producing countries (Ayenan et al., 2017). The development of regional and mini-core collections should be the next step and will be an essential resource for allele mining studies for abiotic and biotic stresses.

Breeding strategies for minor crops such as fonio should perhaps not copy the ones developed for major crops but go beyond the agronomic traits' selection and yield increase. Indeed, in the context of family farming systems, where the neglected underutilized species (NUS) are the most relevant, there are two main challenges: (1) a need to adapt the NUS to accelerating rates of environmental changes; and (2) a general need to optimize the multifunctionality of NUS. Faced with an accelerating rate of environmental change, greater diversity into cropping systems is an increasingly recognized strategy in enhancing agroecosystem functioning and ecosystem services (Hajjar et al., 2008). To reach this objective, the breeding strategy for NUS could be inspired by a new framework, derived from ecological theory, that enables diversity to be incorporated into plant-breeding programs (Litrico & Violle, 2015) and provides another conceptual framework for increased yield target moving from an ideotype to an 'ideomix.'

In smallholder family farming, farmers value fonio for its multifunctionality through its nutrition and health benefits, its tolerance to stress (including drought), its ability to grow under low nutrient input conditions, and its value in traditional foods, different uses, and cultures. Thus, breeding strategies need to go beyond the Green Revolution model of improving and raising the yields of staple crops. Involving farmers in participatory breeding schemes could help solve this problem while meeting farmers' needs for varietal adaptation to a combination function: climate change adaptation, biotic and abiotic resistance, and cultural and culinary needs. Much progress has been made in participatory plant breeding approaches (PPBA), and research must build on these developments (Ceccarelli & Grando, 2020) for a review. Such PPBA requires better consideration of farmers' perspectives, knowledge, and practices through the involvement of such actors and other stakeholders in research projects.

Strategies in Promoting Conservation and Sustainable Use of Fonio

Setting up a global fonio valorization will need to strengthen both *in situ* and *ex situ* conservation. Indeed, while the need to access fonio's seeds/genetic resources for farming and scientific communities is growing, one of the primary losses is the diversity of landraces, the reservoir of genetic diversity and adaptation. Fonio has long since been reduced to the status of a marginal cereal because of its diminutive grains and the difficulties of its traditional processing. Thus, farmers are turning away from fonio production and, by ricochet, from biodiversity conservation. Threat on fonio genetic diversity, along with a wealth of traditional knowledge about their cultivation and use, is already reported in most of the producing countries (Leclerc et al., personal communication), in Togo (Adoukonou-Sagbadja, 2004) and Benin (Dansi et al., 2010; Sekloka et al., 2015) at an alarming rate. Hence, assessment, collection, and conservation of existing fonio diversity is crucial before they are lost forever. This approach is true not only for fonio but for most underutilized crops from West Africa. Of the 7.4 million plant accessions conserved in gene banks worldwide, minor crops and underutilized species are underrepresented (Commission on Genetic Resources for Food and Agriculture, 2010).

Furthermore, conservation efforts are unevenly distributed across the world. In Africa, for example, national gene banks are more dedicated to local genetic resources than conserving the over 10,000 accessions only located in eastern Africa (Commission on Genetic Resources for Food and Agriculture, 2010). Priority action for the conservation of fonio should focus on known collection gaps and wild relatives and on *in situ*/on-farm conservation actions. Indeed, using existing landrace diversity of crop species and favoring crop varietal replacement is viewed as an efficient short-term strategy to adapt to rapid environmental changes (Lobell & Tebaldi, 2014; Pironon et al., 2019; Rojas et al., 2019). A study on pearl millet showed how trans-frontier assisted migration of people could help towards mitigating crop's vulnerability to future climate change (Rhoné et al., 2020). This strategy identifies landraces among currently cultivated, climate-adapted landraces that will still be suitable in future conditions combining spatial genetic structure and spatial climate data (Fitzpatrick & Keller, 2015). This strategy could be particularly relevant for fonio but will require setting action plans at the scale of West Africa.

Besides, conservation is of particular importance in relation to the large interconnection and interdependence of worldwide populations and agriculture, but conservation governance, including exchanges, should also be considered. International treaties provide frameworks to which many countries are now adhering and provide forums for governance changes, including a broadening of stakeholders. As the actors interacting around the NUS are likely to be different from those investing in major species, they are complementary models for considering new modes of governance.

Filling the Gap Between Research and Development: A Need for a Strong Network of Partnerships Beyond Research

Minimal funding is invested in the underutilized crops because they are unknown by the majority (especially for fonio in West Africa), so we innovative promotional strategies for these species. Fonio will greatly benefit from a collective effort from the scientific community in researching, promoting, conserving, and sustainably using fonio. This chapter brings together an interdisciplinary research community (e.g., agronomists, plants geneticists, ethnobotanists, plant breeders) working collectively to develop knowledge and genomic resources within a collaborative framework. Future actions will not only need to bring together all the scientific expertise at a disciplinary (biology, social sciences) and an interdisciplinary level, they will require the development of a strong network of partnerships with research institutions and stakeholders – from smallholder farmers to policymakers. Action plans should concentrate on (1) establishing common approaches, such as multi-environment phenotyping and monitoring on-farm conservation, (2) employing strong leadership able to synergize the various initiatives, (3) sustaining long-term collaborative efforts, and (4) training a new generation of researchers and stakeholders dedicated to NUS.

Conclusion

While the development of agriculture has sometimes been seen as antagonistic with the climatic challenge and the conservation of biodiversity, agriculture is increasingly seen as an important part of the solution. Moving towards sustainable agricultural models is not only one of the keys to promoting the well-being and health of human populations but can have a real and considerable impact on reducing carbon emissions and on biodiversity conservation. Indeed, better utilization of local and often neglected crops such as fonio (*Digitaria exilis*) in diversified cropping systems can be an important first step toward secure food provision in times of uncertainty, while also sustaining the conservation of genetic resources. This chapter provided insight into the importance of fonio and the challenges related to the uses of genetic diversity through either breeding or landraces-assisted migration. For farmers, who are at a high-level risk, to change practices (in our case, to adopt a higher level of diversity), we need to integrate different aspects of the socio-economic environment, including agricultural helping policies. Thus, there must be a comprehensive and coordinated transdisciplinary collaboration across research disciplines (e.g., agronomy, anthropology, sociology, economics, breeding and genetics) and involving actors beyond research to shift the status of fonio out of the 'minor and underutilized' crops' group. NUS, such as fonio, has the potential to 'end hunger, achieve food security and improved nutrition and promote sustainable agriculture', as articulated in the UN SDG 2 and plays a key role in advancing agricultural development beyond the Green Revolution model.

Acknowledgements

We thank farmers and local authorities for their consent and collaboration. Collection of fonio landraces diversity over the last decade was supported through several projects funded by WAAPP/PPAAO 2A (CERA58ID06 SE), by the Agropolis Foundation (ARCAD project), by an ANR grant (AfriCrop project, ANR-13-BSV7-0017), and by the European Commission (EwaBelt, H2020-862848).

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Crop Adaptation and Improvement for Drought-Prone Environments

Editors: Ndjido A. Kane, Daniel Foncéka, And Timothy J. Dalton

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MANHATTAN, KS

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Farmers fields with millet and groundnut grown in rotation in a *Faidherbia albida* park located in the Groundnut Basin (Niakhar, Senegal).

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Digital Version ISBN: 978-1-944548-46-9
Paperback Book ISBN: 978-1-944548-47-6

This book was produced with Pressbooks (https://pressbooks.com) and rendered with Prince.