Crop Adaptation and Improvement for Drought-Prone Environments

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

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Cover image courtesy of: Alain Audebert (CIRAD), August 2021.

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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Foreword

In the 1970s, while the green revolution contributed to a boom in agricultural production across many regions of the world, sub-Saharan Africa faced recurrent periods of drought. Its agriculture has been negatively impacted by socio-environmental constraints (e.g., rural exodus, scarcity, and irregularity of the rainy seasons) and agronomic research has been taken unawares resulting in inadequate management of biodiversity and its potentials, technologies, and agricultural practices to meet the needs of the context.

In 1982, the idea of a specialized African regional center on research, associating skills in physiology and genetics, was born from a common will of the Senegalese Institute of Agricultural Research (ISRA), the Center for International Cooperation in Agronomic Research for Development (CIRAD) and the Universities Paris VII and Paris XII, to develop innovative approaches to improve and stabilize groundnut production in Senegal. This regional dynamic highlighted the need to build a center to accommodate teams from the sub-region and to provide an effective scientific tool that no research institution in the south had the financial and human means to build in isolation.

In 1987, the West and Central African Council for Agricultural Research and Development (CORAF) and ISRA proposed that the expertise of this multidisciplinary research team be extended to the countries of the sub-region, which shared the same issues. This directive materialized in 1989 with the creation of the regional study center for drought improvement (CERAAS), a national center with a regional vocation. In 1997, with the impetus of the Cheikh Anta Diop University of Dakar (UCAD) and the École Normale Supérieure d'Agronomie (ENSA), new research and training facilities were built on the campus of University of Thiès, next to the ENSA. This major development by CERAAS has made it possible to invest in research and a diploma training system in the disciplines related to improving adaptation to drought.

In the early 2000s, the World Bank and the Forum for Agricultural Research in Africa (FARA), to operationalize pillar IV of the Comprehensive Africa Agriculture Development Program, launched the regional initiative for the Multi-country African Agricultural Productivity Program. The objective of this initiative was to improve African producers' access to the technologies they need to increase their productivity and incomes by improving the relevance and efficiency of agricultural technology systems of generation and diffusion. This initiative was operationalized by the West Africa Agricultural Productivity Program (WAAPP), funded under the World Bank's "Adaptable Program Loan," (a progressive program for countries with several phases of implementation), under the leadership of the Economic Community of West African States (ECOWAS) and with the technical coordination of CORAF. Four phases of WAAPP were successively launched in 13 countries in West Africa. Among these countries, nine have a National Center of Specialization (CNS) responsible for conducting cutting-edge research on one or more speculations chosen by the country and included in the regional priorities defined by CORAF. Within this conceptual framework, CERAAS was the National Center of Specialization for dry cereals, including millets [*Pennisetum glaucum* (pearl millet), *Sorghum bicolor* (sorghum), *Digitaria exilis* (fonio)] and associated crops, such as groundnut [*Arachis hypogaea*), cowpea [*Vigna unguiculata*] and sesame [*Sesamum indicum*]). CERAAS benefited from 10-year funding from 2007–2017, provided by the government of Senegal and the World Bank, which offered it new perspectives in terms of mobilizing skills to tackle complex problems requiring multidisciplinary approaches. At the regional level, this partnership takes the form of a greater flow of technologies and expertise between CERAAS and several National Agricultural Research Systems (NARS) in the sub-region. After this ten-year program, CERAAS built up strong regional and international research partnerships and experience in crop adaption to dryland conditions. CERAAS has now fulfilled all requirements for gaining the status of Accredited Center of Excellence of ECOWAS on dryland crops.

Almost 40 years after its creation, CERAAS is in good time to share its contributions on achieving improved crops adaptation to drought. This book, entitled *Crops Adaptation and Improvement to Drought* aims to disseminate key results and technologies from research performed in West Africa and coordinated by an African Center of excellence to reach an international community (including academic and non-academic organizations as well as donors, policymakers, and the general public), interested in improving crop performance under drought conditions.

The book explores the Socioeconomic Analysis of Dryland Crop Production (Part I), the Advanced Phenotyping and Crop Modelling for Adaptation to Drylands (Part II), and the Genetic Diversity and Improvement of Dryland Crops (Part III), providing new insights in biodiversity and agro-systems management and improvement to cope with drought conditions.

The chapters herein, made by contributors who conducted their research at the CERAAS and studied or collaborated with the local staff, present climate-smart technologies, varieties that have been adapted to drought, tools developed, technologies implemented, and methods used to study physiological, genetic, and agronomical bases of crop adaptation to drought.

With such comprehensive topics and very contextualized examples, the book is intended to stand as a legacy in the field for a wide audience: students, research scholars, professionals, and experts. More importantly, this book is the first comprehensive document that addresses the complexity of adapting crops to climate change in the Sahel and West Africa.

Abdou Tenkouano, Executive Director, CORAF – The West and Central African Council for Agricultural Research and Development

Preface

The Sahel region is a semiarid climate zone that stretches from the east to the west of Africa and separates the Sahara Desert to the north and the tropical savannas to the south. During the second half of the 20th century, the Sahel region experienced a major climate shift – from a relatively wetter period in the 1950s and 1960s to a dryer climate in the 1970s and 1980s. This dry period led to major episodes of drought, food shortages, and dramatic environmental and societal effects (Tomalka et al., 2021). Although, the levels of rainfall have increased, they are lower than those in the 1940s and 1950s, with high year-to-year variability and increased unpredictability.

In the Sahel, agriculture is the main pillar of the countries' economy. In this region, 80–90 % of the population is engaged in agriculture, on which they depend for both food and income. Therefore, even minor perturbations could threaten people's livelihoods and food security. Unfortunately, in the Sahel, agricultural production is primarily subsistence-based and rainfed, which makes the region highly dependent on rainfall patterns and thus vulnerable to climate change. Climate change projections indicate that the Sahel will gradually become hotter, with some areas experiencing increased, but erratic rainfall (Tomalka et al., 2021). In this context, droughts and floods are expected to intensify (i.e., become stronger and more frequent), hence the emergency for appropriate adaptation measures to reduce the insecurity and vulnerability in the region.

Sahelian droughts and their effects have been studied extensively since the 1970s. CERAAS, the lead organization behind this book project, is a full-fledged Senegalese research center entirely dedicated to studying drought adaptation and its improvement. It does so through genetic crop improvement in association with other disciplines since its creation 40 years ago. Sound expertise on drought research has earned CERAAS a renowned reputation, which was strengthened by its recognition as a Regional Center of Excellence on dry cereals and associated crops with the mandate to lead research and development on pearl millet, sorghum, fonio, peanut, cowpea, and sesame in West and Central Africa.

Over the years, CERAAS has accumulated a wealth of knowledge and experience on dryland crops improvement, with the collaboration of numerous regional and international partners. This book pays tribute to the excellent work done by dedicated research teams on crop improvement and adaptation to drought-prone environments in West Africa. Rather than compiling 40 years of research on this topic, we opted to share the latest developments relevant to concepts, methods, and technologies associated with dry cereals and legume crops' production in the semiarid West Africa. More specifically, this book highlights key results from both applied and basic research undertaken in West Africa towards the development and deployment of climate-smart technologies, especially drought-adapted varieties. These tools include advanced analysis tools and methods used to characterize drought-prone environments and understand crops adaptation to drought and decision support tools designed to guide a better targeting of necessary technologies to the right environments. This book project was also an opportunity to strengthen young scientists' writing skills and self-confidence as some of them embraced lead author roles. Although, most of the contributors are francophone, to broaden the spectrum of readership, we have undertaken the task of writing and publishing the book in English.

The book encompasses 19 chapters and is organized into three parts – socioeconomic analysis of dryland crop production, advanced phenotyping and crop modelling for adaptation to drylands, and genetic diversity and improvement of dryland crops.

Part 1: Socioeconomic Analysis of Dryland Crop Production illustrates the socioeconomic factors that affect the food systems for these crops. It contains six chapters that provide an overview of crop production and consumption in the region (Chapter 1). Then, important inputs that affect system productivity are presented: preferences for new seed varieties (Chapter 2), yield response to fertilizer (Chapter 3), counterfeit herbicides (Chapter 4), and the way farmers develop expectations about the weather events that shape cropping outcomes (Chapter 5). Chapter 6 is dedicated to understanding urban consumer preferences for processed food products derived from pearl millet.

Part 2: Advanced Phenotyping and Crop Modelling for Adaption to Drylands addresses the state of the art of plant phenotyping and the modeling of crop adaptation to dryland cropping systems. The first three chapters focus on drone-based high throughput phenotyping in field situations. Chapter 1 describes an automated data pipeline to fast-track image data processing and analysis. Using sorghum as a test case, Chapter 2 provides evidence of the effectiveness and accuracy of drones for drought phenotyping. Chapter 3 outlines the prospect of a regional network for phenotyping to mutualize investment. Chapters 4 and 5 focus on root traits and their use in crop improvement programs, while Chapters 6 presents crop ideotypes to guide genetic improvement and variety recommendations.

Lastly, Part 3 investigates the genetic diversity and improvement of dryland crops. The seven chapters in this section focus on biodiversity and agricultural systems sustainability, orphan crops, such as fonio, and the utilization of a regional germplasm collection in the improvement of cowpea, groundnut, pearl millet, and sorghum. Opportunities offered by advances in genetics and genomics for more effective use of genetic resources for varietal development are also highlighted.

The richness of this book lies in the multidisciplinary expertise mobilized by CERAAS through its partnerships, but unfortunately, not all chapters received could be included in this book. To maintain the standards of scientific quality and thematic relevance, some chapters were excluded. However, throughout the review process, which involved both internal and external steps, authors were guided with constructive feedback. In addition, research related to dryland crop management, crop protection, nutrition, as well as technology diffusion pathways, and gender and youth inclusion were deliberately not addressed in this book to keep this first edition concise and focused on CERAAS' core discipline – genetic improvement.

Overall, it has been a long journey since the time the call for chapters was launched in 2020, to the identification of an appropriate publisher in 2021, and the publication of the book in 2022. A lot of time and energy has been spent to compile the information contained in this book. It was a very demanding experience but also very rewarding and satisfying, and a lot has been learned through the process.

We hope that all the parties involved in this project are proud of the outcome of this journey.

We hope that readers will find informative and useful answers herein and better understand the kind of research that is being undertaken to improve crops' adaptation to drought and how the findings can contribute to increasing crop productivity and building more climate resilient cropping and food systems.

We wish you all a happy reading!

The Editors

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PART I

SOCIO-ECONOMIC ANALYSIS OF DRYLAND CROPS PRODUCTION

1. Production and Consumption Trends of Dryland Staples in CORAF Nations

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Timothy J. Dalton, Kansas State University, USA

Abstract

Sorghum, pearl millet, fonio, cowpeas, groundnuts, and livestock form the backbone of the agricultural economy in semiarid regions of West and Central Africa. This chapter presents descriptive statistics on the production, consumption, and trade of five commodities that are the mandate crops of the CORAF regional research center of excellence, Centre d'étude régional pour l'amélioration de l'adaptation à la sécheresse (CERAAS). Over the past decade, changes in the total production of these crops have been driven by land extensification at rates that are two to three times yield growth rates. While the consumption of dryland cereal crops has decreased in most nations, consistent with economic theory, evidence on groundnuts indicates increasing per capita consumption. Very limited quantities of all crops are formally traded across borders, with the exception of groundnuts, which is an important export crop in Senegal. Sorghum, pearl millet, fonio, cowpeas, and groundnuts play critical roles in the food economy of the CORAF region through the supply of calories and proteins to local populations. Strategies to increase the productivity of these crops will be beneficial in different ways to consumers and producers.

Keywords: production, consumption, trade, drylands staples, CORAF

Introduction

This chapter presents recent trends in the production, consumption, and trade of sorghum, pearl millet, fonio, cowpea, and groundnuts in 23 West and Central Africa nations covered by the West and Central African Council for Agricultural Research and Development (CORAF)[1]. These five crops form the basis of the food systems in many Sahelian nations in the CORAF region and are the focus of the research center of excellence, *Centre d'étude régional pour l'amélioration de l'adaptation à la sécheresse* (CERAAS), which has led regional efforts to increase the productivity and resiliency of these crops since 1989.

The purpose of this chapter is to provide strategic country-level information on the dynamics of these staples and consumer needs in the future. This study is restricted to sorghum, pearl millet, fonio, cowpea, and groundnuts to draw attention to the critical role these crops play in the Sahelian food system. It does not focus on the entire basket of staples available in CORAF nations. Approximately 65 million hectares of cereals and 14 million hectares of legumes were planted in CORAF countries in 2019, accounting for 63 and 51 percent of cereal and legume areas in Sub-Saharan Africa. On a global scale, CORAF nations produce approximately 27% (sorghum), 37% (pearl millet), 100% (fonio), 84% (cowpeas), and 23% (groundnuts) of the global annual production.

Overall, production of these crops has increased over the past decade, except in a few countries, and consumption has also increased. Very limited quantities of the crops are traded within the region; a limited amount of sorghum is imported from outside the region, but groundnuts are exported throughout the world. These crops, apart from groundnuts, remain relatively isolated from international markets, unlike maize or soybeans. As such, national and regional production and consumption patterns will influence local prices as international price transmission is limited (Nakelse et al., 2018). We examine each of the five crops independently through discussion and statistics on production, consumption, and trade and then provide a discussion of aggregated trends[2].

Sorghum

Sorghum is harvested from over 15.8 million hectares in the CORAF region, accounting for 56% of the total area in Sub-Saharan Africa. Still, production is dominated by five countries located in the “sorghum belt”: Nigeria, Niger, Burkina Faso, Mali, and Chad. These five countries account for 89% of the regional area (Figure 1), with approximately 51% of the regional total planted in Nigeria. Niger and Burkina Faso combine to occupy only one-half the acreage in Nigeria or approximately 26% of the regional total. From 1999 to 2019, cereal area increased by 52 percent in the CORAF region, sorghum area increased by 22%, and maize by 118%. Areal expansion occurred throughout the region except for in Nigeria, Ghana, Mauritania, and the Central African Republic (Figure 2). The decline in the relative importance of sorghum in the regional cereal economy is largely panterritorial with only Niger, Guinea-Bissau, and Togo showing an increase in their share of total cereal acreage (Figure 3).

Total sorghum production increased by 1.5% per year between 1999 and 2019. Land extensification drives the increase in grain production, with the area harvested increasing by about 1% per year. The average per-hectare yield in the region is less than 1.0 mt/ha, with national differences that flow along with the differences in agroecology. However, yields have not remained stagnant, increasing at 0.9% per year on average, with several nations such as Senegal, Niger, and Cameroon exceeding a 2% annualized rate of growth in average sorghum yields. The combination of higher yields and land expansion underlines the interaction between agroecological potential and sorghum: expansion occurs in less-productive areas where the baseline potential is lower, and the gain in total production is constrained by climatic edaphic conditions interacting with other stress factors.

Sorghum consumption mirrors production patterns. Nations located in the sorghum belt consume more than 50 kg/per capita/per year, while those outside the belt consume far less (Figure 4). Overall, production estimates exceed consumption, indicating surplus grain for loss and seed. The average ratio of production to consumption is 1.75 in the region, but the ratio is lower in the sorghum belt, where the ratio is 1.43. The Chad, Niger, and Nigeria ratio is even lower at 1.13, 1.37, and 1.18, respectively.

Approximately 21,057 mt of sorghum were imported into the CORAF region in 2019, with 99% of the total volume destined for Cameroon. The United States of America was the source of this grain. The remaining tonnage consisted of cross-border trade between neighboring nations (e.g., exports from Burkina Faso into Côte d'Ivoire and Ghana or from the Central African Republic to Cameroon). Overall, the volume of cross-border trade does not exceed 7,000 mt or, in other terms, one-twentieth of 1 percent of total regional production, reinforcing the observation that sorghum is consumed in the country where it is produced. Opportunities for increased trade of sorghum from Mali will depend on a decrease in transportation costs and regional harmonization of trade policies (Kaminski et al., 2013).

Figure 1

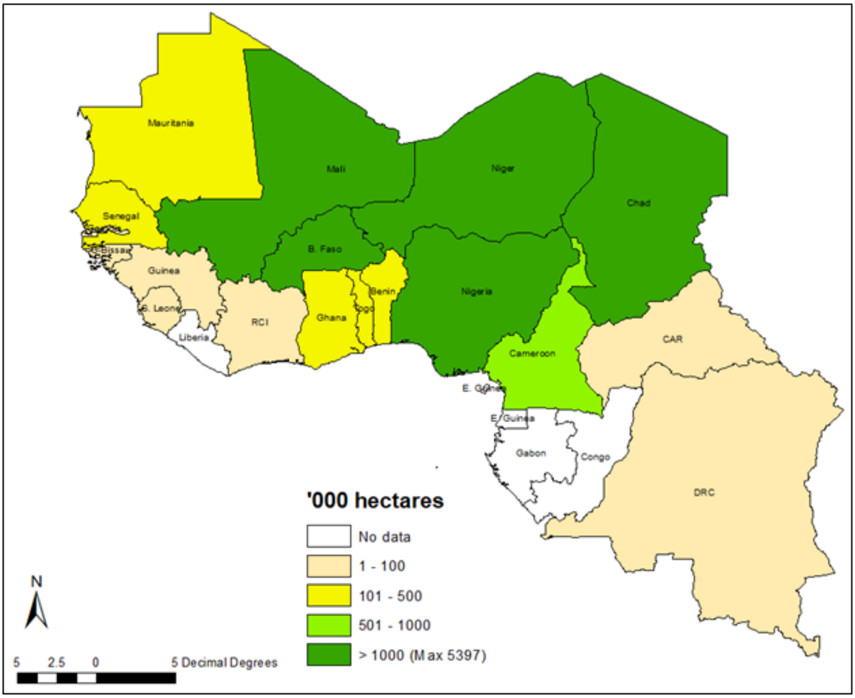

Figure 1 – Sorghum Area in 2019 ('000 hectares)

Figure 2

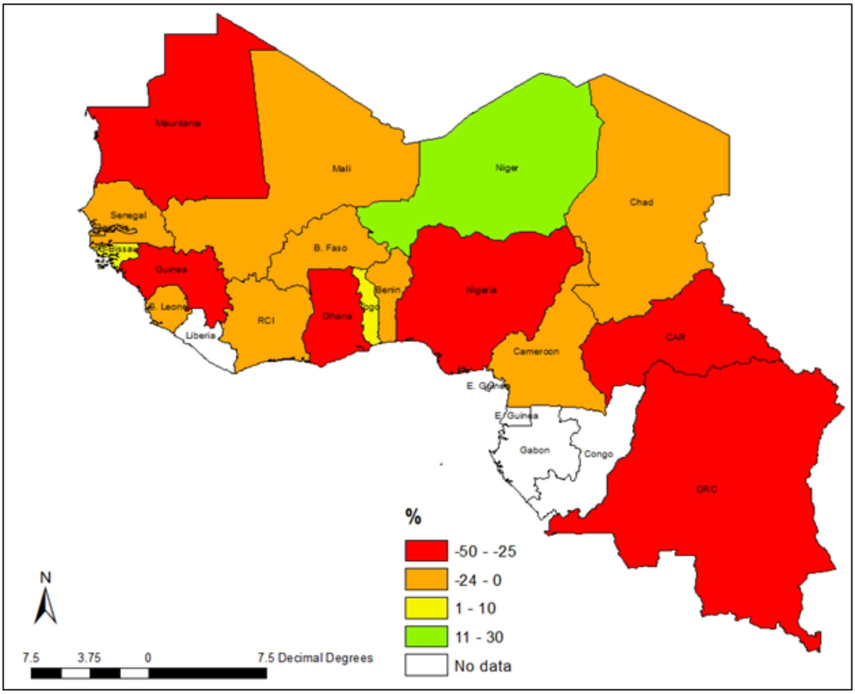

Figure 2 – Relative Change in Sorghum Area Between 1999 and 2019 (%)

Figure 3

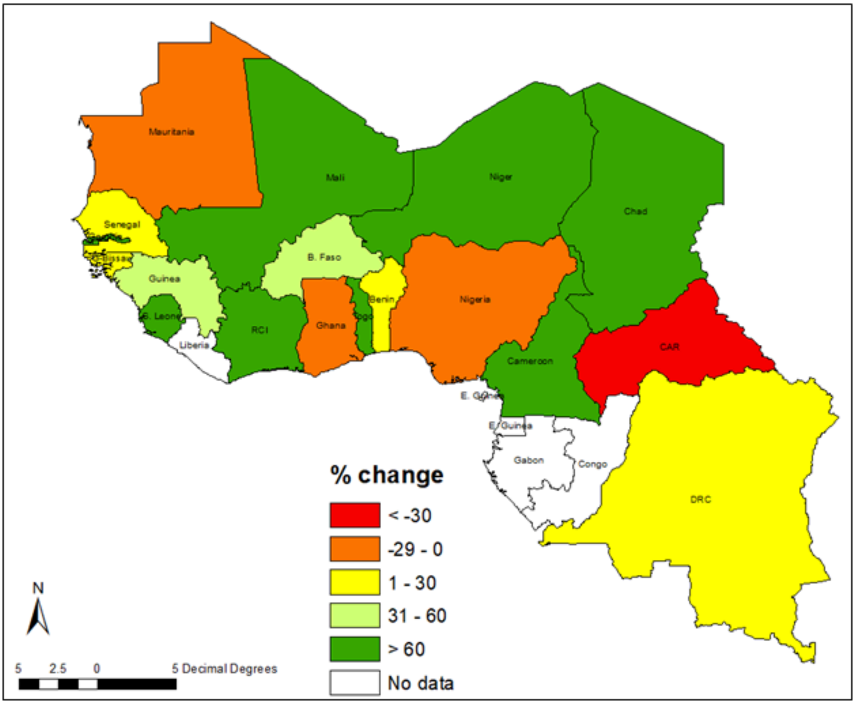

Figure 3 – Change in the Share of Cereal Area Planted to Sorghum Between 1999–2019 (%)

Figure 4

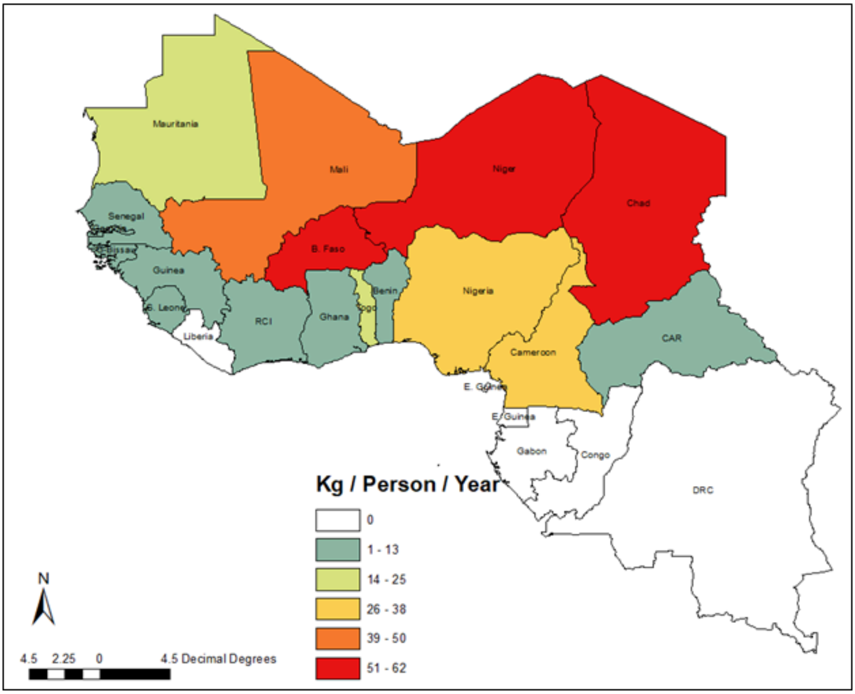

Figure 4 – Annual Per Capita Consumption of Sorghum in 2019 (kg per capita year)

Pearl Millet

Pearl millet production spans nations from west to east in the CORAF region, but it is most intensively cultivated in the Sahelian agroecology (Figure 5). Five nations plant more than a million hectares of pearl millet annually, and Senegal is not far behind with nearly 890,000 hectares (Figure 5). Niger is an outlier among all nations and planted 6.8 million hectares of pearl millet in 2019, Nigeria planted 2.8 million, Mali 2.0 million hectares, and Burkina Faso and Chad about 1.2 million hectares each. The average regional yield is 0.851 mt/ha, and yields in Niger, Burkina Faso, Chad, and Niger are below the regional average (Figure 6).

Millet plays an important role in the cereal economy and occupies a large percentage of cereal area, especially in the dryland areas. In Niger, pearl millet is planted on 64% of all cereal area. In Senegal, it accounts for 51% of the area and about 1/3 of the area in Mali, Burkina Faso, and Chad (Figure 7). Over the past two decades, this share has decreased across the region, despite cereal area increasing, underscoring the faster increase in acreage allocated to other cereals.

Millet remains a very important staple for many nations, but few rely upon millet like Niger. Nigeriens consume an average of 124 kg/per capita/per year, which has declined from 152 kg/per capita/per year in 1999. Mali and Burkina Faso are the next highest consumers of millet but at less than half the amount consumed in Niger (61.3 and 55.6 kg/per capita/per year, respectively; Figure 8). Millet consumption is highly nation-specific, and just five nations (Niger, Nigeria, Mali, Burkina Faso, and Chad) consume 90% of all millet produced in the CORAF region (Figure 9).

International trade in pearl millet is thinner than that of sorghum. Regionally, Niger exported 5,200 mt towards Burkina Faso, accounting for 88% of the total traded volume of 6,362 mt. Trade amounts to approximately one-twentieth of one percent of regional production. Approximately 61 mt of millet were shipped off the continent towards Europe, the United States, and Japan in 2019. Cross-border flows of millet are limited by high transaction costs associated with weak farm and market logistics combined with high transportation costs (Kaminski et al., 2013). In Senegal, high social capital, represented by business networks, increased the opportunities for millet trade despite high freight costs (Jacques et al., 2018).

Figure 5

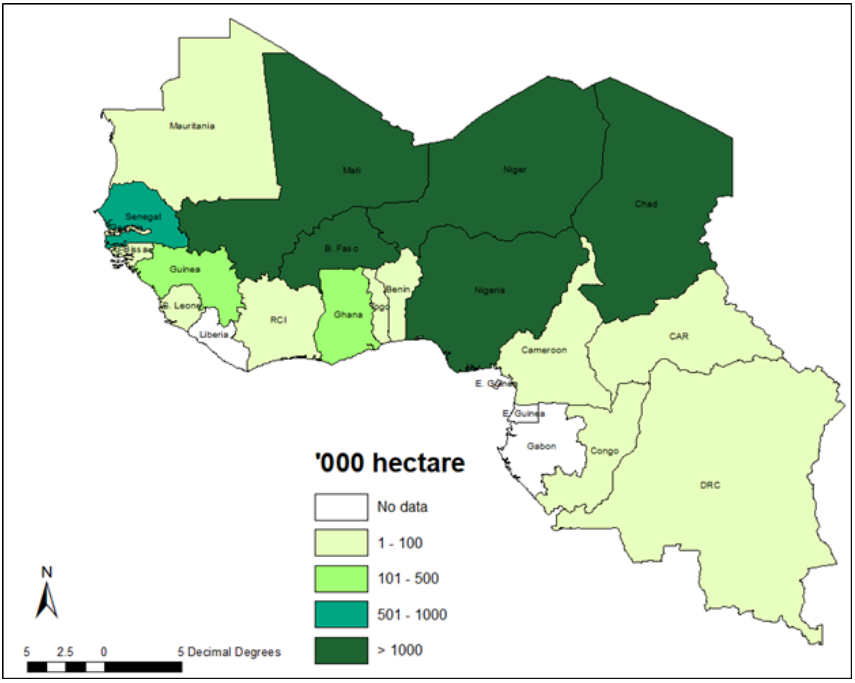

Figure 5 – Pearl Millet Area in 2019 (‘000 hectares)

Figure 6

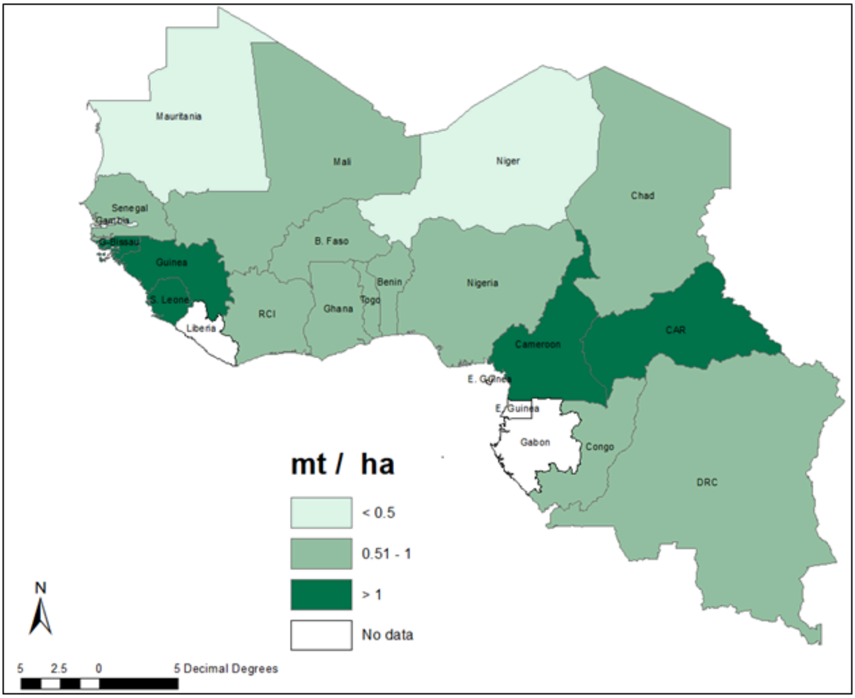

Figure 6 – Pearl Millet Yield in 2019 (mt ha)

Figure 7

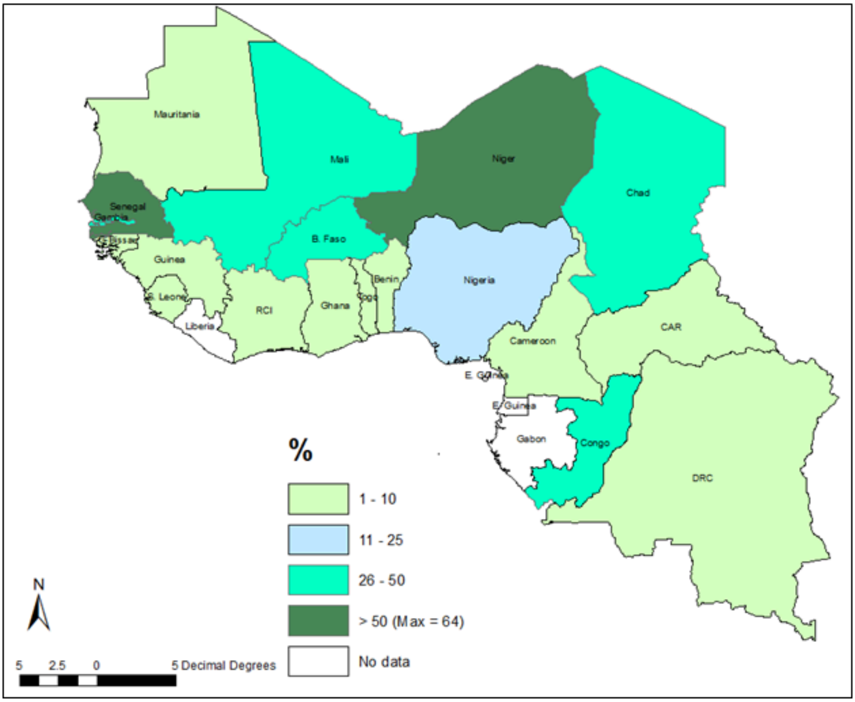

Figure 7 – Share of Cereal Area Planted to Pearl Millet in 2019 (%)

Figure 8

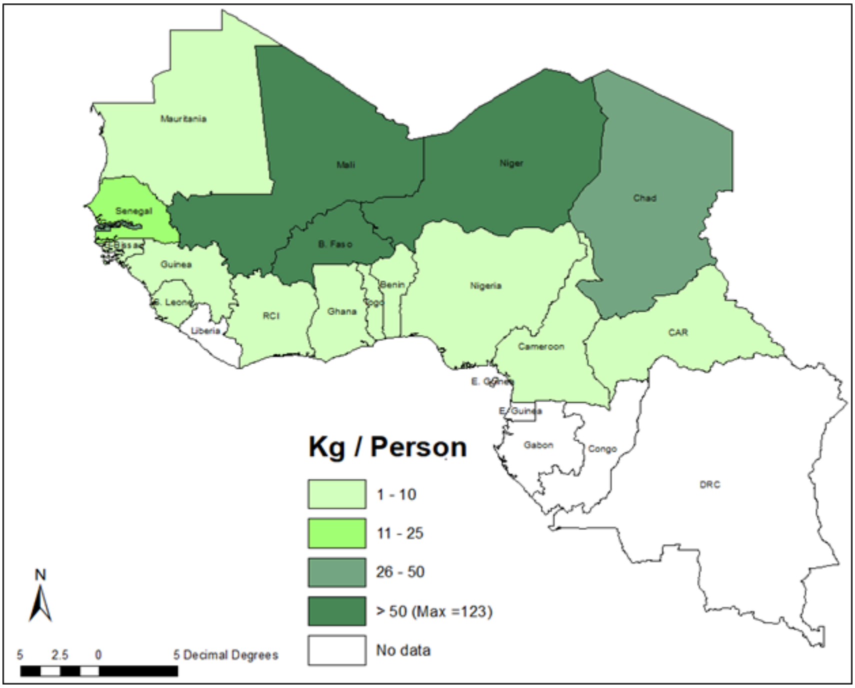

Figure 8 – Per Capita Consumption of Pearl Millet in 2019

Figure 9

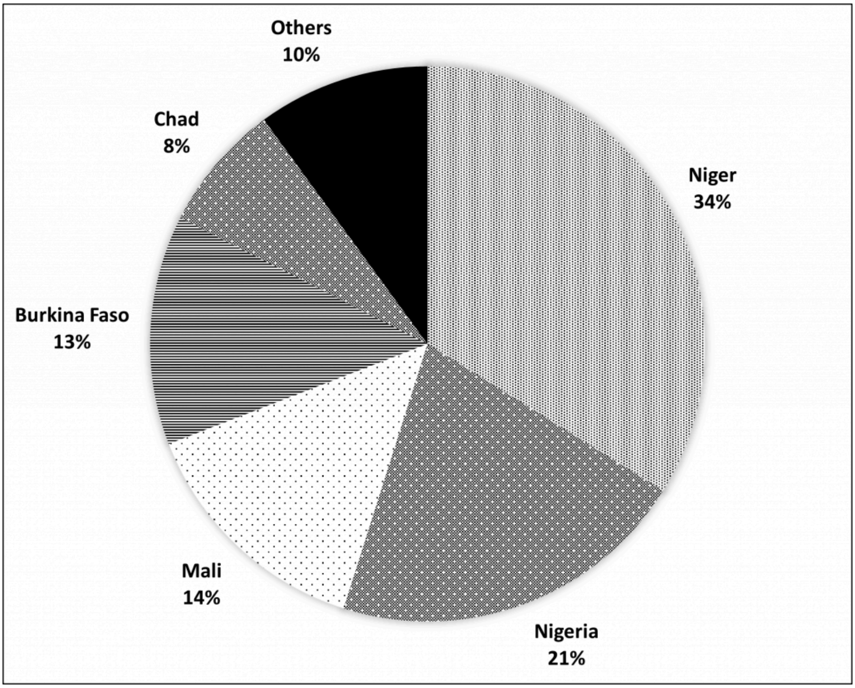

Figure 9 – Top Five Millet Consumers in Terms of the Share of Total CORAF Region Millet Consumed in 2019 (%)

Fonio

Three countries in West Africa account for 95% of all fonio areas: Guinea, Nigeria, and Mali. Nearly 70% of all fonio area is in Guinea, and the nation produces 76% of the total regional output estimated at 701,000 mt (Figure 10). This compares to 10.4 million mt of millet and 15.6 million tons of sorghum.

There is no information on the consumption of fonio. Under the assumption that there is very little trade (as described below) and that nearly all fonio is consumed in the country in which it was produced, per capita consumption is approximately 48.7 kg/per year in Guinea. In comparison, it is less than 2.5 kg/person in all other countries. Fonio in West Africa, outside Guinea, is a specialty crop and is rarely consumed.

Nearly all international trade of fonio (355 mt of 359 mt) was exported to high-income countries in North America and Europe in 2019. Most grains were sourced in Senegal and Mali (124 and 11 mt, respectively), followed by Burkina Faso and Guinea. Like pearl millet, the trade volume of fonio is less than one-twentieth of one percent of production.

Figure 10

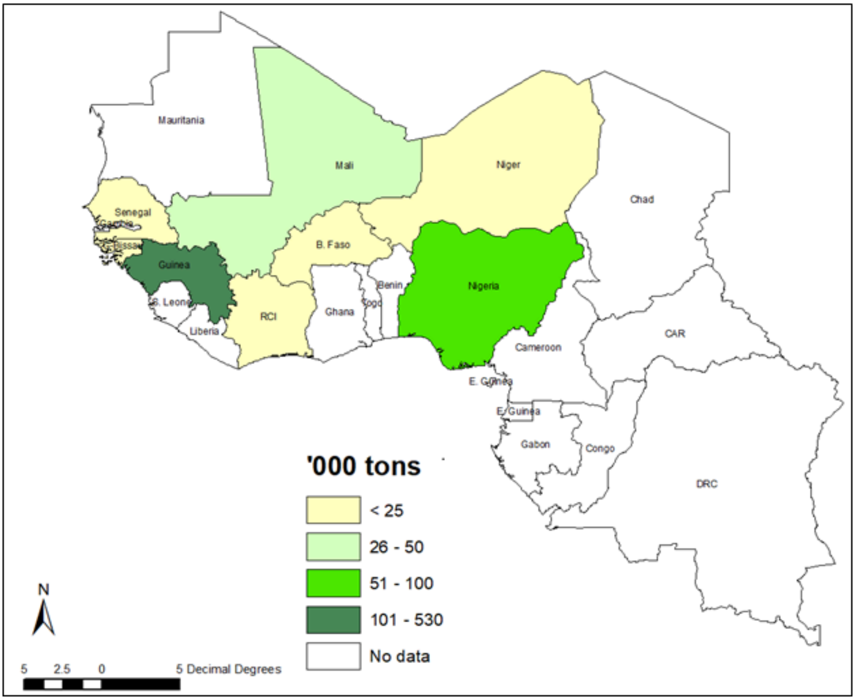

Figure 10 – Production of Fonio in 2019 (mt)

Cowpea

Cowpea, like fonio, is a highly specialized crop, and while grown in ten CORAF nations, it is concentrated in Niger, Nigeria, and Burkina Faso. These three nations account for 93% of all area planted for cowpea in the CORAF region and 82% of the planting across Sub-Saharan Africa (Figure 11). Across the region, cowpea grain production has increased 138% between 1999 and 2019, and the largest increases occurred in Niger, Burkina Faso, Senegal, and Cameroon. Across Sub-Saharan Africa, cowpea production has increased 1.5

times during the same period. There is no recorded systematic information on cowpea hay and fodder production or value despite its economic importance in the livestock sector.

The consumption of cowpea is concentrated in local production areas due to limited trade. Statistical agencies do not record the official trade of cowpeas, and these sources do not capture informal trade across border regions. Based on the production statistics and controlling for seed use and estimated losses, it is approximated that Niger, Burkina Faso, and Nigeria consume, on average, 85, 26, and 14 kg/per capita/per year in each country, respectively (Figure 12). Consumption is estimated to be below 10 kg/per capita/per year in the seven remaining countries with measured production. There are no national trade statistics on cowpea, but a few studies have examined the ex-ante impact of new cowpea technology on trade (Langyintuo & Lowenberg-DeBoer, 2006).

Figure 11

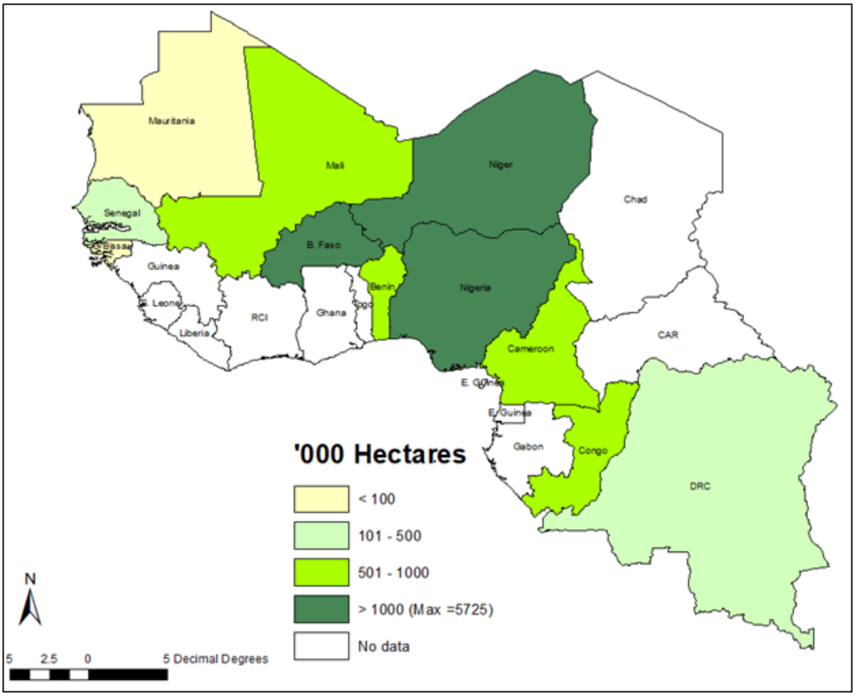

Figure 11 – Area Planted to Cowpea in 2019

Figure 12

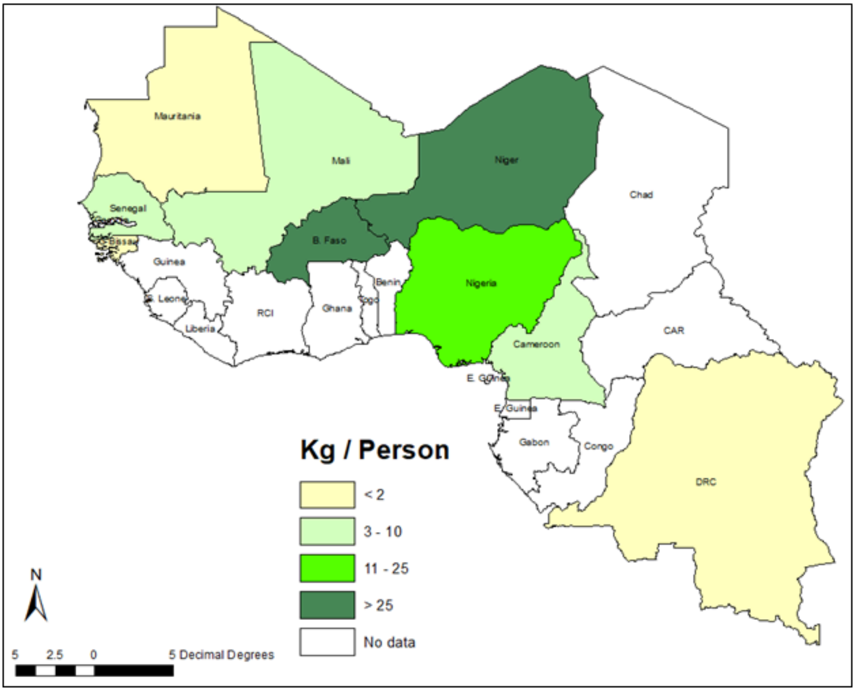

Figure 12 – Cowpea Consumption in 2019

Groundnuts

Groundnut production is widespread across the CORAF region and Sub-Saharan Africa (Figure 13). Approximately 10.7 million hectares of groundnuts were planted in the CORAF region in 2019, accounting for 77% of the total area in Sub-Saharan Africa. In contrast to other crops, where very few nations accounted for 90% of planted areas, ten nations in the region account for 90% of all area and total production. These regions stretch from the western side of the region eastward into central Africa. The region produced 85% of the total output of groundnuts in Sub-Saharan Africa (Figure 14). Nearly all nations in the CORAF region have experienced an increase in the area allocated to groundnuts, resulting in an increase in production over the past twenty years. While the area harvested has increased 89% between 1999 and 2019, total production has increased by a 78%, underscoring the extensification into areas with lower production potential.

The average regional groundnut yield is 1.07 mt/ha, and this level is the highest among all Sub-Saharan African regions, but country-specific averages range between 0.53 to 1.49 mt/ha. Over time, per hectare yield has increased at approximately 0.75% per year in the region, with only four nations exceeding 1% per year (Figure 15). However, our data does not determine whether total factor productivity growth or input use is the driving factor of higher yields.

On average, 6.8 kg/per capita/per year of groundnuts are consumed in the CORAF region, but this ranges from 0.1 kg/per capita/per year in Mauritania to 17.1 kg/per year/per capita/per year in The Gambia. The nations with the greatest consumption of groundnuts include Nigeria, Niger, Burkina Faso, Cameroon, and Ghana. Combined, these nations account for 75% of the total regional consumption (Figure 16).

Trade-in groundnuts is the highest among the five crops discussed in this chapter. Approximately 2.1% of the total production volume in the CORAF region, or 236,069 mt, is traded across international borders, and 95% of the volume is sent to high- and middle-income countries outside of Sub-Saharan Africa. The leading exporter is Senegal, shipping approximately 225,304 mt, or 16% of its total national production, to fifteen countries. Exports from Senegal account for 95.4% of the total trade volume across all CORAF nations. China was the leading destination for Senegalese groundnuts and accounted for 220,877 tons or 93.6% of the total volume of regional exports. Senegal was the only nation in the CORAF region where China purchased groundnuts. The global price for groundnuts ranged from US$1,500/mt to US$2,000 during the first half of the 2020 marketing year, making it a lucrative crop for earning foreign exchange. Sector studies have highlighted strategies to increase the value of the groundnut value chain in Senegal (World Bank, 2015).

Figure 13

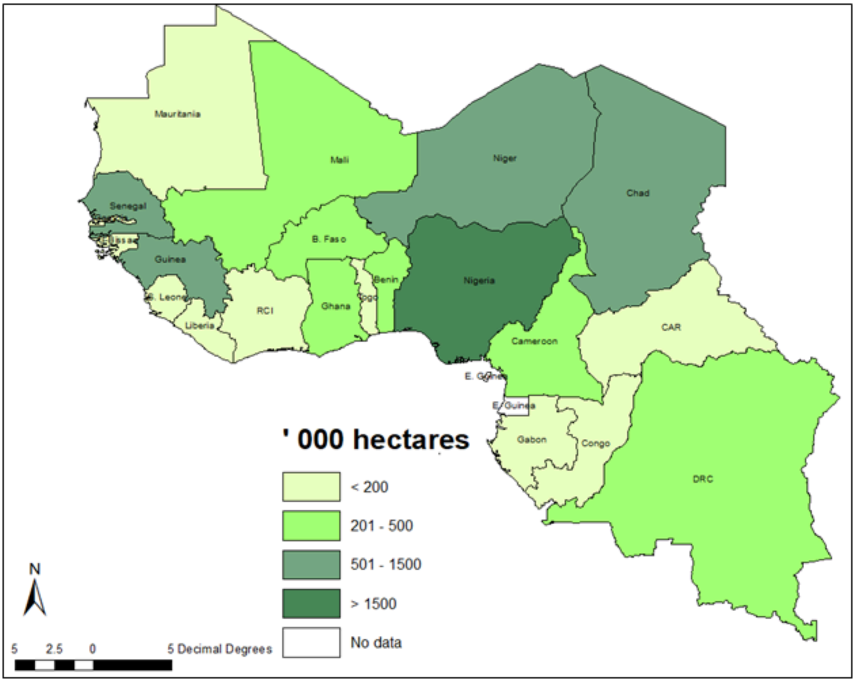

Figure 13 – Area Planted to Groundnuts in 2019 (ha)

Figure 14

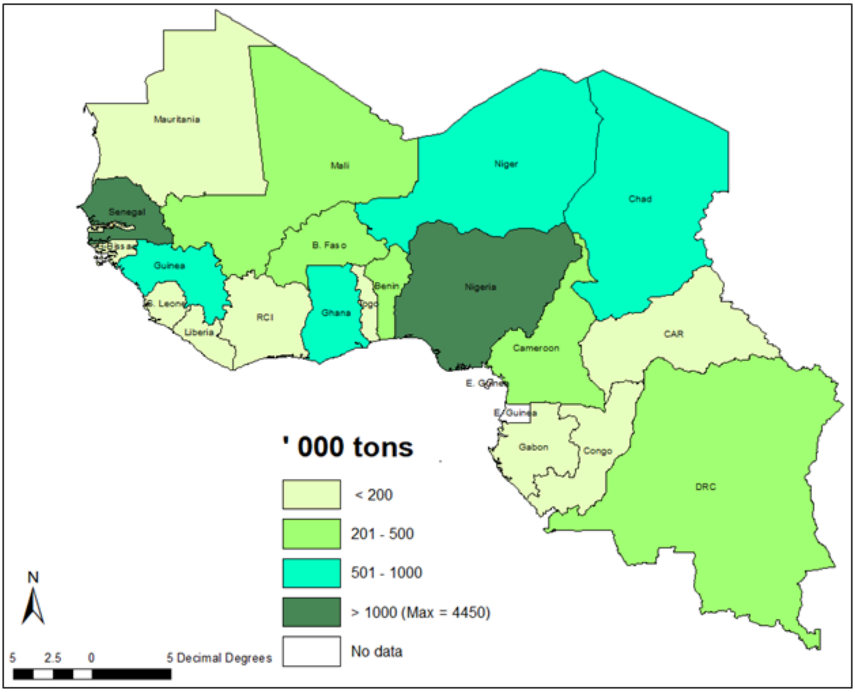

Figure 14 – Total Production of Groundnuts by Nation in 2019 (mt)

Figure 15

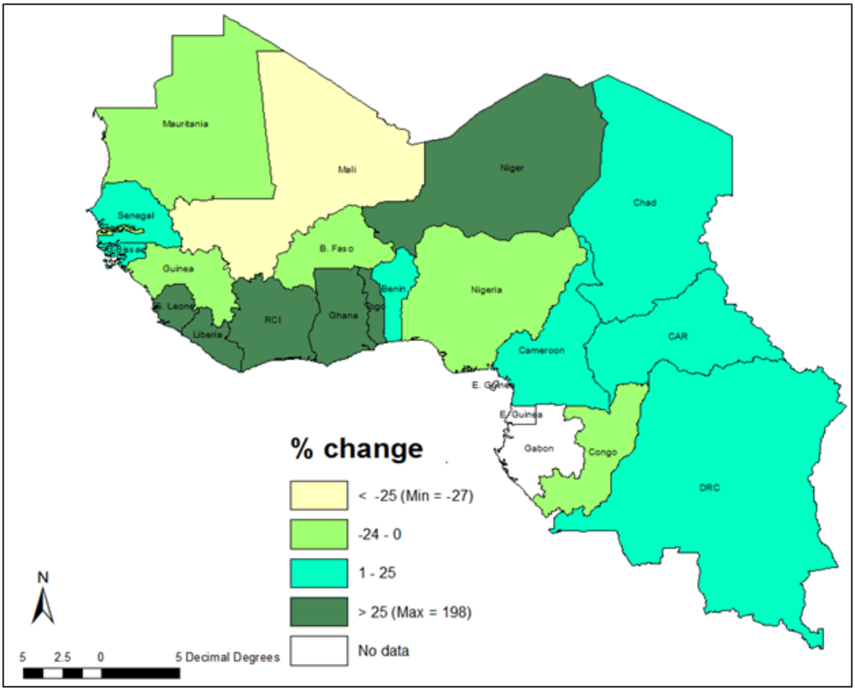

Figure 15 – Change in Average Yield (mt ha) by Nation Between 1999 and 2019 (%)

Figure 16

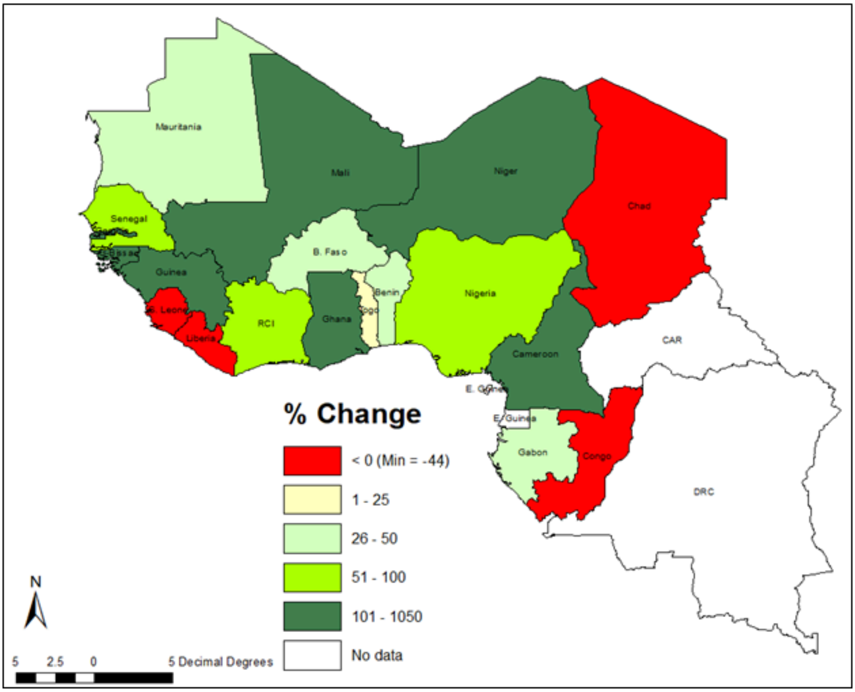

Figure 16 – Change in Per Capita Consumption of Groundnuts Between 1999 and 2019 (%)

Synthesis and Projections

The previous sections have described the production, consumption, and trade of sorghum, millet, fonio, cowpeas, and groundnuts using national statistics. These statistics are pooled into crop-specific data sets to estimate trends across the CORAF region, and these trends are projected into the next decade. The data set covers the period from 1961 until 2019.

Table 1
Annualized Growth Rates Estimated by a Log-Linear Regression (%/year)

Indicator	Sorghum	Millet	Fonio	Groundnuts	Cowpea
Production	2.16	1.70	2.60	1.98	4.29
Acreage	1.42	1.18	2.20	1.26	2.60
Yield	0.59	0.62	0.72	0.52	1.85
Consumption	-0.40	-0.81	*	0.71	*

* Data does not allow an estimation of a log-linear growth rate. ** All trends are significant at 1%.

Total production of all five crops has increased between 1.7% to 4.3% per year (Table 1). Sixty to 85% of the production increase is driven by land extensification. At the same time, the yield component, a combined measure of crop varietal improvement, input intensification, and other elements of total factor productivity growth, accounts for 26% to 43% of the increase in production. The highest yield growth rate is with cowpeas, where yield growth is 2/3rds of the annual rate of areal expansion.

Table 2
Average Rural and Urban Annual Population Growth Rates in CORAF Nations (2009–2018)

	2010's Urban	2010's Rural		2010's Urban	2010's Rural
Benin	2.9%	2.7%	Guinea	3.1%	3.2%
Burkina Faso	2.8%	3.0%	Guinea-Bissau	3.1%	3.0%
Cameroon	2.9%	3.0%	Liberia	1.9%	3.6%
Cape Verde	-0.2%	2.0%	Mali	2.8%	2.4%
Central African Republic	3.2%	3.9%	Mauritania	2.2%	1.9%
Chad	4.1%	4.1%	Niger	2.1%	2.4%
Congo	1.4%	3.4%	Nigeria	2.5%	2.7%
Cote d'Ivoire	3.1%	3.0%	Senegal	2.4%	2.2%
DR Congo	3.7%	3.0%	Sierra Leone	2.2%	2.2%
Gabon	-0.9%	3.6%	Togo	2.1%	2.0%
Gambia	2.6%	2.6%	Sao Tome and Principe	-0.9%	3.8%
Ghana	2.8%	3.0%	Average	2.4%	3.1%

Source: FAOSTAT

We can estimate trends in consumption, and these trends are consistent with economic theory. Sorghum and millet are staple goods that are “inferior” to other cereals, such as wheat, rice, and maize. Over time, as income grows, consumption of these crops (on a per capita basis) decreases as food consumption diversifies into alternative staples and towards proteins, fats, fruits, and vegetables. This does not imply that the aggregate demand for these staples is decreasing. Population growth in the region remains high in many nations (Table 2). Since population growth rates are 2- to 4-times higher than the absolute value of consumption reductions, and there are more mouths to feed, demand for these crops will continue to increase. But as income grows and population growth rates stabilize, consumption of these crops as food will decrease, and alternative usages as feed or industrial products should grow.

Conclusion

Sorghum, pearl millet, fonio, cowpeas, and groundnuts, with livestock, form the backbone of the agricultural economy in semi-arid regions of West and Central Africa. This chapter aimed to explore the graphical distribution of these crops in the region, their productivity and consumption through national averages, and changes over time. The national maps oversimplify the distribution of the crops in the region because the data do not provide resolution to be displayed on a finer scale where agroecological, edaphic, and other constraints can be correlated with outcomes.

Over the past twenty years, cropland has expanded in the CORAF region, but the area allocated to sorghum, millet, and fonio increased more slowly than other crops. Overall changes in the total production of these crops have been driven by land extensification at rates two to three times the growth rate in yields. The consumption of dryland cereal crops has decreased in most nations, consistent with economic theory, while evidence on groundnuts indicates increasing per capita consumption. We do not have data on fonio or cowpea consumption.

There is very limited information on the trade of the five commodities in the region, apart from groundnuts and cowpea (Jacques et al., 2018; Kaminski et al., 2013; Langyintuo & Lowenberg-DeBoer, 2006). Groundnuts have served as an important income-generating crop for farmers in Senegal since the colonial period, and evidence indicates that this is correlated with an increase in consumption (World Bank, 2017). The lack of trade data implies that most production is locally consumed or saved for seed. Future research on regional trade may look to novel data sets that collect information from border crossings where informal exchange occurs.

Sorghum, pearl millet, fonio, cowpeas, and groundnuts play critical roles in the food economy of the CORAF region through the supply of calories and protein to local populations. Strategies to increase the productivity of these three crops will be beneficial in different ways. Increased productivity will accelerate a decline in the share of area allocated to these crops without increased trade or new market opportunities for sorghum and pearl millet. It may also spur innovative food products to meet consumer needs. This will free land to be allocated to other cereals, legumes, or high-valued crops with higher returns to land and labor. In the case of dryland crops in the CORAF region, this is likely to include cowpeas and groundnuts.

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ENDNOTES

[1] CORAF is composed of the national agricultural research systems of Benin, Burkina Faso, Cameroon, Cape Verde, Central African Republic, Chad, Congo, Cote d'Ivoire, Democratic Republic of the Congo, Republic of Congo, Gabon, Gambia, Ghana, Guinea, Guinea-Bissau, Liberia, Mali, Mauritania, Niger, Nigeria, Senegal, Sierra Leone, Togo and Sao Tome and Principe.

[2] This chapter draws upon statistics available from the United Nations Food and Agriculture Organization.

2. Assessment of Farmers' Groundnut Varietal Trait Preferences and Production Constraints in the Groundnut Basin of Senegal

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Maguette Seye, ISRA/CERAAS, Senegal
Daniel Foncéka, CIRAD, France & ISRA/CERAAS, Senegal

Abstract

Groundnut is a cash crop that generates income and improves the livelihoods of smallholder farmers in several developing countries. Although Senegal is one of the major producing countries, the national average grain yield remains low. A participatory rural appraisal was conducted in the Groundnut Basin of Senegal in 2015 and aimed to assess farmer perceptions of production constraints and varietal trait preferences. Ninety farmers were randomly selected in nine villages distributed across three regions of the Groundnut Basin. Data was collected through Focus Group Discussions (FGDs) and Semi-Structured Interviews (SSI). The results of the study indicated that seed availability was the most limiting factor in groundnut production across villages. Low soil fertility and storage insect pests were the second and third most important constraints respectively. Other constraints included limited access to land, drought, and commercialization. Among varietal traits, farmers unanimously considered pod and haulm yields as the most important. Other important traits mentioned were adaptation to drought, high pod weight, and earliness. These production constraints and varietal trait preferences should be taken into consideration when defining the groundnut product profiles of the national breeding program in order to improve productivity and increase the adoption of newly bred cultivars.

Keywords: groundnut, production constraints, farmers, trait preferences

Introduction

Groundnut is one of the most important oilseed legumes grown worldwide. Asia and Africa account for more than 90% of global groundnut area and it is cultivated mostly under rainfed conditions by small-scale farmers. The African continent accounts for 31.1% of total global production (FAOSTAT, 2018). In Senegal, groundnut occupies a central role in the agricultural economy since its introduction by explorers in 1836. Historically, the Senegalese economy has relied on groundnuts, which accounts for up to 60% of GDP, 80% of export earnings, and more than half of the planted area from 1961 to 2020 (FAOSTAT, 2020). The crop was grown throughout the country, and particularly in the central area called the Groundnut Basin.

Over recent decades, the contribution of groundnut to GDP has declined. Groundnut production has been reduced due to numerous factors. These include a long drought period starting in the 1970s and continuing to the present. Added to this is poor soil fertility, climate change, a disorganized value chain, inconsistency of the various governmental and donor policies, and the low adoption of newly developed agricultural technologies. A study conducted by Faye et al. (2019) on the adoption rate of improved varieties of main crops grown in Senegal showed evidence that improved groundnut varieties are not widely adopted by farmers; the reported rate is 55%. In the same report, results also showed that the varieties that are cultivated have an average age of more than 10 years. This shows a low penetration of new varieties in the farming environment. Some authors explain this situation by an inadequate awareness, omission of farmers during the process of cultivar development, and farmers' fear of taking risks in testing varieties that are not yet well known by the majority (Ceccarelli & Grando, 2007; Omanya et al., 2007).

Technology transfer to farmers is one of the major bottlenecks of many agricultural projects in Africa. Efforts should concentrate on improving the access to the developed innovations because technological change in agriculture is essential for reducing poverty and stimulating economic growth, particularly in low-income countries (Dhirifi, 2014). It is also important that the technologies developed and proposed consider the needs of the target users. This shortcoming has opened the way to alternative approaches for increasing the rate of technological adoption by farmers (Chambers, 1994; Duraiappah et al., 2005).

Participatory rural appraisal (PRA) is one of the most popular strategies. PRA enables local farmers to mobilize and participate in the early stages of technology development. In the particular case of plant breeding, the involvement of farmers as an integral part of the process ensures the participation of the most important stakeholders in the definition of breeding objectives and therefore influences the direction of the research. Plant breeders cannot respond to every quirk of farmers' circumstances but the relevance of breeding research in poor nations can be improved (Haugerud & Collinson, 1990; Sattar et al., 2017). The main objective of most PRA approaches is for a better incorporation of farmers' technical knowledge and identification of research priorities into the breeding programs to develop varieties that meet their needs (Morris & Bellon, 2004). PRA results guide the breeder to focus on farmers preferred traits while addressing the constraints prevailing in the production areas. Many studies, such as Ceccarelli and Grando (2009), reported that PRA approaches enhance the adoption of newly bred cultivars.

To date, there is scant formal documentation on the main groundnut constraints and the traits preferred by farmers in Senegal. Existing documents refer to commercialization aspects and to the diagnosis of the problems related to the whole value chain (Dia et al., 2003; Georges et al., 2016; Ndiaye, 2018; Noba et al., 2014). Agricultural extension agencies have often reported low soil fertility and drought as the major constraints to groundnut production in Senegal. However, the scientific method has not been used to ascertain groundnut production constraints and farmers' preferred traits.

Such studies have been conducted and published in most groundnut growing countries of West Africa. In the study conducted by Coulibaly et al. (2017) concerning two main groundnut production zones in Niger, drought appeared as the major constraint affecting production, followed by low soil fertility. In Burkina Faso, besides organizational difficulties (i.e., access to credit and access to material, among others), pest attacks and drought were identified as important constraints followed by diseases (Boubacar et al., 2020). As a starting point for the breeding program in Togo, a PRA was conducted in three regions, identifying leaf spot diseases, rosette, groundnut bud necrosis, and insects, such as pod sucking bug and bruchid, as the most important constraints limiting the production (Banla et al., 2018). High pod yield is the most preferred trait in almost all reported studies. However, pod size and oil content were the second and third preferred traits in the Savanes region in Togo, and early maturing in Niger (Banla et al., 2018; Coulibaly et al., 2017).

The PRA approach has been widely used across Africa for other crops including potato, maize, cowpea, cassava, sweet potato, and pearl millet (Abakemal et al., 2013; Baafi et al., 2015; Egbadzor et al., 2013; Kanfany et al., 2020; Muhinyuza et al., 2012; Njoku et al., 2014). Those studies clearly established that constraints and the trait preferences of farmers for a given crop are location specific. Hence, plant breeders should consider both local adaptation and, when possible, adaptation to a wide range of environments when developing a new cultivar (Omanya et al., 2007). This study applies PRA to gather information and farmers' knowledge to identify groundnut production constraints and to assess traits preferred by farmers in the Groundnut Basin of Senegal. This will serve as important background information to the breeding program and will enable the development of more popular varieties that meet farmers' needs for wide adoption.

Materials and Methods

1. Study Areas and Sampling

The study was conducted between March and April 2015 in the Groundnut Basin located in central Senegal, where groundnut and pearl millet are the predominant crops (FAOSTAT, 2015). Three representative groundnut-growing regions of Senegal, Kaolack, Kaffrine, and Tambacounda, were purposefully selected based on the importance of groundnut in terms of production and area (Table 1). During the 2014 cropping season, these three regions accounted for 39% of the national groundnut area and over 42%

of total groundnut production (FAOSTAT, 2015). With the help of the local extension officers, one department was selected in each region based on the number of farmers and farmers' organizations in the department. Three villages were then selected in each department according to their accessibility and the importance of groundnut production.

Table 1
Characteristics of Selected Groundnut Production Regions in Senegal

Regions	Cultivated area (ha)	Production (mt)	Precipitation (mm)	Selected communities
Kaffrine	209,100	272,570	655	Kathiot, Kahi
Kaolack	169,843	223,001	655	Guinth Kaye, Kaymor, Porokhane
Tambacounda	104,210	161,941	741	Koussanar, Makacolibatang
Senegal	1,134,330	1,432,086		

Nine study sites were considered in the study (Figure 1). The villages were located in seven rural communes: three in Kaolack, two in Kaffrine, and two in Tambacounda. A focus group discussion was held in each of the selected villages to develop a general idea of groundnut cultivation in the corresponding area. In addition, within each village, 10 farmers were randomly selected for semi-structured interviews, creating a sample of 90 producers.

Figure 1

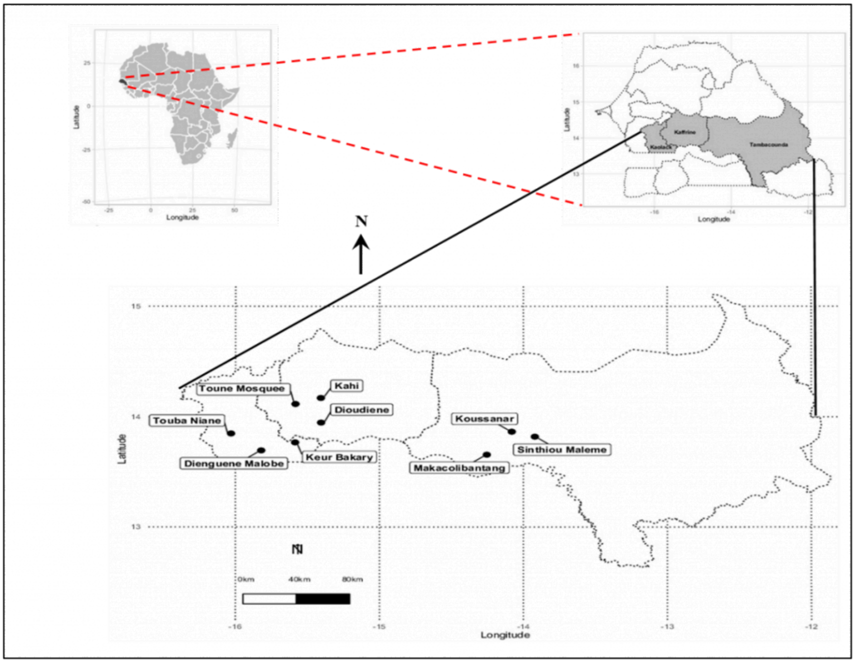

Figure 1 – Map Showing Sampling Locations in the Groundnut Basin

2. Data Collection and Analysis

Local extension staff at the respective localities facilitated the PRA process by mobilizing farmers to participate in the focused group discussions. Both formal and informal approaches were employed to collect data for the study. The informal approach was used to generate information on farmer perceptions at the community level. The discussions involved nine focus group discussions (FGDs) with one at each village. Each focus group comprised of 10 to 17 farmers. The FGDs were standardized using a checklist of topics to be covered. The topics discussed included farm characteristics and farmers' agronomic practices, farmers' trait preferences for groundnut varieties, marketing of their products, and the perceived constraints affecting production.

The group discussions were followed by formal interviews using semi-structured questionnaires to explore issues that were more specific.

Individual farmers were surveyed using a semi-structured questionnaire to collect information on production constraints and farmer's preferences for varieties. This enabled each individual farmer to express their opinion independently.

Scoring and ranking techniques were used to assess farmers' varietal trait preferences and constraints to groundnut production. Data was coded and entered in Microsoft Excel. Analysis was conducted using Statistical Package for the Social Scientists (SPSS version 19) and summarized into percentages and means. Variables were subjected to descriptive statistics, cross-tabulation, one-sample t (two-sided), and Fisher tests. R was used to draw the map showing the PRA sites.

Results

1. Demographic and Socio-economic Characters

In the studied sites, mostly men produce groundnut. The sex ratio is 88.9% males to 11.1% females (Table 2). In our sample, 72.22% of the respondents were farmers by occupation while 27.78% had additional income-generating activities. Most of the interviewed farmers (82.23%) were uneducated. A few (8.89%) possessed a primary school certificate and 5.56% a secondary certificate. The age of respondents ranged between 35 and 60 years. The proportion of the active population that were groundnut producers was 71.11%. Most of the farmers (63%) did not have any form of support or training and only 36% of the farmers belonged to a farmers' association.

Figure 2

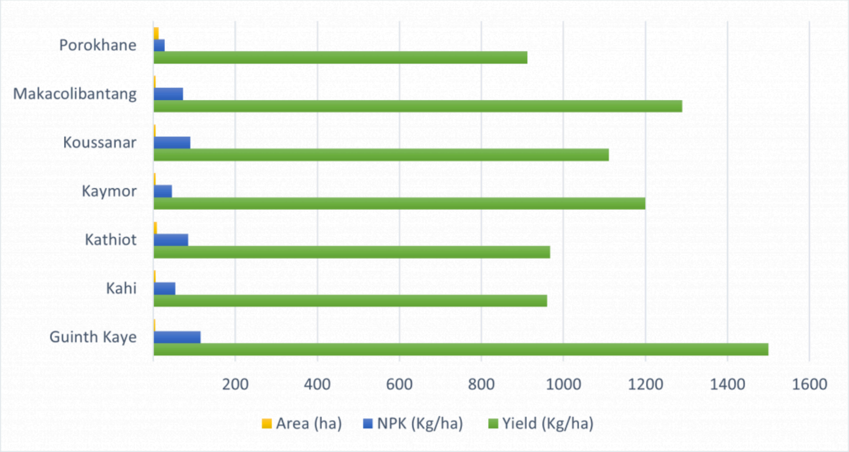

Figure 2 – Average Pod Yield Obtained as a Function of the Area and Application Rate of Mineral Fertilizer

2. Groundnut Importance and Production Level

The selected rural communes were predominantly groundnut producing areas, but other crops, like cereals, played a key role in the agricultural system. The average landholding varied from 1 to 30 ha and there was a significant difference in the importance of the crops grown in each location. A ranking of the importance of groundnut compared to other crops was completed based on the cultivated area allocated to groundnut and the production level. As expected, in almost all rural communes, groundnut occupied the largest share of land and was ranked first with an average mean rank of 1.3. In the central part of the peanut basin (Kaolack, Kaffrine) groundnut was the most important crop followed by pearl millet. Elsewhere in the eastern part of the country (Tambacounda), corn or sorghum were ranked as the second most important crop. Mean comparison of yields reveals significant differences between localities (p = 0.042). The average estimated grain yield in 2014 was 1,112 Kg ha-1. The highest estimated grain yield (1,500 Kg ha-1) was recorded in Guinth Kaye, while the lowest value 0.9 Kg ha-1 was recorded in Porokhane. Both localities are in the same region (Kaolack). A similar trend was observed for the application of fertilizer

(Figure 2). On average, 116 Kg ha-1 of NPK fertilizer (6-20-10) was recorded at Guinth Kaye while 28 Kg ha-1 was recorded at Porokhane.

Table 2
Average Socio-demographic Profile of Interviewed Farmers by Region

Variables					
	Kaolack	**Kaffrine**	**Tambacounda**	**Total**	**%**
Gender					
Female	3	3	4	10	11
Male	27	27	26	80	89
Age					
<15	0	0	1	1	1
15-35	3	5	5	13	14
35-60	18	15	18	51	57
60"}">>60	9	10	6	25	28
Education					
Koranic school	27	20	12	59	66
Local language	1	8	6	15	17
none	1	1	1	3	3
Primary	0	1	7	8	9
Secondary	1	0	4	5	6
Member of a Farmer Organization					
No	26	17	11	54	60
Yes	4	13	19	36	40
Occupation Other than Farming					
No	10	7	8	25	28
Yes	20	23	22	65	72
Subsidy from the Government					
No	25	19	19	63	70
Yes	5	11	11	27	30
Received Training in Groundnut Cultivation					
No	30	24	20	74	82
Yes	0	6	10	16	18

3. Varieties Grown and Their Provenances

Five known and named varieties were cultivated in the surveyed zones: GH119-20, 73-33, 28-206, Fleur 11, and 55-437 (Table 3). There were differences in the most commonly planted varieties by location (Figure 3). Out of the five varieties, 73-33 was the most cultivated and was ranked first in almost all rural communes except in Guinth Kaye, Porokhane, and to some extend Kaymor, where either 28-206 or GH119-20 were more commonly cultivated.

Table 3
Attributes of the Cultivated Varieties

	Attributes						
Varieties	**Released Year**	**Pod Yield (t/ha)**	**Haulm Yield (t/ha)**	**Cycle (Days)**	**100 Seed Weight (g)**	**Seed Size**	**Main Use**
GH119-20	1960	1.5-2	2-2.5	110	85-90	large	confectionery
73-33	1973	2-2.5	1.5-2	110	50-52	medium	oil
Fleur11	1995	2.5-3	2	90	50-55	medium	oil-confectionery
55-437	1994	1.5-2	1	90	35-38	small	oil
28-206	1928	1.5-2	1.5	120	45-49	small	oil

Figure 3

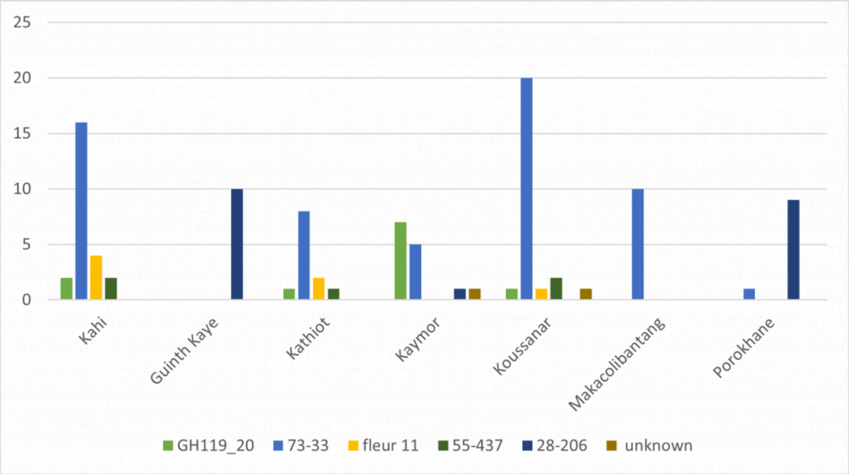

Figure 3 – Popular Varieties Cultivated in the Studied Sites

The variety 73-33 was the most grown across all the studied sites. The 28-206 was specific in Guinth Kaye and Porokhane and the variety GH119-20 was present in Kaymor. Fleur 11 was not very popular in Kaffrine (Kahi and Kathiot). A small portion of respondents (2%) did not have any idea about the type of variety they grew. Most farmers (83%) recycled seed by keeping a portion of the previous harvest. Only 20% obtained government-subsidized seeds or procured them from the local market. It was only in Koussanar, a rural commune of Tambacounda, where farmers were organized in a cooperative and multiplied their seed for the next coming growing season.

4. Trait Preferences

The mean rankings of farmer-preferred traits for groundnut varieties are presented in Figure 4. Characteristics with the smallest mean rank (1) are perceived to be the most important and the highest value (5) is considered as less important. Except for tolerance to biotic stresses (P = 0.007), where a significant difference was observed between rural communes, traits were ranked similarly by farmers interviewed in the study zones. Most of the farmers identified haulm yield as the second most important characteristic after pod yield, except in Koussanar where good pod filling was ranked highest. The same locality identified erect plant stature as an important groundnut characteristic for variety adoption. High seed weight is also a preferred feature for groundnut growers in Kahi, Kathio, Kaymor, and Makacolibatang. Other important traits mentioned were adaptation to abiotic stresses such as short cycle and tolerance to drought. Tolerance to biotic constraints like resistance to leaf diseases is desired in groundnut variety. In general, farmers from the different sites did not consider good taste as an important trait for groundnut variety.

Figure 4

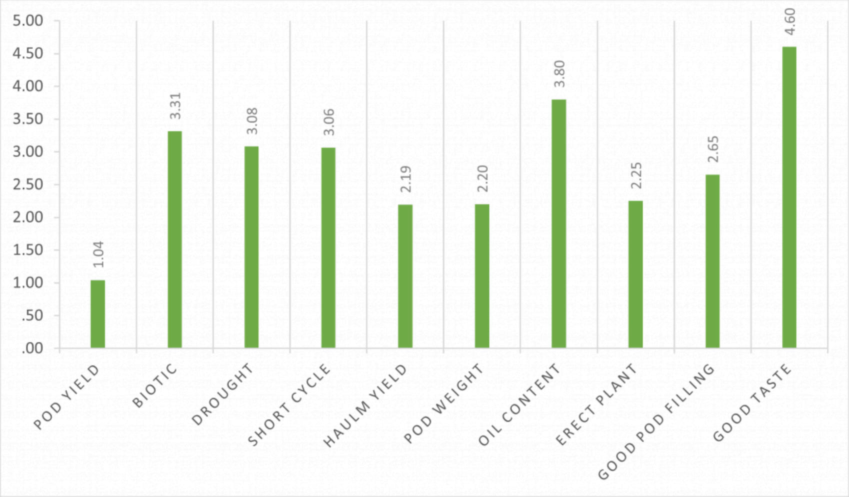

Figure 4 – Farmers Preferences for Groundnut Variety Traits Across Rural Communes

5. Production Constraints

Prioritization of the constraints was based on the mean ranking given by farmers. These constraints were identified and listed during the focus group discussions. Each interviewed farmer further ranked them (Table 4). Characteristics with the lowest mean rank are classified as the most important. The most important constraints mentioned by farmers across sites were seed availability, land degradation, insects at storage, and land availability. Drought was ranked fifth, with a significant difference between sites. Marketing and leaf diseases were ranked sixth and seventh respectively with substantial differences in farmers' responses in ranking marketing.

These constraints were common to groundnut growing areas but the order varied from site to site. Insects, mainly pod-sucking bugs (Pentatomidae and Lygaeidae) and groundnut bruchid (Bruchidae), were considered the most common constraint to groundnut storage and were ranked as the most important in Kathiot alongside leaf diseases. Lack of tools was ranked in Koussanar, Kaymor, and Kathiot as an important constraint. Regarding drought, there was a noteworthy difference between respondents in their respective studied areas. More than half of the respondents (58%) did not classify drought as a major constraint to groundnut cultivation, while the remaining participants (42%) said the opposite. The damages were not so important and drought at the vegetative stage of the life cycle was more frequent. However, terminal drought caused more damage when it happened.

Table 4
Relative Ranking of Major Groundnut Production Constraints by Location

Constraints								**Total**		
	Guinth Kaye	**Kahi**	**Kathiot**	**Kaymor**	**Koussanar**	**Maka**	**Porokhane**	**Mean**	**F**	**Rank**
Land degradation	2.31	2.33	2.2	2.06	1	1	4.66	2	0.47	2
Storage insects	4.01	2	1	3	2.4	1.56	4	2.04	0.063	3
Leaf diseases	3.89	2.78	1	1	2	3.2	3.41	2.56	0.406	7
Drought	4	2.67	3	3.67	1.75	1.75	4	2.36	0.023*	5
Land availability	2.17	1	3	2	3.71	4.1	3	2.13	0.597	4
Seed availability	2.8	1.63	2	1.6	1.67	2.2	2	1.91	0.145	1
Commercialization	3.44	2	2.5	3	1.75	2	2.4	2.5	0.018*	6
Lack of tools	5	3	2	2.4	1.67	2.5	2	2.58	0.047*	8
Cattle damage	5.07	4.22	4.34	3	3.5	4	5	3.33	0.667	9

Note. Characteristic with the smallest mean value is perceived to be the most important. *Significant at 0.05

Discussion

The presence of women farmers (11.1%) in this study was very low and reflects their limited access to land. One major consideration of this situation is socio-cultural. In Senegal, land acquisition is through inheritance from father to son. Another aspect that contributes strongly to this imbalance is the status of the family chief, typically conferred to the man who theoretically is in charge of the family's daily expenses. The limited involvement of women in groundnut cultivation has also been reported in other countries of West Africa (Banla et al., 2018; Oppong-Sekyere et al., 2015). Women do not own land, but they are involved in the cultivation. Arable land access is a real problem for women in West Africa, particularly in Senegal. PRA conducted on sorghum and pearl millet reported limited access to land by women, justifying their low involvement in the production (Kanfany et al., 2020). Conversely, in Burkina Faso, Sinare et al. (2021) highlighted the large involvement of women (more than 50%) in groundnut cultivation despite their limited and unequitable access to production resources. A similar situation was reported in Tanzania where men and women were equally involved in groundnut production (Daudi et al., 2018). Women's engagement in groundnut cultivation is socio-culturally specific.

Because the constraints listed by the farmers in the studied sites involve different actors of the value chain, we classified them into two categories. The first group included seeds availability, land availability, and commercialization. The second group encompassed low soil fertility, insects at storage, drought, and leaf diseases. The consistency of ranking the first group of constraints over the communities suggests that these are major constraints affecting groundnut production in the Groundnut Basin. These difficulties are similar in that the government and the private sector plays a greater role than research in helping farmers solve these problems. However, it is important to underscore the efforts made by the government to reorganize and make the groundnut sector more efficient. The most recent is the Program for Accelerated Pace of Agriculture (PRACAS) with a seed capital reconstitution program of 3.5 billion CFA. This program aims to provide producers with a quantity of quality seeds. These efforts are beneficial, but it is more than important to put in place a system or tool to estimate the needs and consequently establish a production plan of the first generations in terms of seed multiplication (G1, G2, and G3). The traceability of the subsequent levels (G4, R1, and R2) allows one to know in real-time who has which variety, what level, where, and when the product will be available. The answers to these different questions will help resolve in part the availability of seeds, one of the major constraints.

In the second group, low soil fertility, insects at storage, and drought were identified as major constraints limiting the production, followed by leaf diseases. This finding confirms the deteriorating state of soil fertility in Senegal reported earlier by previous studies conducted in the same regions (Kanfany et al., 2020). Senegal falls in the Sahelian zone and is subjected to different scenarios of drought characterized by unequal distribution of rainfall in both time and space. Consequently, the production of many crops is threatened yearly by the interannual and across location rainfall variability. Almost all West African countries identified drought as a major constraint to groundnut production (Banla et al., 2018; Coulibaly et al., 2017; Oppong-Sekyere et al., 2015 ; Ntare et al., 2008). In the present study, drought is perceived to be more important in the eastern part of the Groundnut Basin in the Tambacounda region (annual average rainfall 800 mm) than in the central zone (average annual rainfall between 500–600 mm). This paradoxical situation could results from the rainfall distribution and the type of cultivated varieties. In fact, 73-33, a long cycle variety (110 days), was the most cultivated in the eastern zone; in the central areas a mix of medium and short cycle varieties was grown (55-437 and Fleur 11, 90 days). The most drastic years in groundnut cultivation in Senegal were 2002 and 2011, due to low and erratic rainfall patterns. The impact of such events is not only extremely damaging, but also lasting. Farmers revealed that the rainy seasons become shorter from year to year. Therefore, short cycle varieties are wanted. However, it is important to report that during FGD, farmers in the studied areas did not want extra-early maturing varieties because such varieties might be the first to mature in an area and therefore might suffer from too much rainfall and from livestock damage. They need groundnut varieties that can mature early and escape the drought before it sets in. Drought tolerance was unevenly ranked for any given site, showing that they depended greatly on specific localities. Therefore, the development of varieties better adapted to drought becomes an important breeding objective for each specific location.

In Kathiot and Kaymor (Nioro zone), leaf diseases were the major constraint that affected groundnut production; in other localities, leaf diseases were not perceived by farmers as important. The traditional measure taken by farmers to deal with leaf diseases and soil borne diseases in the study areas was crop rotation. Primarily, groundnut is cultivated in rotation with pearl millet in most of the studied zones or with other cereal species such as sorghum, maize, rice, and fonio. Crop rotation plays an important role in groundnut management. It is known that crop rotation is beneficial to restore soil fertility, as well as to prevent crop pests and soil borne diseases. According to farmers, crop rotation is a good strategy that can restore soil fertility and avoid severe leaf diseases. These results indicated that breeding for improved drought tolerance and leaf disease resistance should constitute major breeding objectives to ensure high yield and varietal acceptance by farmers in specific zones.

High pod yield is the most preferred trait reported in most studies conducted on groundnut across Africa (Banla et al., 2018; Coulibaly et al., 2017; Ntare et al., 2008; Oppong-Sekyere et al., 2015). Contrary to the findings reported by Banla et al. (2018) in Togo, where pod size and oil content followed high pod yield as the most important traits, in the present study, high biomass yield was ranked as the second preferred trait in all study areas. This is attributed to the high feeding values of groundnut haulm to animals and the Sahelian context of Senegal. Hence, breeding for dual purposes, high pod and biomass become essential for variety adoption. Farmers gave much importance to seed and pod size in the study and correlated big pod size to high pod yield. However, scientific studies have shown that there is no correlation between pod yield and morphometric characteristics in the Sahel (Foncéka et al., 2012). Another important consideration for farmers is the attractiveness and the marketability side of large pods and seeds. The fact that groundnut is a cash crop could justify why farmers paid much attention to pod and seed size. These findings corroborate the importance of large pods and seeds reported in West African countries, especially in Togo, Burkina, and Ghana (Banla et al., 2018; Sinare et al., 2021. In the past, groundnut was initially cultivated for its oil correlated to maturity. Oil content and good taste received little attention at the farmers' level in the present study. This result could differ if the survey had considered the perspectives of industrial processors and end-users. These suggest that in the selection process for new improved varieties, yield and yield-related traits must constitute the primary selection criteria for a new improved variety to be accepted by farmers. The agreement between farmers and breeders in some of the criteria used for selecting groundnut varieties suggests the need for collaborative work to improve the efficiency of selection.

Conclusion

In view of the results, it appears that breeding efforts should focus on developing high yielding (pod and biomass) and early-maturing varieties that will minimize crop loss through drought escape. To increase adoption and meet farmers' needs in the Groundnut Basin of Senegal, groundnut breeders should take into consideration the varietal preferences identified. The soil degradation identified by farmers as a major constraint lays down a multidisciplinary research approach based on innovative practices to limit and prevent soil degradation. The findings also call out the government and the private sector on land issues, access to equipment, seed availability, and commercialization, all identified as major constraints to increasing groundnut productivity.

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3. Yield Response of Dryland Cereals to Fertilizer on Smallholder Farms in Mali

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Abstract

In Mali, over 60% of the population lives in rural areas, and about half of them live under the poverty line. Since farming is the primary livelihood of those in rural areas, raising productivity is crucial for decreasing poverty. This chapter explores the effectiveness of nitrogen fertilizer in raising yields of dryland cereals on smallholder farms in Mali, using regional and national datasets. Simple econometric analysis suggests there is minimal effect of nitrogen fertilizer use on crop yields. However, when accounting for the endogeneity of fertilizer use, we find yield response rates within the range reported in the literature. As expected, sorghum has lower response rate to fertilizer than maize. Yield responses are stronger in the Sudan Savanna region than nationwide, highlighting the importance of agroecological factors and the farming system. Soil texture and practices (anti-erosion structures) affect both yields and estimated marginal effects of fertilizer. We also find phosphorus to be a binding constraint in increasing agricultural productivity. While most emphasis in the literature is placed on understanding nitrogen fertilizer use, as recommended by agronomists, it is crucial to promote balanced use of fertilizers so that other complementary nutrients are available in the soil.

Keywords: yield response, cereals, Mali, smallholder farmers

Introduction

In Mali, over 60% of the population is rural, and half that segment lives below the national poverty line (World Bank, 2017). Most rural people depend on agriculture as their main source of livelihood. Dryland cereal crops, such as maize, millet, and sorghum, account for two-thirds and three-quarters of all cultivated land, depending on the years. Over recent decades, the production of dryland cereals has grown primarily through the expansion of cultivated areas rather than intensification, which is unsustainable. Despite the continued release of improved varieties, millet and sorghum yields have stagnated, with national averages hovering below 1 t/ha. Meanwhile, national average maize yields have risen from 1.4 t/ha in 2001/05 to 2.6 t/ha in 2016/18 (http://www.fao.org/faostat/en/#data/QC, November 2, 2020). Mali is West Africa's third-largest producer of maize even though it stands fifth in the area harvested, with the highest average yields among all 15 maize-producing countries in the region (Abate et al., 2015). Nonetheless, as is common throughout Sub-Saharan Africa, maximum yields for improved maize varieties in farmers' fields remain substantially below yield potential based on experimental conditions (4-6 t/ha according to Coulibaly 2008; Macauley & Ramadjita, 2015) given the challenges of growing conditions and incomplete input markets.

Inadequate use of mineral fertilizer has often been pinpointed as a cause of stagnating productivity in dryland cereals in Sub-Saharan Africa (NEPAD, 2003). In 2008, the Malian government decided to reinstate an input subsidy program to boost cereal productivity through improved access to fertilizer while contributing to food and nutrition security via higher income and lower consumer prices (Kone et al., 2019; Smale et al., 2012). Fertilizer subsidies now constitute the largest expense item, accounting for about 25% of government spending on rural development (Theriault et al., 2018). Given that extremely small amounts of fertilizer are currently used on either sorghum or millet, we do not expect the fertilizer subsidy program to have a generalized effect on production decisions nationwide. However, Theriault et al. (2018) found a significant impact on fertilizer use and yields for sorghum and maize in the Sudan Savanna, a region suitable for agriculture. A more resounding critique of policy regarding mineral fertilizer is that the soils of Mali are generally deficient in specific nutrients and that soil organic matter is necessary for effective integration of nutrients (Dicko et al., 2016; Mason et al.,2014). In addition, long-term losses due to soil erosion have been documented (Bishop and Allen 1989). However, these have been offset in some areas by successful resource management programs (Tappan & McGahuey, 2007).

Despite the policy emphasis on mineral fertilizer, few studies have systematically examined the cereal yield response to fertilizer in Mali—which is fundamental for evaluating program impacts. An important exception is the analysis of farm experimental data by Dicko et al. (2016), who estimated response functions for nitrogen (N), phosphorus (P), and potassium (K) on maize, rice, and millet across the four bioclimate-based agro-ecological zones of Mali. In general, the authors found that economic optima of nutrient application rates diverged from recommended application rates, which remain uniform throughout the country and vary only by crop.

We know of only two other studies that address the productivity of dryland cereals in Mali, both of which use data collected in farm household surveys rather than under experimental conditions. Using a 12-year farm household panel dataset (1994-2006) from Mali's Sikasso region, Foltz et al. (2015) found a strongly significant response of maize yields to fertilizer, concluding that increasing fertilizer use has driven most of the maize productivity growth. Sikasso is a region of high productivity potential for maize, where it is grown in rotation with cotton. Applying a stochastic production frontier to nationally representative data from the Living Standards Measurement Survey-Integrated Survey of Agriculture (LSMS-ISA), Ahmed et al. (2017) found no significant response of yields to fertilizer across crops and regions. We know of no published analyses of yield response to fertilizer in sorghum or millet that employ farm household data.

We thus contribute to sparse literature by estimating dryland cereals response functions (maize, millet, and sorghum) using two farm household survey datasets. The first dataset, the Living Standards Measurement Survey-Integrated Survey of Agriculture (LSMS-ISA), is nationally representative and includes information on all three crops (maize, millet, and sorghum). The second dataset, collected by a research team from the Institut d'Economie Rurale, was collected only in the Sudan Savanna and focused on sorghum and maize. Both datasets were collected during the 2014/2015 growing season. In estimating our yield response functions, we employ a combination of econometric approaches to compare and check the robustness of our findings.

Methods

1. Data Sources

We utilize data from the Living Standards Measurement Survey-Integrated Survey of Agriculture (LSMS-ISA), conducted in Mali in two visits during the 2014-15 growing season. Summary information about the survey is provided in a document compiled by the Planification and Statistics Unit (2016). With the probability of selection proportional to population size as of the 2009 Census, the statistical sample is nationally representative of rural and urban areas, excluding the region of Kidal. The total sample size was limited by the inability to collect data in some regions because of political insecurity, with the largest sample losses in the Mopti, Tombouctou, and Gao regions. The final sample includes about 3,804 households compared to the planned sample of 4,218. The number of standard enumeration areas (SEs, or grappes) was 1070, with 80% in rural areas, including 2-3 households per *grappe*. Compared to LSMS surveys which focused on household consumption, expenditures and income, the LSMS-ISA survey also contains plot-level data on input use and crop production. One-third of all plots inventoried by households in each SE were randomly sampled after grouping them by crop and crop association.[1] This procedure was necessary given that in Mali, large numbers of plots may be simultaneously cultivated by extended family farms, augmenting respondent burden and survey costs. We conduct our analysis only on data from the main rural agricultural regions of Mali, excluding Tombouctou, Gao, and some observations around Bamako. Therefore, our analytical sample covers the regions of Kayes, Koulikoro, Sikasso, Segou, and Mopti.

The second data source is a case study undertaken in the sorghum belt of Mali, which we use as a comparison since it is more focused on a specific farming system. Survey details are provided in Smale et al. (2015). The sample was drawn from a baseline census of all sorghum-growing households in 58 villages in the Cercles of Kati, Dioila (both Koulikoro Region), and Koutiala

(Sikasso Region) of Sudan Savanna, within the 800 mm isohyet. Villages surveyed included fewer than 1000 persons listed as sites where the national research program and farmer associations had implemented activities since 2009. The multi-visit survey was conducted in four rounds from August 2014 through June 2015 by a team of experienced enumerators employed by the Institut d'Economie Rurale. The sample is representative of areas in the Sudan Savanna with some exposure to agricultural research outreach activities. For cereals, many sorghum growers also grow maize and millet in this region. Millet is also grown, but due to budget constraints, detailed plot information was collected only for sorghum and maize.

The sample of households was drawn with simple random sampling and augmented by five percent to account for possible non-responses, leading to a total of 623 households and an overall sampling fraction of 25%. Enumerators listed all plots operated by each sampled household. One plot was randomly sampled per crop and management type per household. After removing yield and fertilizer use outliers, the total analytical sample employed here is 1,086 plots, including 421 sorghum plots and 665 maize plots.

In addition to the household survey data, this dataset includes soil nutrient indicators measured in laboratory tests conducted on soil samples by the Institut d'Economie Rurale, Sotuba, Mali. Due to budget constraints, soil samples could not be collected from all sorghum and maize plots. Plots were subsampled randomly within crop (maize and sorghum) and plot management (collective, individual) groups. After the harvest, soil samples were obtained following a standard protocol with 8 sub-samples per plot collected in a zig-zag pattern to assure overall plot representation. Laboratory analysis followed Sparks et al. (1996). The analytical sample for soil nutrients is 643 plots.

The two household datasets are not directly comparable with respect to sampling methodology or statistical representation of the farming population. We exploit both datasets because each provides information on nitrogen use and response on cereal crops grown in farmers' fields in Mali. Information of this type is scarce. The Sudan Savanna dataset is structured on a village list reflecting organizational structure and agroecology. The LSMS-ISA dataset is structured according to administrative units with census-based, standard enumeration areas. No georeferenced identifiers enable us to link one dataset to the other and directly compare results. Finally, variables are not identical between the two datasets.

Rainfall data were downloaded and compiled from the Climatology Resource for Agroclimatology site of the National Air and Space Administration.[2]

2. Econometric Approach

Our objective is to quantify the effect of fertilizer use on the yields of dryland cereal crops using household survey data. First, we estimate the yield response model:

$$Y_i = \beta_1 F_i + \boldsymbol{\beta_2 I_i} + \boldsymbol{\gamma X_i} + \varepsilon_i \,. \qquad (1)$$

The dependent variable Y_i denotes the crop yield (kg/ha) on plot *i*. The key explanatory variable is F_i, the quantity of fertilizer applied on plot I, with coefficient β_1. Fertilizer quantity is measured in nitrogen kg/ha to standardize different fertilizer types. Quantities are summed across the nitrogen content of the urea (46%), NPK (14%), DAP (18%), and other fertilizer (16.5%) applied on plot *i*.

Other than fertilizer, agricultural inputs $\mathbf{I_i}$ are applied to plots, and these are typically included in yield response functions estimated with either experimental or survey data. Accounting for other inputs is important because fertilizer is often used in conjunction with other inputs. For example, plots that apply more fertilizer may have more labor allocated. If we do not control for labor quantity, the coefficient on fertilizer will include the effect of labor and will overestimate the effect of fertilizer on crop yield. $\mathbf{X_i}$ is a vector of factors other than inputs that affect crop yield, such as plot characteristics.

The estimation strategies for equation (1) are tailored to the two data sets. Despite controlling for plot characteristics, $\mathbf{X_i}$, the estimate of β_1 may be inconsistent if other omitted variables explain crop yield and correlate with the fertilizer quantity applied. For example, wealthier households may have higher crop yields because they can acquire more efficient agricultural practices from radio, television, or agricultural extension agents. They may also apply more fertilizer because they have money or credit available to purchase fertilizer. Farmers may also apply fertilizer on plots with soils that they observe to be more responsive.

To eliminate household level confounding factors, in the LSMS model, we use household fixed effects to estimate model (1). In addition, since the survey is cross-sectional and contains data from a single year, we compare yields on plots within the same household with varying fertilizer levels applied. This allows us to control for any unobserved household-level factors that explain crop yields and correlate with the fertilizer quantity applied.

While this estimation strategy can provide reliable estimates for β_1, we may still be concerned about omitted variables bias. Unobserved plot-level characteristics are likely to affect crop yields. We can measure such variables, as in the case of soil samples collected in the Sudan Savanna, and include them as explanatory variables. For example, the soil's organic matter partly determines the responsiveness of nitrogen fertilizer (Marenya & Barrett, 2009).

With the LSMS data, we use instrumental variables estimation, combined with household fixed effects, to provide more robust estimates of the effect of fertilizer on crop yields. The instrument captures the general diffusion of fertilizer in the region where the household is located. We use the average fertilizer rate used across all other plots of households growing that crop in the *grappe* (1 to 30 plots, with an average of 3.5 plots).

Since the identification strategy combines household fixed effects with instrumental variables estimation, the instrument must vary within households. The diffusion rate of fertilizer differs across crops, and hence the instrument varies within households when we consider more than one crop. If we estimate a yield-response function for each crop separately, the instrument will not vary within households, and we are unable to use household fixed effects combined with instrumental variables estimation. Thus, we estimate separate regressions for millet, sorghum, and maize with only household fixed effects.

We expect the instrument to be correlated with the potentially endogenous variable Fi, because it captures the general availability of fertilizer in the locality. We do not expect the fertilizer allocation of households to directly influence the crop yields of other households – except through the increased use of fertilizer. Under these assumptions, we obtain consistent estimates of β_1. The instrument will not be valid if it affects yields through mechanisms other than more fertilizer being applied on that plot. For example, it would be problematic if the instrument was correlated with more intensive use of other inputs. Since we include the quantity of other inputs allocated to the plot as explanatory variables, we overcome this problem by controlling for the instrument's effect through other inputs.

In the regressions estimated with nutrients measured in laboratory tests on soil samples, we combine both dryland cereals in one regression, given the even smaller number of observations. Binary and interaction variables are included to control crop effects on grain yield and yield response to nitrogen nutrients per ha. We also test a quadratic term for nitrogen nutrients per ha, which expresses whether a turning point in yield response to nitrogen is observable in the data. In the set of regressions estimated with farmer-perceived soils classes, along with the combined regression, we have also estimated separate regressions for maize and sorghum because sample sizes are larger.

As a robustness check, we also test the final combined model with farmer-perceived soil classes (the largest sample) with the Control Function Approach. A Control Function Approach is applied instead of instrumental variable methods because of the potential endogeneity of multiple variables (nitrogen fertilizer applied, interaction, and squared terms). As instruments, we utilize whether the plot manager has benefited from the fertilizer subsidy and the village share of plot managers who are registered cooperatives. Theriault et al. (2018) found that Malian farmers who are members of cooperatives have better access to fertilizer than non-members. Participation in the subsidy program and cooperative is likely to affect fertilizer use but unlikely correlated with unobserved variables. All Sudan Savannah regressions are estimated with robust standard errors, clustered by household.

3. Variables

In the two analyses, explanatory variables differ somewhat to reflect underlying differences in the data. Variables used in the LSMS analysis are listed in Table 1. The plot area, measured in hectares, allows us to examine whether productivity differs across plot sizes. Vector ***I*** includes manure, compost, other organic fertilizer (i.e., crop residues), pesticides, herbicides, fungicides, other protecting liquids, improved and local seed. The distance of the plot from the homestead is related to the time taken to reach the field for crop management. It is also, potentially, a measure of fertility since those located farther away may have been more recently cleared and brought into cultivation. Also, households may choose to invest more in nearby plots since they are more secure (Gebremedhin & Swinton 2003) and easier to reach. A dummy variable is included to control for whether there is an anti-erosion structure on the plot, such as stone contour bunds or dikes—which have been promoted in certain regions of the country to offset the heavy loss of soil nutrients during the rainy season and enable farmers to retain moisture (Tappan & McGahuey, 2007).

Location in the toposequence (lowland, plain, slope, plateau) and soil texture are important indicators of soil quality in this region and are highly correlated with the crops grown (Guirkinger et al., 2015; Udry, 1996). Bazile et al. (2008) explain that farmers define soil type according to the position of the field in the toposequence. Farmers distinguish the shallow soils of the plateaus or higher areas from medium-depth soils and alluvial, low-lying soils ('*bas-fonds*'). Soil differentiation observed within and among farms explains growing multiple varieties and crops per farm and across a landscape. To capture the location of the plot in the toposequence, we include binary indicators of location in the plain, lowland, on a slope, or plateau. Dummy variables for soil type are also included, representing farmer-perceived soil classes (sandy, silty, clayey).

Table 1
Descriptive Statistics, LSMS-ISA Data

Variable	**Mean**	**S.D.**	**Min**	**Max**
Millet Yield (kg/ha)	695	629	0.660	3759
Sorghum Yield (kg/ha)	735	686	0.530	3930
Maize Yield (kg/ha)	1492	1221	1.26	6000
Material Inputs				
Nitrogen Fertilizer (N nutrient kg/ha)	6.74	23.6	0.000	288
Manure (kg/ha)	1594	3800	0.000	29850
Compost (kg/ha)	25.8	247	0.000	4889
Other Organic Fertilizer (kg/ha)	5.64	60.6	0.000	1708
Pesticides (liter/ha)	0.053	0.51	0.000	10.5
Fungicide (liter/ha)	0.033	0.42	0.000	19.7
Herbicide (liter/ha)	0.270	1.17	0.000	19.1
Other Protecting Liquids (liter/ha)	0.007	0.11	0.000	3.14
Local Seed (kg/ha)	10.3	15.4	0.000	236
Improved Seed (kg/ha)	1.00	4.45	0.000	50.7
Labor				
Total Labor (no. of days/ha)	45.1	84.8	0.000	1031
Plot Characteristics				
Plot Area (ha)	3.07	6.12	0.020	52.7
Distance to plot from house (km)	2.81	4	0.000	60.0
Plain (0/1)	0.7	0.464	0.000	1.00
Plateau (0/1)	0.147	0.355	0.000	1.00
Lowlands (0/1)	0.034	0.18	0.000	1.00
Sloped (0/1)	0.13	0.34	0.000	1.00
Soil Sandy (0/1)	0.536	0.498	0.000	1.00
Soil Clay (0/1)	0.357	0.479	0.000	1.00
Soil Lateritic (0/1)	0.11	0.31	0.000	1.00
Anti-Erosion Structure (0/1)	0.043	0.2	0.000	1.00

Source: Authors, based on LSMS-ISA, Mali. Number of plot observations=3733

Explanatory variables used in the analysis of the Sudan Savanna data are listed in Table 2. We estimate maize-sorghum yield (grain harvested per ha) response to nitrogen but do not include millet plots, for which we do not have production data. Fertilizer application is computed in the same way as in the LSMS analysis. All regressions include conventional inputs, a common set of plot characteristics, and a rainfall indicator at the village level. Manure application is measured as a binary variable because of difficulties in measuring quantities reliably. Labor days, liters of herbicides, and hours of equipment use are computed per ha. Common plot characteristics are the distance (in minutes walking) from the homestead to the plot, presence of a soil erosion structure on the plot, association of the primary crop with a leguminous (groundnut, cowpea) intercrop. Average rainfall during the period of fertilization in the survey year is recorded at the geographical scale of the village.

We test two sets of soils characteristics. In the first, soils characteristics are by soil nutrient content as tested in the laboratory: percentage soil organic matter (C), sand, silt, and clay, the percentage total nitrogen (N), assimilable phosphorus (P), exchangeable potassium (K), and soil pH (KCl). Since total carbon content (C) changes over centuries and active carbon changes over 3-5 years (Weil et al., 2016), these are not affected by recent fertilizer applications. Similarly, recent fertilizer use does not affect total nitrogen content (N), which includes the nitrogen in the soil organic matter. Nor can farmers deduce the specific nutrient content of their soils (P, K). In the second, we use farmer-perceived soils characteristics. Binary variables are entered for the location of the plot in the toposequence and farmer-perceived soil classes.

Table 2
Descriptive Statistics, Sudan Savanna Data

Variable	Mean	S.D.	Min	Max
Maize yield (kg/ha)	1497	945	12.5	4730
Sorghum yield (kg/ha)	642	681	0.000	4286
Nitrogen fertilizer (nutrient kg/ha)	19.5	25.7	0.000	100
Sorghum plot (0/1)	0.609	0.488	0.000	1.00
Manure (0/1)	0.641	0.479	0.000	1.00
Labor (days/ha)	68.0	66.6	0.000	800
Herbicide (liters/ha)	1.68	2.24	0.000	25.0
Equipment (hours/ha)	475	474	0.000	5294
Distance from House (minutes)	17.4	17.5	1.00	160
Soil Erosion Structure	0.188	0.391	0.000	1.00
Legume Intercrop 0/1)	0.112	0.316	0.000	1.00
N (% total nitrogen)	0.028	0.023	0.010	0.200
C (% organic matter)	0.522	0.334	0.020	2.63
P (assimilable phosphorus)	1.29	1.31	0.210	15.9
K (exchangeable K)	0.246	0.210	0.020	1.87
Ph (KCI)	5.34	0.400	3.15	7.25
0.05)"}">Sand (% > 0.05)	59.6	12.8	7.00	90.0
Silt (%0.05-0.002 mm)	36.2	12.3	8.00	90.0
Clay (% < 0.002 mm)	4.26	2.88	0.000	23.0
Rainfall (mm, period of fertilization)	220	31.0	164	299
Plain	0.865	0.341	0.000	1.00
Lowlands	0.015	0.122	0.000	1.00
Slope	0.119	0.324	0.000	1.00
Sandy (0/1)	0.381	0.486	0.000	1.00
Silty (0/1)	0.203	0.403	0.000	1.00
Clayey (0/1)	0.269	0.444	0.000	1.00
Gravelly (0/1)	0.147	0.354	0.000	1.00

Source: Authors, based on Sudan Savanna case study data. n=1222 for all except manure (1096).

Results

1. Descriptives

Millet, sorghum, and maize are grown on 39, 32, and 29 percent of the plots in the LSMS sample, respectively. Fertilizer application rates differ significantly across crops. Table 3 shows average use rates calculated from the LSMS and Sudan Savanna datasets by cereal crop and region, compared with recommended rates and economically optimal rates estimated with response functions based on experimental data (Dicko et al., 2016). They also differ in major ways by region.

Agronomic recommended rates of N per ha are 32 for sorghum and millet, and 84 for maize, throughout the country (Dicko et al., 2016). These correspond to 100 kg/ha on all three crops for cereal complex, 100 kg/ha of NPK (16-16-16) for millet and sorghum, 250 kg/ha of NPK (23-10-5) for maize, 100-150 of DAP on cereals, and 50-400 kg/ha for other crops and fertilizers (see also Thériault et al., 2016). The overall mean for N kg per ha on millet, sorghum, and maize in the LSMS data is 6.7, but use rates on maize are considerably higher except for the region of Kayes. For all three cereals and all five regions except millet in Sikasso, estimated mean rates of use are but a fraction of economically optimal rates. In Koulikoro, Segou, and Mopti, average N use rates on sorghum and millet are in the single digits or lower, while economic optima range from 21 to 26. Again, the mean rate of N applied per ha to maize in Sikasso (36.2) is closest but is still far from the economic optimum (56-65). Mean phosphorus application rates for the entire LSMS sample are only 1 kg/ha and 1.9 kg/ha for millet and sorghum, respectively, but 6.7 kg/ha for maize—which is close to recommended levels. Recommended use rates for P are 10 for sorghum and millet, and economically optimal rates are estimated to be higher (Dicko et al., 2016). Overall, applying their fertilizer optimization tool, Dicko et al. (2016) found that the economically optimal rates of N were well below recommendations for maize, sorghum, and millet, varying by bioclimate.

Mean applications rates of N per hectare on maize and sorghum are also shown in Table 3 for the Sudan Savanna. In this relatively high potential area, mean rates of use on sorghum (6.41) are closer to rates in Sikasso in the LSMS

(9.38) than in Koulikoro at (<1), and even roughly the same on maize (39.8) as in Sikasso (36.2). Again, both are but a fraction of the economically optimal rate estimated by Dicko et al. (2016), which is, in turn, but a fraction of the nationally recommended rate.

Table 3
Average Use Rates for N, Compared with Recommended and Economic Optima, by Region and Crop

	Average use rates (N kg/ha)	Economically optimal rate	Recommended rate
LSMS-ISA			
		Millet	
Kayes	0.000	no data	32.0
Koulikoro	0.316	no data	32.0
Sikasso	8.19	8.00	32.0
Segou	3.65	21.0	32.0
Mopti	1.50	21.0	32.0
		Sorghum	
Kayes	0.182	26.0	32.0
Koulikoro	0.722	26.0	32.0
Sikasso	9.38	26.0-28.0	32.0
Segou	7.15	20.0-26.0	32.0
		Maize	
Mopti	0.360	20.0	32.0
Kayes	0.453	54.0	84.0
Koulikoro	17.3	54.0	84.0
Sikasso	36.2	54.0-65.0	84.0
Segou	11.7	31.0-54.0	84.0
Sudan Savanna			
		Sorghum	
Koulikoro, Sikasso	6.41	26.0	32.0
		Maize	
Koulikoro, Sikasso	39.8	54.0	84.0

Source: Authors, based on LSMS and Sudan Savanna survey data; recommended and economically optimal rates from Dicko et al. (2016).

Note: Tombouctou, Gao and Mopti (for maize) excluded because of very few observations.

2. Yield Response Functions

Tables 5-8 present yield response models estimated with the LSMS data. The yield and input variables, including the quantity of fertilizer, are included in logarithms to smoothen their distributions, which are concentrated in lower values and skewed in shape. β_1 and β_2 are interpreted in terms of percentage changes of yield. The coefficients have been converted into marginal products by computing the marginal change in yield (in kg/ha) from a one percent increase in the quantity of fertilizer (N kg/ha) at the mean and are indicated in the bottom rows of the tables.

In preliminary regressions, the coefficients on nitrogen fertilizer across the household fixed effects models that do not use instrumental variables suggest that a one percent increase in the quantity of nitrogen fertilizer applied to the plot results in only a 0.04-0.07 percent increase in yields of dryland cereals. These elasticities correspond to marginal physical products of only 5.2 to 8.8, on average, for dryland cereals (maize, millet, and sorghum).

FE-IV estimates for more robust inference of the effect of fertilizer on yields are shown in Table 4. In all specifications, the first-stage F-statistic is much greater than 10, which is often used as a rule of thumb for the inclusion restriction. The first-stage F-statistic is also greater than the Stock-Yogo 10 percent maximal IV size critical value of 16.38, suggesting that the inclusion restriction is satisfied. The FE-IV estimates for fertilizer are several times as large as those reported above, suggesting that not controlling for endogeneity may diminish estimates of the yield response to fertilizer. In all specifications, the effect of nitrogen fertilizer applied is statistically significant. A one percent increase in the quantity of fertilizer applied to the plot results in a 0.1-0.2 percent increase in yields of dryland cereal crops. This translates to a 17-27 kg/ha increase in dryland cereal crop yield for an additional nitrogen kg/ha fertilizer.[3]

Other control variables described above are included sequentially to see whether the coefficient on fertilizer is sensitive to these. We find that yields are decreasing in plot size – consistent with the inverse productivity relationship that has also been observed in this region (Guirkinger et al., 2015; Kazianga & Wahhaj, 2013; Udry 1996). Plots where manure has been applied, and those with anti-erosion structures, achieve greater yields. Yields are increasing in the quantity of local seed and increasing even more in the quantity of improved seeds. More labor allocated to a plot also raises yields. This effect is strong throughout and with a relatively high elasticity—suggesting that labor constrains productivity. We find no effects of pesticides, fungicides, or other protecting liquids, which are used in very limited amounts. The presence of anti-erosion structures has a meaningful effect on yields. Controlling for toposequence and soil type reduces the marginal product attributable to fertilizer. Models were also estimated with specifications that contained squared terms for fertilizer and interaction terms between fertilizer and crop dummy variables. The point estimates of these square and interaction terms were close to zero and not statistically significant, so we retained more parsimonious specifications.

Table 4
Dryland Cereals Yield Response to N Fertilizer Applied, Instrumental Variables-household Fixed Effects Model

Variables	**-1**	**-2**	**-3**	**-4**
Nitrogen Fertilizer	0.190***	0.218***	0.162**	0.149*
	(0.073)	(0.081)	(0.075)	(0.080)
Manure		0.026***	0.024***	0.026***
		(0.008)	(0.009)	(0.010)
Compost		-0.058	-0.044	-0.033
		(0.038)	(0.037)	(0.041)
Other Organic Fertilizer		0.051	0.024	0.022
		(0.066)	(0.066)	(0.067)
Pesticide		0.253	0.304	0.304
		(0.211)	(0.201)	(0.280)
Fungicide		0.076	0.029	0.082
		(0.272)	(0.248)	(0.259)
Herbicide		0.104	-0.063	-0.095

Variables	**-1**	**-2**	**-3**	**-4**
		(0.137)	(0.134)	(0.144)
Other Protecting Liquids		0.673	0.769	0.967
		(1.285)	(1.178)	(1.202)
Total Labor		0.447***	0.335***	0.283***
		(0.030)	(0.033)	(0.039)
Local Seed			0.353***	0.294***
			(0.039)	(0.044)
Improved Seed			0.488***	0.417***
			(0.073)	(0.085)
Millet	-0.159*	0.071	0.249***	0.295**
	(0.090)	(0.093)	(0.096)	(0.117)
Sorghum	-0.393***	-0.188**	-0.036	0.053
	(0.075)	(0.077)	(0.079)	(0.101)
Plot Area				-0.025***
				(0.005)
Distance (km) from House				0.017*
				(0.009)
Plain				-0.008
				(0.130)
Plateau				-0.019
				(0.170)
Lowland				-0.005
				(0.210)
Sandy				-0.032
				(0.210)
Clay				-0.028
				(0.212)
Anti-Erosion Structure				0.486**
				(0.198)
Observations	2,453	2,043	1,707	1,307
Number of households	776	671	548	425

Variables	-1	-2	-3	-4
Kleibergen Paap F statistic	218.6	155.8	148.3	112.5
Marginal Effect of N Nutrient Applied	23.13	26.95	19.49	16.81

Source: Authors, based on LSMS data. Standard errors in parentheses. *** p<0.01, ** p<0.05, * p<0.1. Sample sizes drop with missing observations in more complete models, particularly those including seed quantities.

Separate household fixed effects regressions are shown in Tables 5-7 by crop. The results suggest that millet and sorghum yields are unaffected by fertilizer use. For maize, in one of the simpler models, a one percent increase in the quantity of fertilizer applied to the plot results in about 0.15 percent higher yields, corresponding to a marginal product of 11. These models have a smaller sample size than the pooled household fixed effects model. Additionally, these coefficients may be downward biased, given that the estimates from the pooled household fixed effects models are smaller than the FE-IV estimates. However, we consider these estimates as lower bounds for the true effect of fertilizer on crop yields.

Table 5
Millet Yield Response to N Fertilizer Applied, Household Fixed Effects Model

Variables	(1)	(2)	(3)	(4)
Nitrogen Fertilizer	0.0392	-0.00945	0.00449	-0.00372
	(0.0724)	(0.0685)	(0.0642)	(0.0714)
Manure		0.0271**	0.0222*	0.0156
		(0.0122)	(0.0122)	(0.0137)
Compost		-0.0774	-0.0518	-0.0751
		(0.0754)	(0.0744)	(0.0862)
Other Organic Fertilizer		0.0832	0.0806	0.0803
		(0.0720)	(0.0676)	(0.0657)
Fungicide		-0.668	-0.630	-1.261
		(1.004)	(0.938)	(0.923)
Herbicide		2.565	0.960	2.138
		(10.59)	(9.893)	(9.408)
Total Labor		0.470***	0.314***	0.156***

Variables	**(1)**	**(2)**	**(3)**	**(4)**
		(0.0481)	(0.0529)	(0.0602)
Local Seed			0.409***	0.360***
			(0.0652)	(0.0698)
Improved Seed			0.550***	0.350
			(0.208)	(0.259)
Plot Area				-0.0310***
				(0.00828)
Distance to plot				0.0334**
				(0.0150)
Plaine				0.0543
				(0.186)
Plateau				0.0202
				(0.314)
Lowland				-0.220
				(0.383)
Sandy				-0.00658
				(0.411)
Clay				0.411
				(0.448)
Anti-Erosion Structure				1.789***
				(0.369)
Constant	5.996***	4.633***	4.267***	4.635***
	(0.0282)	(0.139)	(0.150)	(0.466)
Observations	1,376	1,182	1,018	813
Number of households	771	688	585	476
Marginal Effect of N Nutrient Applied	10.37	-2.34	0.99	-0.81

Source: Authors based on LSMS data. Standard errors in parentheses. *** p<0.01, ** p<0.05, * p<0.1. Sample sizes drop with missing observations in more complete models, particularly those including seed quantities.

Table 6
Sorghum Yield Response to N Fertilizer Applied, Household Fixed Effects Model

Variables	**-1**	**-2**	**-3**	**-4**
Nitrogen Fertilizer	0.0503	0.0663	0.0265	0.0399
	(0.0590)	(0.0545)	(0.0582)	(0.0579)
Manure		0.0356	0.0411*	0.0301
		(0.0220)	(0.0245)	(0.0250)
Compost		-0.184	0.432	4.949
		(0.441)	(1.146)	(5.166)
Other Organic Fertilizer		-1.010	-1.025	-0.910
		(1.889)	(1.878)	(1.724)
Fungicide		2.347**	2.081*	4.539***
		(1.168)	(1.157)	(1.726)
Herbicide		0.0986	0.0539	0.0319
		(0.281)	(0.310)	(0.295)
Total Labor		0.496***	0.316***	0.309***
		(0.0567)	(0.0704)	(0.0761)
Local Seed			0.269***	0.264***
			(0.0828)	(0.0864)
Improved Seed			0.655***	0.444**
			(0.202)	(0.213)
Pesticide		-0.727	-3.386	-23.47
		(1.605)	(5.036)	(23.03)
Plot Area				-0.00449
				(0.00972)
Distance to plot				-0.0140
				(0.0151)
Plaine				-0.0652
				(0.250)
Plateau				-0.291
				(0.388)
Lowland				0.0337
				(0.310)

Variables	-1	-2	-3	-4
Sandy				-0.325
				(0.432)
Clay				-0.456
				(0.401)
Anti-Erosion Structure				-0.171
				(0.441)
Constant	5.961***	4.389***	4.351***	4.985***
	(0.0297)	(0.175)	(0.202)	(0.462)
Observations	1,170	1,001	816	664
Number of households	767	666	534	445
Marginal Effect of N Nutrient Applied	9.56	11.70	4.73	6.44

Source: Authors based on LSMS data. Standard errors in parentheses. *** p<0.01, ** p<0.05, * p<0.1. Sample sizes drop with missing observations in more complete models, particularly those including seed quantities.

Table 7
Maize Yield Response to N Fertilizer Applied, Household Fixed Effects Model

Variables	-1	-2	-3	-4
Nitrogen Fertilizer	0.0658	0.146**	0.00067	-0.0620
	(0.0541)	(0.0676)	(0.0638)	(0.0747)
Manure		0.00286	0.00169	0.0125
		(0.0268)	(0.0237)	(0.0275)
Compost		-0.0796	-0.0520	-0.0646
		(0.0639)	(0.0585)	(0.0755)
Other Organic Fertilizer		0.218	0.435*	0.420
		(0.147)	(0.231)	(0.290)
Fungicide		-0.0489	-0.367	0.0470
		(0.509)	(0.442)	(1.038)
Herbicide		-0.0469	-0.236	0.129
		(0.226)	(0.276)	(0.329)
Total Labor		0.540***	0.403***	0.443***

Variables	**-1**	**-2**	**-3**	**-4**
		(0.0786)	(0.0849)	(0.111)
Local Seed			0.662***	0.706***
			(0.114)	(0.186)
Improved Seed			0.719***	0.572***
			(0.133)	(0.182)
Pesticide		0.366	0.459	-0.242
		(0.290)	(0.291)	(0.669)
Other Protecting Liquids		0.887	0.891	-0.176
		(1.170)	(1.014)	(1.168)
Plot Area				-0.0541***
				(0.0147)
Distance to plot				0.0902
				(0.0768)
Plain				0.0520
				(0.590)
Plateau				-0.564*
				(0.335)
Lowland				1.806*
				(0.923)
Sandy				0.368
				(0.589)
Clay				-0.207
				(0.627)
Anti-Erosion Structure				1.016*
				(0.514)
Constant	6.603***	4.623***	3.614***	3.386***
	(0.0787)	(0.260)	(0.319)	(0.710)
Observations	781	657	512	357
Number of households	559	481	369	264
Marginal Effect of N Nutrient Applied	5.01	11.33	0.049	-3.83

Source: Authors, based on LSMS data. Standard errors in parentheses. *** p<0.01, ** p<0.05, * p<0.1. Sample sizes drop with missing observations in more complete models, particularly those including seed quantities.

Overall, analysis of the LSMS data demonstrates that nitrogen fertilizer has positive and statistically significant effects on yields of dryland cereals. When we account for the endogeneity of fertilizer use, predicted magnitudes raise the range of elasticities to 17-23 for the three crops combined. For maize, in particular, these fall within the expected range. Ahmed et al. (2017) found no statistically significant effects of mineral fertilizer on crop yield. Foltz et al. (2012) estimated significant maize yield elasticities of 0.2-0.3 for fertilizer—higher than we found here. However, they used total fertilizer kg and utilized data only from the highly productive region of Sikasso.

The Sudan Savanna has the greatest agricultural potential in Mali to produce both sorghum and maize (Dicko et al., 2016). Despite this, anecdotally, farmers surveyed reported that sorghum yields were lower than expected due to declining soil fertility, moisture problems, and pest damage—encouraging a switch from sorghum to maize. The data indicate a very modest yield response rate to fertilizer for either crop. One reason why, in sorghum, could be the extremely low rate of application—application rates per ha on maize plots in our survey averaged 158 kg total of fertilizer, or 39.8 N nutrients/ha, compared with only 27 total kg of fertilizer on sorghum (6.4 N nutrients/ha). There are many zeros in our sample for sorghum (66%), compared with only 14% on maize plots.

Three response function specifications are shown in Table 8, each including soils characteristics measured in laboratory tests on samples. Model 8(1)[4] is a simple linear regression, with sorghum plot entered only as a binary variable affecting overall yields. The effect on yield is strong and negative, reducing average grain yields by about 600 kg/ha relative to maize, controlling for other factors. Model 8(2) includes an interaction effect between N nutrient kg/ha and sorghum plot. The effect is negative but not statistically significant. In Model 8(3), the squared term is added for N applied and is negative in sign but not statistically significant. The interaction effect becomes significant, indicating that growing sorghum reduced yield response by 9 N nutrient kg/ha relative to maize. On average, Model 8(3) suggests that an additional kg of N nutrients per ha contributes 10.4 kg of maize grain per ha. This suggests a response rate of only about 1.3 for sorghum combined with the interaction effect.

Consistent across the three specifications, other coefficients of interest include a positive and significant effect of labor and equipment use and a negative and significant effect of distance to the plot and legume intercrop on yields. The magnitudes and significance of the input effects suggest that these may constrain productivity. This is supported by the negative effect on time walking to the plot from the homestead. The inverse relationship between yield and the legume intercrop is explained by the fact that we were unable to control for the area planted to primary and secondary crops—leading to a downward bias in the yield of the primary crop. On the other hand, any long-term, positive effects of intercropping would be difficult to discern in a single year's survey data of this type. Similarly, erosion structures were often constructed earlier and may not be repaired. Most are stone contour lines to control erosion on slopes, but most of the plots in the sample are on the plain. The insignificance of the manure variable may reflect the fact that while most farmers apply manure (64%), there is considerable variation in the quantity and quality applied.

Among measured soil nutrients, the effect of P is strongly significant (at 1%), suggesting that it poses a constraint to productivity. In many of Mali's sorghum-growing areas, we believe that phosphorus is a more binding constraint than N (Dicko et al., 2016; Kihara et al., 2016).

Table 8
Maize-sorghum Yield Response Including Measured Soil Nutrients, Sudan Savanna

	(1)	**(2)**	**(3)**
	linear	**interaction**	**quadratic and interaction**
N nutrients/ha	2.864	4.356	10.42*
	(1.974)	(2.646)	(5.543)
Sorghum plot	-596.8***	-502.7***	-351.7*
	(131.5)	(156.6)	(197.8)
Sorghum plot x N nutrients/ ha		-5.593	-9.134*
		(3.576)	(4.669)
(N nutrients/ha)2			-0.0381

	(1) linear	(2) interaction	(3) quadratic and interaction
			(0.0300)
Manure	80.4	73.3	83.28
	(117.1)	(117.4)	(117.9)
Labor	3.099***	3.051***	3.155***
	(1.020)	(1.015)	(1.013)
Herbicides	15.05	17.00	18.11
	(27.43)	(27.46)	(27.03)
Equipment	0.721***	0.724***	0.724***
	(0.153)	(0.153)	(0.152)
Distance to plot	-3.374*	-3.338*	-3.343*
	(1.744)	(1.732)	(1.731)
Soil erosion structure	-78.13	-81.10	-82.52
	(100.8)	(101.7)	(103.3)
Legume intercrop	-238.8***	-233.1***	-236.5***
	(88.85)	(86.80)	(85.86)
lnN	-90.00	-94.77	-81.98
	(71.55)	(70.75)	(69.99)
lnC	-92.00	-84.60	-89.99
	(61.40)	(62.12)	(61.85)
lnP	137.2***	146.6***	149.7***
	(47.61)	(47.33)	(47.14)
lnK	-58.34	-65.67	-61.44
	(65.13)	(66.11)	(65.56)
lnPh(kcl)	191.6	150.2	286.6
	(430.7)	(436.8)	(434.8)
Sand	14.18	15.36	14.66
	(17.97)	(18.41)	(18.48)
Silt	17.07	17.93	17.23
	(18.35)	(18.76)	(18.82)
Clay	60.80**	63.77**	62.86**

	(1) linear	(2) interaction	(3) quadratic and interaction
	(27.67)	(28.17)	(28.01)
Rainfall	-0.552	-0.306	-0.0562
	(1.339)	(1.335)	(1.363)
Constant	-1,707	-1,891	-2,230
	(2,235)	(2,279)	(2,305)
Observations (n plots)	643	643	643
R-squared	0.518	0.520	0.523

Source: Authors, based on Sudan Savanna data. Robust standard errors in parentheses. *** p<0.01, ** p<0.05, * p<0.1

Table 9 shows models for maize and sorghum in combined and separate regressions. The combined results in Model 9(3) are similar to those shown in Table 4 (4), both in terms of response magnitudes and significance and in terms of other main inputs (labor, equipment) influencing productivity. However, they cannot be directly compared because of differences in sampling and covariates. The yield response rate for maize taken separately is 14.4 and significant but is insignificant at 3.6 for sorghum. Some differences appear in key factors across the regressions reported in Table 9. Statistically, the maize regression is statistically weaker, with far fewer observations than the sorghum regression.

Table 9
Maize-sorghum Yield Response Including Farmer-perceived Soil Types, Sudan Savanna

	(1) Combined	(2) Maize	(3) Sorghum
N nutrients/ha	10.52**	14.43***	3.634
	(4.501)	(5.427)	(4.065)
Sorghum plot	-273.1**		
	(112.1)		
Sorghum plot x N nutrients/ha	-6.608**		
	(3.238)		

	(1) **Combined**	(2) **Maize**	(3) **Sorghum**
(N nutrients/ha)2	-0.0102	-0.0471	-0.00551
	(0.0454)	(0.0569)	(0.0653)
Manure	89.49	229.4**	-43.94
	(58.60)	(90.18)	(68.72)
Labor	2.184***	4.015***	1.802**
	(0.693)	(1.084)	(0.800)
Herbicides	-0.835	-7.904	4.472
	(14.89)	(26.35)	(16.08)
Equipment	0.391***	-0.0169	0.541***
	(0.103)	(0.182)	(0.0723)
Distance to plot	-1.344	-1.193	-2.053*
	(1.656)	(4.444)	(1.099)
Soil erosion structure	161.5**	195.8	149.0**
	(71.43)	(120.4)	(75.23)
Legume intercrop	-386.8***		-320.8***
	(54.41)		(56.26)
Plain	-65.03	-10.85	3.302
	(127.2)	(158.1)	(81.89)
Lowland		-67.34	144.9
		(504.9)	(150.9)
Slope	-63.54		
	(152.2)		
Sandy	137.2*	-27.07	77.6
	(74.00)	(119.0)	(52.43)
Silty	114.8		
	(78.54)		
Clayey	149.8*	-159.2	168.2**
	(81.99)	(123.7)	(78.65)
Gravelly		-176.5	-80.07
		(159.3)	(68.94)

	(1) Combined	(2) Maize	(3) Sorghum
Rainfall	0.447	3.576**	-1.603*
	(0.936)	(1.657)	(0.911)
Constant	402.2	-404.1	666.5***
	(262.3)	(456.5)	(251.1)
Observations	1,086	421	665
R-squared	0.410	0.198	0.387

Source: Authors, based on Sudan Savanna data. Robust standard errors in parentheses. *** p<0.01, ** p<0.05, * p<0.1

Table 10 shows the coefficients from the second stage, yield response function estimated with the Control Function Approach. The yield regression is based on the combined maize-sorghum model with farmer-perceived soils classes to benefit from as many observations as possible. In the first-stage regression, which tests and controls for potential endogeneity of fertilizer use in yield response, both the coefficient on the binary variable indicating that the plot manager benefited from the fertilizer subsidy and the coefficient on the village proportion of plot managers who belong to a registered cooperative, are statistically significant at the 1% level. So too is the residual entered in the yield regression, failing to support exogeneity of fertilizer use in the yield response function. As was true in the LSMS estimates, the marginal product of nitrogen fertilizer rises meaningfully when we control for endogeneity.

The estimated response rates for maize reported for the Sudan Savanna fall within the range of other estimates for the same crops based on data collected from farmers' fields in Sub-Saharan Africa. A review conducted by Yanggen et al. (1998) shows that maize's response rates to nitrogen are generally lower in West Africa than in East and Southern Africa, with most in the 10-15 range. Based on nationally representative cross-sectional and panel datasets, Koussoubé and Nauges (2017) and Theriault et al. (2017) estimated a yield response rate of about 19 kg/ha to nitrogen on maize in Burkina Faso, respectively. By contrast, Marenya and Barrett (2009) estimated a marginal product of 40-44 kg/ha in Western Kenya, while Sheahan et al. (2013)

reported marginal products ranging from 14 to 25 kg/ha across the agro-ecologies of Kenya. Xu et al. (2009) reported response rates for Zambia varied from under 10 to 30 kg/ha, with a median of 16.

Estimates of sorghum yield response to fertilizer are statistically insignificant. Analysis of trial data by Institut de Recherches Agronomiques Tropicales (IRAT) from 1978-82 in Burkina Faso showed experimental responses of 10.3 kg grain of sorghum per N nutrient kg, with much lower figures measured in farmers' fields (Matlon, 1983). In an early review of literature on this topic, Yanggen et al. (1998) found that the marginal physical product of nitrogen nutrients in sorghum production was similar in Sub-Saharan Africa to other regions of the sorghum-producing world such as India, but were lower in West Africa, were most reported rates were in the 4-5 range. In a recent analysis conducted in Nigeria, Omonona et al. (2016) found response rates of only around 1 kg of sorghum in cereal-root crop and agro-pastoralist farming systems.

Table 10
Maize-sorghum Yield Response to Nitrogen Applied, Control Function Approach

	(1)
Nitrogen fertilizer	23.98***
	(5.035)
Residual, stage 1	-16.33***
	(3.916)
Sorghum plot	622.1***
	(236.6)
Sorghum plot x N nutrients/ha	-5.565*
	(3.110)
(N nutrients/ha)2	0.00795
	(0.0439)
Manure	180.7***
	(60.61)
Labor	3.365***
	(0.777)
Herbicides	-3.601

	(15.01)
Equipment	0.351***
	(0.101)
Distance to plot	-3.118*
	(1.816)
Soil erosion structure	115.5
	(70.55)
Legume intercrop	-524.4***
	(65.38)
Plain	-100.5
	(119.9)
Slope	-120.4
	(144.2)
Sandy	-10.72
	(76.59)
Silty	35.67
	(80.92)
Clayey	173.7**
	(77.86)
Rainfall	-0.54
	(0.979)
Constant	-18.04
	(262.7)
Observations	1,086
R-squared	0.424

Source: Authors, based on Sudan Savanna data. Robust standard errors in parentheses. *** p<0.01, ** p<0.05, * p<0.1

Conclusion

In Mali, raising the production of dryland cereals (maize, millet, and sorghum) to improve food security must be achieved through higher yields rather than a further extension of cultivated area. Although maize yields on farms have increased in recent years, they are far below their potential. Generally, yields of millet and sorghum on farms have remained low. Inadequate use of inorganic fertilizer has been pinpointed as a cause of low agricultural productivity in these crops. To encourage fertilizer use and spur productivity, the Malian government has implemented a fertilizer subsidy program since the global food price crisis in 2008. Beginning in rice, the program now also targets dryland cereals. Yet, little is documented about the responsiveness of those crops to fertilizer under farmer's conditions. This study aims to fill this gap by examining dryland cereal yield responses to fertilizer using two farm household datasets. The first, the LSMS-ISA, is nationally representative. The second, collected in the Sudan Savanna region, is representative of a relatively high-potential zone for sorghum and maize production.

We applied a combination of econometric techniques to control for potential endogeneity and check the robustness of the results. Four key findings emerge. First, it is important to control for endogeneity to avoid underestimating the effect of fertilizer use on yields. Second, soil texture and practices (anti-erosion structures) affect both yields and estimated effects of fertilizer. Third, sorghum yields have a lower response to fertilizer than maize yields. Fourth, dryland cereal yield responses to fertilizer are stronger in the Sudan Savanna region than nationally representative data, highlighting the importance of agroecological factors and farming systems. Together, these findings suggest that the use of mineral fertilizer can boost productivity, especially for maize, but in complementarity with other practices that reduce soil erosion and improve soil quality.

One key aspect that we have not addressed is the profitability of fertilizer use. Related work by Dicko et al. (2016), which supports the need for varied recommendations, also suggests that economic optima are generally lower than agronomic optima recommended by national programs. Given that maize yields do respond to fertilizer use, can inadequate application rates be explained by low economic incentives? How does the subsidy program affect economic incentives, and at what social cost? When response rates are so low, does it make sense to include millet and sorghum in the subsidy program? Further research is needed to tackle those important questions and make sound policy recommendations on the subsidy program and other mechanisms to promote agricultural intensification in Mali.

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[3] These figures are calculated by multiplying the estimated coefficients by the average yield and fertilizer quantities of the regression sample.

[4] The first number refers to table and second number refers to model.

4. Counterfeit Herbicides, Productivity and Family Labor Use on Farms in Mali: A Multivalued Treatment Approach

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Abstract

Rapid growth in private sector herbicide imports has led to a dramatic rise in use of these commercial products by Malian smallholder farmers. Given weak regulatory capacity to monitor markets, the recent proliferation in herbicide products and brands has been accompanied by widespread sales of unregistered products. We test the effects of herbicides applied to Mali's major dryland cereals, sorghum, and maize, on yield and labor use per ha, differentiated by gender and age. We employ a multivalued treatment model with data collected from 623 households and 1,273 plots. We find that registered herbicides provide significant productivity benefits to farmers. Registered herbicides reduce the intensity of weeding labor of adult males nearly twice as much as unregistered herbicides, also reducing the weeding labor of female and child household members. Unregistered herbicides negatively affect maize and sorghum yields, while registered herbicides control weed damage without reducing yield.

Keywords: herbicides, multivalued treatment, agricultural policy, Mali

Introduction

Raising the productivity of dryland cereal crops among smallholder farmers in Mali depends critically on their use of modern inputs combined with practices that protect soil and water resources. Yet, despite long-term investments in seed improvement and more recently, government subsidy programs for fertilizer, adoption rates for these inputs remain low on dryland cereals (Kelly et al., 2015; Theriault et al., 2018). In contrast, spurred entirely by commercial supply and farmer demand, herbicide use by smallholder farmers has proliferated. The number of herbicides imported has more than doubled since 2000, even though farmers pay the full commercial price (Haggblade et al., 2017b; INSTAT, 2016).

Rising rural wages, urbanization, and market access are thought to underpin these patterns across Sub-Saharan Africa (Sheahan & Barrett, 2017; Tamru et al., 2017). Similar growth in herbicide use is apparent in other developing regions as well, driven by growing availability of generic products and falling prices (Haggblade et al., 2017a). In China, as in Africa, herbicide use has increased rapidly since the mid-2000s because of rising rural wage rates and falling herbicide prices (Huang et al., 2017).

In Mali, as is often the case elsewhere, not all of these herbicides are registered. While regulators effectively screen new herbicide products for efficacy and safety prior to registration, monitoring of the quality of herbicides actually sold in local markets following registration remains weak. As a result, a large volume of unregistered herbicides finds its way into Mali's agricultural input markets. Recent market surveys indicate that roughly a quarter (24%) of herbicides sold in Mali are unregistered (Haggblade et al., 2019b). Moreover, laboratory analysis of the most widely used herbicide active ingredient suggests that unregistered herbicides are underdosed by about 8–10% compared to duly registered products (Haggblade et al. 2019a). Broadly speaking, counterfeit and low-quality agricultural inputs are thought to be widespread in Sub-Saharan Africa (Ashour et al., 2018; Bayoumi, 2021; Bold et al., 2017; Gharib et al., 2021; MirPlus, 2012; Yao, 2020).

The survey data from the Sudanian Savanna, an area of high productivity potential for sorghum and maize, demonstrates that most Malian farmers who apply herbicides do not know the difference between registered and non-registered products and that many of the herbicides they use are not registered. Clearly, a situation like this has important ethical considerations in addition to economic implications. Misuse of herbicides has consequences for on-farm yields and potential negative externalities for human and environmental health. Counterfeit inputs have caused considerable problems in fertilizer and seed use, but there has not been much analysis of this problem with respect to herbicides (Ashour et al., 2018).

Published analysis of herbicide use on farms in Sub-Saharan Africa also remains limited. A recent analysis by Haggblade et al. (2017b) examined the origins and consequences of the rapid growth in herbicide use in Mali, finding adoption rates that range from 25% of farmers in remote areas to 75% of farmers in areas better served by market and road infrastructure. The authors found that on average, herbicides costs 50% less per ha than hiring labor to weed and documented a strong relationship between adoption and rising wage rates for weeding labor. In Ethiopia, Tamru et al. (2017) found a similar rapid rise in herbicide use that was driven by the private sector, strongly correlated with access to all-weather roads, and contributed to significantly higher labor productivity on farms. Sheahan and Barrett (2017) documented overall levels of input use in several countries of Sub-Saharan Africa, including agro-chemicals (i.e., insecticides, herbicides, fungicides). Among the six countries examined, Ethiopia and Nigeria showed substantial use of herbicides in particular. Sheahan et al. (2017) demonstrated the positive relationship of agro-chemical use with value of agricultural output, along with its negative consequences for indicators of human health. They analyzed nationally representative datasets from Ethiopia, Tanzania, Uganda, and Nigeria, finding the rate of use of agro-chemicals surpassed 10% of growers.

This chapter contributes to an emerging, still sparse knowledge about the use of herbicides by smallholder farmers in Sub-Saharan Africa, and in particular, to information about counterfeit herbicides. We contribute to the body of research cited above in several ways. First, we tested the effect of herbicide product quality on yield and labor productivity on Malian farms. In the absence of accredited testing laboratories in Mali, we use registered as compared to non-registered herbicides as a proxy for herbicide quality. Via registration of the product, we also tested the effects of regulations.

Second, we are able to disaggregate labor intensity, which we measured as weeding labor per ha, by gender and age (i.e., male, female, and child labor). The heavy demand for female labor generated by a combination of domestic and farm work has long been considered an impediment to their productivity in Sub-Saharan Africa, although Palacios-Lopez et al. (2017) recently questioned women's share of farm labor.

Third, to test our hypotheses, we applied a multivalued treatment effects model to observational data collected in 58 villages of Mali's Sudanian Savanna zone from 2014 to 2015. Many treatment effects in agricultural development involve binary assignment (e.g., program participation or not). In the case of binary treatment when employing observations in cross-sectional data, matching has become a popular approach (Imbens & Wooldridge, 2009), especially given the challenges of identifying appropriate instruments for two-stage least squares analysis. To our knowledge, propensity score matching methods have not yet been fully extended to multivalued treatments. Multivalued models have been described by Wooldridge (2010) and Cattaneo (2010), but so far, we have found only one application in agriculture (Esposti, 2017). Here, we tested three multivalued effect estimators with regression methods and, for completeness, used propensity score matching to test the overall effects of herbicide use.

Methods

1. Data

The sampling frame is a baseline census of all 2,430 sorghum-growing households in 58 villages located in the Cercles of Kati, Dioila, and Koutiala, regions of Koulikoro and Sikasso. Sikasso and Koulikoro regions lie largely within the Sudan Savanna zone, which has the greatest yield potential in Mali (Dicko et al., 2017). These two regions constitute the "sorghum belt" of the nation in terms of area cultivated and total production; as of the 2012–2013 season, the year before our survey, the two regions represented more than 51% of total sorghum area planted in the country (Cellule de Planification Statistique du Secteur du Développement Rural [CPS-SDR]). The zone is also favorable for maize production, an increasingly popular food and cash crop.

The enumeration unit in the baseline census, and generally in Mali, is the Exploitation Agricole Familiale (EAF), also known as the family farm enterprise. According to the national agricultural policy act (*Loi* *d'Orientation Agricole*), the EAF is a production unit composed of several members who are related and who use production factors collectively to generate resources under the supervision of the head of household. The head can be a female or male household member, but female headship remains rare. The head's primary economic activity is to encourage the optimal use of production factors, as these are defined by the extended family. For the EAFs we studied, the first priority was universally food security. The head represents the EAF in all civil acts, including representation and participation in government programs. They may designate a team leader (*chef de travaux*) to supervise field work and manage the EAF on behalf or to assist the head when they have physical or other limitations.

The family farm enterprise is a complex organization that consists of numerous plots on which multiple crops are grown. Plots are managed collectively and individually by various family members. Members generally include the head, their spouse and children, married sons and their wives and children, unmarried daughters and brothers of the head, and other relatives. Collective plots belonging to the whole EAF are managed by the household head or the team leader on behalf of the EAF. Individual plots belong to the EAF but are planted and managed by individual members, including both men and women. The production from these plots is not managed collectively. At each cropping season, the head distributes individual plots based on the needs of the family.

Sorghum and maize are the major dryland cereals in this region of Mali, although some millet is also grown. For more detailed analysis of input use in sorghum and maize production, we drew a sample of EAFs with simple random sampling. The final sample size was 623 EAFs, with an overall sampling fraction of 25%. Enumerators inventoried all plots operated by each sampled EAF, grouping them by crop and plot management type. Considering sorghum and maize plots only (because of budget constraints), one plot was randomly sampled per management type per EAF. The total sample of sorghum and maize plots analyzed, including those collectively and individually managed, was 1,273. We controlled for plot manager in the analysis, and included all sorghum and maize plots, having obtained more detailed production data compared to other crops.

The multi-visit sample survey was conducted in four rounds from August

2014 through June 2015, with a combination of paper questionnaires and computer-assisted personal interviews, by a team of experienced enumerators employed by the Institut d'Economie Rurale. Modules included (a) inventories of plots, livestock, agricultural equipment, and household assets, utilizing the harvest from the previous season; (b) input use and labor use on sorghum and maize plots; (c) measurement of area and production on sorghum and maize plots; (d) consumption expenditures and migration remittances.

2. Econometric Strategy

Our aim was to test the impacts of counterfeit and registered herbicides, as compared to use of neither, on farm productivity (output per ha) and labor intensity (weeding labor per ha). We further differentiated labor intensity by gender and age.

Herbicide use has recently expanded in rural Mali, in the absence of any deliberate program or policy intervention. We expected the decision to use herbicides to be non-random in farming communities given that the input was novel and it was introduced entirely by local traders or other farmers. We imagined that at this early stage of adoption, users and non-users would be systematically different. Users may "self-select," leading to potential bias in estimates of productivity impacts.

The Randomized Controlled Trial (RCT) is often seen as the "gold standard" of evaluation approaches because it eliminates selection bias (Imbens & Wooldridge, 2009). Bias due to non-random selection can occur because of program placement, participation criteria, or through processes of self-selection. Various approaches have been recommended to address the challenge of establishing a counterfactual with non-experimental data, including the class of treatment effect models, which we employed here. These models make treatment and outcome independent by conditioning on covariates or controls.

Various methods were used to address the question of establishing a counterfactual with non-experimental observations, including the class of treatment effect models, most of which involved a single treatment level represented by a binary (0,1) variable. Our interest in distinguishing the effects of herbicide quality (no herbicides at all, counterfeit herbicides, registered herbicides, or 0,1,2 respectively) led us to apply a multivalued treatment effects model. The case of multivalued treatment effects was developed by Wooldridge (2010), Cattaneo (2010), and Cattaneo et al. (2013). Wooldridge (2010) presented the example of participation in a training program that occurred at different levels (part-time or full-time), or in different forms. Cattaneo (2010) developed a more general theory for semiparametric estimators and applied it to estimate quantile treatment effects. The Wooldridge (2010) conceptualization best represents our situation, where 0 represents the control group and higher integer values indicate different treatment options.

To our knowledge, propensity score matching methods have not been fully developed for more than a single value of treatment (Cattaneo et al., 2013). As in the binary case, multivalued treatment effects can be estimated by applying other regression approaches. Wooldridge (2010) recommended regression adjustment (RA) as a baseline approach and a simple extension of the binary case to the multivalued case. RA estimators model the potential outcome of treatment without any assumptions about the treatment model. Augmented, inverse-probability weighted (AIPW) and inverse-probability weighted, regression adjustment (IPWRA) estimators address the outcome model $Y_i = f\,(\mathbf{X_i}, \boldsymbol{\beta}) + \varepsilon_i$, as well as the treatment model for 1,…G treatments, $Pr\,(T_i=1,\ldots G) = h\,(\mathbf{Z_i}; \boldsymbol{\lambda}) + \omega_i$.

X is a vector of covariates that influence the outcome Y and Z is a set of covariates explaining treatment assignment T, which may overlap. By exploiting inverse-probability weights derived from propensity scores estimated with multinomial, nested, or ordered logit, these estimators control for selection on observables. We utilized multinomial logit.

When either the outcome model or the treatment model or both are specified correctly, AIPW and IPWRA furnish consistent estimators of the treatment model parameters. Reflecting this property, the AIPW and IPWRA have been termed “doubly robust” (Wooldridge, 2010, p. 930). Cattaneo (2010) referred to the AIPW as the “efficient influence function”. AIPW and IPWRA estimators can be more efficient than RA (Cattaneo, 2010; Cattaneo et al., 2013; Glynn & Quinn, 2010). Use of these approaches in agricultural analyses appears to be infrequent. Esposti (2017) applied the multivalued Cattaneo

(2010) model to evaluate the impact of the 2005 reform of the Common Agricultural Policy on farm production choices using treatment intervals.

Identification of the treatment effect relies on satisfying the properties of conditional mean independence, which stipulates that the treatment does not affect the mean of the outcome variable. Apparently, the multivalued case relies on a weaker assumption than in the binary case (Esposti, 2017; Cattaneo, 2010). Among our estimators, weighting by the inverse of the estimated propensity score achieved covariate balance and created a sample in which the distribution of covariates was independent of treatment status (Karamba & Winters, 2015).

Potential bias generated by unobservable characteristics remained. We applied the bounds approach proposed by Rosenbaum (2002) to examine the robustness of our results to these unobserved characteristics. The Rosenbaum bounds approach determines how strongly an unobserved factor must affect the outcome variables to undermine the matching estimates. The technique calculates the confidence intervals for different level of Γ based on the following equation

$$\frac{1}{\Gamma} < \frac{P_i}{P_j} \times \frac{1-P_j}{1-P_i} < \Gamma$$

where P_i and P_j are odds for two individuals i and j. γ is the effect of unobserved factor on the treatment selection

$$\Gamma = exp(\gamma)$$

The smallest value of Γ for which the confidence interval contains zero is the critical odds ratio for which we questioned the estimated impact. If the value of Γ is small (less than two), we considered that the effect of the estimated treatment was sensitive to unobservable factors (Duvendack & Palmer-Jones, 2012).

We also improved the covariate balance by introducing plot management type and education into the treatment model. Plot management type is highly correlated with observed and intrinsic characteristics of the manager (relationship to head, gender, age) that affect access to resources within the extended family household (EAF). We also examined the common support condition.

In addition to the multivalued models, we estimated a binary model with propensity score matching to test the effects of use vs. non-use of herbicides. All models were estimated in STATA 14 using plot-level data.

3. Model Specification

The objective of the econometric strategy was to quantify the potential outcomes that expressed changes in the output per ha and labor use in weeding per ha. For both outcomes, we used the same econometric specification

$$Y = \alpha + \beta' \mathit{outcomecovar} + \Theta' \mathit{treatmentcovar} + \mu,$$

where Y is grain yield in kg/ha or weeding labor/ha and *outcomecovar* is a vector of agricultural inputs applied on dryland cereals plots, which covary with the outcome. Corresponding to a notional yield response function, we included input quantities per ha (seed, fertilizer, adult male labor, adult female labor, children's labor, machinery use, manure), as well as plot characteristics (time in minutes to travel from homestead to the plot, whether any structure was built on the plot to offset soil and water erosion). These were the same covariates we expected to influence the intensity of labor use.

Treatmentcovar is a vector of plot manager, household, and market covariates that influence incentives for use (covarying with treatment), including the cost per ha of hiring weeding labor, the total household labor supply, and whether or not the EAF received a fertilizer subsidy. In Mali, access to formalized extension structures (encadrement) substitutes to some extent for commercial markets, influencing farmer access to inputs and services of various kinds, including subsidized fertilizer. The estimate of weeding costs per ha is derived from responses to a question asking how much weeding labor costs if herbicides were not applied. Since market infrastructure extends to weekly fairs conducted in villages, we included a dummy variable for the presence of a weekly fair in the village of the EAF. Finally, as described above, we recognized the social organization of production in this region of Mali, and added the characteristics of the plot manager (education of the manager, whether the plot is managed by the head or another individual member of the household) among our explanatory variables.

Following the potential outcomes framework, we expressed the observed outcome Y as

$$Y=D_0Y_0+D_1Y_1+D_2Y_2$$

where D_0, D_1, and D_2 were dummy variables indicating the level of treatment. $D_{t=\{0,1,2\}}$ equals to one if the plot received treatment level t and zero otherwise. Y_0, Y_1, and Y_2 were the corresponding potential outcomes.

Letting t and s act as two treatment levels, the average treatment effects were given by the following equation:

$$ATE = E[Y_t\text{-}Y_s]$$

If we were in a randomized experiment setting, we could estimate the average treatment effect (ATE) of level t relative to level s by the sample means of observed outcomes. Given the observational nature of our data, to estimate ATE we needed to fulfil the weak unconfoundedness or conditional independence assumption, which required independence of each treatment level with the corresponding potential outcomes knowing X. Hence, formally

$$D_t \perp Y_t|X, \forall t\in \{0,1,2\}$$

where X= *outcomecovar* + *treatmentcovar*, $\perp$ denotes independence and t treatment level.

In addition, the overlap or common support assumption, which implies positive probability of being in any treatment level, must be satisfied. The overlap assumption in multivalued treatment can be assessed using generalized propensity score (GPS) proposed by Imbens (2000) and computed with the following equation:

$$r(x,t) = P\,[T = t|X=x] = E[D_t|X = x]>0$$

The GPS is used in the empirical implementation because it overcomes the problem of high dimensionality that might arise by conditioning directly on vector X.

Under these assumptions, we estimated the mean of the potential outcome for the treatment level t knowing the vector of covariates X by taking the average of the conditional expectation of the potential outcome or by weighting the observed outcomes with the generalized propensity score through the below equation:

$$\mu_t = EE[[Y/T = t, r(t, X) = r]] \text{ or } \mu_t = E[\frac{YD_t}{r(t,X)}]$$

The ATEs were then determined by pairwise comparison of these means of the potential outcome.

Model control variables are defined in Table 1. Outcome variable definitions are shown in Table 2, along with differences in the means of each outcome variable by treatment. Without controlling for other factors, lower mean yields were associated with unregistered herbicide use compared with no herbicide use, but the highest mean yields were associated with registered herbicide use. The lowest labor use per ha for adult males, adult females, or children was on plots receiving registered herbicides. In interpreting our labor outcome variables, it was important to recognize that hired labor use on farms surveyed was negligible. Absence of labor markets, and dependence on the extended family or labor sharing arrangements with neighbors, was a prominent feature of the dryland cereals farming system in our zone of study. These were the hypotheses we carried to the estimation.

Table 1
Definition of Control Variables in Multivalued Treatment Effect Model

Control variable	**Definition**
Treatment covariates	
individually-managed	plot managed individually by male or female who is not the EAF head or designate=1, else 0
manager	head=1; individual male not head=2; individual female not head=3
education	plot manager attended primary school=1, 0 else
labor supply	number of adults in EAF between 12 and 55 years of age (inclusive)/total area operated by EAF
weeding cost	cost of hiring weeding labor per ha
subsidy	EAF benefited from fertilizer subsidy=1, 0 else
market	weekly market fair in village=1, 0 else
village	village fixed effect
Outcome covariates	
seed	quantity of seed in kgs used per ha
fertilizer	kgs of fertilizer applied per ha
male labor	number of adult male person-days (14 years and above) per ha
female labor	number of adults female person-days (14 years and above) per ha
child labor	number of children person-days (under 14 years) per ha
machinery use	hours of equipment use her ha
manure	manure use on plot=1, 0 else
location	time in minutes to travel from home to the plot
erosion control	any anti-erosion structure built on plot=1, 0 else

Table 2
Outcome Results by Treatment

Outcomes	Definition	No herbicide	Unregistered herbicide	Registered herbicide
crop productivity	yield=grain kgs harvested/ ha	1183	890	1346
male labor intensity	days weeding labor per ha for adult males;	21.1	20.5	17.9
female labor intensity	days weeding labor per ha for adult females	6.13	8.01	3.77
child labor intensity	days weeding labor per ha for children (12 years and under)	3.38	4.18	2.83
N=1273 plots, 623 EAFs.				

Results

1. Descriptives

Glyphosate, a broad-spectrum, non-selective herbicide which was developed by Monsanto under the trademark name of Roundup, is the world's most popular herbicide. Importers and input vendors also report that glyphosate is their top-selling herbicide in Mali (Diarra, 2016). Our survey data indicated that glyphosate accounted for about two-thirds of herbicide volumes applied by farmers to their sorghum and maize plots. Selective herbicides, intended for use on cotton, maize, and rice, represented the other third. Since many households surveyed belonged to the cotton growers' associations, use of selective herbicides may have reflected their experience and access to inputs via their membership. Based on Table 3, only slightly more than half of sorghum and maize plots (53%) or volume of total herbicides used by farmers surveyed (55%) were registered. The remainder were of unregistered and of uncertain quality, meaning either "knock-offs" or counterfeit.

Table 3
Farmer Use of Herbicides by Category (in %), Sudan Savanna of Mali, 2014/15

Herbicide type	Herbicide registration		
	registered	unregistered	total
% of plots	53	47	100
% of volume	55	45	100

Aside from the practice of full soil inversion (plowing) during land preparation, farmers in this region of Mali rely on hand and hoe to control weeds, and generally on the labor of family members or shared labor with friends. When asked what it would cost to hire labor to accomplish this task rather than apply herbicides, surveyed farmers indicated that they would have spent $52. In comparison, those who used herbicides instead would spend an average of only $23 per hectare.

Among households surveyed, female household members (primary wives of the household head, but also daughters-in-law) managed about one-quarter of sorghum plots, but none of the maize plots. Sorghum and maize plots managed by male family members who were not heads of household were relatively few in number, although these men often managed plots of cotton or other cash crops. Larger plots managed by the household head and worked collectively by members constituted over 80% of all sorghum plots and 95% of maize plots.

The data in Table 4 indicates that individual plot managers were more likely to apply herbicides on their plots than household heads were to use the input on family fields. According to social norms, the head reserves the right to demand labor on these plots, since the output benefits the family as a group; individuals must meet labor needs on their own fields after satisfying their duties—potentially, a powerful incentive for using herbicides. Female plot managers applied herbicides on their individual fields at nearly twice the rate applied on collective fields (2.6 liters per hectare compared to 1.1 liters). Male-managed individual plots received doses that were even higher per hectare.

Table 4
Herbicide Use by Plot Management Type

		Crop grown		
Plot manager	**Plot type**	**Sorghum**	**Maize**	**All**
	Percent of plots using herbicides			
Household head	collective	47	69	58
Female	individual	79		79
Male	individual	90	60	80
All		56	69	61
	Herbicide application rate (liters/ha)			
Household head	collective	1.1	1.7	1.4
Female	individual	2.6		2.6
Male	individual	3.3	2.5	3.1
All		1.6	1.7	1.6

2. Econometric Findings

Before discussing the ATEs, it is important to examine the quality of the matching process. Conditional probabilities of herbicide use by treatment level are shown in Figure 1. Across all three treatment levels, the density distribution of the estimated probabilities confirmed that there was not much high-density mass near the values 0 or 1. Thus the common support condition was satisfied: there was substantial overlap in the distribution of the probability for non-users of herbicides, users of unregistered herbicides, and users of registered herbicides.

Figure 1

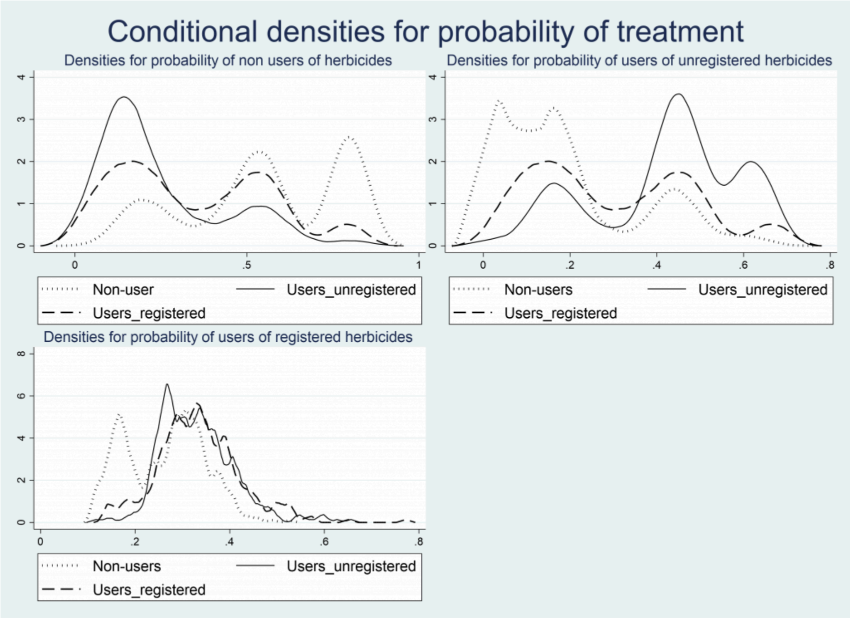

Figure 1 – Conditional Densities for Probability of Treatment, by Category

In addition, Figure 2 presents the probability distribution of propensity scores (lowest to highest) and the region of common support for users and non-users. The data indicated that the common support condition was satisfied as there was overlap in the distribution of the propensity scores between the two groups. This is reflected in Figure 3, which shows the probability density functions of users and non-users. The results of the covariate balancing tests in Table 5 show that good balance was achieved after matching by reducing the percentage of balance bias up to more than 70% overall.

Figure 2

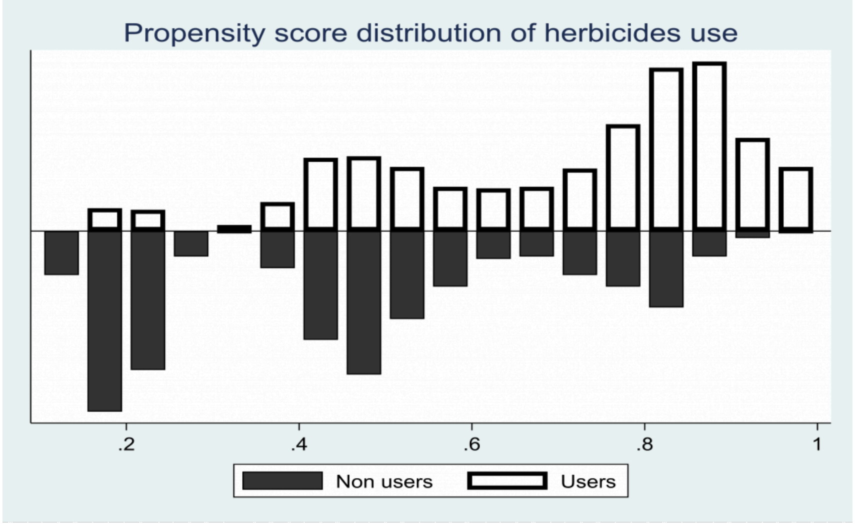

Figure 2 – Propensity Score Distribution of Herbicide Use, Users, and Non-users

Figure 3

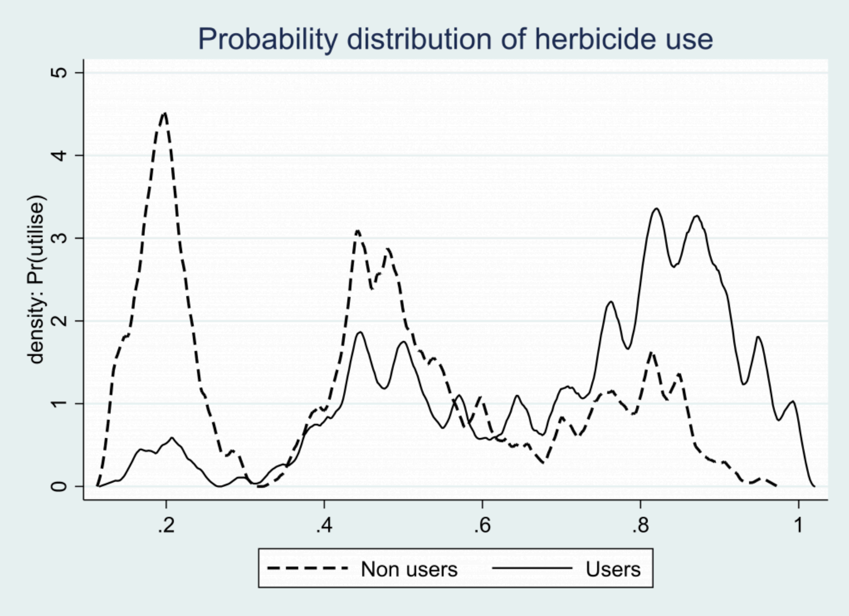

Figure 3 – Probability Distribution of Herbicide Use

Table 5
Covariates Balancing Test

	Standardized	Differences	Variance	Ratio
	Raw	Weighted	Raw	Weighted
Not registered herbicides				
manager	0.538	0.538	2.662	2.660
village	-1.401	-1.401	0.451	0.451
subsidy	-0.283	-0.283	1.158	1.157
age	-0.192	-0.192	1.012	1.011
education	0.278	0.278	1.647	1.645
market	-0.301	-0.301	0.654	0.654
labor supply	0.334	0.334	1.216	1.215
weeding cost	0.732	0.732	12.777	12.768
individually-managed	0.559	0.559	2.745	2.743
seed	-0.069	-0.069	2.048	2.046
fertilizer	0.031	0.031	0.891	0.890
male labor	-0.141	-0.141	1.043	1.043
female labor	-0.192	-0.192	0.569	0.568
child labor	0.194	0.194	1.742	1.740
location	-0.033	-0.033	1.108	1.107
erosion control	-0.070	-0.070	0.999	0.999
machinery use	-0.313	-0.313	0.667	0.666
manure	0.020	0.020	1.016	1.015
Registered herbicides				
manager	0.189	0.189	1.600	1.599
village	-0.824	-0.824	0.716	0.716
subsidy	-0.140	-0.140	1.099	1.098
age	-0.072	-0.072	1.022	1.021
education	0.180	0.180	1.427	1.426
market	-0.222	-0.222	0.751	0.750
labor supply	0.318	0.318	1.156	1.155
weeding cost	0.535	0.535	21.569	21.555
individually-managed	0.198	0.198	1.643	1.642

	Standardized	Differences	Variance	Ratio
	Raw	**Weighted**	**Raw**	**Weighted**
seed	0.180	0.180	1.887	1.886
fertilizer	0.521	0.521	2.954	2.952
male labor	0.146	0.146	1.423	1.422
female labor	-0.185	-0.185	0.710	0.709
child labor	0.154	0.154	1.518	1.517
location	-0.172	-0.172	1.092	1.092
erosion control	-0.251	-0.251	0.797	0.796
machinery use	-0.095	-0.095	0.967	0.966
manure	0.324	0.324	1.138	1.137

Furthermore, Table 6 presents the critical values of gamma (Γ) for each of the four outcome variables. The critical gamma values indicated that yield and male labor were sensitive to unobserved characteristics at Γ = 1.4 and Γ = 1.6, respectively. These values suggested that the unobserved characteristic would need to increase the odds ratio by 40% for yield and 60% for male labor before we started questioning the estimated effects of treatment. The degree of vulnerability to unobserved factors for these two outcome variables was within an acceptable range and was not a critical issue (Rosenbaum, 2005). The critical gamma values for female and children labor were greater than two. This result implies that the treatment effects are more robust to the hidden biases arising from unobserved characteristics for these two outcome variables. Our estimates of treatment effects were overall robust to the influence of unobserved factors.

Table 6
Rosenbaum Bounds Analysis for the Main Outcomes

Outcome variables	Gamma	CI+	CI-
Yield	1	-401.395	-189.458
	1.2	-512.604	-77.024
	1.4	**-609.629**	**16.257**
Male labor	1	-7.902	-4.134
	1.2	-10.132	-2.312

Outcome variables	Gamma	CI+	CI-
	1.4	-12.194	-0.802
	1.6	**-14.034**	**0.524**
Female labor	1	-0.003	-0.003
	1.2	-0.003	-0.003
	1.4	-0.004	-0.003
	1.6	-0.004	-0.004
	1.8	-2.013	-0.004
	2	-2.885	-0.004
	2.2	-3.962	-0.004
	2.4	**-4.878**	**0.553**
Children labor	1	-0.003	-0.004
	1.2	-0.003	-0.004
	1.4	-0.704	-0.004
	1.6	-1.676	-0.003
	1.8	-2.102	-0.002
	2	-3.106	-0.003
	2.2	-3.484	-0.003
	2.4	**-3.896**	**0.549**

As described in the econometrics section, we applied RA, AIPW, and IPWRA to estimate the impacts of herbicide use on yield and intensity of adult male, adult female, and child labor with a multivalued treatment model (non-use, use of unregistered, and use of registered herbicides). For completeness, we used overall propensity score matching (PSM) to estimate the binary impact of herbicide use compared to non-use.

The results reported in Table 7 showed no significant impact of registered herbicide use on yield. In fact, herbicides reduced damage from weeds rather than enhancing the yield potential of the crop (Lichtenberg & Zilberman, 1986). Still, *ceteris paribus*, we might have expected a larger harvested output per acre if damages had been offset by use. On the contrary, the regression indicates that the use of unregistered herbicide has a significantly negative effect on harvested yields, controlling for other covariates. Household members who managed plots where they applied unregistered herbicides expected an average yield loss of 218 kg/ha. Considering that the overall mean yield was only 1,141 ha, this amount is important in terms of magnitude. Overall, the binary PSM model confirms that the overall impact of herbicide use on crop yields is not significantly different from zero.

Table 7
Average Treatment Effects by Outcome and Model

	RA	**AIPW**	**IPWRA**	**PSM**
ATE on Yield				
not registered	-219.4*	-204.0**	-152.1	
registered	66.1	108.2	137.3	
use herbicide				1.876
ATE on men weeding labor				
not registered	-4.686**	-5.441**	-6.284***	
registered	-7.973***	-8.674***	-9.327***	
use herbicide				-8.061***
ATE on women weeding labor				
not registered	-1.055	-0.92	-1.318	
registered	-1.397	-1.788*	-2.144**	
use herbicide				-1.599
ATE on children weeding labor				
not registered	-1.62	-1.785	-2.279*	
registered	-1.913*	-2.241**	-2.706**	
use herbicide				-1.342
N	1136	1136	1136	1136

$^{*}\ p < 0.10,\ ^{**}\ p < 0.05,\ ^{***}\ p < 0.01$

Impacts on weeding labor appear to be stronger, as might be expected given that labor bottlenecks are the primary incentive for using this input. Among the households surveyed, adult male labor was by far the largest category. The labor of adult male household members was heavily demanded on the collective plots, particularly in land preparation and weeding. The labor of adult female household members was deployed across a broad range of household and farming activities; their individual plots were small in size, and generally intercropped with legumes. The data shows low overall levels of female labor use in weeding. Child labor efforts were also relatively minor compared to those of adult males.

Consequently, the impacts of all categories of herbicide use on the labor use intensity of adult males is strong and positive (corresponding to a negative sign since the variable was labor days per hectare). Registered herbicides had the greatest impact, almost twice as large as unregistered herbicides (an average decrease of 7.9 vs. 4.6 days). The use of registered herbicides was associated with lower amounts of weeding labor by women and children in the household, reducing it by an average of 1.7 and 2.2 days, respectively. This implies that children in households who use registered herbicides are less likely to be asked to weed, which has important ethical and, possibly, health implications.

Conclusions and Policy Implications

This study contributes in general to a sparse, emerging knowledge about the use of herbicides by smallholder farmers in Sub-Saharan Africa and in particular to information about counterfeit herbicides. We found that the use of unregistered herbicides is associated with lower yields and that the use of all herbicides, and in particular, registered products, reduces the intensity of labor use (per ha) of male, female, and child labor in weeding.

Use of registered herbicides improves child welfare by reducing the demand for their labor. Policies and regulations to support the use of registered herbicides could be beneficial, but more research is needed on health and environmental implications. Future research might further test these hypotheses using techniques for quality directly through laboratory testing, and a sample of farmers from more regions of Mali.

Clearly, the large volume of unregistered herbicides currently in use poses a problem for farmers as well as potential problems for consumers and the environment. These findings suggest a need for improved regulatory practices. It is important to distinguish between the pre-registration review system, which works very well, and the post-registration market monitoring, which functions very poorly (Diarra & Haggblade, 2017; Haggblade et al., 2021). For over 20 years, Mali has participated in a regional regulatory review process. Since 1994, the Comité Permanent Inter-Etats de Lutte contre la Sécheresse dans le Sahel (CILSS) has operated a regional regulatory body, the Comité Sahelien des Pesticides (CSP), to review and certify all pesticide products sold throughout the Sahelian member countries, including Mali. Under these common rules, any pesticide passing CSP efficacy and safety reviews and registered for sale in one member country becomes automatically authorized for sale throughout all nine member countries. By centralizing this regulatory review process, the CSP provides a one-stop-shop for manufacturers and importers, facilitating the review process and enabling suppliers to reduce bureaucratic costs by standardizing and centralizing review procedures. This model economizes on scarce technical manpower and laboratory facilities by pooling talent from across the member countries. Specialists at the Food and Agriculture Organization of the United Nations (FAO) and across West Africa consider the CSP regulatory model to be “probably the most successful example of regional harmonization in Sub-Saharan Africa” (Traoré et al., 2011, p.16) and one increasingly emulated in other sub-regions of Africa (Haggblade et al., 2021).

In contrast, post-regulatory monitoring remains very weak. The growing numbers of unregistered and counterfeit herbicide products available on the market lead to mounting farmer concerns about product quality and safety. Yet the environmental impacts of herbicide use remain largely unmonitored in Mali (Haggblade et al., 2017b).

Looking forward, policy makers in Mali will increasingly require better monitoring of pesticide product quality and environmental impact. The CILSS model of regional regulatory review, which economizes on scarce scientific personnel and laboratory facilities, has proven efficient in vetting herbicide products prior to release. Regional sampling and studies across common Sahelian agro-ecological zones can perhaps offer parallel economies in environmental monitoring.

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5. Economic Risks and Uncertainties in a Context of Climate Change: Teachings on the Use of Information Systems in the Senegalese Groundnut Basin

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Abstract

This chapter aims to show the benefits of systematically using information systems as a basis for agricultural decisions and strategies in the Senegalese groundnut basin. The research involved two surveys conducted by ISRA/Bame in 2016. The first, which focuses on market information, was conducted on a sample of 105 cowpea farmers who use the *Yeugglé* Market Information System (MIS) to obtain information on the current price in the markets of Diourbel, Bambey, and Fatick from weekly telephone messages. The second, based on a sample of 82 farmers in the regions of Diourbel, Kaolack, and Kaffrine, focuses on Climate Information (CI). The approach is based on a statistical analysis of variables related to the influence of market and climatic information on production, marketing, and agricultural input investment decisions. The results show that for 49% of farmers, market information influences their choice of markets. For most farmers (85%), market information influences the decision of sale, period, and allows farmers to make trade-offs in time and space. Regarding climate information, the results show that 67% of respondents use it and that the national meteorological service is the main provider (52%), followed by the radio (6%), and the *Yeugglé* platform (4%).

Keywords: Information system, risks, groundnut basin, climate change, Senegal

Introduction

In economics, “the principle of rationality means that individuals act by making the best use of the resources available to them, given the constraints they face” (Simon, 1965,). However, the rationality of agents basing their decisions only on prices and maximizing the difference between the value of inputs and the value of outputs is not a reality. In fact, agents do not and cannot behave in a way that maximizes utility, but instead adopt strategies that consider cognitive limits (i.e., the limits encountered in the knowledge and processing of information). Rationality is therefore linked to information mastery (Fraval, 2000).

According to neoclassicists, the “market game” allows economic agents to coordinate the best possible individual decisions. Indeed, economic and social activity is often characterized by situations where the well-being of an economic agent depends, not only on their own actions, but also on the decisions of other agents. Being aware of the existence of this type of interdependence, everyone takes it into account and incorporates it into their decision-making (Fraval, 2000).

In the agricultural sector, production and marketing decisions are often dependent on the level of information available to farmers. For that reason, Senegal, like most of the countries in the Sahel, has had a few Market Information System (MIS) experiments beyond that of the Food Security Commission (CSA), which was set up in the 1980s. These MISs, both public and private, do not all have the same objectives or targets. The channels and frequencies of information dissemination may differ as some use traditional channels (e.g., radio, word of mouth) while others use second generation channels to transmit information through the website and/or cell phone.

In the groundnut basin of Senegal, cowpea producers use the *Yeugglé*[1] MIS to obtain information on the product's price. This MIS, like others, broadcasts weekly information on cowpea prices in the markets of Diourbel, Bambey, and Fatick via telephone short message services (SMS). It is managed by the cowpea sector table set up by the Support Program for Agricultural Sectors (PAFA). Like other MIS's, cowpea prices are collected weekly at urban and rural markets (Ngom, 2018).

Another experiment was developed on a large scale in the Groundnut Basin (which includes Diourbel, Fatick, and Kaffrine) in 2016 on the use of Climate Information (CI) and the impacts that it could have on farm management and more specifically on securing income. To this end, representatives of the PAFA network attended a training session on the concept of climate-smart agriculture with a particular focus on climate products.

This information impacts producers' production and marketing decisions, even if they also face the risk and uncertainty inherent in agricultural activity. Indeed, risk and uncertainty are two fundamental notions for understanding the strategies of rural households in Sub-Saharan Africa, particularly Senegal. They are so important that uncertainty is omnipresent in this context, whether it relates to climatic conditions, crop pest problems, the internal functioning of commodity chains (i.e., production, transport, marketing) or product prices. This raises the question of what influence the use of information can have on the economic decisions of producers? These decisions have the sole aim of maximizing their utility (i.e., consumers) or their profit (i.e., firms).

Overall, this chapter aims to show the benefits of using information systems in decision-making and on agricultural strategies of the farms in the Senegalese groundnut basin.

This chapter is structured as follows: first, we will analyze the influence of market information use on cowpea farmers' economic decisions. Next, we focus on access to and use of climate information by farms. Finally, following the conclusion, we provide recommendations.

Methodology

1. Sample

Three communes were chosen: Ndinguiraye (Bambey), Ndindy (Diourbel), and Niakhar (Fatick). In total, 14 villages belonging to these three communes benefit from the *Yeugglé* information system. We adopted a sampling rate of 50% to randomly select 7 villages through stratification by village. In each village, 15 producers were randomly selected. Thus, a group of 105 cowpea producers using the *Yeuggl*é MIS were surveyed.

1.1 Market Information

We conducted a survey targeting cowpea producers in the Senegalese groundnut basin with a sample made up of cowpea producers who use the *Yeugglé* information system. This system is managed by the cowpea commodity chain sector setup within the framework of the Support Program for Agricultural Sectors (PAFA). Like other MISs, cowpea prices are collected weekly at the markets—mainly the markets of Diourbel, Bambey Serère, Ndiguiraye, and Gaouane—and are distributed by SMS to the producers of this commodity chain sector, which has become a national framework for sector consultation.

1.2 Climate Information

With regard to climate information, the complexity and heterogeneity of the farms as well as the size of the study area led us to adopt a "multi-stage" sampling methodology, which consists of consecutive stages developed to arrive at the selection of basic observation units (i.e., farms) where the requirements of representativeness are respected. A reasoned choice was made for the selection of the PAFA zone as well as for the villages, which were dictated by the option of the millet/sorghum and sorrel (bissap) sectors, the focus of the PAFA. For the farms, all the members who participated in the training sessions were retained, as well as those with extensive experience in climate information at the Kaffrine level. The trainings were organized for the representatives of the PAFA network to share with them the concept of climate-smart agriculture with an emphasis on climate products. These were three-day workshops that trained farmers, defined the needed products, and identified a framework for transmission of climate information. These were held in Diourbel for the northern Groundnut Basin area and in Kaolack for the southern Groundnut Basin, with each workshop bringing together about 20 producers.

Our sample consisted of 82 farmers in three regions (Diourbel, Fatick and Kaffrine) as presented in Table 1. For the controls (i.e., no training in climate information), they were chosen at random from similar villages.

Table 1
Type of Actor

Region	**Type of Actor**				**Total**
	Participated in the Training	**Extensive Experience on CI**	**No Training but CI**	**No Training and No CI**	
Diourbel	14	4	2	0	20
Fatick	17	2	11	9	39
Kaffrine	9	13	0	1	23
Groundnut Basin	40	19	13	10	**82**

Source: Author based on ISRA/BAME survey data, 2016. Farmers answered a questionnaire with three modules: farm characteristics; access, use and appreciation of climate information; and usefulness of climate information.

1.3 Approach Analysis

The approach is based on a statistical analysis of variables related to the influence of market and climate information in production, marketing, and agricultural input investment decisions. Additionally, as far as climate information is concerned, the comparative analysis of these two sites will make it possible to: (i) define the added value of the adoption of climate information by farmers; (ii) observe how it can be integrated with other CSA technologies or practices; and (iii) identify the factors that facilitate or limit the diffusion of these technologies and practices.

Teachings on the Influence of MIS Use on Cowpea Farmers' Economic Decisions

1. Market Information Does Not Always Influence the Point of Sale

For half of the cowpea producers (51%), the market information received does not influence the choice of the market where to make the sale. The reason given is the lack of means of transportation and the related costs to be borne. On the other hand, for 49% of the producers, this information influences the place of sale because it allows them to sell at more remunerative prices. Thus, as Egg et al (1996) points out, MIS are supposed to enable producers to make special trade-offs.

2. Market Information Guides the Timing of Sales

For the vast majority of cowpea producers (85%), the market information received influences the time of sale. Actually, the sale is made when the price of cowpea on the market is remunerative, showing that MIS allows farmers to make trade-offs by considering their opportunities. However, for 15% of producers, the time of sale is not influenced by the information received, but depends on social needs and to a lesser extent on the lack of storage infrastructure, hence the need to continue to focus on storage infrastructure for better management of opportunities.

3. Cowpea Price Trends in Reference Markets Drive Pricing

For the majority of cowpea producers (62%), market information influences their choice of selling price. The decision to sell is not made without first knowing the price trends of cowpeas in reference markets, which has a positive impact on their bargaining power vis-à-vis traders who are considered to be better informed. For slightly more than a third (38.1%), market information does not influence the selling price because producers generally engage in tied or loyalty transactions to avoid the risk of not finding any buyer for their produce. The uncertainty that results from the way a farmer finances their campaign can also influence the price. It can include the rising cost of capital, interest rate, limited availability, and degree of creditworthiness (Wade, 2009).

4. Privileging Group Sales Means that Market Information Does Not Influence the Quantity to be Sold

Market information does not influence the choice of the quantity to sell for most cowpea producers (75%). The reason given is that generally the sale of the crop is not done in a sequential manner but rather grouped together, which avoids post-harvest losses. On the other hand, for nearly 25% of these producers, market information influences the choice of the quantity to sell. The quantity sold is greater when the price is high. Conversely, it is low when the price is not remunerative. In other words, the higher the price, the greater the incentive for producers to sell a large quantity.

5. Market Information Influences the Choice of Crop

Market information influences the majority of producers (56%) in their choice of crop. It allows them to cultivate the crops for which prices are the most remunerative, beyond millet, which is a food crop in this zone. In fact, more and more food crops are being sold on the markets, which is why it is important to be able to identify the most profitable crops for the zone in order to have a substantial cash income to meet the family's financial needs. Indeed, when the price of a good increases, suppliers are encouraged to increase their supply in order to increase their profit.

6. Market Information Influences the Choice of Plot Size

For the vast majority of cowpea producers (82%), market information influences the choice of plot size. Depending on the prices of the crops observed on the markets during the past raining season and during the dry season, producers decide to increase or maintain a given plot size for a given crop for the next season. This decision is influenced by market risk and environmental uncertainty. In fact, being in a situation of uncertainty, farmers favor flexibility by minimizing the investments (i.e., monetary or in time) that they devote to production. In the event that the crops are effectively destroyed, the loss of investment will be less important with this posture than if the feared event were not to occur (i.e., as if it were a certain universe). In a certain (favorable) universe, producers can safely make the investments required to maximize their production, which they know from the outset will be good at harvest time (Fraval, 2000).

7. Market Information Influences the Decision to Invest in Agricultural Inputs

For most cowpea farmers (94%), market information influences the decision to invest in agricultural inputs. Thus, producers prefer to invest in agricultural inputs for which prices are much more remunerative. In other words, prices guide producers towards the use of production factors. Nevertheless, they face production uncertainty because agriculture is affected by many uncontrollable events that are often related to climatic conditions (i.e., excessive or insufficient rainfall, extreme temperatures, hail), as well as diseases and pests. These factors have a direct impact on the quantity and quality of production (Wade, 2009). Such influences create an increase in the quantity of inputs used (58%) and with particular attention paid to the quality of inputs used (34%)

Access and Use of Climate Information

1. ANACIM: The Main Provider of Climate Information

The information on the climatic and meteorological forecasts are broadcasted every day by the National Agency of Civil Aviation and Meteorology (ANACIM) via radio and television. Their information includes temperature, rainfall, and humidity. Sometimes, if there are abnormal situations in sight (i.e., strong wind, heavy rains, etc.), the weather service alerts producers, and even fishermen, so that they can make arrangements. However, as part of its collaboration with projects in certain areas, particularly in Kaffrine, in addition to training, ANACIM broadcasts weekly climate information during production periods, particularly the rainy season, via radio and SMS. The forecast period is generally 1, 3, and 10 days.

In the groundnut basin, 67% of producers are accustomed to receiving climate information (Table 2). ANACIM is the main provider of this information (52%), a trend that can be explained by the presence of the CCAFS project in the area since 2010, which instilled in farmers the importance of using climate information. Various annual training sessions and the ANACIM's sharing of seasonal forecasts have finally convinced farmers, who have confidence (94%) in the information provided by ANACIM. This confidence is owed to the accuracy of past forecasts. However, 5% still do not trust ANACIM and 1% do not follow its information.

Besides ANACIM, the radio, with 6%, ranks second because of its widespread use in rural areas. The *Yeugglé* platform (4%), however, is becoming increasingly important, particularly in Diourbel, where ¾ of the "highly experienced CI" group get their information the platform, especially after it integrated climate information into its services. These services are followed by the decentralized services of the Ministry of Agriculture, the sector tables (PAFA), television, and traditional news, each with 1%. Thus, the sharing of climate information is more important when there is a regrouping of actors during training workshops or other meetings.

Table 2
Habit of Receiving Climate Information

Region	Type of Actor	**Habit of receiving climate information?**							
		No	Yes						
			Source						
			Agriculture	ANACIM	Yeuglé Platform	Cowpea Sector Platform	Radio	Television	Traditional Information
Diourbel	Participated in the Training	29%	–	57%	–	7%	7%	–	–
	Extensive Experience on CI	–	–	25%	75%	–	0%	–	–
	No Training but CI	100%	–	0%	–	–	0%	–	–
	No Training and No CI	–	–	–	–	–	–	–	–
Fatick	Participated in the Training	12%	–	82%	–	–	0%	6%	–
	Extensive Experience on CI		–	100%	–	–	0%	–	
	No Training but CI	64%	–	9%	–	–	18%	–	9%
	No Training and No CI	89%	–	11%	–	–	0%	–	–

Region	Type of Actor	**Habit of receiving climate information?**							
		No	Yes						
			Source						
			Agriculture	ANACIM	Yeuglé Platform	Cowpea Sector Platform	Radio	Television	Traditional Information
Kaffrine	Participated in the Training	11%	11%	67%	–	–	11%	–	–
	Extensive Experience on CI	15%	–	77%	–	–	8%	–	–
	No Training but CI	–	–	–	–	–	–	–	–
	No Training and No CI	100%	–	–	–	–	–	–	–
Sample		33%	1%	52%	4%	1%	6%	1%	1%

Source: Author based on ISRA/BAME survey data, 2016.

2. Community-Based Learning Promotes the Use of Climate Information

The use of climate information is generally community-based, especially for the two groups that "attended the training" and "had a lot of experience on CI." In short, these trainings, in addition to providing climate information, promote dialogue between actors for better decision making and especially for knowledge sharing. In contrast, for the other two groups—"no training but CI" and "no training and no CI"—the use of climate information is individualized with little sharing at the community level (Table 3).

Among those who received climate information (whether they were involved in the program or not), 84% actually used it. In Diourbel and Fatick, all of those who received climate information used it, while in Kaffrine, only 11% of those in the "attended the training" category did not. Several reasons were given by the latter, including not having received the information, not trusting the information because of its randomness, and that the information was not in the local language.

Table 3
Use of Climate Information

Region	**Type of Actor**	**Did you use the climate and weather information you received to conduct your campaign?**		
		Yes	No	Not Received
Diourbel	Participated in the Training	93%	0%	7%
	Extensive Experience on CI	100%	0%	0%
	No Training but CI	100%	0%	0%
Fatick	Participated in the Training	100%	0%	0%
	Extensive Experience on CI	100%	0%	0%
	No Training but IC	82%	9%	9%

Region	Type of Actor	Did you use the climate and weather information you received to conduct your campaign?		
		Yes	No	Not Received
	No Training and No CI	11%	0%	89%
Kaffrine	Participated in the Training	89%	11%	0%
	Extensive Experience on CI	100%	0%	0%
	No Training and No CI	0%	0%	100%
Sample		84%	2%	13%

Source: Author based on ISRA/BAME survey data, 2016.

3. More Information Means More Choices on Crops and Varieties

Climate information has enabled farmers to better orient their agricultural activities, including the choice of crop (48%), the variety to be sown (35%), and what was needed to complete the cycle and the sowing periods (12%). Producers, through their experience, have some knowledge of the crops or varieties that are best suited to the given seasonal forecast. Sometimes they ask agricultural advisors for information. At this point, they can choose to plant more peanuts than another crop, for example. Thus, we note that climatic information allows farmers to implement a strategy in relation to their agro-climatic environment. Indeed, farmers would like to have information on the nature of the rainy season (54%), and therefore its course (seasonal forecast), along with the duration of the season (25%). In addition, they would also like to have daily information on rainfall in order to have better control over resource allocation. Finally, 1% would also like to have information at the beginning of the rainy season (Table 4).

Table 4
Types of Use of Climate Information

Region	Type of actor	Types of use of climate information						
		Crop Selection	Variety Selection	Plot Preparation	Ploughing Period	Sowing/Seeding Period	NPK Application Period	Weeding/ Hoeing Period
Diourbel	Participated in the Training	54%	39%	0%	0%	8%	0%	0%
	Extensive Experience on CI	50%	50%	0%	0%	0%	0%	0%
	No Training but CI	50%	50%	0%	0%	0%	0%	0%
Fatick	Participated in the Training	18%	65%	0%	6%	12%	0%	0%
	Extensive Experience on CI	0%	0%	50%	0%	50%	0%	0%
	No Training but CI	22%	11%	0%	0%	44%	11%	11%
	No Training and No CI	100%	0%	0%	0%	0%	0%	0%
Kaffrine	Participated in the Training	100%	0%	0%	0%	0%	0%	0%
	Extensive Experience on CI	77%	23%	0%	0%	0%	0%	0%
	No Training and No CI	–	–	–	–	–	–	–

Region	**Type of actor**	**Types of use of climate information**						
		Crop Selection	Variety Selection	Plot Preparation	Ploughing Period	Sowing/Seeding Period	NPK Application Period	Weeding/ Hoeing Period
Sample		48%	35%	1%	1%	12%	1%	1%

Source: Author based on ISRA/BAME survey data, 2016.

4. Consent to Pay (WTP) for Climate Information

All farmers in the area have heard of weather and climate information. Almost all (99%) agree with the usefulness of climate information, but 1% of them, and particularly the “no training and no CI” category (11% in Fatick), still doubt the usefulness of this tool. This doubt can be explained by attachments to traditional practices, but also by a lack of information on this tool.

As for the effective use of climate information for agricultural activities, we see the same trend with an affirmative response for the Kaffrine and Diourbel zones. However, in Fatick, 10% of the “no training but IC” category and 55.6% of the “no training and no IC” category claim not to have used weather information in their production. Thus, it would be interesting to know if farmers are willing to spend money to have this information.

5. Experience in Using Weather Information Favors Producers’ WTP

The willingness to pay for weather information is quite ambiguous even though a slight majority (58%) are willing to pay for it (Table 5). However, the category with a large experience in CI is the most willing to pay for weather information, perhaps due to the experience these producers had in using climate information over the years. The “participated in the training” and “no training but IC” categories are also in favor of payment, but a significant portion (between 40 and 45%) remain hesitant to pay.

Table 5
Willingness to Pay for Climate Information

Region	Type of Actor	Are you willing to pay for weather information for your farming operation?	
		Yes	No
Diourbel	Participated in the Training	57.1%	42.9%
	Extensive Experience on CI	75%	25%
	No Training but CI	50%	50%
Fatick	Participated in the Training	58.8%	41.2%
	Extensive Experience on CI	100%	0%
	No Training but CI	50%	50%
	No Training and No CI	56.6%	44.4%
Kaffrine	Participated in the Training	56.6%	44.4%
	Extensive Experience on CI	61.5%	38.5%
	No Training and No CI	0%	100%
Sample		58%	42%

Source: Author based on ISRA/BAME survey data, 2016.

Two main reasons may explain this trend: not knowing payment methods (44%) and lack of means (44%) (Table 5). We also note the weak structuring of farmers' organizations (7%) and others who think they can get the information through their acquaintances (4%) (Table 6).

Table 6
Reasons Given for Not Paying for Climate Information

Region	**Type of Actor**	**Main reasons for not wanting to pay for climate information**			
		Availability of other sources to capture information	Lack of knowledge of payment methods	Lack of resources	Lack of organized structure
Diourbel	Participated in the Training	0%	25%	50%	25%
	Extensive Experience on CI	0%	100%	0%	0%
	No Training but CI	–	–	–	–
Fatick	Participated in the Training	13%	38%	50%	0%
	Extensive Experience on CI	–	–	–	–
	No Training but CI	0%	0%	67%	33%
Kaffrine	No Training and no CI	0%	67%	33%	0%
	Participated in the Training	0%	50%	50%	0%
	Extensive Experience on CI	0%	60%	40%	0%
	No Training and No CI	0%	100%	0%	0%
Sample		4%	44%	44%	7%

Source: Author based on ISRA/BAME survey data, 2016.

Farmers are willing to pay for different products: seasonal forecast, decadal information, daily information, and for agrometeorological advice (Table 7). Respondents in the "extensive CI experience" and "participated in the training" categories are the most willing to pay for all of these products, especially in Kaffrine. Reasons why include the fact that prices fluctuate greatly and this variability is explained by the fact that the service is not well appreciated.

As noted above, the information that is really sought concerns the nature of the rainy season, its duration, and other daily information. The vectors for accessing this information are quite diversified but focus on the latest generation of communication tools (e.g., SMS, email, telephone, television, etc.) and information provided through the sharing workshops. Depending on the area, the actors, and the communication channel selected, the prices offered vary in relation to their income level. Thus, farmers understand the importance of climate information for the proper conduct of their agricultural activities and are willing to invest in this tool to secure their production.

Table 7
Types of Climate Information and Willingness to Pay

Region	Type of Actor	Types of Ready-to-pay Climate Information	Minimum Price	Average Price	Maximum Price
Diourbel	Participated in the Training	Seasonal Forecasts	100	167	280
		Decadal information	100	125	150
		Daily information	50	50	75
		Agro-meteorological advice	100	150	200
	Extensive Experience on CI	Seasonal Forecasts	25	50	70
		Agro-meteorological advice	2000	2500	2500
Fatick	Participated in the Training	Seasonal Forecasts	500	750	750
		Daily information	200	300	500
	Extensive Experience on CI	Seasonal Forecasts	18	20	23
		Daily information	15	20	25
		Agro-meteorological advice	500	500	1000
	No training but CI	Seasonal Forecasts	667	833	1000
		Decadal information	1750	1875	2000

Region	Type of Actor	Types of Ready-to-pay Climate Information	Minimum Price	Average Price	Maximum Price
Kaffrine	No Training and No CI	Daily information	500	600	600
	Participated in the Training	Seasonal Forecasts	1900	2650	4000
		Decadal information	513	765	1025
		Daily information	500	500	1000
		Agro-meteorological advice	750	1000	1500
	Extensive Experience on CI	Seasonal Forecasts	2168	3188	3821
		Decadal information	353	228	541
		Daily information	38	58	58
		Agro-meteorological advice	2365	751	3504
	No Training but CI	Decadal information	1000	1000	1000
	No Training and no CI	Daily information	500	600	600

Source: Author based on ISRA/BAME survey data, 2016.

Conclusion

This chapter aimed to show the benefits of using information systems in decision-making and on agricultural strategies of the farms in the Senegalese Groundnut Basin using surveys conducted in that basin. The methodological approach conducted statistical analysis of variables related to the influence of market and climatic information on production, marketing, and agricultural input investment decisions.

The analyses show that for almost half of the cowpea producers (49%), this information influences their choice of markets. For most cowpea producers (85%), the market information received also influences the decision of when to sell the crop. This allows producers to make trade-offs in time and space.

For the majority of cowpea producers (62%), market information influences their choice of selling price. However, it does not influence the choice of the quantity to sell for most cowpea producers (75%). For more than half of the cowpea producers (56%), market information influences the choice of which crop to grow. In addition, market information influences the choice of plot size and the decision to invest in agricultural inputs for 82% and 94% of cowpea producers respectively.

The analyses show that climate information has enabled various actions to be taken to ensure that agricultural activities run smoothly. The availability of climatic information has made it possible to better orient the choice of crops and the sowing period, as well as the preparation of soil and the period for spreading fertilizer. In addition, the majority (67%) of respondents are accustomed to using climate information, and ANACIM (52%) is the main provider of this information, followed by the radio (6%) and the *Yeugglé* MIS (4%). The use of climate information is generally community-based and is effectively used by 84% of those who have received it. This climatic information allowed farmers to choose the crop to be cultivated (48%), the variety to be grown (35%) in order to complete the cycle, and the sowing periods (12%). Thus, almost all (99%) agree that climate information is useful, but only a small majority (58%) agree to pay for it. The main reasons given were not knowing how to pay (44%) and lack of means (44%).

However, the price of the product is not the only criterion influencing producers' economic decisions. They are also confronted with the risk and uncertainty of markets and environmental factors. Agricultural activity depends on climate, cultivation practices, government policies, and global markets, all of which have a definite impact on agricultural supply in the long and short terms. However, there is no optimal reference situation that agents can use to take measures that will allow them to get closer to that optimal situation. With respect to uncertainty, the producer can seek to: i). transfer it by concluding a purchase or sale contract; ii). limit its effects by choosing several complementary productions, in order to stabilize income through diversification; iii). reduce it by improving knowledge of the environment, by resorting to futures markets for example. (Wade, 2009). Thus, the producer adopts mechanisms that Robison and Barry (1987) describe as managerial.

In terms of recommendations, we propose: an extension of agricultural information systems to all agro-ecological zones. This information system will consider all the information needed by the actors in the value chain (i.e., market information, climatic, and agronomic information). It will also be necessary to promote the establishment of consultative frameworks to discuss information and technologies related to climate change and their repercussions for the development of agro-sylvo pastoral activities (agriculture, livestock and forestry).

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ENDNOTES

[1]*Yeugglé* means to inform in *wolof*.

6. Consumer Willingness to Pay for Millet-based Food Attributes in Niger

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Abstract

This chapter assesses urban consumers' preference for quality attributes of value-added food products derived from cereals. We combine qualitative and quantitative methods to assess the preferences of 205 randomly sampled consumers and derive their willingness to pay for those quality attributes. We account for taste and preference heterogeneity inherent in consumers' responses to a change in quality attributes. Consumers are sensitive to health quality attributes as measured by the expiration date, the presence of a micronutrient, and the product's country of origin. The resulting market demand for quality-improved products suggests the marketing of novel attributes through a promotion strategy that includes quality labeling to improve product differentiation.

Keywords: labeling, expiration date, fortification, choice experiment

Introduction

Several studies show that nutrition and safety information positively affect consumers' food choices, depending on whether they are price conscious or not (Chowdhury et al., 2011; Drichoutis et al., 2005; Lusk and Schroeder, 2004; Nayga et al., 1998). The introduction of new or improved food quality attributes has a primary goal of a market differentiation of the product from competing ones and creates new market segments (Henson & Reardon, 2005; Roy & Srivastava, 2022). Indeed, income growth and relative price changes also induce a gradual shift toward processed foods in developing countries (Barrett et al., 2017). Successful introduction of an improved or a new food product requires a deep understanding of consumers' preferences and valuation of intrinsic and extrinsic attributes. Hence, knowing consumers' willingness-to-pay (WTP) for food attributes is critical to achieve effective policy intervention. Furthermore, it provides information about the market demand of those attributes to food processors for strategic marketing and segmentation (Caswell & Mojduszka, 1996).

Another important consideration is that consumers consider price premiums the most decisive limiting factor cereal products demand in West Africa (Naseem et al., 2013). For example, high premiums combined with limited availability might restrict market growth, especially in populations that need these micronutrients (O'Donovan & McCarthy, 2002). Therefore, WTP estimates can analyze the marketability of new products and develop Pareto-improving public policy where warranted (Van Loo et al., 2011).

Several studies investigated consumers' preferences for food quality attributes in developing countries. For example, biofortification of micronutrients (e.g., zinc, pro-vitamin A, or iron) translates to substantial premiums in Uganda, Ethiopia, and Senegal (Chowdhury et al., 2011). Fiamohe et al. (2015) conducted a study in West Africa on extrinsic and intrinsic characteristics finding that Togolese consumers are willing to pay a premium of up to 46% of the actual price for cleanliness and 53% for whiteness in locally produced rice.

This chapter presents the results of a framed choice experiment to determine the relative values of food product fortification and marketing information. The study assesses consumers' preferences for intrinsic (i.e., the expiration date on products, the dietary composition of iron in food) and extrinsic (i.e., family-friendly promotion and country-of-origin) characteristics of high-quality millet flour-based agglomerated cereal products. This chapter explicitly models consumers' marginal rate of substitution of income for quality attributes, accounting for preference heterogeneity across consumers, using mixed multinomial logit models in both preference and WTP spaces proposed by Train and Weeks (2004) and Scarpa et al. (2008). We applied these models to consumer data elicited from a collective conjoint-based choice experiment conducted in the capital of Niger. Our contribution to the literature and policy debate is twofold. First, in the global debate on the implications of date labeling for food waste, we evaluate consumers' valuation of expiration dates. Second, we assess the relevance of accounting for preference heterogeneity in evaluating consumer valuation of quality attributes. Additionally, we provide empirical evidence for a plausible market-driven micronutrient supply through fortified food products in developing countries.

Choice Experiment Methods

We evaluated a random sample of 205 consumers WTP for quality attributes of value-added cereal food product locally known as Dègué which is an agglomerated food product, similar to couscous, but of a larger diameter.[1] Traditionally it has been marketed as a homogenous food commodity and developed for subsistence purposes. However, some small firms, owned mainly by women, use modern technologies to produce high-quality products, especially in urban areas. Quality characteristics of those products are not made explicit to consumers in a way that can be directly analyzed through market purchases to determine relative demand for these quality attributes. As such, this experiment has been conducted to determine consumers' preferences for selected quality attributes embedded in these food products.

Packages of five hundred grams (500 g) of Dègué with varying quality attributes are the unit of analysis. Because the products with these quality attributes were either new or unavailable in the local market, demand for the attributes was uncertain. Consequently, this study represents a classical use of Choice Experiments (CE) to determine relative preference for the product attributes and estimate the associated marginal WTP (Louviere, 1991). Revealed preference data —groceries or scanner data—often estimate WTP in high or middle-income countries. Such data are not readily available in Niger, where grocery stores with electronic scanning systems are at an early stage of development. Also, Lusk and Schroeder (2004) noted the difficulty of finding survey participants in such studies adding to the challenge of collecting demographic characteristics from each purchaser of

Dèguè in a store setting. It may not be possible to identify market niches by classifying consumers with the same preference structure.

Hence, random participants who were going to, or returning from the market, were recruited on the spot. To include a random factor during sampling, we approached every fifth male or female passer-by with an estimated age between 18 and 65. Following the methods of Demont et al. (2012), whenever we approached a group, we selected a maximum of one participant so that none of the participants knew each other. Subjects were offered 2000 FCFA ($4) cash to participate in "Consumers' willingness to pay for quality attributes of cereal value-added food products," a study conducted in a schoolroom near the market site. We assigned participants a random identification number for anonymity and directed them to the experiment site. One and a half hour sessions occurred once or twice per day, depending on the difficulty of recruiting participants, between July 4 and July 10, 2017. The experiment was conducted in the five districts of Niamey to ensure the spatial representativeness of the sample to the city population.

Prior to the focus group discussion on May 30, 2017, we conducted a literature review and reviewed expert interviews to identify the main drivers of consumer food choices. As a result, ten attributes were selected for the focus group discussion, including: price and brand, food safety, ecological certification, production process, health-related characteristics, and nutritional attributes. Through a series of pre-tests and expert advice, subsequent refinement led to four customized and improved attributes (Figure 1).

Upon arrival at the session, subjects completed a short demographic questionnaire and examined a packaged sample of Dèguè made locally by processors in town without labels. An information sheet and cheap talk script were read aloud, after which subjects responded to a series of eight repeated questions on product choice. Each question or choice set appeared on the board, read aloud in French, and translated into the two major languages of Hausa and Djerma, which are spoken in the town.

Three package options (Figure 2) were presented to the subjects in each set, including a "None of these" option. Subjects were asked to indicate which package was preferred (or none) in each scenario. Package price ranged between 450 FCFA, 500 FCFA, 550 FCFA, and 600 FCFA. During focus group discussions, the price levels were chosen to straddle the range of prices available in the market.

Figure 1

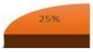
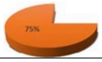
Attribute	Description	Attribute levels			
		1	2	3	4
Limit date of consumption	Limit Date of Consumption (DLC) “Date of Expiration”	No	Yes		
Product Nutritional Content	Highlight the content of the product in Iron relative to the daily value requirement.	0 % of Daily Value	25 % of Daily Value 	75% of Daily Value 	100% of Daily Value 
National origin claim	Highlight the origin of the product and the pride related to the country	None	 Made in Niger		
Family “friendly” product	Whether the image associated with the product Is suitable for all family members	None	 Family		
Product price (per 500g)	The buying price of the product per 500g in FCFA	450	500	550	600

Figure 1 – Attributes and Levels for the Choice Experiment

In this experimental design, there are three options of packages (including none) built using four price levels, micronutrient content levels, country-of-origin declaration, and a modern family image (See Figure 1). Subjects would have to be shown 22 × 22 × 22 × 42 × 42 = 16,384 different choice sets if presented with every package at every combination of price, micronutrient level, date of expiration, the origin of the product, and family image. An orthogonal fractional of the full factorial design was generated to reduce the number of questions respondents had to answer. In this design, attributes are uncorrelated between packages. The resulting design consisted of 64 sets of scenarios or choice sets, which were then formed into eight blocks of eight choice sets each. An example choice card is presented in Figure 2.

Figure 2

Attribute	Package A	Package B	Package C
Expiration Date	Yes	No	None
Origin	 Made in Niger		
Image			
Micronutrient: Iron	0 % Daily Value	 75% Daily Value	
Price	550	450	
I would Choose *(Check (√) only one choice)*	☐	☐	☐
Rank			

Figure 2 – Sample Choice Set Presented to Participants

Empirical Methodology

Consider a consumer's utility maximization problem under a budget constraint, with an exogeneous level of a good's quality (q). In the case of agribusiness applications, q is most applicable as a measurement or index of a good's quality (Lusk & Hudson, 2004). The consumer chooses the market good (x_m) that maximizes utility, producing the traditional Marshallian demand curve $x_m(p, y, q)$, where p is the market price of the good and y is income. The resulting indirect utility function is $V(p, y, q)$. Now assume that an agribusiness food processor and retailer consider improving the quality of an existing product from q_0 to q_1. A measurement of the consumer's value on this improvement can be derived by determining the magnitude of a WTP such that the following equality holds: $V(p, y - WTP, q_1) = V(p, y, q_0)$. WTP measurement is often conducted using a Choice Experiment (CE) composed of hypothetical sets of questions for novel products or attributes without an existing market.

In each CE question or choice set, respondents had to choose between two packages and the "none of these" option. Let V_{njt} be the deterministic component of n^{th} consumer's utility of choosing package *j* at choice occasion *t*. For simplicity, the utility derived from alternative *j* chosen by consumer *n* at choice occasion *t* is separable in *price* and quality (non-price attributes) x_{njt},:

$$U_{njt} = -\alpha_n price_{njt} + \beta_n x_{njt} + u_{njt}, \quad j=A, B, C \qquad (1)$$

where scalar α_n is the price coefficient, and vector β_n represents the marginal utility associated with the quality attributes. Both sets of parameters vary randomly by consumer n = 1, ..., N., u_{njt} is the stochastic component of utility that is Gumbel distributed with a variance $Var(u_{njt}) = \mu_n^2(\pi^2/6)$, and μ_n is the scale parameter for consumer *n*. Train and Weeks (2004) demonstrated that the scale of utility is irrelevant to consumer behavior. The utility can then be divided by μ_n without changing behavior, which results in an *i. i. d.* new error term ε_{njt} of type-one extreme value, distributed with constant variance $(\pi^2/6)$:

$$U_{njt} = \lambda_n price_{njt} + c'_n x_{njt} + \varepsilon_{njt} \qquad (2)$$

where $\lambda_n = -\alpha_n/\mu_n$ and $c_n = \beta_n/\mu_n$. Train and Weeks (2004) call this specification the "utility model in preference space." It can be seen from Equation 2 that λ_n and c_n are correlated unless the scale parameter does not vary over individuals since μ_n appears in the denominator in both expressions. Specifying the coefficients to be independent implies that the random term is homoscedastic, which may not be a realistic assumption. By using the fact that the WTP is given by $w_n = -\beta_n/\alpha_n = c_n/\lambda_n$, Equation 2 can be written as:

$$U_{njt} = \lambda_n[price_{njt} + w_n x_{njt}] + \varepsilon_{njt} \qquad (3)$$

This model is what Train and Weeks (2004) and Scarpa et al. (2008) called "utility in WTP space." Models (2) and (3) are, of course, behaviorally equivalent. However, the key thing to note is that a standard assumption regarding λ_n and c_n in the preference space (equation 2) can lead to an unusual distribution for the WTP. For instance, if the price coefficient has any positive density setting over zero, then the distribution of this ratio has undefined moments (Daly et al., 2012). In addition, if λ_n and c_n are both normally distributed, it implies that w_n is a ratio of two normal distributions, which does not have defined moments. This choice of distribution is unlikely if we were to specify the distribution for the WTP directly as we did in the

WTP space model. We estimated the coefficients in the preference space and WTP space models using maximum-simulated likelihood. We followed Scarpa et al. (2008) as described in the next section.

Estimation Method

This section presents the method of estimating coefficients in equations 2 and 3. We adopt the mixed logit specification under repeated choices by consumers with continuous taste known as panel mixed logit developed by Revelt and Train (1998). In our study, consumer *n* faces a choice among j alternatives (package A, Package B, or C-Neither) in each T choice situation. For the simplicity of the exposition, let θ_n represent the random terms entering utility, which are λ_n and c_n in the preference space (equation (2)) and λ_n and w_n in the WTP space (equation (3)).

Consumer *n* chooses package *j* in period *t* if $U_{njt} \geq U_{nkt}\ \forall j \neq k$. Denote the consumer's chosen alternative in choice occasion t as y_{nt}. The consumer sequence of choice over the T_n choice occasions t as $yn = \langle y_{n1},\ldots,y_{nTn}\rangle$. Hence, conditional on θ_n, consumer's n sequence of choice probability is:

$$L(Y_n|\theta_n) = \Pi_{t=1}^{t=8} \frac{exp(\theta_n z_{njt})}{\sum_{k=1}^{3} exp(\theta_n z_{nkt})} \qquad (4)$$

The unconditional probability of consumer *n*'s sequence of choice is the integral over all values of θ_n weighted by its density

$$P_n(Y_n|\Omega^*) = \int L(y_n|\theta_n) f(\theta_n|\Omega^*) d\theta_n \qquad (5)$$

where *f*(.) is the density of θ_n, which depends on parameters Ω* to be estimated. The goal is to estimate Ω*, which is the population parameter that describes the distribution of individual parameters (Revelt & Train, 1998) using the log-likelihood function $LL(\Omega) = \sum_n \ln P_n(Y_n|\Omega^*)$. The exact maximum likelihood is not possible since the integral of equation (4) cannot be calculated analytically. Hence $P_n(Y_n|\Omega^*)$ is approximated via simulation. The simulation is done by first drawing a θ^r values of θ_n from $f(\theta_n|\Omega^*)$ with Ω^* fixed at a given initial value.

With a given R number of draws: $\mathrm{P}_n^{\mu}\widehat{(Y_n|}\Omega^*) = \frac{1}{R}\sum_{r=1}^{R} L_{n,j}(\theta^r)$ is an unbiased estimator of $P_n(Y_n|\Omega^*)$. Finally, substitute $\widehat{\mathrm{P}_n^{\mu}}$ into the Log-Likelihood function to yield the simulated Log-Likelihood: $SLL = \sum_n \sum_j d_{njt} ln \mathrm{P}_n^{\mu}\widehat{(y_n|}\Omega^*)$ where d_{njt} = 1 if consumer n chooses alternative *j* at choice situation *t*.

In this study, we first estimated a range of models in both preference and WTP space and afterward selected the "best" model among a set of non-nested models using the Akaike likelihood Ratio Index proposed by Ben-Akiva and Swait (1986). We compute Akaike Likelihood Ratio Index (ALRI) for each model to measure how well the models best fit the data. We chose the model with significantly higher ALRI1.

RESULTS

1. Descriptive Statistics

Table 1 presents sampled consumer distributions concerning gender, age groups, marital status, education, and their corresponding average household monthly expenditure group. The table also compares our sample structure with our target population at the city and national levels, even though our survey was exclusively in Niamey. These comparisons were chosen because the generalization of the findings will critically depend on the sample representativity of the targeted population: consumers between 18- and 60-years old living in the city of Niamey. Our sample distribution was also compared to the national level to understand similarities and differences between the sample and the target population. Specifically, our sample is stratified concerning the town districts and has similar spatial distributions as our targeted population. Overall, the randomization appeared to be well-conducted since our sample is relatively representative of consumers in Niamey. In addition, this similarity is extended to the national level despite some noticeable dissimilarities for education and marital status variables. When the city sample is compared to the national level population, consumers without any level of education are underrepresented in our sample.

Specifically, 17.5% of our sample had no education, which is low compared to the 47.7% for the city of Niamey and 73.4% for the national level. The reticence in participating in the survey may concern a lack of trust in the recruiter and the delivered message. Finally, a noticeable fact is a discrepancy about the top and bottom classes of participants' household food expenditures in Niamey. The low-income class is overrepresented, while the higher class is underrepresented in our sample. This situation is probably due to the incentives we proposed (US $4), which is 25% of the average monthly food expenditure in our sample. This may be a significant incentive for the lower-income group, but not for the higher-income group.

Like Niamey and the national level, our typical consumer is relatively young, between 18 and 34 years old, married, with a monthly food expenditure of fewer than 12,000 FCFA (USD 22), and lives in a household with 6-8 members. Specifically, about two-thirds of the participants have a monthly food expenditure level of fewer than 16,000 FCFA (USD 29).[2]

Regarding food poverty, 36.5% of the participants live in households with a per capita food expenditure lower than the town threshold, calculated to be 9,925 FCFA (USD 18) per capita per month by official statistical services (INS, 2011). Comparatively, the chronic food insecurity estimated by the National Institute of Statistics was 33.5%.

Table 1
Average Sample Socioeconomic and Demographic Characteristics by Class

	Sample	**Niamey**	**Diff. Sample-Naimey**[a]	**t-stat**	**National**	**Diff. Sample National**[b]	**t-stat**
	(1)	(2)	(3)		(4)	(5)	
Gender							
Male	42.27	48.91	-6.64***	-2.70	49.37	-7.1***	2.60
Female	57.73	51.09	-8.82***	-2.70	50.63	-8.36***	2.60
Age Group							
18-24 years	25.26	27.27	-2.01*	-1.92	23.99	1.27	-0.86
25-34 years	27.32	29.74	-2.42*	-.032	28.12	-0.8	0.16
35-44 years	24.23	17.5	6.73*	1.91	18.35	5.88	1.64
45-54 years	14.95	12.99	1.96	0.40	13.87	1.08	0.07
55-64 years	6.19	7.81	-1.62	0.30	9.06	-2.87	-0.30
65 years or +	2.06	4.99	-2.93	0.31	6.61	-4.55	-0.84
Marital Status							
Single	33.51	35.11	-1.6	-0.56	19.26	14.25***	4.77
Married	60.82	55.68	5.14	1.51	71.78	-10.96***	-2.87
Divorced	4.12	3.8	0.32	0.09	2.64	1.48***	-15.37
Widow	1.55	5.37	-3.82*	-1.74	6.01	-4.46***	-60.37

	Sample	Niamey	Diff. Sample-Naimey[a]	t-stat	National	Diff. Sample National[b]	t-stat
	(1)	(2)	(3)		(4)	(5)	
Education							
None	17.53	47.7	-30.17***	-10.62	73.41	-55.88	-19.64
Primary	24.23	22.04	2.19***	-26.40	13.47	10.76	-15.58
Junior High	24.23	14.54	9.69***	2.52	7.43	16.8	5.06
Senior High	10.31	2.72	7.59**	2.84	1.07	9.24	7.16
Professional	5.67	4.5	1.17	-1.38	1.91	3.76	3.93
Koranic	8.25	0.8	7.45	-0.39	0.23	8.02	3.11
Higher Education	8.25	7.6	0.65	0.40	2.42	5.83	2.87
Other	1.53	0.1	1.43***	3.39	0.06	1.47	3.59
Per capita monthly household food expenditure (FCFA)[c]							
Less than 4000	10.4	0.66	9.74	0.40	1.89	8.51***	2.77
4000-6000	10.98	1.76	9.22**	2.00	7.47	3.51	-1.46
6000-8000	12.14	5.29	6.85	1.50	13.30	-1.16**	-2.33
8000-10000	12.14	9.14	3.00	0.43	16.39	-4.25*	-2.77
10000-12000	4.62	9.03	-4.41	0.71	14.78	-10.16*	-1.76
12000-14000	6.94	10.46	-3.52	0.32	12.53	-5.59	-0.54

	Sample	Niamey	Diff. Sample-Naimey[a]	t-stat	National	Diff. Sample National[b]	t-stat
	(1)	(2)	(3)		(4)	(5)	
14000-16000	9.25	11.23	-1.98**	2.33	9.15	0.1	3.05
More than 16000	33.53	52.42	-18.89***		24.48	9.05	1.38

Note. *** $p<0.01$, **$p<0.05$, * $p<0.1$, with p the p-value of the one-sample t-test. [a] is the difference between Niamey and the sample estimate, [b] represents the difference between national and the sample estimate, [c] Per capita monthly household food expenditure (FCFA). Niamey and National level information are official statistics by the National Institute of Statistics.

2. Estimated Model Parameters

In this section, we compare results from the estimated choice models. The models are estimated using maximum simulated likelihood with 1000 Halton draws. Table 2 presents estimation results for both preference and WTP spaces models as discussed in the methodology. In both spaces, models are estimated across random utility coefficients. The first two columns are the estimation results of models in preference space (Equation 2) without and with the correlation between estimated coefficients, respectively. The two last columns display estimation results of models in the WTP space, again without and with the correlation between the estimated coefficients.

Table 2

Estimation Results of Utility Parameters in Preference and WTP Space With and Without Correlation Among Coefficients

	Preference Space		**WTP Space**	
	Without correlation	**With correlation**	**Without correlation**	**With correlation**
	(1)	(2)	(3)	(4)
Price	-0.006***	-0.006***	-5.090***	-4.930***
	(0.0005)	(0.000551)	(0.0986)	(0.0896)
Expiration date	1.638***	1.709***	276.2***	242.6***
	(0.108)	(0.123)	(20.40)	(17.81)
Micronutrient (less than 25 % of DR)	0.387***	0.400***	65.20***	63.60***
	(0.0461)	(0.0526)	(7.789)	(8.428)
Product origin	0.752***	0.737***	122.0***	138.3***
	(0.107)	(0.121)	(15.12)	(16.61)
Family image	0.129	0.0908	19.1	41.07**
	(0.109)	(0.122)	(18.12)	(18.60)

	Preference Space		WTP Space	
	Without correlation	With correlation	Without correlation	With correlation
	(1)	(2)	(3)	(4)
L* at Convergence	-1136.574	-1104.79	-1135.927	-1093.286
Akaike Information Criterion	2299.148	2265.58	2299.853	2256.572
ρj2	-1.24	-1.18	-1.24	-1.16
Pr (ρ42-ρj2)	0	0	0	a
Pr (ρ22-ρj2)	0	a	0	b
Observations	4272	4272	4272	4272

Note. Standard errors in parentheses, *** $p<0.01$, **$p<0.05$, * $p<0.1$, [a] Probabilities are not calculated because of the auto-comparison. [b] The statistics are not computed because ρ22-ρ42 is negative in this case.

Table 3
Marginal Willingness to Pay for All Consumers by Gender and Income Classes in FCFA Using Utility Model in WTP Space

	Observation	Expiration Date	Micronutrient	Origin	Family Image
All Classes	4272	242.6***	63.60***	138.3***	41.07**
		(17.81)	(8.428)	(16.61)	(18.60)
Gender					
Male	2,520	203.4***	62.24***	147.8***	44.53*
		(19.05)	(10.39)	(20.01)	(23.52)
Female	1,752	317.4***	70.82***	132.4***	49.69
		(40.31)	(16.17)	(28.66)	(35.92)
Monthly Income Class[a]					
Less than 60	888	297.6***	32.40*	145.2***	66.29
		(40.51)	(17.63)	(33.89)	(44.67)
60-120	1368	226.2***	55.05***	203.3***	92.84*
		(46.50)	(19.22)	(45.11)	(51.36)
More than 120	2,016	225.2***	84.89***	104.0***	30.75

	Observation	Expiration Date	Micronutrient	Origin	Family Image
		(24.08)	(12.17)	(22.20)	(24.07)
Age					
Less than 28 years old	1,704	249.8***	41.08***	114.7***	28.05
		(21.71)	(10.54)	(20.46)	(23.10)
28-38 years old	1,104	221.9***	89.24***	151.4***	77.59**
		(18.38)	(10.78)	(30.60)	(35.44)
More than 38 years old	1,464	266.7***	51.34***	185.1***	44.61
(35.42) (15.64) (32.04) (40.10)					

Note. Standard errors in parentheses, *** $p < 0.01$, $**$ $p < 0.05$, * $p < 0.1$, with p the $p-value$. ^{a}Income class in thousands of FCFA

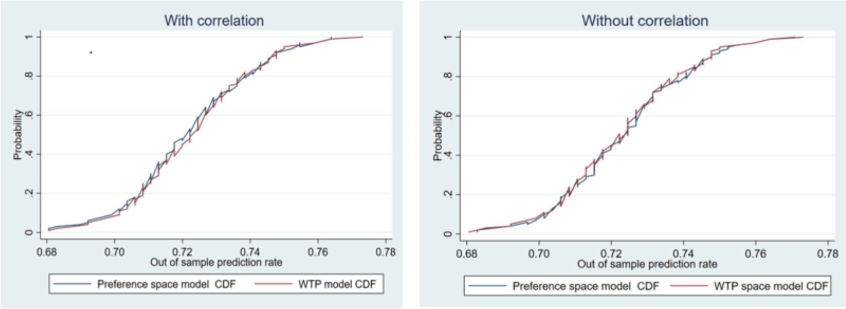
The fit of alternative models of heterogeneity was compared using the Akaike Likelihood Ratio Index because the models estimated are non-nested. In addition, based on this index, a test procedure developed by Ben-Akiva and Swait (1986) was implemented to test the statistical difference of fit between models. The general result is that the model in WTP space with correlation outperforms all others because the probability of incorrectly specified functional form is almost equal to zero, as shown in the lower panel of Table 3. The result strongly suggests the suitability of its structure in explaining consumers' preferences in our sample case and is the basis of subsequent model interpretation. Also, the fact that preference heterogeneity exists is evident by the improvement in the likelihood of the model with random parameters from that with fixed random parameters. Appendix A provides details on the model selection procedure.

3. Robustness Analysis

We further test model performance by bifurcating the total sample into two subsets containing 80 and 20 percent of the sample. We drew one hundred iterations with replacement and models estimated using 80 percent of the sample. The resulting parameters predicted the results for the 20 percent held aside. Then we compared the predicted choice with the actual choice to calculate the out-of-sample prediction success rate. We did this to test the model's predictive ability and to determine a preferred model based on comparing success rates.

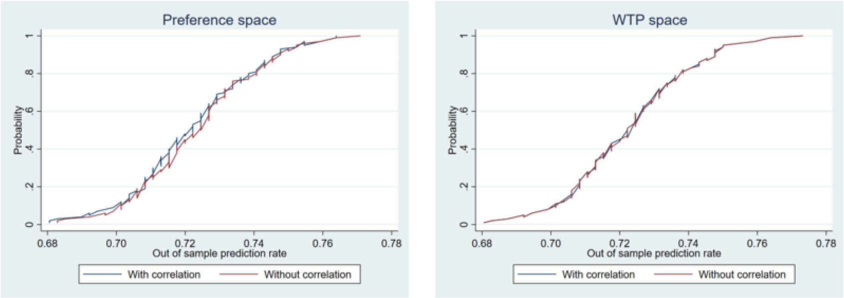
The cumulative probability distribution curves allowed us to illustrate the distribution of correct predictions for the out-of-sample selection for each of the four models. These results are presented in figure 3. A distribution to the right indicates a higher prediction rate for a given probability. We used these tests to determine whether models with correlation (or not) better predict choice and whether models in preference space out predict those in willingness-to-pay space. Overall, models have had little difference in terms of predictive power since the prediction rate is around 74 percent for all four models; however, those with a correlation between coefficients have had a slightly higher success rate (Table D.1). As a result, models equally perform well in an out-of-sample setting. No curve first-order or second-order dominates another, indicating that no model better predicts the out-of-sample choice.

Figure 3



(a) With correlation between variables

(b) Without correlation between variables



(c) Preference space models

(d) WTP space models

Figure 3 – Cumulative Distribution Functions (CDF) of Out of Sample Prediction Success Rates

Figure 4 presents the posterior distributions of parameter estimates. These graphs emphasize the range of heterogeneity of consumer valuation of the product's intrinsic and extrinsic traits under alternative specifications. Since there are interesting spread and multimodal distributions, we attempt to explain these phenomena by disaggregating models into market segments to enhance understanding of the robustness of these models.

Figures 4a-4e Individual Posterior Means Distributions of Marginal WTPs Across Sample Respondents

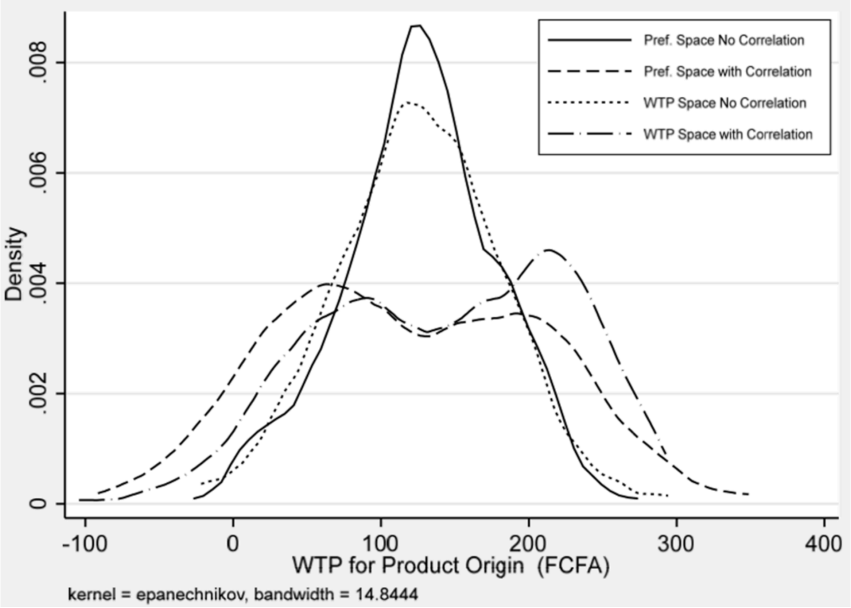


Figure 4a Distributions of WTP for Product Origin for estimated models

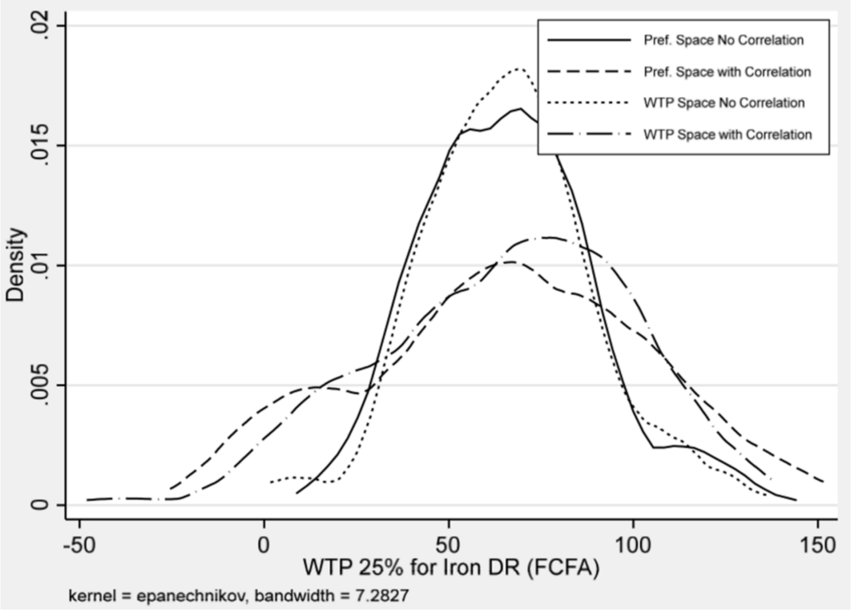


Figure 4b Distributions of WTP for Micronutrient for estimated models

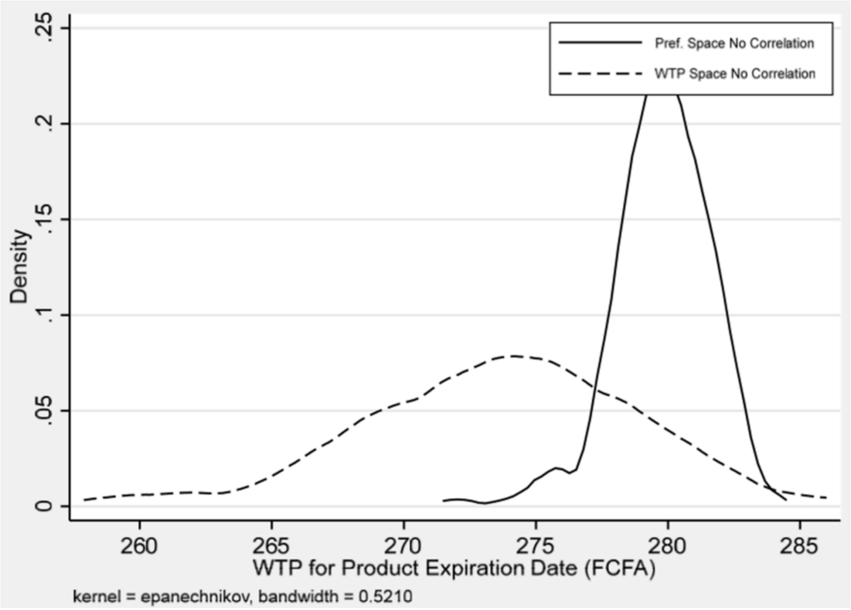


Figure 4c Distributions of WTP for expiration date in both WTP and preference spaces without correlation

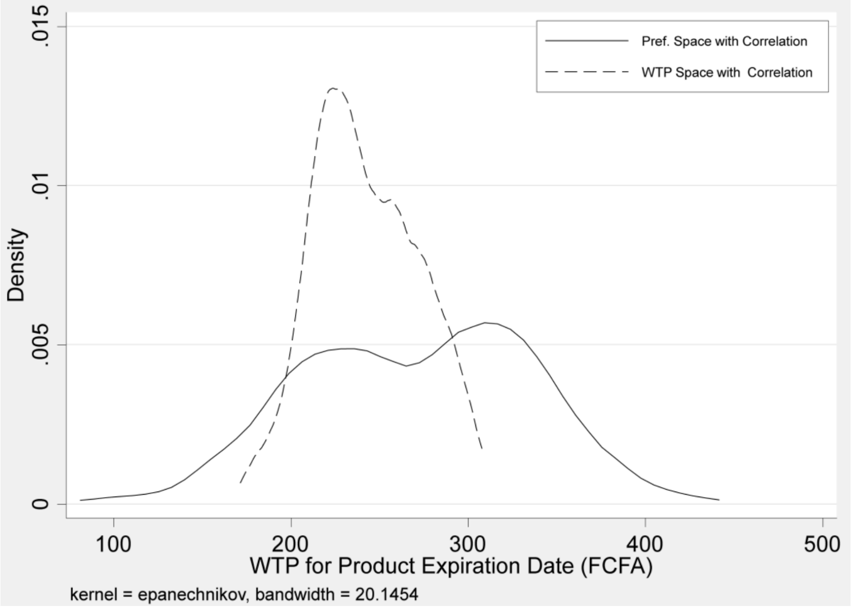


Figure 4d Distributions of WTP for expiration date in both WTP and preference spaces with correlation

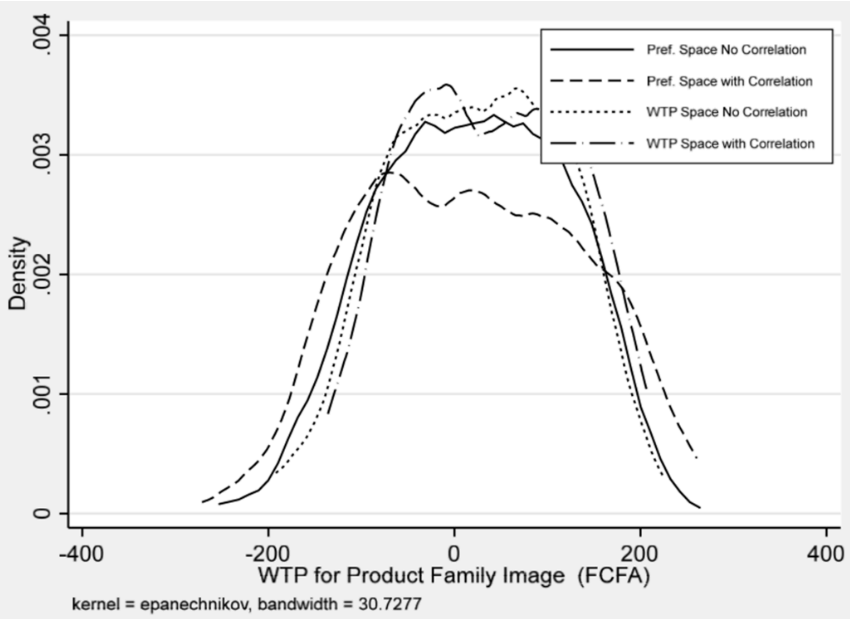


Figure 4e Distributions of WTP for Family Image

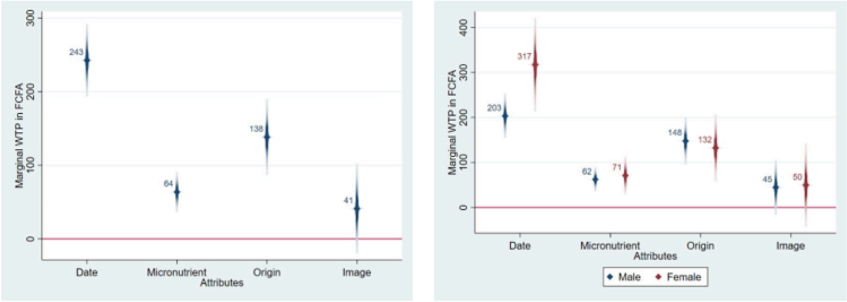
4. Parameter Interpretation and Heterogeneity

All models produced reasonable estimates. The price coefficient is negative, while consumers strongly prefer the expiration date, micronutrient information, and the product's origin. The family image attribute is less critical, although significant. Also, all standard deviations associated with the marginal utilities of attributes are statistically significant at the one percent level, denoting significant preference heterogeneity of consumers concerning attributes. The expiration date, which informs consumers about a product's safety for consumption, increases utility by 1.7 (Column 3). As a result, consumers are willing to pay a premium of 242.6 FCFA for this attribute or information. Initially, the result of 242.6 FCFA seemed to be an implausibly large value since it is roughly 1/3 of the average producer price of the product. Nevertheless, this high value may reveal a consumer's WTP to avoid expenditure on an outdated and unhealthy product. Several studies highlight this strong social desirability of food safety and calls for labelling policy (Liu et al., 2020; Wongprawmas & Canavari, 2017).

The second-most important attribute is micronutrients—the percentage of daily iron requirements or daily value—needed by a human body. The willingness to pay for 25% of the Recommended Dietary Allowance (RDA) of iron is 65 FCFA. Since micronutrients have three levels, WTP for one additional daily requirement level will be linear because our experimental design does not allow for estimating nonlinear effect by integrating dummy variables representing each level. As a result, the willingness to pay for 50%, 75%, and 100% of daily requirements could be estimated as equal to 127 FCFA, 191 FCFA, and 254 FCFA, respectively. Nevertheless, 25% of RDA for 500g of the product is a technological threshold since iron taste is distinguishable above that level, possibly confounding consumer taste and preference.

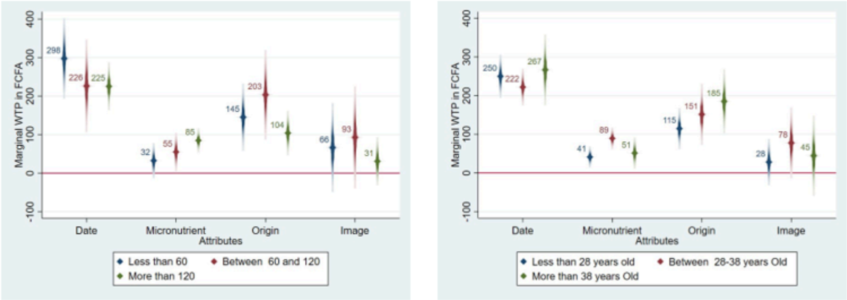
Table 3 and Figure 5 present the marginal WTP for attributes by income classes, and gender, using the utility model in WTP space with the correlation between the marginal utility of attributes. The product's origin is the third attribute consumers strongly prefer. They are willing to pay a premium of 138 FCFA for the product to be made in their country rather than an uncertain place of origin. Women have a strong preference for iron content and the product's expiration date, making them more inclined to pay a higher premium for those attributes. This situation is not surprising because the team nutritionist highlighted the benefit for pregnant and lactating women, and their babies, in the "Cheap Talk Information" given to the participants.

Figure 5



(a) WTP for all Sample

(b) WTP by Gender



(c) WTP by Income Group

(d) WTP by age Group

Figure 5 – Marginal Willingness to Pay for All consumers by Gender and Income Classes in FCFA

Men strongly prefer "*Made in Niger*" and the expiration date, which translates to higher WTP than women. Also, younger consumers are even more ethnocentric than older ones based on their willingness to pay a higher premium for products that carry an image of the Nigerien flag. The willingness to pay for the expiration date is higher for low-income classes and lower for higher-income classes. This finding suggests that risk-averse consumers are willing to pay a higher premium to purchase a product with a more certain quality as defined by the expiration date in WTP space.

Finally, consistent with Bennett's law on the relationship between income and food quality, WTP for micronutrients is significantly higher for higher-income classes of consumers. Indeed, Bennett's law reflects the seemingly universal desire for variety in diet and diversification towards higher quality.

Discussion and Conclusion

Our study focuses on urban consumers in one of the poorest nations in the world. The hypothetical market setting provides information on a range of intrinsic and extrinsic attributes of the food product. Our experiment's design provided signals to consumers on product freshness, as described by the date of expiration, nutritional content, as described by the micronutrient density, the national origin of the product, and family friendliness as described by the family image. Specifically, we inferred consumer demand for product safety through a statistically significant WTP for a product that bears a date of expiration compared to a product that does not have such information. In these treatments, consumers showed a strong preference for the quality attributes compared to the situations where they were uncertain on attributes. Also, consumers strongly prefer products made in their home country.

These results reveal how consumers may react when they are certain about product information when making food choices. This finding indicates the value of transforming credence attributes into search attributes through labeling. The uncertainty reduction drives a higher willingness to pay for product-related attributes. Furthermore, consumers are willing to pay a price premium for iron fortification. These results are consistent with theoretical predictions derived by Falconi and Row (1990) in their study on the economics of food safety. They show that consumers' beliefs, the certainty of beliefs, and the presence of information (signals), are important determinants of demand for goods as the demand for health drives them.

The attributes and the information provided to participants enhanced those beliefs. In addition, the effectiveness of how information is supplied to consumers has been crucial on consumers' WTP. For example, the low level of micronutrient WTP may be related to consumer-limited knowledge of its health benefit. Consumers widely understand the date of expiration or product origin, which is not the case with micronutrients. Hence, participants may be uncertain about any associated health benefit. Aside from these results, findings are heterogeneous across socioeconomic characteristics, such as gender and income class, which segments the market.

Because market demand is high for health-related attributes such as date of expiration, public policy could be undertaken to create an enabling environment for the supply of such attributes. This policy could first sensitize food processors on the economic benefit of following quality standards and informing consumers on those attributes. This information could be provided to consumers using harmonized and high-quality labels and packaging. High-quality labels are critical in developing consumer trust in the claimed attributes. Furthermore, governments could set guidelines on the type of label that food processors should adopt. Several countries already implement such guidelines in West Africa following FAO and WHO (2010) Codex Alimentarius Commission standards.

In addition, our study suggests that micronutrient demand is higher in wealthier income classes and for women. This finding is consistent with Abdulai and Aubert (2004), who found that in Tanzania, the diets of high-income households were richer in all micro-and macronutrients. Likewise, Ecker and Qaim (2011) generally found that higher household incomes were associated with a more diversified diet in Malawi as measured by the number of different food items consumed.

Our findings suggest that micronutrient demand, especially by women and higher-income classes, in addition to necessary policies, may reduce malnutrition. Those critically in need of such micronutrients are less willing to pay for them mainly because of financial constraints and a lack of information on short and long-term health benefits. Government intervention may be necessary to achieve the optimal provision of such attributes. This kind of intervention could target those most in need, such as women in low-income classes. However, this approach could be costly for the entire population, mainly when based on income. Indeed, such an intervention would require records of all consumers, ultimately deciding who could benefit from the intervention or who could not. Instead of income targeting, gender targeting seems easier to implement and could have the highest return per dollar invested because pregnant and non-pregnant women of childbearing age are the most in need of iron.

Finally, our study found that consumers are likely to be ethnocentric, especially younger consumers, when purchasing processed food products. This is consistent with findings by Jin et al. (2015) in their study on consumers' preference for a product image representing a country of origin.

One explanation of this result is that with increased globalization and economic development, consumers in low-income countries may have realized that locally produced products are becoming increasingly competitive with imported products. This finding is important for food processors from both high and low-income nations because they have the opportunity to exploit and support the country associated with their companies. Therefore, such research remains of significant relevance to international agribusiness (Chabowski et al., 2013).

This study has some limitations that could be considered in future research. First, the quality issue of alternatives in each choice set is essential for avoiding any problem of price endogeneity. For example, a high price of an alternative could be interpreted as a signal of a higher quality product. Omitting the quality aspect in choice experiments could cause biased and inconsistent estimates, potentially inducing sign flipping of coefficients, especially the price. One solution is to build the quality aspect in the choice experiment by selecting choice sets for which price will be positively correlated with quality. In addition, to better manage the choice experiment, especially in developing countries, it may be helpful to have fewer attributes, and limited levels since the number of choice sets could impose power requirements of a larger sample size to detect effects.

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Appendix A. Model Selection Test Procedure

In order to test the appropriateness of alternative specifications, we applied the test on non-nested choice models, which was based on the AIC proposed by Ben-Akiva and Swait (1986). The test proceeded as follows. Assume that there are two models (model 1 and model 2). Model 1 explains choices using K_1 variables and model 2 explains the same choices using K_2 variables. Assume that the models are different either by their functional form or by the number of variables. The fitness measured is defined as follows:

$$\rho_j^2 = 1 - \frac{L_j - K_j}{L(0)}$$

where L_j is the log (simulated) likelihood for model $j = 1,2$. The denominator $L(0)$ is the log-likelihood for a model—multinomial logit in our case—with constant only. Under the null hypothesis that model 2 is the true model, its fitness measure will be higher. More importantly, the difference between the two fitness measures of both models is:

$$Pr(|\bar{\rho}_2^2 - \bar{\rho}_1^2 > Z) \leq \Phi(-\sqrt{-2ZL(0)})$$

where Z is the difference of the fitness measures between models. This probability was calculated for all the pairwise combinations of models 2 and 3 estimated with and without correlation. Using the above definition, we calculated that the probability that model 2 under correlation of the coefficients is incorrectly specified functional form is almost equal to zero, as shown in Table 2.

Appendix B. Survey Materials

Appendix B.1. Questions on Choice Experiment

Imagine you are purchasing a package of Dègué at your local store or market. You can choose between two packages of Dègué that Package A and B. Package A has a date of expiration on it so that you know if it is expired or not. Package B did not have this information that is you do not know if it is expired or not. In addition, on package A has a Family picture on while package B does not.

Package A has zero percent of iron daily requirement in that is it does not contain iron micronutrient to satisfy your body daily requirement. By contrast, Package B contains iron that represents 75% (three quarters) of your body daily requirement. But to have Package A you must pay 550FCFA and to have package B you must pay 450. If you choose package A, check the corresponding box; if you decide to choose package B check its corresponding Box. If you do not prefer package A nor B then check the box corresponding to package C.

Appendix B.2. Information on Micronutrient (Iron)

Iron is important and effects red cell production in quantity and quality, the productivity that comes from having good quality blood, the relationship of a healthy pregnant woman to have a healthy baby, role in the prevention of anemia allows the brain to function properly, allows a good growth and learning skills of the child, prevent certain diseases of the liver and pancreas, etc. Without enough iron, your body can't produce enough of a substance in red blood cells that enables them to carry oxygen. As a result, iron deficiency anemia may leave you with the following symptoms: extreme fatigue, weakness, pale skin, chest pain, fast heartbeat or shortness of breath, cold hands and feet, headache, dizziness or light-headedness, poor appetite, especially in infants and children with iron deficiency anemia. One of the causes of a lack of iron is in your diet. Your body regularly gets iron from the foods you eat. If you consume too little iron, your body can become iron deficient over time. Examples of iron-rich foods include meat, eggs, leafy green vegetables, and iron-fortified foods. For proper growth and development, infants and children also need iron from their diets. Women, infants, and children are at greater risk of iron deficiency anemia. Infants, especially those who were low birth weight or born prematurely, who don't get enough iron from breast milk or formula, may be at risk of iron deficiency. Children need extra iron during growth spurts. If your child isn't eating a healthy, varied diet, he or she may be at risk of anemia.

Appendix B.3. Cheap Talk Script

We are here today to conduct a study on your preferences for millet products. In particular, we want to know how you will react if we give you information on the Dègue̊. We will give you information about two packets of Dèguè and ask you what you will choose. Your answers will be anonymous. At the end of the study, you will be paid an amount of 2000 FCFA for your time.

In addition, the information we gather from this study will be very useful in designing an appropriate labeling and promotion strategy that will improve the sales of women producing this product and also the nutrition of the population. Therefore, it is important that you understand the experience and think carefully before making your answers. In a recent study, several different groups of people were asked whether they would purchase a new food product similar to the one you are about to be asked about. This purchase was hypothetical for these people, as it will be for you. No one actually had to pay money when they indicated a particular preference. The results of this study were that over 80% of people said they would buy the new food. However, when a store actually put the same new food on their shelf, but where payment was real and people really did have to pay money if they decided to purchase the new food, the results were that only 43% of people actually bought the new food. That's quite a difference, isn't it? We call this "hypothetical bias." Hypothetical bias is the difference that we continually see in the way people respond to hypothetical purchase questions as compared to real situations.

Why this is so? In my opinion when you go to the market and wants to buy a product, you have a limited budget to make purchases for you or your household. You really think twice before spending your money, so you don't waste your money buying something that you or your household doesn't need. This is what is happening in the real life. But in the hypothetical life you may think that you really don't lose money or since you don't have to eat the product you are more inclined to make a decision that may not represents what you will do in real market. So, if I were in your place, I would ask myself: if I was really shopping at the local store or market and I had X FCFA to purchase a package of Dèguè, do I really want to spend X FCFA to have package A or Y to have package B? If the answer is yes in either of the cases, check the corresponding box and left blank the other cases. If the answer is no in both of the cases, *check the last box. In any case, I ask you to respond to each of the following purchase questions just exactly as you would if you were really in a local store or market and were going to face the consequences of your decision: which is to pay money if you decide to buy a food.*

Appendix C. Estimation outputs

Table C.1.
Cholesky Matrix from MSL Estimates in Preference Space

	Expiration Date	**Micronutrient**	**Origin**	**Family Image**
Expiration Date	0.811*** (0.139)			
Micronutrient (25 % of DR)	-0.595*** (0.158)	0.207** (0.0844)		
Origin	-0.0457 (0.213)	0.0904 (0.153)	0.196 (0.188)	
Family Image	0.178 (0.654)	0.240 (0.149)	-0.973*** (0.192)	-0.105 (0.534)

Standard errors in parentheses, *** p < 0.01, * * p < 0.05, * p < 0.1, with p the p − value.

Table C.2.
Cholesky Matrix from MSL Estimates in WTP Space

Parameter	**ln(λn)**	**Expiration Date**	**Micronutrient**	**Origin**	**Family Image**
ln(λn)	-116.5*** (19.95)				
Expiration Date	41.38* (21.69)	-33.23*** (11.56)			
Micronutrient (25 % of DR)	3.163 (27.68)	0.438*** (0.105)	-25.73 (21.30)		
Origin	1.407 (16.65)	-82.36*** (31.01)	0.291** (0.134)	40.46*** (10.92)	
Family Image	-85.62*** (30.37)	0.128 (0.131)	-42.21 (46.82)	0.0163 (0.178)	0.0518 (0.182)

Standard errors in parentheses, *** p < 0.01, ** p < 0.05, * p < 0.1

Appendix D. Model robustness check using out of sample prediction rate

Table D.1.
Models' Out-of-Sample Performance

	Without correlation		**With Correlation**	
	Preference space	**WTP space**	**Preference space**	**WTP space**
Out of sample prediction success rate	73.8%	73.8%	74.1%	74.1%
Chi2	146.27	146.27	150.00	146.27
p-value	0.000	0.000	0.000	0.000

ENDNOTES

[1] In some countries, "Dègué" comprises agglomerated cereal and dairy products such as yogurt or sour milk. Our study focuses on the cereal product and none of the other co-products.
[2] The exchange rate of USD 1 in 2017 was 550 FCFA.

PART II

ADVANCED PHENOTYPING AND CROP MODELLING FOR ADAPTATION TO DRYLANDS

7. UAV Method Based on Multispectral Imaging for Field Phenotyping

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Abstract

In many countries, particularly in West Africa, there is a strong social demand for increased cereal production. Responding to this demand involves the improvement of cereal varieties. Modern varietal breeding programs in the sub-region need to establish the relationship between plant genotype and phenotype to select high-yielding stress-tolerant plants and to enhance agricultural production. However, in most cases, accurate phenotyping of large mapping populations is a limiting factor. The Regional Study Centre for the Improvement of Drought Adaptation (CERAAS) has developed a robust drone-based data collection and spatial modelling process to better measure cereal crops' traits for the benefit of plant breeding programs. Herein, we report an unmanned aerial vehicle (UAV) driven crop characteristics analysis throughout the crop cycle. We present a fully automatic pipeline based on a multispectral imaging system for the indirect measurement of agronomic and phenological characters of crops in agricultural field trials. The pipeline is made up of different stages including image acquisition, georeferencing, generation of orthoimages, creation of masks to delimit individual plots, and calculation of proxies. The incorporation of the UAV into agricultural field experiments has the potential to fast-track the genetic improvement of adaptation to drought.

Keywords: UAV, multispectral, field phenotyping, sorghum

Introduction

If the world's population and food demand continue to grow, food production will need to increase 60% by 2050. It is urgent to develop new strategies to feed future generations. Over the last few decades, many breeding programs have focused on the improvement of major traits for crop varieties such as yield, disease resistance, and resistance to other environmental constraints (Cuenca et al., 2013). Nowadays, breeding methodologies employ innovative digital tools such as artificial intelligence, bioinformatics, genomics, and statistical advances to enable the speedy creation of cultivars (Vardi et al., 2008). A fundamental condition to new breeding methods such as genomic selection is the development of a training population with an exceedingly high genetic diversity (Aleza et al., 2012). Therefore, carrying out large-scale plant phenotyping experiments is critical; the fast and precise collection of phenotypic data is especially important to explore the association between genotypic and phenotypic information.

In Africa, sorghum is the second major staple cereal and constitutes the only viable food for the most food-insecure populations of the world (Hariprasanna & Rakshit, 2016). However, its genetic improvement relies mostly on manual phenotyping. Traditional phenotyping techniques are often expensive, labor-intensive, and time-consuming (Cruz et al., 2017; Luvisi et al., 2016). Using unmanned aerial vehicles (UAV) equipped with sensors has recently been considered as a cost-effective alternative tool for rapid, accurate, non-destructive, and noninvasive high-throughput phenotyping (Pajares, 2015). However, the measurements of plant traits using UAVs are carried out through vegetation indices obtained by image processing. Many studies demonstrated the efficient use of UAV to monitor plant biomass (Lussem et al., 2019), crop health status, nitrogen content, plant water need estimates (Romero et al., 2018), or even to help in the detection of plant diseases (Abdulridha et al., 2018). Unlike satellites, UAVs represent a relatively low-cost method for image acquisition with high resolution and they are increasingly used for agricultural applications. Hunt et al. (2010) established a good correlation between leaf area index (LAI) and normalized difference vegetation index (NDVI) by using UAV multispectral imaging for crop monitoring. Ribera et al. (2018) deployed UAV trichromatic imagery to count the number of leaves in sorghum. Nebiker et al. (2008) reported the successful application of UAV imagery to evaluate grapevine crop health.

The use of high-performance sensors for plant imaging has resulted in the generation of enormous amounts of image data that required processing to extract useful information. Here, we present our full image processing pipeline to store, preprocess, and analyze sorghum UAV images in a holistic way to extract the spectral indices that correlate the most with structural and physiological variables measured. The pipeline provides valuable information about key priority traits for breeding programs, and it can be used as a decision support tool.

UAV Image Data Acquisition

For this study, images were collected with a hexacopter UAV (FeHexaCopterV2, MikroKopter, Germany) at an altitude of 50 m and a constant speed of 4.5 $m.s^{-1}$. This UAV can fly by either remote control or autonomously with Global Positioning Systems. The UAV's support software (MikroKopter tools, MikroKopter, Germany) implements a flight plan, monitors the flight, and allows information such as drone position. An Airphen multispectral camera (Hyphen, France) with 6 spectral bands (blue = 450 nm, green = 532 nm, green-edge = 568 nm; red = 675 nm; red-edge = 730 nm; NIR = 850 nm) combined with a thermal infrared camera (Flir Ltd, USA) was used. In addition, a RGB SONY ILCE-6000 digital camera (Sony, Japan) with a 6000 x 4000-pixel sensor equipped with a lens of 60 mm focal length was used. To reduce the effects of ambient light conditions, we limited data capturing missions to clear and cloudless days.

Both the RGB and the Airphen multispectral cameras acquired images continuously at 1 Hz frequency. The Hexacopter tools were used to design the flight plan so that it covered all the area and ensured 80% of overlapping both across and along the track. We used a 2.5 m² carpet reference panel placed horizontally on the ground at 1.5 times the height of the closest plants, as recommended by Ahmad et al. (2021). Besides, 6 circular panels of 50 cm diameter were placed in the 4 corners of the field as ground control points (GCPs) (Kääb et al., 2014). The exact positions of these GCPs were defined with GPS GNSS (Global Navigation Satellite System) equipment, providing an accuracy of 2 cm.

Regarding phenotyping in RGB, we calculated proxies from the literature such as the Brightness Index, the Soil Color Index, etc. These indices were shown to have a positive correlation with measured traits.

Figure 1

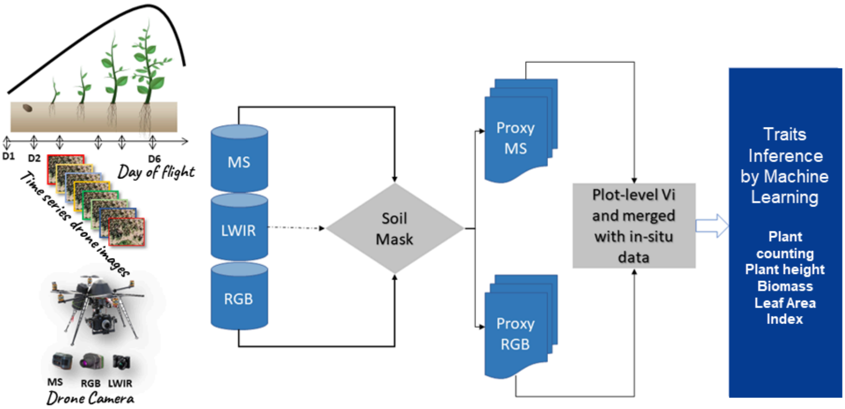

Figure 1 – Field-based UAV Aerial Phenotyping Platform and Methodology Used to Extract the Multispectral Image

Note. MS is the multispectral camera, LWIR is the thermal camera, and RGB is the red-green-blue camera. D1 to D6 are the flight dates.

Flight dates are optimized according to the traits of the measured plants. Some traits cannot be measured at certain stages of plant development. For example, if the leaf area is 2 cm, the determination of biomass becomes extremely difficult. Thus, the flight date D1 is used to create a Digital Elevation Model (DEM), which is the field's reference height (h0). Flight dates D2-D3-D4 are used to measure a plant's agro-morphological traits, such as biomass, Leaf Area Index (LAI), and plant height. Flight dates D5-D6 are used to assess varieties' performances at the maturity stage (yield estimation and panicle number). Specific flights are carried out for the characterization of stresses including water, nitrogen, and thermal stresses. The thermal imaging camera is used more during stress characterization to calculate temperature distribution according to cereal varieties.

After the flights, images were uploaded to Agisoft software (Agisoft LLC, St. Petersburg, Russia) to create a geo-referenced multi-layer orthoimage of the flight for each date. A subsample of microplots was designed in both sites and georeferenced using FieldImageR package (Matias et al., 2020). The plot-level reflectance data and vegetation indices were calculated using R (Hijmans & van Etten, 2016). The entire process of spectral index extraction is fully automated, and the outputs are directly obtained in a CSV file.

Workflow of the Image Processing Pipeline

1. Generation of the Orthomosaic Image

All the image datasets collected from every flying date for both cameras were processed separately to generate mosaics of the entire plantation. The RGB imagery was assembled using Agisoft PhotoScan software fully automated scripting API by applying three consecutive phases of superimposed image alignment, field geometry construction, orthoimage, point cloud, and dense surface model (DSM) generation using structure-from-motion algorithms. The final ortho-product is a three-band orthomosaic. Multispectral images were assembled using Agisoft PhotoScan and the multi-band imaging plugin Airphen. The final product was a six-band orthomosaic and a DSM.

2. Radiometric Calibration

Depending on the lighting conditions, sensor configuration, sun position, and measurement angle, the luminance measured by the multispectral sensor occasionally differed from the energy reflected by the crop due to radiometric distortions. To ensure radiometric consistency between the different drone images, radiometric distortions and inconsistencies were accurately processed for subsequent analysis of the images. Radiometric correction consists of converting a digital number of multispectral images into reflectance by absolute or relative calibration (Liang, 2008). In this pipeline, we calibrated the reflectance using a reference surface: the carpet located on the ground at a distance from the plot which was imaged at each flight, and the radiometric calibration tool (Agisoft PhotoScan and the Airphen plugin) which used known reflectance indices of the carpet from laboratory measurements.

3. Geometric Correction

Due to the drone's speed, altitude, and the angle of sensor view, geometric distortions are possible. As a result, the pixels recorded in the different images might not project onto the same geographical grid due to these distortions. Thus, corrections must be made to increase the spatial coincidence between the images. Firstly, we carried out geometric correction through multiband co-registration to modify and adjust the image coordinate system to decrease geometric distortions and make pixels in different pictures coincide to the similar map grid points. The co-registration process is simply based on internal GPS from raw image metadata. Ortho-rectification was then completed using the GCPs to increase the accuracy of the generated orthomosaic.

4. Extraction of Spectral Vegetation Indices

Automated scripts were developed to load RGB and MS orthoimages. Then we used RGB orthomosaic to segment and separate sorghum plants from the soil background by converting mosaics from RGB to HSV colour space and by performing thresholding operations over green pixels to create a sorghum mask. Escadafal's (1993) modified HUE index was used for effective soil masking of both MS and RGB images. Figure 2 illustrates the output of the soil masking operation. This process is important for reducing bias since the spectral signature of soil mixed with vegetation layers tend to introduce strong outliers.

Figure 2

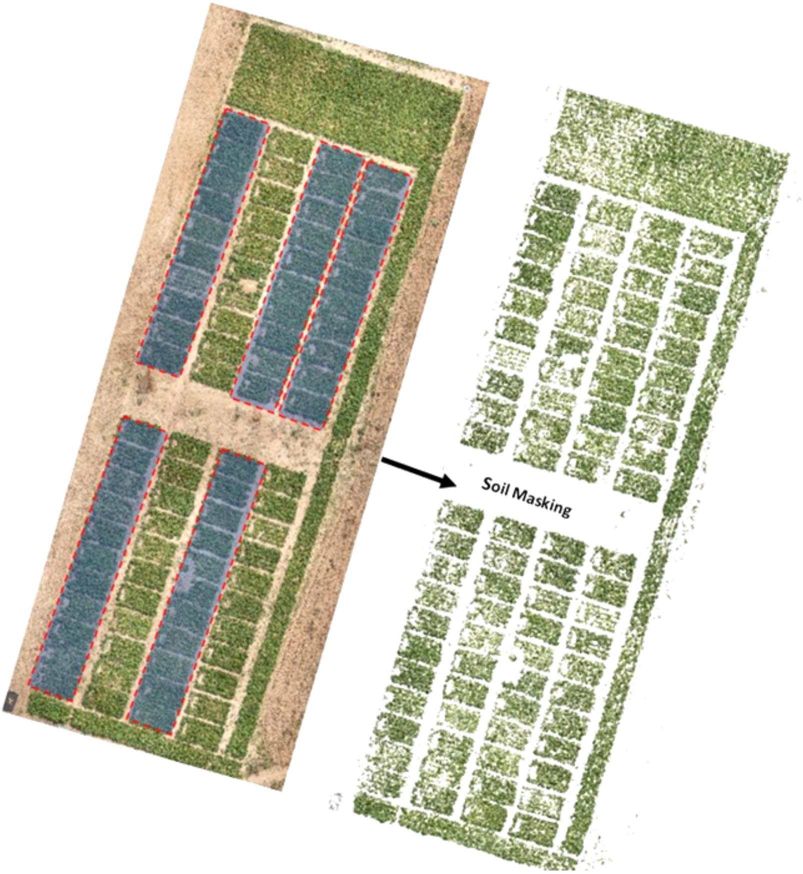

Figure 2 – Image Obtained After Using the Soil Masking Technique to Extract Both Soil and Vegetation Layers with the Traditional HUE Index Thresholding

We extracted calibrated reflectance in red, green, and NIR bands using that mask raster. Modified scripts from RSToolbox (Leutner et al., 2017) and FieldImageR (Matias et al., 2020) libraries were used to derive the following well-known spectral indices for crop physiology and biomass monitoring: NDVI, GNDVI, MSAVI2, RVI, CTVI, and NDWI (Table 1). In total, automated extraction of 15 proxies with 7 spectral bands from drone imagery was operated. In addition, the GPS coordinates of each plot were extracted using the QGIS geographic information system software (Menke et al., 2016) and exported as spatial vector data. The extraction of the average values of each vegetation index was performed according to the GPS coordinates extracted on QGIS using the features of the sf and raster packages.

Table 1
Popular Vegetation Indices are Used in Drone Phenotyping with the RGB Camera.

Vegetation index	Formula
Normalized Ratio Vegetation Index	$NRVI = \frac{R/N-1}{R/N+1}$
Normalized Difference Water Index	$NDWI = \frac{G-N}{G+N}$
Ratio Vegetation Index	$RVI = \frac{R}{N}$
Green Leaf Index	$GLI = \frac{2R-G-B}{2R+G+B}$
Green Normalized Difference Vegetation Index	$GNDVI = \frac{N-G}{N+G}$
Normalized Difference Vegetation Index	$NDVI = \frac{N-R}{N+R}$
Visible Atmospherically Resistant Index	$VARI = \frac{G-R}{G+R-B}$
Soil Color Index	$SCI = \frac{R-G}{R+G}$
Brightness Index	$BI = \frac{\sqrt{R^2+G^2+B^2}}{3}$
Spectral Slope Saturation Index	$SI = \frac{R-B}{R+B}$
Overall Hue Index	$HUE = \frac{\arctan(2(B-G-R))}{30.5(G-R)}$
Difference Vegetation Index	$DIV = s * (N - R)$
Corrected Transformed Vegetation Index	$CTVI = \frac{NDVI+0.5}{\sqrt[2]{NDVI+0.5}}$

Figure 3 shows different combinations of orthomosaic bands from the multispectral sensor on field trials of water-stressed and irrigated plots. For each combination, important information can be deduced as parts of the test subjected to water stress or experimental units that are less developed. Figure 3(c) is an overlay of the shapefile of the experimental units with the generated orthomosaic. On each experimental unit, vegetation indices were calculated and further analysis on the spatial modelling on crop characteristics was conducted.

Figure 3

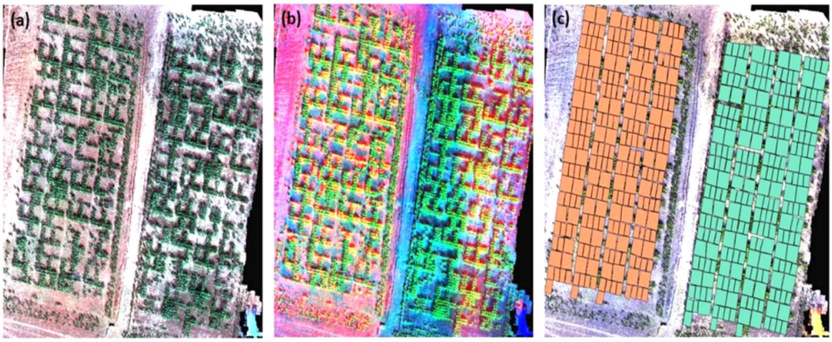

Figure 3 – Outputs of an RGB Image Showing Spatial Variation Based on Some Vegetation Indices (VIs) on Soil-free Orthomosaic Data

Note. 3(a) is a True-Color map, while 3(d) is a false-color. 3(c) shows the shapefile generated from each variety.

5. Regression Analysis

Two approaches have been developed in our image processing and analysis pipeline. The first approach uses statistical modelling and machine learning regression to link the agronomic traits to vegetation indices, especially the NDVI. Nevertheless, more than 15 other vegetation indices have been determined including the Soil Color Index (CSI), the Simple Ratio Vegetation Index (SRI), the Green Normalized Difference Vegetation Index (GNDVI), and the Modified Soil Adjusted Vegetation Index (MSAVI). The leaf area index calibrated with data from previous sorghum tests with measurements of NDVI derived from the drone images was estimated according to the statistical model proposed by Gano et al. (2021). An exponential regression law with a coefficient variation of 0.92 was used to estimate the LAI.

Figure 4 illustrates the spatial-temporal evolution of biomass, NDVI, and LAI of plants grown under water stress and non-stress conditions. This time series plot allowed us to make a rapid survey of how crops are sensitive to stress conditions. It appears from the figure that biomass, as well as LAI, shows a similar trend as the NDVI. This correlation is also noted for other vegetation indices such as GNDVI. Most importantly, water stress decreased the biomass of all the three varieties tested. However, the magnitude of this decrease was not homogeneous across varieties. For example, the variety V3 stands better water stress.

Figure 4

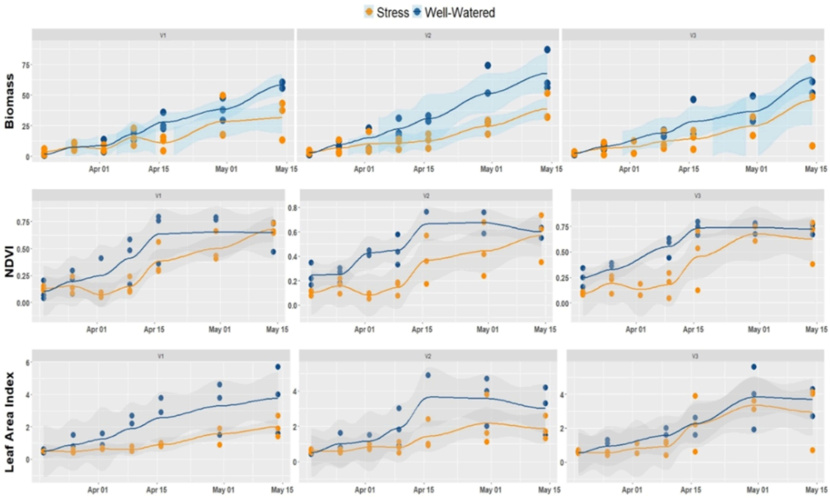

Figure 4 – Time Series Analysis of Plant Traits (biomass, NDVI, LAI) in 3 Sorghum Varieties (V1-V3) at Different Dates of Crop Cycle

In this report, the regression models developed showed an excellent correlation between LAI and vegetation indices such as NDVI, CTVI, and GNDVI ($0.76 < R^2 < 0.96$). Figure 5 illustrates regression analysis and indirect estimation of the LAI. The logarithmic transformation of the LAI shows a linear correlation between the estimated vegetation indices. These indices also have a strong linear dependence of the order of 0.99. From a modeling point of view using one of the indices would give the same result in terms of LAI prediction.

Figure 5

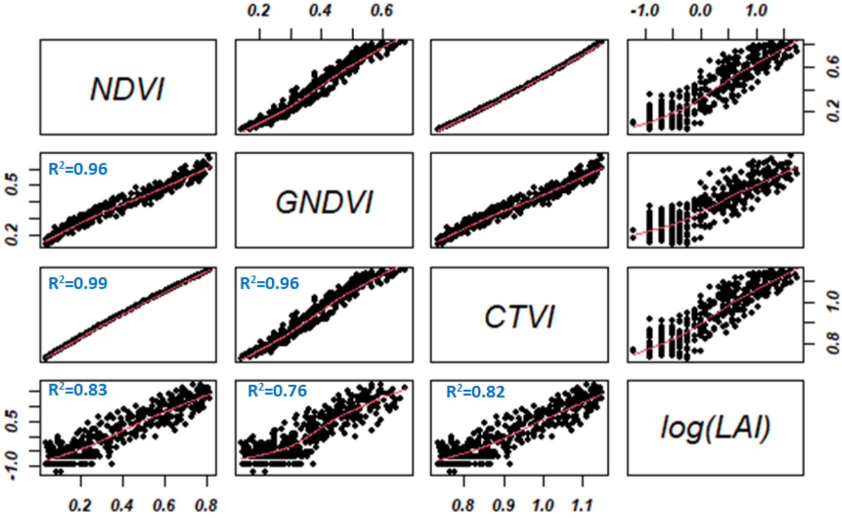

Figure 5 – Regression Analysis of Linear Dependency Between Drone Vegetation Index & in Situ LAI

For the second approach, we used a densely connected neural network to estimate the LAI based on drone vegetation indices and the RGB bands. Our network consisted of four hidden layers with the succession of two drop-out and batch normalization layers. The hidden layers consisted of 128, 64, 128, and 11 units respectively. The drop-out rate was 40% (first layer) and 30% (second layer). We used the Mean Absolute Error as metrics and the Mean Standard Error as loss. For the optimizer, the Gradient Descent with the Root Mean Squared Propagation was used. Deep learning with the above-mentioned vegetation indices showed a better linear relationship with an error of 2% and a coefficient of determination of 0.99. However, deep learning with RGB optical bands produced a 10% error with an R^2 of 0.7. Figure 6 shows the deep learning regression model for LAI estimation with the deep learning model architecture and the output of the loss function for two different regression models (drone RGB and multispectral).

Figure 6

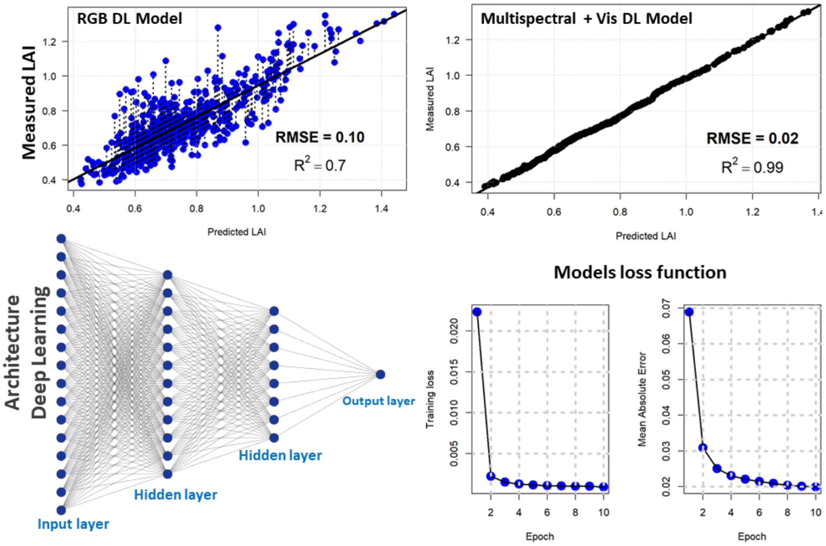

Figure 6 – A Densely Connected Neural Network for LAI Estimation

The use of statistical regression or deep learning approaches depends on the volume of field data and the experimental data acquisition protocol. However, statistical regression models are more likely to produce bias and prediction errors compared to deep learning models. It is important to note that for large-scale phenotyping, it is much easier to implement statistical models.

Conclusion

In this study, we evaluated the use of multispectral UAV imagery coupled with a fully automated image processing pipeline for the phenotyping of cereal crops. To optimize the computation, we developed 6 proxies from the RGB camera and around 10 other proxies for the multispectral camera. The generation of the shapefile from the experiments is now simplified and allows an easier extraction of the vegetation indices. However, due to the high resolution of the images, the computation time is still long with the processors at our disposal. With this process, we were able to accurately estimate agro-morphological traits using machine learning regression or deep learning architecture.

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8. Agro-physiological Responses of 10 West Africa Sorghum Varieties to Early Water Deficit Assessed by UAV and Ground Phenotyping

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Abstract

Sorghum is a staple food for many in the Sahel. However, it often faces early-stage water deficit resulting in production decrease. Research is focusing on developing early drought tolerant varieties. This study assessed the effects of early drought stress on 10 elite varieties of West African sorghum collection tested over 2 years (2018-2019) in Bambey (Senegal). Water stress was applied by withholding irrigation 25 days after sowing for one month, followed by optimal irrigation until maturity. Soil moisture and agro-physio-morphological traits were monitored. Results showed highly significant effects of early drought stress on sorghum plants growth. The combined analysis of variance revealed highly significant differences ($P \leq 0.01$) between varieties in the different environments for most traits studied. Under water deficit, the genotypic adaptation was linked to the capacity of varieties to increase the dead leaves weight and the roots length density and to reduce photosynthesis rate, stomata conductance, and leaf transpiration. The analysis of spectral indices across water treatments revealed significant variation. However, the differential responses between varieties remained the same. Fadda (V1), Nieleni (V2), Soumba (V8) and 621B (V9) showed promising behavior under drought stress and could be suitable for further use in West Africa.

Keywords: early drought tolerance; genetic variability; root adaptation; sorghum

Introduction

Plant adaptation to water deficit is one of the key factors that will determine the severity of climate change on food production, because in the next decade, water availability will be greatly affected by climate change (Molden, 2007). Currently, agriculture uses 75% of the world's total water consumption and that is likely to increase (Molden, 2007). Food production increases at only 1.2% for the four key global crops—maize, rice, wheat, and soybean—and future demands will cause it to double (Ray et al., 2013). This is also valid for sorghum (Sorghum bicolor (L.) Moench), which is a staple food for millions of people in arid and semiarid tropical regions (Agrama et al., 2003). Its production in Africa has been estimated at 29.83 million tons from 30.54 million hectares of land (FAOSTAT, 2019).

However, the production remains unstable despite cultural practices farmers implemented to adapt and cope with the growing needs and population rise (Chaléard, 2010; Sanchez, 2002). Indeed, the latter has caused strong pressure on the arable land leading to soil depletion.

Actions to promote food security in the Sudano-Sahelian zones include the promotion of local cereal production through the identification of high-performance varieties and the breeding of new varieties. In Senegal, sorghum is one of the most important local cereals grown in the various agro-ecological zones of the country. However, climate change has increased the risk of rainfall shortage during July—the beginning of the growing season (Salack et al., 2012). This could be the cause of the low production (291.171 tons in 2019) (DAPSA, 2019). Early-stage water deficit is experimented with in many research studies by withholding water supply at the beginning of the crop growth cycle, about 3 weeks after germination, for 3 to 4 weeks (Debieu et al., 2018; Qazi et al., 2014; Zegada-Lizarazu & Monti, 2013). This causes a decrease in leaf appearance, transpiration, and photosynthesis through leaf senescence (Craufurd & Peacock, 1993; Dwivedi et al., 2008; Tari et al., 2013). The combined effects of drought and rewatering are still not well-known, especially regarding sorghum. The ability to recover from early water deficit during rewatering can explain in some cases the yield difference between varieties at harvest (Zegada-Lizarazu et al., 2013). The drought recovery index (DRI) represents rewatering-induced recovery of the growth traits related to biomass, height, etc., and would be suitable for investigating drought tolerance. According to Perrier et al., (2017), recovery capacity is an important trait for future phenotyping, genetic and breeding studies while its process and genotypic variability are poorly understood. Late maturity genotypes appeared to be more tolerant to early drought because the stress occurs before the panicle initiation phase, when plants have more ability to recover after rewatering. However, these genotypes no longer suit the farming systems of semiarid regions because of the shortened rainy season. Thus, the solution would be to identify improved short-cycle varieties capable of adapting to early season water stress. This requires a characterization of sorghum behavior under early season water stress and the identification of relevant selection criteria to facilitate the decision on the choice of varieties for cultivation and breeding programs.

Root response is of prime importance to crop productivity under drought stress. This is because the root size, architecture, and distribution determine the ability of plants to access and take up the water for proper physiological functioning of shoots (Henry, 2013; Taiwo et al., 2020). Sorghum's ability to adapt to water shortage is also due to its root system, which can extend into the deep soil layers. The investigation of this trait through the measurement of root length density (RLD) trait revealed useful (Masi & Maranville, 1998). Researchers have been working to identify specific root traits targeted for plant improvement under drought and limited nutrients conditions (Comas et al., 2013; Girma et al., 2020; Lynch et al., 2014). Recently, greater focus was given to root system architecture, especially the RLD distribution in the soil, which is a key factor for water and nutrient uptake (Chopart et al., 2008; Gregory, 2006). However, field assessment of RLD is not obvious. Among other methods, the trench profile method for mapping root intersection in a soil profile was identified as more efficient and feasible to provide information on roots distribution (Böhm, 1976; Chopart et al., 2008; Tardieu, 1988).

Another method investigated in this study is the use of vegetation indices (VIs) calculated from Unmanned Aerial Vehicle (UAV) multispectral images to phenotype sorghum varieties under drought. Previous findings have promoted VIs related to normalized difference vegetation index (NDVI) as an important multi spectral index to track the agro-physiological dynamics of key traits such as biomass, leaf area index (LAI), yield, etc. (Foster et al., 2017; Magney et al., 2016; Samborski et al., 2015). However, breeders are not aware and have less understanding about the application of the different reflectance bands ratio on monitoring crops development and adaptation. Higher level of NDVI is associated with faster growth rate, higher biomass accumulation during the vegetative stage, and a longer grain filling period by delaying leaf senescence during the ripening phase thereby increasing yield (Babar et al., 2006).

The objectives of this study were to investigate the effects of early water deficit in sorghum to determine the main adaptation mechanisms and simultaneously highlight an interesting method and criteria for the agro-physiological characterization of sorghum in water deficit conditions.

Material and Methods

1. Plant Material

The plant material used in this study consisted of 10 elite varieties of sorghum from Senegal, Mali, and Nigeria (West Africa) (see Table 1). They differ in terms of phenology (from 90 days to 128 days cycle duration), plant architecture (120 cm to 450 cm height), response to inputs (hybrid vs. open pollinated varieties caudatum or guinea), and yield (2 t/ha to 4.5 t/ha) (Dembele et al., 2020). These varieties are widely cultivated by the farmers because of their adaptability and agronomic characteristics (Dembele et al., 2021; Gano et al., 2021; Ndiaye et al., 2018; Ndiaye et al., 2019).

Table 1
Characteristics of the Varieties Studied

Variety	Code	Type	Cycle (days)	Height (cm)	Potential yield (t/ha)	Panicle form	Photoperiod-sensitivity	Isohyet (mm)	Origin
Fadda	V1	Guinea (hybrid)	128	200-300	4.5	noncompact	mean	700-1000	Mali
NIELENI	V2	Guinea (hybrid)	115	300	4	semicompact	low	700-800	Mali
IS15401	V3	Guinea-Caudatum	115	400-450	2	semicompact	high	900-1200	Mali
PABLO	V4	Guinea (hybrid)	125	400	4	noncompact	mean	700-1000	Mali
CSM63E	V5	Guinea	90	400	2	noncompact	low	600-1000	Mali
SK5912	V6	Caudatum	170	200	2.5-3.5	semicompact	high	700-900	Nigeria
GRINKAN	V7	Caudatum	90	120	4	semicompact	non	500-800	Mali
SOUMBA	V8	Caudatum	115	250	2.5	semicompact	low	600-1000	Mali
621B	V9	Caudatum	105	175	2.5-3	semicompact	non	600-900	Senegal
F2-20	V10	Caudatum	110	210	3-5.3	semicompact	low	600-900	Senegal

2. Methods

2.1 Trial Conditions

Trials were conducted at Bambey (14°42'N; 16°28'W) (Senegal) in the Centre National de la Recherche Agronomique (CNRA) on a sandy soil (sand = 94.2%, silt = 3.5%, clay = 2.3%) with a previous cowpea crop. Three trials were carried out between 2018 and 2019 during the dry seasons, which allowed control of the water supply by irrigation. The experimental design is a randomized complete block design, with irrigation as the main factor, and varieties randomized in three replications in each main block. The two water treatments (well-watered [ww] and drought stress [ds]) were placed 10 m apart to avoid involuntary irrigation. A sprinkler method of water supply was provided twice weekly with 25 mm per irrigation (50 mm per week) until physiological maturity. The amount of irrigated water was calculated to cover the weekly average evapotranspiration of sorghum that varied between 25 mm to 37 mm (see Figure 1D). One irrigation was applied before and after sowing to promote good seedling emergence. Fertilizers were applied after sowing and at 21 days after sowing (DAS) as NPK and urea respectively following standard recommendation (i.e., 150 kg ha^{-1} of NPK [15-15-15] and 100 kg ha^{-1} of urea). Water stress was applied by withholding irrigation in the drought stress environment for 1 month from the 25th DAS.

2.2 Weather Conditions

Figure 1 shows the climate conditions (vapor pressure deficit [VPD], solar radiation, relative humidity, and temperature) during both experiments. There was a high evaporative demand during these dry seasons as shown by the VPD data that reached 5 KPa during the day. The dry season is characterized by high temperature (above 30°c) and high solar radiation (800 w.m^{-2}) during the day. These climate conditions are representative of the dry season, allowing control over water supply.

Figure 1

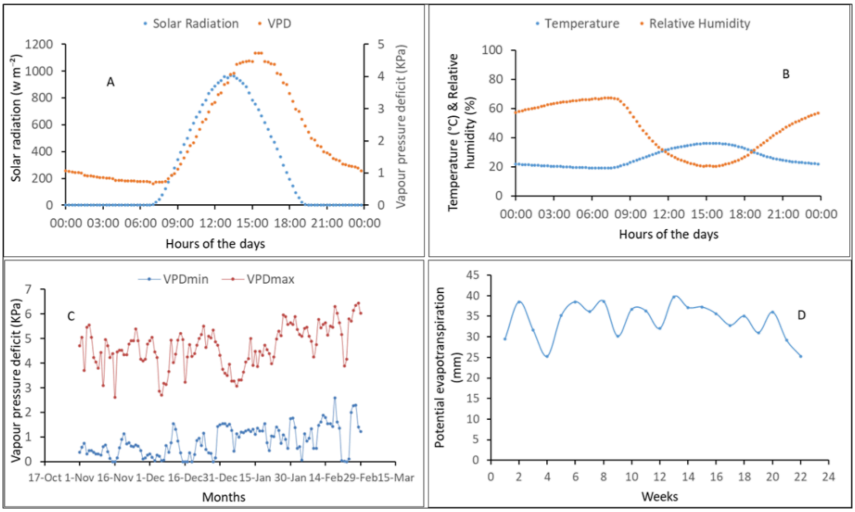

Figure 1 – Climate Conditions During the Experiments in Bambey in 2018 and 2019.

Notes. (A) Daily averages of vapor pressure deficit (VPD) and solar radiation; (B) Temperature and relative humidity; (C) Minimum and maximum VPD; (D) Potential evapotranspiration. Although climate conditions were measured in both years, only representative annual graphics were presented. (A) and (B) were recorded during 2018 experiment and (C) and (D) during the 2019 experiment.

2.3 Monitoring Water Stress

Water stress in the field was monitored by measuring the volumetric soil moisture (Diviner 2000, Sentek Pty Ltd) once a week during the irrigated period and twice a week during the stress period to assess the fraction of transpirable soil water (FTSW) (Debieu et al., 2018; Sinclair & Ludlow, 1986). Diviner probe tubes of 1.6 m length were used to record water stock at every 10 cm of depth. In this work, a total of 1.6 m depth water stock was considered to assess the FTSW as this depth represents the sorghum's root activity zone. Soil moisture measurements allowed us to follow the level of stress down to FTSW = 0.3 at the end of the stress period. The average of the three most contrasted varieties was used to evaluate the general trend. We also monitored the predawn leaf water potential once a week using the pressure chamber (PMS Instrument Co., Corvallis, Oregon, USA) according to the protocol of Peyrano et al. (1997). The plant's water potential was measured before sunrise, when there is a balance between plant and soil for water potential.

2.4 Assessment of Agro-physiological Traits

Plants' agro-physiological traits—such as number of leaves appeared (NLA) and plant height after stress (PHS)—were measured on three tagged plants per plot. The photosynthesis rate (Pn), leaf temperature (Tleaf), transpiration (Tr), and stomata conductance (C) were measured on the last ligulate leaf using the CI340 handheld photosynthesis system (CID Bio-science, USA). Biomass production was evaluated by estimating plant dry weight (DWP) and dead leaves weight (DLW) using six plants per plot at seven different dates (before the stress, at the end of the stress, and after recovery [2 weeks after rewatering]). At physiological maturity, grain yield, plant height (PHT) and straw dry biomass (SDW) were measured. The specific leaf area (SLA) was calculated as the ratio between plant leaf area and biomass.

Moreover, other morphological traits were measured weekly during drone flights on three randomly tagged plants per plot, from crop emergence (25 DAS) to flowering-maturity stage (89 DAS). Seven sampling weeks' data were used for LAI and biomass. LAI was measured using the SunScan septometer (Delta-T Devices, Cambridge, England). Nondestructive measurements (LAI) were performed just before UAV flights. Plants were sampled, dried outdoors for 2 weeks, and oven-dried for 3 days before biomass measurements were taken using ad-venturer pro precision balance (OHAUS Corporation, Pine Brook, New Jersey, NJ, USA).

To better study the recovery performance and classify varieties, we introduce a new parameter that we have named the DRI. The DRI represents the relative recovery of the growth traits (NLA, PHS, DWP, Pn) after a freely defined time of drought stress followed by rewatering. This approach was inspired by the drought factor index (DFI) used by Strauss et al. (2006) for the detection of dark chilling tolerance in soybean genotypes and by Oukarroum et al., (2007) for probing the response of barley cultivars under drought stress conditions. DRI was calculated by applying the formula:

$$\mathbf{DRI} = \log A + 2 \log B \quad (1)$$

in which A is the relative trait measured at the end of the drought period and B is the relative trait measured 2 weeks after rewatering. The relative trait is calculated as trait drought over trait control. The principle of the DRI is that recovery efficiencies should play an important role on the production capacity of some genotypes. Varieties with DRI near to zero have good recovery and varieties with DRI around -1 have bad recovery index (Oukarroum et al., 2007).

2.5 Roots Phenotyping

Root measurements were done on two tagged plants per plot. We used the described methods, to count the number of adventitious roots and estimate RLD from intersections between the roots and the face of a soil trench profile (Chopart et al., 2008; Dusserre et al., 2009; Faye et al., 2019). The trench profiles were dug perpendicular to the rows of seedlings and at two distances (20 cm then 10 cm) from the plant stem. Iron grids of 60 cm length by 30 cm width, in relation to the spacing between rows and between plants, were used to count root impacts. Square meshes of 10 cm side length were made inside the grids to facilitate the measurement of the number of impacts. At the end of the stress period, the plants were dug up for additional measurements on the tilling tray, such as the number of adventitious roots.

2.6 UAV Data Capture and Image Analyses

Time series flights were done at the altitude of 25 m and a constant speed of 2.2 $m.s^{-1}$ with the hexacopter drone (FeHexaCopterV2, MikroKopter Company, Moormerland, Germany). Seven UAV weekly flight data, from emergence to maturity, were recorded. Nine grey colored ground control points (GCPs) were uniformly distributed over the entire field area with fixed position for all the flights throughout the experiment. These were surveyed using Precis BX305 Real Time Kinematics (RTK) GNSS unit (Tersus GNSS Inc., Shanghai, China). The GCPs were made of painted PVC disks of 60 cm diameter where the central disk of 40 cm diameter was 20% gray level and the outer disk 60% gray level color. These gray levels were selected to avoid saturation and allow automatic target detection on the images. The

UAV system, equipped with six motors, can perform user-defined waypoint flights with a differential global navigation satellite system (GNSS) receiver. The UAV support software (Mikrokopter tools, Mikrokopter Company, Moormerland, Germany) that implements the flight plan also monitors the flight and records information such as drone position. The flight was performed with an RGB ILCE-6000 digital camera (Sony Corporation, New York, NY, USA) with a 6000×4000-pixel sensor equipped with a lens of 60 mm focal length. To minimize the blurring effect and noise in the images, the camera was set on speed priority (1/1250 sec) and auto ISO mode. Another flight was performed with an Airphen multispectral camera (hiphen, Avignon, France, https://www.hiphen-plant.com/) equipped with a lens of 8 mm focal length and acquiring 1280×960-pixel images. The Airphen consists of six individual cameras equipped with filters centered on 450 nm, 530 nm, 560 nm, 675 nm, 730 nm, and 850 nm, with a spectral resolution of 10 nm. For each camera (RGB and MS), the flight lasted about 15 minutes with a break of approximately 10 minutes in between to prepare the second flight. The cameras captured images at 1-second intervals and recorded them in JPG and Tiff format on the SD memory card. The drone did round trips spaced by 4 m that allowed a side and forward overlapping fraction of 0.75. To reduce the effects of ambient light conditions, such as plant shadow that can greatly affect spectral measures especially between rows at maturity stages, the flights were limited to clear and cloudless days between 10:00 a.m. and 12:00 a.m. UTC.

An automatic image-processing pipeline was designed to generate radiometrically calibrated and geometrically corrected multiband orthoimages using Agisoft PhotoScan digital photogrametric software version 1.4.0 (Agisoft LLC, St. Petersburg, Russia, https://www.agisoft.com/downloads/installer) (see Part 2 Chapter 1, Mbaye et al. in this book). Radiometric calibration included automatic correction of vignetting effects (Iqbal et al., 2018). Real reflectances were computed using a reference target positioned to the ground during UAV flights. This target was previously spectrally characterized in controlled conditions. Geometric correction involved firstly, multiband coregistration to modify and adjust the images' coordinate system to decrease geometric distortions and make pixels in different pictures coincide with the corresponding map-grid points. The coregistration process was based upon the internal GNSS from raw image metadata. Orthorectification was then performed using GCPs to increase the accuracy of the generated orthoimage. As Agisoft Photoscan manages multilayer images, we used the 450 nm band for tie point searching. For a better plots segmentation, we uploaded the RGB orthoimage in QGIS (Geographical Information SYSTEMS, version 3.10.0, QGIS Development Team, open source 2019, https://www.qgis.org/fr/site/forusers/download.html) and designed the plots boundaries. The created shapefile with the GNSS coordinates of each plot was exported as spatial vector data. The extraction of the average values of the varieties' vegetation index in each plot was performed according to the GNSS coordinates of plots, extracted on QGIS and MS orthoimage. The computation was performed using R software (version 3.6.0) libraries (sf, raster, rgdal, RSToolbox and uavRst) (R Core Team, 2020). Four vegetation indices (NDVI, CTVI, MSAVI2 and SR) were used to estimate LAI and biomass during the dry seasons of 2018 and 2019. These vegetation indices are single values computed by grid calculation.

They are invariant to the difference in illumination conditions, slope, seasons, etc. They represent a quick way to distinguish green leaves from other objects and to estimate the relative biomass present on the image, therefore, distinguishing stressed vegetation from nonstressed (Li et al., 2018; Shi et al., 2016; Steven et al., 2015; Zhang et al., 2017).

2.7 Statistical Analyses

The raw data were analyzed using R software version 3.6.0 (www.r-project.org). An analysis of variance was performed for each environment (ww and ds) to verify statistical differences between varieties. Subsequently, a combined analysis of variance was performed to test the effects of water stress and years on varieties. The homogeneity between residual variances was tested using Bartlett's test (Bartlett, 1937). RLD was modeled on the basis of measurements of root intersections density (RID) on a vertical perpendicular plane within a sorghum row because this method is most commonly used for studying roots in a soil profile. Relationships between RLD and RID were evaluated taking the slope, the standard error of the slope (SE), the intercept, and the regression (r^2) into account. Ordinary least squares linear regression models were applied. Regression models were developed to predict LAI and biomass using vegetation indices. The performance of regression models in estimating LAI and biomass were evaluated by calculating the root mean squared error (RMSE), the coefficient of determination (r^2) and p-values at the probability level of 0.05.

Results

1. Water Stress

During the irrigation period, FTSW and predawn leaf water potential showed a very low variation and revolved around 0.7 and -1.5 bars, respectively (see Figure 2). However, when the plots in the ds treatment were let to dry down, FTSW and predawn leaf water potential decreased progressively and reached 0.3 and -5 bars respectively, showing an effective drought stress experience that occurred between 35 DAS and 55 DAS. Thereafter, after resuming irrigation, these parameters increased again and stabilized around the initial values with a slight drop (0.6 and -2 bars for FTSW and predawn leaf water potential, respectively).

Figure 2

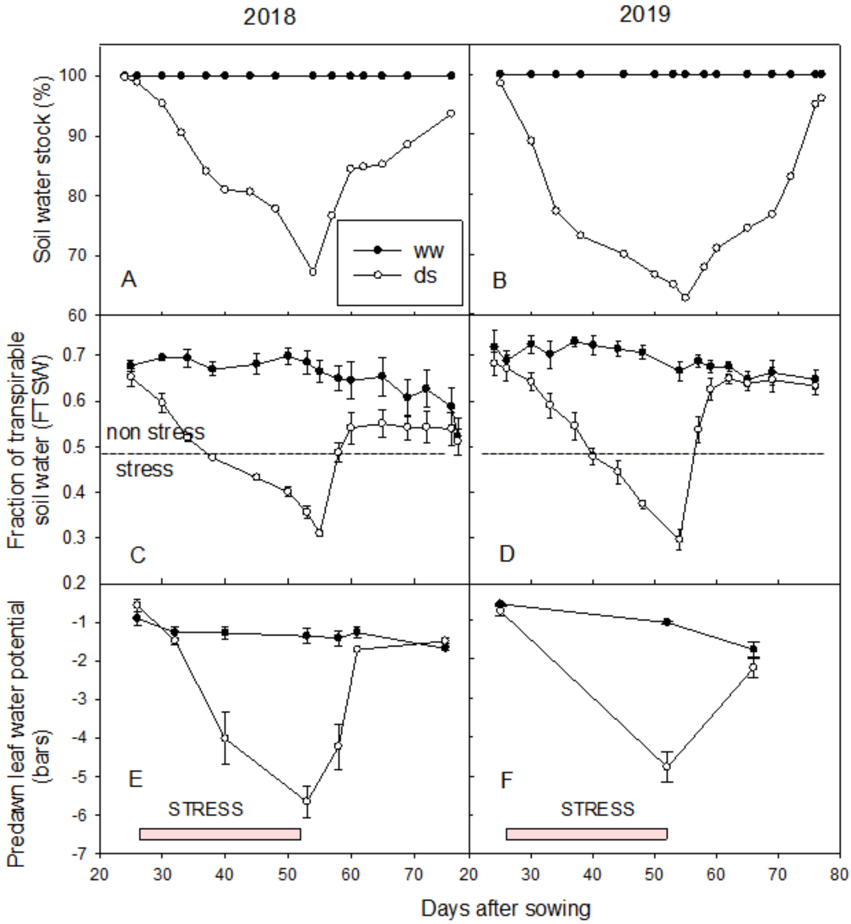

Figure 2 – Monitoring of Water Stress Parameters in Well-watered (ww) and Drought Stress (ds) Treatments

Notes. (A) Evolution of soil moisture stock (%) in 2018 and (B) in 2019; (C) Fraction of transpirable soil water in 2018 and (D) in 2019; (E) Predawn leaf water potential (bar) in 2018 and (F) in 2019.

2. Effects of Early Water Deficit on Growth, Recovery, and Yield

Table 2 presents the effects of water deficit on agro-physiological traits assessed in the experiments. The results showed highly significant differences (P ≤ 0.01) between the different environments for all the characters under study. The early water deficit led to a reduction of leaf appearance (NLA) (-9.18% in 2018 and -6.75% in 2019); PHS (-16.37% and -48.99%); Pn (-12.45% and -27.75%); C (-18.37% and -35.32%); and Tr (-26.37% and -25.92%). After maturity and harvest, we observed a decrease in yield (-22.78% and – 28.15%), SDW (-18.25% and -27.79%) and PHT (-15.01% and -23.23%). However, we noticed an increase in the DLW (+43.29% and +15.10%) and Tleaf (+1.29% and +7.64%).

Table 2
Average Performance and Statistical Parameters of Some Agro-, Physio- and Morphological Traits of Sorghum Genotypes Under Well-watered (ww) and Drought Stress (ds) Conditions of 2018 and 2019 Field Trials

	Year 2018				**Year 2019**			
Traits	Mean ww	Mean ds	ΔWS	Signif.	Mean ww	Mean ds	ΔWS	Signif.
NLA	15.33a	13.92b	-9.18	***	15.30a	14.26b	-6.75	***
PHS	143.89a	120.33b	-16.4	***	130.55a	66.59b	-49	***
DLW	13.65b	19.56a	43.29	***	14.22b	16.37a	15.1	***
PHT	174.83a	148.58b	-15	***	165.75a	127.24b	-23.2	***
SDW	453.38a	370.61b	-18.3	***	427.35a	308.60b	-27.8	***
Yield	3271.85a	2526.21b	-22.8	***	2419.84a	1738.64b	-28.2	***
Pn	39.32a	34.43b	-12.5	***	41.38a	29.90b	-27.8	***
C	184.94a	150.97b	-18.4	***	179.14a	115.88b	-35.3	***
Tr	7.43a	5.47b	-26.4	***	7.04a	5.22b	-25.9	***
Tleaf	39.02b	39.53a	1.29	**	39.16b	42.15a	7.64	***

NLA: number of leaves appeared; PHS: plant height after stress (cm); DLW: dead leaves weight (g); PHT: plant height (cm); SDW: Straw dry weight (g); Yield: grain yield (kg/ha); Pn: photosynthesis rate; C: stomata conductance; Tr: leaf transpiration; Tleaf: leaf temperature; Signif: significance at p:s 0.001 (***) and p:s 0.01 (**); ΔWS: delta water stress (%). For a given trait, numbers followed by the same letters are not significantly different between water treatments.

Figure 3 represents the monitoring of C, SLA per plant, plant height, NLA on the main stem. DWP, and Pn of varieties under both conditions (ww and ds). The results showed that the number of leaves on the main stem, plant height, and dry weight per plant gradually increased in a similar way between varieties, but the advent of water stress induced a drop. These results indicated that water stress causes significant reduction in biomass production and shoots growth in sorghum. The SLA of the plant, which reflects the thickness of the leaves, the C, and the (Pn) initially increased to reach their maximum at the 30th DAS, before gradually decreasing until maturity. In the water-stressed environment, the drop in SLA, C, and Pn was greater than in the nonstressed conditions. After the end of the stress period, these traits rebounded but without recovering to the SLA, C, and Pn values of the nonstressed environment. In terms of height and biomass, the varieties have all lost pace despite the high plasticity found in sorghum.

Figure 3

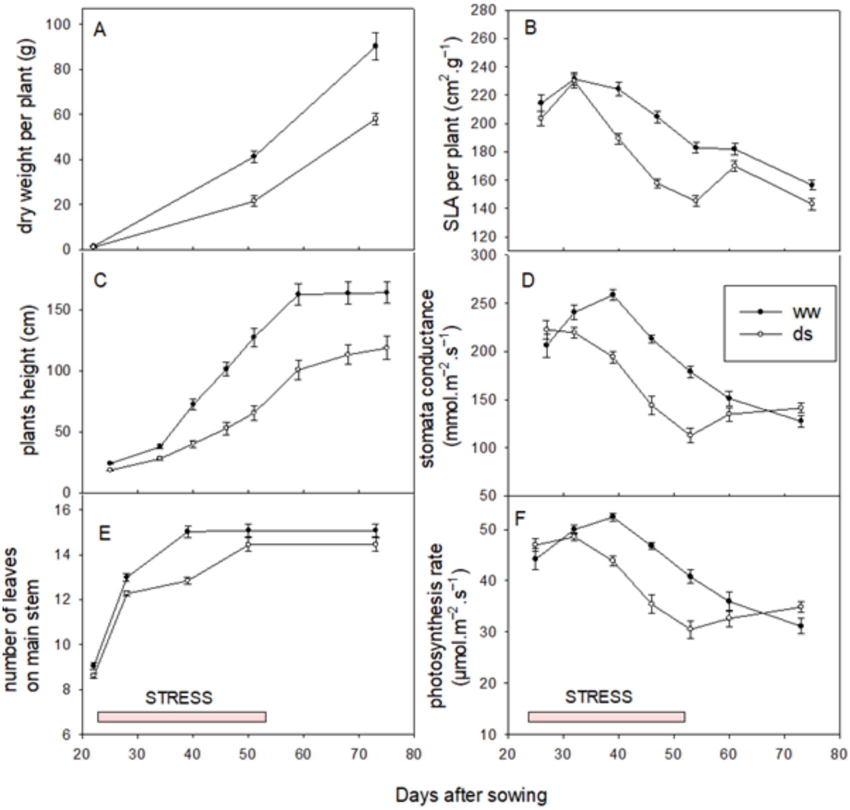

Figure 3 – Evolution of Agro-physiological Traits of Sorghum Varieties Under Well-watered (22) and Drought Stress (ds) Conditions

Note. (A) Dry weight per plant, (B) Specific leaf area (SLA) per plant, (C) Plant height, (D) Stomata conductance, (E) Number of leaves, (F) Photosynthesis rate

Sorghum varieties that exhibited the smallest values of DRI had more problems recovering. We noted that varieties had good recovery in the NLA and Pn with a DRI of -0.11 and -0.04 respectively. However, varieties' recovery on PHS and the DWP was more difficult with a DRI of -0.62 and -0.65 respectively (see Table 3). The results indicated a best recovery on plant height and dry weight for the variety V3 and V1 respectively; varieties V4, V5, and V6 revealed the worst recovery on the same traits.

Table 3
Drought Recovery Index of Sorghum Varieties on Some Growth Trait

Drought Recovery Index (DRI)				
Varieties	**NLA**	**PHS**	**DWP**	**Pn**
V1	-0.04	-0.54	-0.32	-0.22
V2	-0.1	-0.43	-0.6	-0.24
V3	-0.12	-0.33	-0.75	-0.08
V4	-0.13	-0.81	-0.98	0.07
V5	-0.1	-0.68	-0.64	0.35
V6	-0.09	-0.8	-0.97	-0.16
V7	-0.13	-0.55	-0.93	-0.05
V8	-0.11	-0.77	-0.57	0.12
V9	-0.12	-0.62	-0.44	-0.18
V10	-0.12	-0.69	-0.32	0
MEAN	-0.11	-0.62	-0.65	-0.04

NLA: number of leaves appeared; PHS: plant height after stress; DWP: dry weight per plant; Pn: photosynthesis rate

3. Adaptation Responses to Early Water Deficit

The combined analysis of variance revealed highly significant differences ($P \leq 0.05$) between varieties; environment; and the interactions between variety (V), environment (E), and year (Y), (V*E, V*Y, E*Y and V*E*Y) (see Table 4). Variety V7 showed the smallest number of leaves and PHS; V6 and V3 recorded respectively the highest values for these traits. Varieties V8 and V4 had the highest DLW in both years; V1, V6, and V9 recorded the smallest values. At harvest, variety V5 exhibited the highest plant height and SDW but the lowest grain yield. V7 and V9 exhibited the lowest plant height and SDW respectively. V1 and V10 recorded the highest grain yield under ww conditions in 2019 and 2018 respectively; V1 and V9 recorded the highest one under ds conditions in 2019 and 2018 respectively.

Table 4a

Performance of 10 Sorghum Varieties Under Two Water Treatments (Well-watered and Drought Stress) for Agro-morphological Traits Measured During 2018 and 2019 Field Trials

		NLA		**PHS**		**DLW**	
	V	**ww**	**ds**	**ww**	**ds**	**ww**	**ds**
Year 2018	**V1**	14.6cd	13.5bc	133.7bc	111.7bcd	5.7e	13.9cd
	V2	15.3bc	13.6bc	125.7bc	101.6bcd	16.8ab	28.7a
	V3	15.5abc	13.2bc	204.3a	179.3a	12.6bcd	25.8a
	V4	15.5abc	13.8bc	200.6a	137.5b	10.7cde	17.3bc
	V5	15.0bc	13.5bc	186.3a	193.5a	6.0e	16.6bc
	V6	16.6a	15.9a	108.5cd	91.2cd	7.8de	9.9de
	V7	13.5d	12.4c	92.5d	86.2cd	14.2bc	19.2b
	V8	16.0ab	14.4ab	147.5b	111.8bcd	22.4a	26.9a
	V9	15.7abc	14.9ab	98.4d	74.0d	18.3ab	8.6e
	V10	15.1bc	13.8bc	141.0b	116.1bc	21.4a	28.3a
	Grand mean	15.3a	13.9b	143.8a	120.3b	13.6b	19.5a
	ANOVA						
	V	***	***	***	***	***	***
	E	***		***		***	
	V×E	ns		**		***	
Year 2019	**V1**	15.7ab	13.7a	120.4a	77.5a	13.7d	15.1e
	V2	16.5a	14.2a	140.6a	83.5a	14.9ab	16abcd
	V3	15.0ab	13.8a	163.1a	103.1a	11.9f	15.7de
	V4	15.2ab	14.3a	107.3a	38.3a	15.3a	16.1cd
	V5	15.5ab	14.3a	154.6a	68.5a	14.8ab	16.3bcd
	V6	16.0a	15.3a	107.1a	60.8a	12.6e	16.1cd
	V7	13.5b	14.1a	106.5a	55.3a	14.5bc	16abcd
	V8	15.8ab	14.4a	124.5a	49.0a	15.1ab	17.2a
	V9	15.1ab	14.4a	99.4a	53.5a	15.0ab	17.1ab
	V10	14.3ab	13.7a	149.4a	66.3a	14.0cd	16.7abc
	Grand mean	15.3a	14.2b	130.5a	66.5b	14.2b	16.3a
	ANOVA						

		NLA		PHS		DLW	
	V	ww	ds	ww	ds	ww	ds
	V	*	ns	ns	ns	***	***
	E	***		***		***	
	V×E	ns		ns		***	
Both years	Y	ns		***		***	
	V×Y	*		***		***	
	E×Y	ns		***		***	
	V×E×Y	ns		**		*	

Table 4b

		PHT		SDW		YIELD	
	V	ww	ds	ww	ds	ww	ds
Year 2018	V1	172.5cd	148.9cd	427.6bc	358.7abc	4183.4abc	3182.3b
	V2	162.8d	140.4cde	470.2abc	349.3abc	3715.9d	3359.3b
	V3	191.2bc	193.6ab	498.7ab	409.0abc	2001.5e	1817.6de
	V4	205.6b	161.3bc	530.0ab	449.8ab	1606.4ef	1540.3e
	V5	235.3a	215.6a	603.2a	461.4a	1473.1f	1168f
	V6	159.8d	133.6cde	408.0bc	424.4ab	3926abcd	2598.3c
	V7	127.2e	108.9e	315.0c	294.5bc	3812.1cd	2006.9d
	V8	168.1d	126.0de	496.8ab	339.9abc	3922bcd	3132.8b
	V9	152.2d	117.1de	321.5c	259.3c	4246.0ab	3851.7a
	V10	169.3cd	140.0cde	451.0abc	359.3abc	4349.3a	2643.02c
	Grand mean	174.8a	148.5b	453.3a	370.6b	3271.85a	2526.21b

		PHT		SDW		YIELD	
	V	**ww**	**ds**	**ww**	**ds**	**ww**	**ds**
	ANOVA						
	V	***	***	***	**	***	***
	E	***		***		***	
	V×E	*		Ns		***	
Year 2019	**V1**	173.2cd	127abcd	494.2bc	377.3abc	3876.8a	2424a
	V2	149.4de	120.1bcd	404.5bcd	259.0bc	2127.7cd	2070.3abc
	V3	216.7ab	170.4abc	329.6cd	323.0abc	1886.4d	1752.5bc
	V4	204.6bc	183.2ab	791.2a	399.4ab	1233.9e	1124.5de
	V5	250.8a	198.2a	564.5b	428.4a	771.2f	817.4e
	V6	137.9ef	88.4d	413.2bcd	274.0abc	3429.2ab	1582bcd
	V7	109.2f	93.4d	380.8bcd	246.5c	3166.7b	2027.6abc
	V8	143def	106.1cd	330.4cd	267.8abc	2514.8c	2087.6ab
	V9	131.4ef	101.8cd	303.7d	272.0abc	2105.5cd	2037abc
	V10	140def	102.6cd	382.6bcd	278.3abc	3085.8b	1462.9cd
	Grand mean	165.7a	127.2b	427.3a	308.6b	2419.84a	1738.64b
	ANOVA						
	V	***	***	***	**	***	***
	E	***		***		***	
	V×E	*		**		***	
Both years	**Y**	***		***		***	
	V×Y	***		**		***	
	E×Y	ns		**		*	
	V×E×Y	ns		ns		***	

ww: well-watered; ds: drought stress; NLA: number of leaves appeared; PHS: plant height after stress; DLW: dead leaves weight; PHT: plant height at harvest; SDW: Straw dry weight; Yield: grain yield; V: variety; E: environment; Y: year; *** significant at *p* = 0.001; ** significant at *p* = 0.01; * significant at *p* = 0.05; ns: not significant. The means with the same letters are not significantly different. The bold values indicate the highest and lowest value measured.

Physiological traits like photosynthesis rate, stomata conductance, leaf transpiration, and leaf temperature revealed a wide range of genetic variability among the varieties under both ww and ds conditions (see Table 5). The effects of variety, environment, and their interaction (V× E) were highly significant in both years. Under ww conditions, variety V1 recorded the highest photosynthesis rate, stomata conductance, and leaf transpiration; V5, V9, and V2 recorded respectively the lowest values for the same traits in 2018. However, the occurrence of drought stress induced various responses in these varieties. Variety V10 recorded the lowest photosynthesis rate in 2018 but the highest rate in 2019, showing variation in the behavior of this variety from year to year. Overall, a decrease of photosynthesis rate, stomata conductance, and leaf transpiration—and an increase of leaf temperature—were the physiological responses of the studied varieties to early water deficit (see Table 5).

Table 5

Performance of 10 Sorghum Varieties Under Two Water Treatments (well-watered and drought stress) for Physiological Traits Measured During 2018 and 2019 Field Trials

		Pn		**C**		**Tr**		**Tleaf**	
	V	**ww**	**ds**	**ww**	**ds**	**ww**	**ds**	**ww**	**ds**
Year 2018	**V1**	43.14a	31.92abc	213.06a	119.35cd	9.34a	5.06ab	36.34cd	40.70ab
	V2	41.57ab	33.29abc	189.14ab	101.85d	7.00b	4.00b	34.80d	39.12abc
	V3	39.88ab	39.66a	179.04ab	169.84ab	7.12b	6.42a	40.30ab	39.83abc
	V4	38.99ab	38.61a	169.08b	140.07abcd	7.38b	5.58ab	40.77a	39.77abc
	V5	35.64b	26.05bc	169.11b	128.31bcd	7.13b	4.45ab	39.87ab	39.08bc
	V6	42.17ab	39.83a	202.09ab	181.85a	7.56ab	6.16a	39.32ab	40.94a
	V7	40.69ab	37.81a	194.62ab	181.45a	6.39b	5.89a	40.40ab	39.54abc
	V8	38.16ab	38.02a	182.93ab	183.21a	7.68ab	6.36a	40.83a	38.51c
	V9	36.05ab	35.74ab	166.88b	166.72ab	7.50ab	6.53a	39.34ab	39.02bc
	V10	37.70ab	22.96c	186.72ab	147.17abc	7.22b	4.61ab	37.83bc	38.75c
	Grand mean	39.32a	34.43b	184.94a	150.97b	7.43a	5.47b	39.02b	39.53a
	ANOVA								
	V	*	***	**	***	**	***	***	**
	E	***		***		***		**	

	Pn		**C**		**Tr**		**Tleaf**	
V	**ww**	**ds**	**ww**	**ds**	**ww**	**ds**	**ww**	**ds**
V×E	***		***		***		***	

		Pn		**C**		**Tr**		**Tleaf**	
	V	**ww**	**ds**	**ww**	**ds**	**ww**	**ds**	**ww**	**ds**
Year 2019	**V1**	47.03a	22.66c	193.03a	78.41c	7.28ab	4.00b	38.75b	42.86ab
	V2	42.37abc	29.28abc	189.03a	108.90bc	7.25ab	5.17ab	39.98a	42.72ab
	V3	41.56abc	35.05ab	191.45a	140.03ab	6.70abc	5.73ab	40.44a	41.68bc
	V4	37.76bc	34.51ab	137.08b	135.79ab	6.12c	5.40ab	38.30bc	43.11a
	V5	41.08abc	27.06abc	167.77ab	96.88bc	7.24ab	4.96ab	39.94a	40.73c
	V6	38.79abc	26.58abc	165.52ab	94.97bc	6.89abc	5.23ab	40.50a	42.12ab
	V7	43.72ab	35.59ab	194.77a	177.36a	7.65a	6.18a	37.36c	42.34ab
	V8	34.15c	27.81abc	164.44ab	98.39bc	6.56bc	4.78ab	40.00a	40.62c
	V9	43.24ab	25.57bc	190.44a	93.53bc	7.14abc	4.64ab	37.63bc	43.27a
	V10	44.10ab	36.41a	197.92a	134.17ab	7.61a	6.11a	38.67b	42.06ab
	Grand mean	41.38a	29.90b	179.14a	115.88b	7.04a	5.22b	39.16b	42.15a
	ANOVA								
	V	**	***	***	***	***	*	***	***
	E	***		***		***		***	
	V×E	***		***		**		***	

		Pn		C		Tr		Tleaf	
	V	**ww**	**ds**	**ww**	**ds**	**ww**	**ds**	**ww**	**ds**
Both years	**Y**	ns		***		**		***	
	V×Y	***		***		***		*	
	E×Y	***		***		ns		***	
	V×E×Y	***		***		**		**	

ww: well-watered; ds: drought stress; Pn: photosynthesis rate; C: stomata conductance; Tr: leaf transpiration; Tleaf: leaf temperature; SDW: Straw dry weight; V: variety; E: environment; Y: year; *** significant at p = 0.001; ** significant at p = 0.01; * significant at p = 0.05; ns: not significant. The means with the same letters are not significantly different. The bold values indicate the highest and lowest value measured.

The RLD was estimated by RID along the soil profiles using the geometrical model for both ww and ds treatments at the end of the stress. Our results showed a strong and significant effect of water deficit on the number of total roots (NTR) and RLD profiles (see Table 6).

Varieties V1 and V8 exhibited the highest NTR in ww and ds conditions respectively, while V2 and V10 exhibited the lowest in ww and ds conditions respectively. Among varieties, V4 exhibited the lowest RLD (0 cm – 120 cm) in both the ww and ds environment. Under drought stress, V1 and V8 recorded the strongest RLD in the shallow horizon (0 cm – 50 cm) and deep horizon (60 cm – 120 cm) respectively (see Table 6). From the data presented in Table 6, the global trend of the varieties' root system's responses to early drought stress is highlighted on Figure 4. Drought stress induced significant reduction of RLD in the 0 cm – 50 cm soil horizon; it increased in the 60 cm –120 cm deep soil layers.

Table 6

Average Performance of Sorghum Varieties for Root Traits Under Well-watered and Drought Stress Conditions

	NTR		**RLD [0-120cm]**		**RLD [0-50cm]**		**RLD [60-120cm]**	
V	ww	ds	ww	ds	ww	ds	ww	ds
V1	63.00a	28.66ab	1922.80a	1687.83g	3457.35c	2764.00a	800.02c	1578.33c
V2	32.00f	22.33cd	1760.68bc	2041.48c	3286.61e	2698.90b	654.07f	1571.89c
V3	40.33c	26.00bc	1751.29bc	1769.92f	3358.45d	2435.41f	648.08f	1294.57e
V4	50.33b	31.66a	1467.24e	1574.29h	2519.95h	2236.74g	715.29e	1090.53f
V5	62.66a	28.66ab	1781.89bc	1945.37e	3245.57e	2641.44c	719.73e	1448.18d
V6	40.00cd	28.66ab	1739.46bc	1993.00d	3564.50b	2520.00e	873.33a	1421.00d
V7	36.00e	25.33bc	1827.72b	2190.90b	3311.3de	2598.55d	772.75cd	1807.34b
V8	42.00c	30.66a	1991.88a	2453.95a	3659.27a	2704.23b	800.89c	2266.67a
V9	37.00de	25.00bcd	1625.93d	1687.83g	2738.30g	2271.24g	831.38b	1271.11e
V10	37.00de	21.33d	1696.45cd	1757.95f	3121.66f	2428.02f	763.37d	1279.32e
Grand mean	44.03a	26.83b	1758.61b	1897.27a	3214.64a	2522.88b	757.89b	1502.8a
ANOVA								
V	***	***	***	***	***	***	***	***
E	***		***		***		***	
V×E	***		***		***		***	

ww: well-watered; ds: drought stress; NTR: number of total roots; RLD: root length density (m m^{-2}); [0–120 cm], [0–50 cm] and [60–120 cm] represent the depth considered; V: variety; E: environment; *** significant at *p* = 0.001. Means with the same letters are not significantly different. The bold values indicate the highest and lowest value measured.

Figure 4

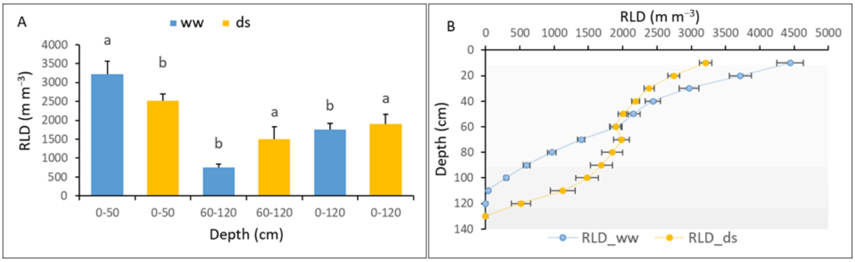

Figure 4 – Root Length Density (RLD) of Sorghum Varieties Under Well-watered (ww) and Drought Stress (ds) Conditions at the End of the Stress Period

Notes. (A) RLD distribution at [0-50], [60-120] and [0-120] depth horizons (B) Impact of water deficit on RLD profile. Data are means +/- standard error. Significant differences are indicated by different letters.

4. Relationship Between Vegetation Indices and Sorghum’s Growth Traits

Results presented in Table 7 show the relationship between LAI, biomass, and vegetation indices. Nonlinear and linear regression models were fitted using the 2018 field data set (n = 390, calibration data). Regression analysis revealed a good relationship between LAI or biomass with NDVI, CTVI, GNDVI, MSAVI2, and SR. To assess the performance of vegetation indices to estimate LAI, we compared the coefficients of determination (r^2) of the relationships between NDVI, CTVI, MSAVI2, SR, and LAI that were respectively of 0.83, 0.82, 0.76 and 0.77 with highly significant p values. However, the r^2 for biomass estimation using the same indices were comparatively lower than those for LAI (0.6, 0.6, 0.57, and 0.47).

Table 7
Regression of Sorghum LAI and Biomass on Vegetation Indices (n = 390)

Vegetation indices	Regression models	r	r²	P-value
NDVI	$LAI=0.3732*e^{2.9648*NDVI}$	0.91	0.83	<0.001
CTVI	$LAI=0.0069*e^{5.5322*CTVI}$	0.9	0.82	<0.001
MSAVI2	$LAI=0.3392*e^{2.7498*MSAVI2}$	0.9	0.82	<0.001
SR	$LAI=0.4438*SR+0.0126$	0.87	0.77	<0.001
NDVI	$Biomass = 3.1153*e^{3.7021*NDVI}$	0.77	0.6	<0.001
CTVI	$Biomass = 0.0206*e^{6.9446*CTVI}$	0.77	0.6	<0.001
MSAVI2	$Biomass = 2.7357*e^{3.4587*GNDVI}$	0.77	0.6	<0.001
SR	$Biomass = 6.0128*SR + 0.8947$	0.68	0.47	<0.001

NDVI, CTVI, MSAVI2 and SR: vegetation indices; r: coefficient of correlation; r^2: coefficient determination; LAI: leaf area index.

Figure 5 shows the NDVI plots with the corresponding LAI. The LAI values varied from 0.3 m^2 m^{-2} to 5.7 m^2 m^{-2} per plant across varieties, treatments, and developmental stages during the calibration trial in 2018. A saturation of the different vegetation indices was observed above LAI values higher than 4 m^2 m^{-2} per plant. To test the variance of calibration models, an ordinary least squares linear regression between calculated and measured LAI was done, and it revealed an r^2 value of 0.8 for LAI (see Figure 5). The ANOVA revealed highly significant effect of varieties, environment, and the interaction (V*E) ($p<0.05$) on both calculated and measured LAI and biomass with almost the same values (see Tables 8 and 9).

Figure 5

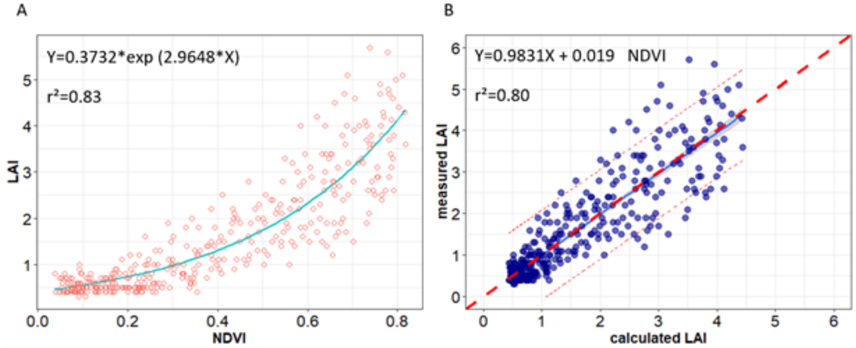

Figure 5 – Calibration of LAI prediction model from NDVI vegetation index

Notes. (A) Relationship between normalized difference vegetation index (NDVI) and leaf area index (LAI); (B) Measured LAI vs. corresponding LAI values predicted using empirical equation in Figure 5A. The dashed red line in the graph is the 1:1 line.

Table 8
ANOVA of Leaf Area Index Measured (LAIm) and Calculated from Vegetation Indices (LAIc) and Average Performance of the Varieties Under Well-watered and Drought Stress

	LAIc_NDVI		**LAIc_CTVI**		**LAIm**	
V	ww	ds	ww	ds	ww	ds
V1	1.5	0.62	1.53	0.62	1.9	0.6
V2	1.56	0.61	1.59	0.61	1.9	0.8
V3	2.09	0.7	2.12	0.72	1.57	0.9
V4	1.6	0.58	1.63	0.57	1.4	0.45
V5	1.95	0.56	1.97	0.56	2.23	0.6
V6	1.39	0.7	1.43	0.7	1.63	0.57
V7	2.01	0.53	2.03	0.52	1.9	0.47
V8	1.93	0.68	1.96	0.69	2.63	0.8
V9	1.78	0.64	1.81	0.65	1.53	0.67
V10	1.74	0.48	1.77	0.47	1.57	0.53
Mean	1.75	0.61	1.78	0.61	1.83	0.64
V	*		*		**	
E	***		***		***	

	LAIc_NDVI	LAIc_CTVI	LAIm
V*E	*	*	*

V: varieties; E: environment; ww: well-watered; ds: drought stress; CTVI and NDVI: vegetation indices; Significance codes: ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05

Table 9
ANOVA of the Biomass Per Plant Measured (BPPm) and Calculated from Vegetation Indices (BPPc) and Average Performance of the Varieties Under Well-watered and Drought Stress

	BPPc_MSAVI2		BPPc_SR		BPPm	
V	ww	ds	ww	ds	ww	ds
V1	17.62	5.53	21.12	9.69	18.3	15.7
V2	18.27	5.38	22.08	9.54	22.55	10.79
V3	25.85	6.65	27.56	10.5	19.11	12.36
V4	18.73	4.96	22.38	9.01	17.38	7.9
V5	23.94	4.73	26.1	8.93	29.82	11.84
V6	15.77	6.62	20.49	10.49	23.87	11.39
V7	24.47	4.35	28.25	8.57	35.72	8
V8	23.59	6.32	26.84	10.36	27.32	9.21
V9	21.52	5.76	24.51	9.87	22.49	18.88
V10	21	3.75	24.55	7.91	18.28	5.86
Mean	21.08	5.42	24.39	9.5	23.48	11.31
V	*		*		***	
E	***		***		***	
V*E	*		**		***	

V: varieties; E: environment; ww: well-watered; ds: drought stress; MSAVI2 and SR: vegetation indices; Significance codes: ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05

5. Assessment of the Impact of Water Treatment on UAV Derived Traits

The combined analysis of variance revealed highly significant effect ($P \leq 0.05$) of the environment (E), variety (V), and their interaction (V*E) on all the vegetation indices under study (see Table 10). In ww conditions, the varieties recorded on average 0.6, 1.08, 0.76, 7.37 for NDVI, CTVI, MSAVI2, and SR respectively; the stressed plants showed lower values (i.e., 0.37, 0.90, 0.44, and 3.01). In ds conditions, the variety V3 exhibited the highest indices (0.59, 0.94, 0.66 and 4.02 for NDVI, CTVI, MSAVI2, and SR); V10 had the lowest (0.20, 0.83, 0.25, and 1.74).

Table 10
Average Performance and ANOVA of the Vegetation Indices of the Varieties Under Well- watered and Drought Stress

	NDVI		**CTVI**		**MSAVI2**		**SR**	
V	ww	ds	ww	ds	ww	ds	ww	ds
V1	0.63	0.38	1.06	0.92	0.71	0.46	6.83	3
V2	0.68	0.37	1.08	0.91	0.76	0.44	6.77	3
V3	0.73	0.59	1.11	0.94	0.81	0.66	7.97	4.02
V4	0.7	0.33	1.09	0.89	0.77	0.4	7.53	2.71
V5	0.71	0.39	1.1	0.94	0.79	0.47	7.91	2.85
V6	0.62	0.36	1.05	0.89	0.7	0.42	5.69	3.24
V7	0.74	0.28	1.11	0.88	0.81	0.35	8.59	2.2
V8	0.74	0.45	1.11	0.94	0.81	0.53	8.17	4.46
V9	0.7	0.4	1.09	0.94	0.78	0.49	6.99	2.92
V10	0.67	0.2	1.08	0.83	0.75	0.25	7.33	1.74
Mean	0.69	0.37	1.08	0.9	0.76	0.44	7.37	3.01
V	**		**		***		*	
E	***		***		***		***	
V*E	*		*		*		*	

V: varieties; E: environment; NDVI, CTVI, MSAVI2 and SR: vegetation indices (VIs); ww: well-watered; ds: drought stress; Significant codes: '***' 0.001 '**' 0.01 '*' 0.05

Results presented in Figure 6 showed the general trend of the evolution of VIs during plants growth in both ww and ds conditions. The vegetation indices of nonstressed plants gradually increased to reach their maximum at the 60th DAS (flowering time) before dropping slightly. In the stressed plots, the vegetation indices initially recorded a slight increase but then water deficit induced a reduction that was followed by a progressive increase after rewatering.

However, the VIs values of stressed plants did not recover values of the nonstressed plants. The results highlighted in this study testify the relevance of VIs to capture the differences induced by drought and that occurred from the 30th DAS to the 55th DAS. The post flowering decrease of the VIs observed in the ww treatment was due to the saturation of the VIs as plants have grown up enough in this environment.

Figure 6

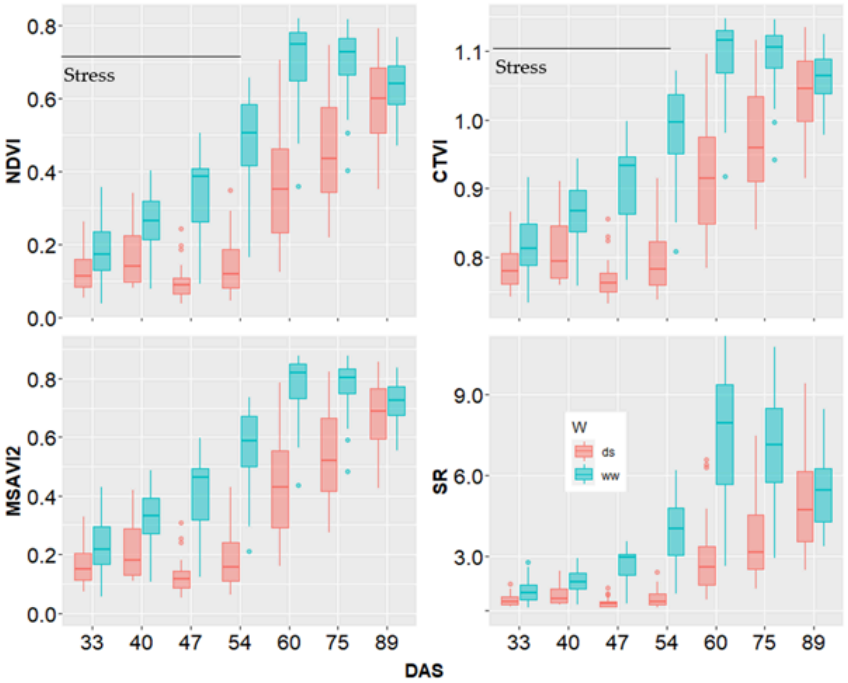

Figure 6 – Dynamics of Estimated Vegetation Indices Under Well-watered and Drought Stress Conditions

Note. Box plots represent the estimations for all the 10 sorghum varieties at a given stage. NDVI, CTVI, MSAVI2 and SR: vegetation indices; DAS: days after sowing; ds: drought stress; ww: well-watered.

Discussion

1. The Adaptive Behavior of the Sorghum Varieties Studied

The stress characterization revealed very negative values of water potential (WP = -5 bars) at the end of the stress period. This can be explained by the intensity of the stress experienced by the plants (FTSW = 0.3). To counteract the water deficit that occurs in their tissues, plants implement water retention mechanisms with very high energy. Consequently, it is necessary to provide equivalent energy to extract this water from the tissues (Brou et al., 2007). The behavior of the sorghum varieties, which consists in maintaining a high level of hydration despite the stress pressure, reflects a dehydration tolerance mechanism, with a low water potential of the tissues (Levitt, 1985). This limits cell growth because of loss of turgidity.

Water-limiting conditions lead to altered cell elongation, mainly due to low water flow from the xylem to neighboring cells (Fahad et al., 2017; Nonami, 1998). The number of leaves and the size of each leaf were reduced in drought conditions because their expansion depends on the turgor pressure and the amount of water assimilated. This induced a decrease in plant biomass accompanied by a reduction in leaf appearance and plant growth. Regarding physiological traits, drought stress causes a decrease in the transpiration rate, photosynthetic activity, and stomata conductance (Dwivedi et al., 2008; Fracasso et al., 2016). This adaptation mechanism also was revealed in pearl millet (Kholova et al., 2009, 2010) and cowpea (Belko et al., 2012). Under water deficit, the diffusion of CO2 to the carboxylation sites is limited because of stomata closure and increased mesophyll resistance. This inhibits the transport of electrons, leading to an imbalance between the electron transport rate and

CO2 fixation rate (Verma et al., 2018). The photosynthetic performance is one of the parameters providing useful and quantitative information on plants condition and vitality (Banks, 2018; Oukarroum et al., 2007; Zegada-Lizarazu & Monti, 2013). Tingting et al. (2010) showed that the process of photosynthesis is sensitive to changing environmental conditions, and the way in which plants adapt to their environment is propitious to photosynthesis. The recovery of photosynthesis upon rewatering indicates that the PSII systems had recovered their ability to deal with the absorbed light and the accumulated energy. Hence, oxidative permanent damage may not have occurred at the early growth stages, or as suggested by Oukarroum et al. (2007), the maximum quantum yield of photochemistry was not affected by the drought. The drop of plant growth rate caused by the lack of water during a given period often leads to difficulties in covering the normal development in terms of height or biomass (Hud et al., 2016). This behavior is not always a disastrous consequence. It could be a means of adaptation that allows the plant to maintain its development but at a slower pace. This was the case of the variety V6, for instance, which produced well despite a low DRI in height and biomass. These are part of physiological functioning that confer drought tolerance to sorghum (Hadebe et al., 2017; Harris et al., 2007; Kapanigowda et al., 2013). The agro-physiological behavior of a plant depends on the genotype, the severity of the drought, and the time of occurrence (Chaves et al., 2002; Jaleel et al., 2008). Early water stress acts differently on sorghum varieties depending on the variety's stage of development. It is well-known that when drought occurs at the vegetative stage before panicle exertion, plants recover better. This may explain why the agronomic performances of some long-duration varieties of the *guinea* and *bicolor* breed (V1, V4) were weakly affected by early cycle drought. Long-duration varieties were able to catch up and stabilize production despite a lack of water at the early stage. According to Araus et al. (1989), this phenomenon is due to stomata control, which is more effective in the young growth stages. This could have been the case of variety V1, which responded to water deficit by closing its stomata, thus allowing it to limit exchanges with the environment until water conditions become favorable and the growth could resume and compensate for the losses due to drought. Contrariwise, V4 showed the lowest DRI and a slight variation of stomata conductance and yield under drought stress. A hypothesis is that this variety recovered well after the 2 weeks allowed for recovery measurement. However, the drought adaptation conferred by the long cycle is not sufficient to consider such varieties appropriate for the future. Previous studies have shown that the duration of drought episodes at the beginning of the season is likely to increase with the worsening of global climate change impacts (Blanc, 2012; Vadez et al., 2012), therefore even long-duration varieties may be affected by early drought stress if the duration is long.

Roots play an important role as a support, but also provide the plant with the water and mineral elements it needs. Thus, their study represents a very effective means of characterizing drought adaptation. Some authors showed that the spatial distribution of root length density determines water and nutrient uptake (Intergovernmental Panel on Climate Change, 2014). In the present study, the varieties V1 and V8 turned out to be very interesting. They yielded well under drought, and their adaptations were mainly based on a high RLD (60 cm – 120 cm) (V8) and the increase of dead leaves (V8 and V1) contrarily to V4, which had the lowest RLD (60 cm – 120 cm) and a low grain yield. Additionally, some varieties have densified their root system to be able to exploit a larger surface area of soil and to increase the absorption of water and mineral nutrients (Comas et al., 2013). The high root density at depth allows them to reach moisture in the deeper soil layers and compensate for the lack of water supply.

Although the varieties V3, V4, and V5 were less productive, they could be of high interest for height or fodder breeding programs. Varieties V1, V2, V8, and V9 could be devoted for grain yield breeding. Phenotypic evaluation of germplasm can be useful for characterization, conservation, and maintenance of genetic resources (Naoura et al., 2019). This study revealed a large agro-morphological diversity of quantitative traits. Overall, the results showed that plant response to early drought was genotype dependent (Sinclair et al., 2018) and some varieties expressed a strong ability to reduce water loss by decreasing leaf transpiration rate through stomata closure and increasing the number of dead leaves. These were among the adaptation strategies used by the studied varieties to tolerate drought stress conditions in both seasons.

2. Monitoring Plant Growth by UAV Based Phenotyping

Recent advances in high throughput field phenotyping have boosted the power of physiological breeding (Araus & Cairns, 2014; Fahlgren et al., 2015; Hu et al., 2018; Reynolds & Langridge, 2016). Currently, UAV technology is an alternative to the manual collection of crop data, offering information on traits and factors affecting crop development and productivity with relatively shorter time and lower cost (Du & Noguchi, 2017; Yu et al., 2016). The moderate to strong relationships (see Table 7) found between the UAV-derived plant spectral traits and the leaf area index and the biomass indicate that UAVs could be useful for phenotyping West Africa sorghum genotypes (Gano et al., 2021). The NDVI is an indicator of the combined effects of chlorophyll concentration, canopy leaf area, and yield (Erdle et al., 2011). The estimation of the NDVI can be used as a reference index for the dynamic monitoring of the biomass changes during the growth season of sorghum. NDVI estimates are influenced by many factors, such as measurement time, sensors, and environmental conditions (Crusiol et al., 2017), and there is no one absolutely accurate measurement method for NDVI estimation.

Improved precision would also contribute to further applications for field management (Foster et al., 2017). Results presented herein demonstrate the importance of using NDVI related vegetation index as indirect selection criteria by reporting genetic variation for VIs among varieties, the effect of water treatment on VIs and their interaction with varieties, and the relationships between VIs and LAI and biomass of sorghum. This attests the ability of VIs in estimating growth rate, biomass accumulation during the vegetative stage and yield set up (Babar et al., 2006).

3. Key Traits Involved in Drought Tolerance for Breeding

As a major challenge for agricultural production, drought tolerance is a prime target for molecular approaches to crop improvement. To obtain significant results, these approaches must be based on phenotyping protocols that are appropriate at all stages of plant development (Salekdeh et al., 2009). Because drought adaptation traits are complex and polygenic, the understanding of their physiological and genetic basis is still incomplete. This challenge comes at a time when plant biologists are witnessing an explosion in the availability of new high-throughput technologies and genomic information. However, the identification of preferred selection criteria remains unclear and still makes phenotyping laborious. According to Passioura (1977), the conceptual framework for drought phenotyping is based on the equation expressing the product yield of WU (quantity of water used), WUE (conversion of WU into dry biomass), and HI (the fraction of dry matter converted into grain). Therefore, it is important to design experiments to test these factors by distinguishing the impact of WU and WUE on production. In other words, when looking at productivity, it is important to identify the effects of growth stress that may affect assimilations transport. By considering these components of performance individually, it is possible to target traits more effectively in relation to environmental constraints. In the case of early-cycle water stress, there are several key phenotypic traits highlighted (see Table 11) to help target phenotyping. In addition, it would be useful to select high yielding genotypes that are stable across environmental conditions and years. To do so, it would be interesting to follow growth-related traits such as plant height and NLA, DWP, Tr and Pn because these traits are susceptible to environmental changes.

Table 11
Example of Traits Associated with Different Yield Factors Worth to Phenotype Under Conditions of Early-cycle Water Stress in Sorghum

Traits	Stage	Phenotyping technique	Interest for breeding
Root Length Density (RLD)	Growth	Count	Yield
Number of adventitious roots	Growth	Count	Yield
Soil water stock	Growth	Metric	Yield
Biomass rate	Growth	Metric	Biomass
Plant height rate	Growth	Metric	Biomass
Dead leaves weight	Growth	Metric	Yield
Photosynthesis rate	Growth	Metric	Yield
Transpiration rate	Growth	Metric	Yield
NDVI	Growth	Metric	Biomass
Grain weight	Harvest	Metric	Yield
Number of grains	Harvest	Count	Yield
Stem dry weight	Harvest	Metric	Biomass

Moreover, this study demonstrated successful and rapid assessment of NDVI related VIs (CTVI, MSAVI2 and SR) using a UAV platform that showed high accuracy in assessing variation in plant development. The accuracy of the UAV platform was validated by ground truth data, and it proved a significant advantage of UAV over the handheld data acquisition platform from the stem elongation stage to late grain filling stage, especially under water- limited conditions.

Drought-prone environments are diverse and the biotic and abiotic stresses that affect yield during drought periods are numerous (Richards et al., 2002). Therefore, our objective is not to propose unique criteria for drought stress phenotyping. Rather, we suggest that each experiment be conducted with a specific, realistic goal and with WUE and yield set up as reference traits (Venuprasad et al., 2007). Such reference traits will ensure the relevance of field results that are assessed and deposited in public databases for a standardized recording and reporting of drought-related phenotypic data.

Conclusion

This study is justified by the challenge that researchers have set to improve adaptation to early drought stress in cereals, particularly sorghum. We have shown the impact of water deficit on sorghum growth and development. The early stress is a major factor in the evolution of biomass, height, and leaf development. Even though it occurred early, its impact leads to yield instability. This study also highlighted plant adaptation mechanisms under early water deficit based on growth; photosynthesis and transpiration reduction; senescence increase; stomata closure; and roots length density increase. We also highlighted the ability of UAV platform to phenotype drought stress in West Africa sorghum varieties. Finally, we proposed key phenotyping traits that involve the different factors that govern production for a more efficient characterization of drought adaptation. Future areas of study could include phenotyping entire sorghum collections in different growing conditions during the year to better fix the adaptation mechanisms. Based on the predictions of precariousness linked to climate change, it would be more than necessary to select varieties that are able to adapt and stabilize performance independently of the season and year.

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9. Toward a Regional Field Phenotyping Network in West Africa

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Abstract

Phenotyping plays an important role in crop science and breeding programs. The accurate, rapid acquisition of phenotypic information on plants in different environments helps researchers explore the genomes' inheritance and expression patterns and determine the association of genomic and phenotypic information and ultimately increase crop yields. Traditional methods for acquiring crop traits (e.g., plant height, biomass, yield, etc.) rely on manual sampling, which is laborious and time-consuming. Fortunately, technological advances are resolving the high-throughput phenotyping bottleneck. To optimize the benefit of breeding programs in West Africa (WA) on the sustainability and performance of cropping systems (considering climate change and agroecological transition) developing high throughput field phenotyping methods is essential. However, the establishment of this type of activity requires infrastructure, equipment, management, and most importantly, dedicated and trained staff. Also, new technologies like Unmanned Aerial Vehicles (UAV) have recently become an important tool for fast and non-destructive high throughput phenotyping. This technology is flexible, practical, and provides easy access to data and high spatial resolution. UAVs are powerful tools for phenomics and genomics studies. As such, CERAAS and its partners are developing a field phenotyping network

in the West African sub-region—the general scheme of which is presented below.

Keywords: Breeding, Field phenotyping, High-throughput, Regional network, West Africa

Introduction

Crop production must double by 2050 to respond to predicted demands of the global population (Ray et al., 2013). To meet this demand, crop yields should be increased by 2.4% annually, but currently, the average rate of yield increase is only 1.3%, with yields stagnating in up to 40% of the land under cereal production (Fischer & Edmeades, 2010). To ensure improved agricultural productivity, developing new varieties that are well adapted to specific environments is one of the main avenues for agricultural research centers. An effective approach to achieve this objective is the design of marker-assisted breeding programs which requires scientists to better understand the connection between a plant's observable characteristics (phenotype) and its genetic makeup (genotype). By establishing the connection between genotype and phenotype, it is possible to select high-yielding stress-tolerant plants and improve agricultural production to satisfy the requirements of the growing human population (Li et al., 2014; Thorp et al., 2015, 2018; White et al., 2012).

In the last two decades, genome sequencing of crops has proceeded at a rapid pace, but the translation of these data into the identification of desirable traits has been constrained by the lack of knowledge of the associated phenotypes (Furbank & Tester, 2011; Zaman-Allah et al., 2015). Besides, marker assisted breeding programs often require working with large mapping populations (more than 250 lines in most cases). Depending on the experimental design used or the number of treatments applied, phenotyping may require thousands of individual plots to be measured. To relieve this bottleneck and to fully benefit from the available genomic information, reliable, automatic, multifunctional, and high-throughput phenotyping platforms should be developed to offer plant scientists new insight into all the aspects of living plants. In recent years, high-throughput phenotyping platforms (HTPPs) have been developed (Araus & Cairns, 2014; Yang et al., 2013). However, most of these are fully automated facilities in greenhouses or growth chambers, equipped with a precise environmental control. Although HTPPs enable the capture of detailed, non-invasive information throughout the plant life cycle, the results from controlled environments are distinct from the actual situations that plants will experience in the field, making it difficult to extrapolate data from controlled environments to the field. As a regional center of excellence that focuses on the genetic improvement of dryland crops (e.g., sorghum, pearl millet, fonio, groundnut, cowpea and sesame), CERAAS/ISRA proposes to engage the breeding community in the development of a field phenotyping network of testing sites. The goal is to provide a rich ground for interactions across disciplines in order to develop improved varieties and management packages adapted to specific stress scenarios and sensitive to socio-cultural contexts, and hence address the multiple complex challenges facing plant breeding in West Africa. Family farming is essential, and it must meet an increasing food demand in diverse and changing agro-climatic environments and in connection with changing agricultural sectors (i.e., food, non-food agricultural products, seeds). This chapter's objective is to propose a roadmap to associate different technologies—varying from manual measurements to image analysis and UAV onboard sensors—in a field phenotyping network in the Sahelian sub-region.

1. Institutional Positioning

CERAAS, Centre d'Études Régional pour l'Amélioration de l'Adaptation à la Sécheresse, is a research center of ISRA (Institut Sénégalais de Recherche Agronomique) specialized in drought adaptation studies. In 2018, CERAAS was elevated from a National Center of Specialization to an ECOWAS Regional Centre of Excellence (RCE) on dryland cereals (e.g., millet, sorghum and fonio) and associated crops (e.g., peanut, cowpea and sesame). The RCE is a joint entity between CERAAS, two other centers of ISRA (the Bureau d'Analyse Macroéconomique – BAME and the Centre National de Recherche Agronomique – CNRA), the Institut de Technologie Alimentaire (ITA) and the Ecole Nationale Supérieure d'Agronomie (ENSA-University of Thies). The primary mandate of RCE is to lead research on suitable drylands-cereal technologies and varieties in the West and Central African region.

With its historical partner, CIRAD (Centre de Coopération Internationale pour la Recherche en Agronomie pour le Développement), CERAAS is running a partnership network dedicated to innovation in crop improvement in Western Africa (dP-IAVAO which stands for dispositif en partenariat-Innovation et Amélioration Variétale en Afrique de l'Ouest, in French). The proposal of the dP-IAVAO is to rethink varietal improvement that has so far focused mainly on specialized agricultural and social systems. The aim is to recognize the plurality of agricultural systems and corresponding varietal demands, and to mobilize more disciplines and advanced tools towards more agile breeding programs that respond to the diversity and complexity of these agricultural systems.

Interdisciplinarity is key to this proposal, and it needs to be effectively integrated into innovative breeding programs. The scientific vision of the dP-IAVAO is thus structured around four research domains involving multiple disciplines and constitutes a platform fostering dialogue and interactions between its components:

– *Understand the crop improvement system*. This first domain aims at better describing the different components of the agri-food system in which crop improvement operates.

– *Genetic analysis and crop improvement*. This domain, which constitutes the historical heart of crop improvement, aims to mobilize modern genetic tools to explore the diversity and complexity of agricultural systems.

– *Variety adoption and innovation management*. The effective implementation of redefined breeding objectives and the creation of corresponding varieties provides the subject of an iterative analysis on the adoption and dissemination of this new diversity within traditional diversity.

– *Partnership modalities and research practices*. The context in which life sciences research operates has become significantly more complex over the past 30 years: international regulations on access to and sharing of genetic resources have evolved considerably, and at the same time, research products are increasingly subject to intellectual property constraints related, for example, to the development of the seed sector and biotechnology.

The dP-IAVAO was also part of an evolving West African partnership context with a new research structure led by CORAF and supported by

WAAPP/PPAAO, which aims at the emergence of Regional Centers of Excellence (RCE). The dP-IAVAO, which is based on existing research facilities and projects, is improving coordination at the regional level, but also guiding the design of new flagship projects and the development of infrastructures and technical capacity. Education and training are also an essential component of the dP-IAVAO as it contributes to the training of a new generation of plant breeders.

The geographical boundaries of the dP-IAVAO include the Sahelian and Sudanese (200 – 1200 mm) areas of West Africa where the cultivation of dry cereals such as millet, sorghum, fonio, and their associated crops such as cowpea, groundnut, and sesame is predominant. In this area, several breeding programs working on these species, notably from Senegal, Mali, Burkina Faso, and Niger, are involved in projects focused on innovative approaches for crop improvement (participatory selection, marker-assisted selection, etc.). However, other countries located in these areas, (Chad, Guinea, Cameroon, Côte d'Ivoire, Ghana, Togo, and Benin) and with research activities on one or more of the crops listed above, are also associated with the dP to develop collaborations on specific topics, in particular field phenotyping and training activities. The central theme of the dP-IAVAO is therefore the integration of a multidisciplinary approach in the design and effective implementation of innovative varietal breeding programs in response to the complexity of the agro-ecological systems encountered in West Africa. In terms of design, the breeding program is considered an integration place enabling the production of genetic materials responding to the demand.

2. High-throughput Phenotyping Methods

The crop phenotype is an expression of the genotype (G) and the environment (E) in which it grows. Crop phenotyping generally includes agro-morphological traits that provide indications on the dynamics of yield establishment and its genotypic and environmental variability (e.g., plant height, counting LAI, lodging, crop canopy cover), canopy spectral texture (i.e., spectral features), physiological traits (e.g., chlorophyll, biomass, pigment content, photosynthesis), abiotic/biotic stress indicators (e.g., stomatal conductance, canopy temperature difference, leaf water potential, senescence index), nutrients (e.g., nitrogen concentration, protein content), and yield. Field phenotyping is a critical component of plant breeding programs, as the ultimate expression of the genetic factors, environmental factors, and their interaction on critical production traits, such as yield potential and tolerance to abiotic/biotic stresses (Araus & Cairns, 2014; Neilson et al., 2015). Field phenotyping is increasingly recognized as a key approach capable of delivering the required throughput and an accurate description of trait expression in real-world cropping systems. However, for a higher precision, the performances of breeding materials must be evaluated through a wide range of environmental conditions (González-Dugo et al., 2015; González-Recio et al., 2014; Rahaman et al., 2015).

Traditionally, phenotyping was done manually, and it was time consuming and expensive. To move towards high throughput methods, new phenotyping approaches relied largely on imaging technologies. Different methodological approaches that use spectral reflectance, canopy temperature by thermal imaging, and visible light imaging have been proposed to evaluate phenotypic traits in the field (Araus & Cairns, 2014). The agro-morphological traits of a crop can be estimated using an RGB camera (visible) by building the digital surface model (DSM) or the digital elevation model (DEM) and by conducting image classification analysis, which can be used to estimate the plant height, the proportion of lodging area, seedling emergence, etc. (Bendig et al., 2015; Hunt et al., 2005, 2010; Li et al., 2015). The absorption and reflectance characteristics of crops can be used to calculate vegetation indices related to agro-morpho-physiological traits (Nigon et al., 2015; Øvergaard et al., 2010; Swain et al., 2010). For instance, the temperature of the canopy is closely related to the cooling capacity of the plant, which depends on the transpiration of the crop, itself reflecting the plant water potential, stomatal conductance, etc., under stress or non-stress conditions. Crop yield can be predicted using proxies based on the combination of hyperspectral and thermal infrared data (Berni et al., 2009; González-Dugo et al., 2015).

Currently, advanced field-phenotyping platforms use high throughput ground wheeled or aerial vehicles deploying multiple types of sensors to measure plant traits on a timescale of a few seconds per plot. Although phenotyping with ground vehicles such as phenomobiles is extremely precise, the process can be time-consuming if there are too many plots to phenotype (Cobb et al., 2013; Zhang and Kovacs, 2012). Therefore, this approach would be unsuitable for an African cross-regional network due to the cost, heavy maintenance, transport, and lack of maneuverability.

Satellite imaging technologies have become extremely useful when collecting data for various agricultural applications (Li et al., 2014; Sankaran et al., 2015). However, the major limitations of using the currently available satellite sensors are the high cost, the lack of spatial resolution for the identification of desirable traits, the risk of cloud cover, and long revisit periods (Gevaert et al., 2015; Han-Ya et al., 2010). For breeding programs, the resolution of the satellite sensor is still not enough to compare individual lines or plants. In contrast, UAVs have demonstrated capabilities for large-scale monitoring of crop condition due to the high spatial and spectral resolutions of the sensors.

In recent years, the use of UAVs has increased considerably in agricultural research programs due to the drop in prices, the miniaturization, the higher resolution of sensors, the ease of use (piloting, programming of flight plans), the improvement of computing (image analysis) and its strong potential for applications in breeding programs (Ballesteros et al., 2014; Berni et al., 2009; Candiago et al., 2015; Chapman et al., 2014; Gómez-Candón et al., 2013; Hunt et al., 2005; Liebisch et al., 2015; Zhang & Kovacs, 2012). This technology provides a low-cost approach to meet the critical requirements of spatial, spectral, and temporal resolutions. To assess the precision and efficiency for field-based phenotyping in small plots by different remote sensing techniques, three remote sensing approaches including UAV, proximal sensing, and satellite-based imagery, were compared. This study demonstrated that the UAV-based remote sensing was the most suitable approach for acquiring canopy temperature and normalized difference vegetation index (NDVI) in breeding populations (Tattaris et al., 2016). Therefore, UAVs are becoming critical in the high-throughput phenotyping of many plots and field trials in a near real-time and dynamic manner. UAVs can be used to execute autonomous tasks through the use of radio remote control equipment and an auto-control system, which can be divided into several types according to the flight mode (Sankaran et al., 2015). Field phenotyping platforms that use UAV tools have a higher potential thanks to the development and use of adapted sensors such as digital cameras, multispectral cameras, hyperspectral sensors, and infrared thermal imagers, which are commonly deployed UAV-RSP sensors. With advances in miniaturization, new sensors based on light detection and ranging (LiIDAR) are upcoming. The main applications of these sensors for breeding programs include the use of visible imaging for canopy surface modeling, crop height, and biomass estimation (Diaz-Varela et al., 2014; Mathews & Jensen, 2013; Zarco-Tejada et al., 2014); the use of visible–near-infrared spectroscopy to identify physiological status (Nigon et al., 2015; Overgaard et al., 2010; Sugiura et al., 2005; Swain et al., 2010); thermal imaging to detect water stress (González-Dugo et al., 2013, 2014); LIDAR cloud point to measure plant's fine-scale geometric parameters with high precision (Wallace et al., 2012); and microwave imaging to estimate soil moisture and canopy structure parameters by combining different spectral bands (Acevo-Herrera et al., 2010; Han-Ya et al., 2010).

3. Network Construction

At the national level, the field phenotyping network relies on three levels. The first level is centered on fine phenotyping. The second level is focused on varietal evaluation in different environments, while the third level consists of evaluations in farmers' fields. In addition to the breeding aspect, the network is also of significant interest for all research and development activities in agronomy. The diagram presented in Figure 1 lists the possible research actions at the different levels.

Figure 1

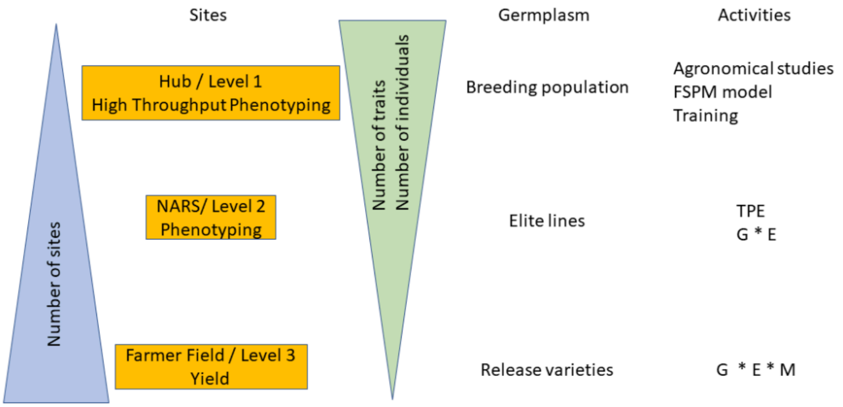
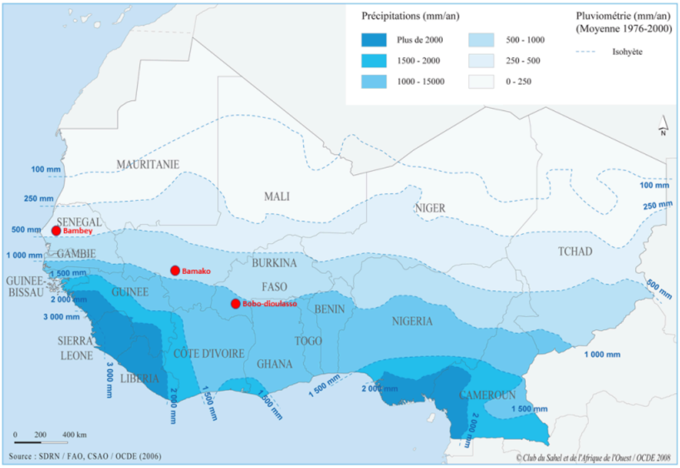


Figure 1 – Diagram of Activities Within the Field Phenotyping Network

Level 1: The fine phenotyping is done at a hub that is fully equipped and highly specialized to meet the needs of high throughput (i.e., the ability to conduct experiments with a large number of germplasms tested and to carry out precise measurements in a short time step). These representative high throughput phenotyping locations must also present all the guarantees to manage experiments with different agronomic treatments and should be selected based on environmental characterization, build on existing experimental sites that are functional, and back up the most advanced NARS (e.g., ISRA in Senegal, IER in Mali). This may require the development or rehabilitation of infrastructures like weather stations, drip irrigation systems, fencing, and modern data capture tools. There might be a scope for working in collaboration with the private sector at certain sites (e.g., Adventa or Corteva). The necessary equipment to carry out high-throughput phenotyping measurements should be available at these sites. Occasionally and depending on the resources, this equipment can be deployed to other sites (levels 2 and 3). These fine high-throughput phenotyping sites should also have all the advantages to conduct studies that aim to understand better crop adaptation mechanisms using functional-structural plant models. The development of infrastructures needs to be paired with a massive long-term training of students, technicians, and scientists/breeders ("multi-purpose breeders," capable of doing both breeding and reliable phenotyping) in order to develop a sense of ownership. Hence, three sites were chosen as potential high throughput phenotyping hubs across the subregion. Each hub is representative of the diversity of climate and soil conditions in the region (Figure 2): Bambey (ISRA research station, Senegal; 14.710825° N; -16.483797° E), Sotouba (IER research station, Bamako, Mali; 12.659558° N; -7.924943° E) and Farako-ba (INERA research Station, Bobo Dioulasso, Burkina Faso; 11.094251° N; -4.332719° E).

Figure 2



Source : SDRN / FAO, CSAO / OCDE (2006)

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Figure 2 – Regional Isohyets Mapping & Possible Location of High Throughput Phenotyping Hubs in Bambey, Bamako, Bobo Dioulasso

Level 2: This level is based on the national agricultural research sites, which generally form a good network throughout the country. The main objective of this network is to evaluate the performances of the breeding lines in different environments, including hot-spots for specific stresses and then to study genotype-environment interactions. Studies carried out at this level are of great importance to define the target population environment (TPE) at the national and regional levels. Robust crop simulation models exist that can be used to: (i) characterize climatic scenarios in all target regions (main TPE) and (ii) guide the choice of trait-management packages to optimize productivity locally, even in the context of different socio-cultural contexts. This work requires good quality agronomic data from the network of Level 2 sites. The proposed work would engage breeders in generating input data and knowledge for crop models in order to guide breeding decisions. Breeding programs would then have greater insight on breeding targets (i.e., an area with known and prevalent stress type, required traits and management options, as well as appropriate breeding approaches). Besides, enriching the analysis of TPE with a socio-cultural analysis of potential cropping system variants within the TPE is essential to better design technical solutions, in particular to target cultivar/management improvement, to local constraints.

Level 3: Farmers' fields are used to test promising breeding lines that are foreseen for release in this production system. At this level, only yield and yield components will be measured. This level is characterized by uncontrolled crop management. Therefore, to have a good estimation of varieties' performances, the number of farmer fields should be as large as possible to integrate the diversity of cropping conditions.

4. Data Management

Much of the power of this field phenotyping network is in the way the data it generates are connected across sites and years. An efficient data management system needs to be established to ensure that evaluation and breeding data are integrated and shared across sites, network levels, and breeding programs. CERAAS, as a partner of IBP (Integrated Breeding Platform), benefits from logistic support for the use of the BMS (Breeding Management System). BMS is a complete software suite designed to boost the efficiency of plant breeding programs. This database combines crop information management, data analysis and decision-support tools to conduct most routine breeding activities, including the integration of different levels of molecular marker use. In other words, BMS represents an ideal tool to integrate data across the regional field phenotyping network.

5. Field Phenotyping Methodologies Developed in the Field Phenotyping Network

Based on the capacities of each partner/country and their financial possibilities, the development of the field phenotyping network is not synchronous among participating West African countries. The fine phenotyping hubs (level 1) and the evaluation sites (level 2) are generally located in national agricultural research stations. These sites have been well characterized previously and soil maps are usually available. They are equipped with a functional weather station, agricultural equipment, and have local manpower familiar with the requirements of research activities. For some sites, a renewal of the equipment is in progress. The field phenotyping network is expected to double in the next few years with the integration of a near infrared spectroscopy (NIRS) network that will enable high-speed phenotyping in the field of biochemistry.

Currently, Senegal is the most advanced in setting up the network since level 1 (hub) and level 2 sites are operational. For Mali, the phenotyping equipment is missing. The purchase of the UAV, pilot training, as well as the use of the image processing pipeline, are all under consideration. Burkina-Faso is lagging behind mostly due to funding reasons. Its level 1 site meets all criteria, but it still needs to be equipped with an irrigation system and UAV equipment, while in the level 2 sites, some weather stations are missing.

Across the different projects that allowed the start of West African field phenotyping network, UAVs technical solution has been chosen as an optimal solution to deploy across sites and trials. In Senegal the equipment consists of a FeHexaCopterV2 hexaCopter UAV system (Flying Eye Ltd., Sophia Antipolis, France). This UAV can carry three cameras fixed on a two-axis gimbal to point vertically downward. The first camera was an RGB ILCE-6000 digital camera (Sony Corporation, New York, NY, USA) with a 6000×4000 pixels sensor equipped with a 60 millimeter (mm) focal length lens. To minimize the blurring effect and noise in the images, the camera was set on speed priority (1/1250sec) and fixed on 100 ISO. The second camera is the AIRPHEN multispectral camera (Hiphen, Avignon, France) equipped with a 4.2 mm focal length lens and acquiring 1280×960 pixels images. The AIRPHEN includes six individual sensors equipped with filters centered on 450, 530, 560, 675, 730 and 850 nm, with a spectral resolution of 10 nm. The third camera is an infrared thermographic camera Tau 2 (Flir system, Oregon, USA) with 19 mm focal length.

The flight plan is defined with MikroKopter-Tools software (MikroKopter, Germany) to cover the entire area to be mapped and ensure an 80% frontal and lateral overlap along the track. Flight speed and image triggering depend on the flight altitude.

Figure 3

Figure 3 – View of an UAV Used for Image Acquisition with Its Onboard Sensors

A semi-automatic image-processing pipeline developed by ISRA/CERAAS and CIRAD generates radiometrically calibrated and geometrically corrected multiband orthoimages using Agisoft PhotoScan digital photogrammetric software (PhotoScan Professional 1.4, Agisoft LLC, Russia) (See Part 2-Chapter 1). Real reflectance is computed using a radiometric reference target positioned to the ground and imaged at every UAV flight. This reference target is previously spectrally characterized in controlled conditions. Geometric correction is done using ground control points (GCPs) that have already been georeferenced. Orthorectification is then performed using GCPs to increase the accuracy of the generated orthoimages; vegetation indices can be extracted from the orthoimages. Using this UAV image processing pipeline, a good correlation between field measurements and proxies from the UAV images was observed in a study conducted during the 2019 cold dry season in Senegal which involved a sorghum panel (African population) of 202 entries (Gano et al., 2021) (Figure 4 and Figure 5). Similar correlation levels were observed on pearl millet and peanut populations (Diop et al., 2021) and calibration work is currently underway for cowpea.

Figure 4

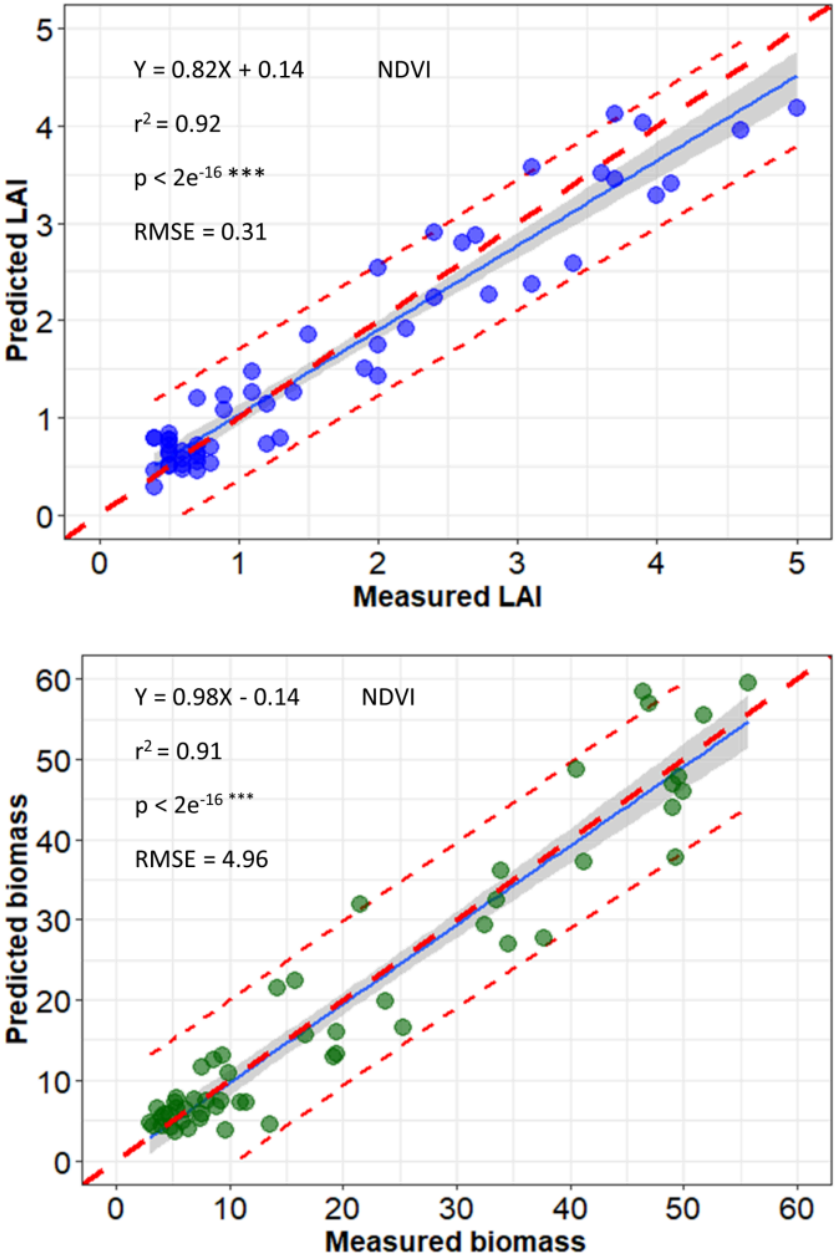

Figure 4 – Relationship Between Measured LAI and Biomass and Predicted LAI and Biomass Using the NDVI Extracted from UAV Images

6. Training

The training activities are already underway in different countries of the phenotyping network. A significant number of students have carried out their internships in the field with the network researchers. Two postdocs worked on the UAV phenotyping platform in order to develop the image analysis pipeline. Two PhD students are finalizing their thesis, and since the onset of the project a total of 15 MSc students have been supervised. A training session on eco-physiological and biochemical phenotyping as well as crop modeling were organized within the network or by the network's partners for PhD students, postdocs, and young scientists. It is expected that such training will be repeated over time in the framework of various projects. A sub-regional pilot contingent is already being built with two graduated pilots in Senegal.

Conclusion

The field phenotyping network initiated in 2016 is now in its second phase of construction. The activities in Senegal are ahead of schedule, but there is little doubt that other countries participating in the network will catch up. The drone-borne imaging phenotyping methodology is now functional for sorghum and millet culture but still under construction for peanut. The existing capacities meet the requirements of field high-throughput phenotyping and for training. The field phenotyping network is being rapidly strengthened by a biochemical phenotyping network with the deployment of NIRS equipment. Accordingly, West African crop improvement programs will become autonomous for the acquisition and analysis of phenotypic data in the fields of biochemical and morpho-physiological traits, thus meeting the requirements to better support breeding programs in their goal of contributing to the food security of future generations.

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10. High-throughput Root Phenotyping: Opportunities and Challenges for the Adaptation of Arid and Semi-arid Crops to Future Climates

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Abstract

Emerging constraints associated with climate change are posing an increasing threat to crop yields. In the arid and semiarid regions of Africa, crop failure, due to extreme events such as drought, is predicted to cause major food security issues. Root traits can improve crop resilience to drought and poor soil conditions by increasing the crop's ability to acquire water and soil nutrients. However, selection based on root traits in agronomically meaningful contexts poses practical challenges. In fact, phenotyping represents a major bottleneck for root traits breeding, with trade-offs between precision and throughput. In this chapter, we will describe advances in low- and high-throughput root observation and sampling methods that can be easily deployed to measure root traits in field conditions. We will further describe a high-throughput root phenotyping pipeline that has recently been implemented to phenotype root architectural and anatomical traits in pearl millet grown in West African Sahelian conditions. These new methods can facilitate the selection of next generation crops with improved root systems that are more adapted to future climates.

Keywords: root, field, drought, pearl millet, shovelomics, laser ablation tomography

Introduction

Changing climatic conditions are challenging crop production worldwide. Therefore, it is important to develop crop varieties that are more resilient to extreme weather conditions (e.g., temperature, floods, or drought). Such efforts are particularly required for crops grown in low income Sahelian areas, where guaranteeing crop yields is of major importance for food security. Crops with improved root systems that better capture water and nutrients have recently demonstrated utility in adapting to future climates (Lynch, 2018, 2019; Rogers & Benfey, 2015; Uga et al., 2013).

Several root architectural and anatomical traits (see Figure 1) have been described as beneficial for improving drought tolerance. In maize, plants developing fewer crown roots with steeper growth angles developed more roots at depth (more carbon is invested in growth of individual roots) and showed increased drought tolerance (Gao & Lynch, 2016; Lynch, 2018). In crops growing in arid and semiarid environments—such as sorghum, pearl millet or chickpea—deep rooting may improve access to water and grain production, especially when drought occurs at reproductive and grain-filling stages (Lynch, 2013; Thorup-Kristensen et al., 2020; Vadez et al., 2013). Reduced xylem diameter may also improve transpiration efficiency (biomass produced/water used) and grain production under drought in dryland cereals (Vadez, 2014; Vadez et al., 2014; Zhang et al., 2018). Breeding programs specifically targeting reduction in xylem diameter in wheat led to new varieties having more parsimonious use of water that yielded 11% more grains under drought conditions (Richards & Passioura, 1989).

Figure 1

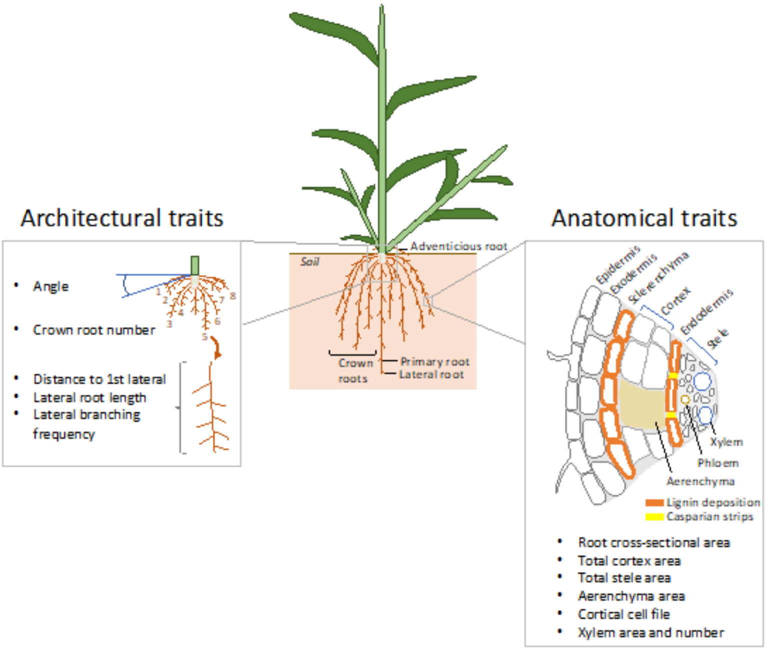

Figure 1 – Scheme of the Root Architecture and Anatomy of a Pearl Millet Plant at Vegetative Stage (1)

Note. The main architectural and anatomical root traits measured in high-throughput root phenotyping field studies are represented in the left and right boxes, respectively.

However, roots are complex organs constantly developing and adapting to the spatio-temporal heterogeneity in soil properties and resources (Maqbool et al., 2022). Although single traits have shown to improve drought tolerance in specific contexts, it is likely that more significant progress will be accomplished when considering root trait synergisms and integrated phenotypes (Lynch, 2022). Recently phenotyping multiple root traits, along with yield and yield-component related traits in field conditions, revealed that clusters of root phenotypes allowing greater soil exploration, restriction of water uptake, and greater soil penetrability could be considered breeding ideotypes for drought tolerance in maize (Klein et al., 2020).

Identification of markers controlling these root traits through genetic approaches rely on robust high-throughput root phenotyping techniques. For pre-breeding approaches, ideally these techniques should be deployed in agronomical conditions (Lynch, 2022). Still, the high dependence of root development on the environment does not guarantee the successful use of these markers in breeding programs (Lynch et al., 2021). For that matter, identification of easy to measure root phenotypes that could represent a proxy for integrated phenotypes, and development of easy to deploy phenotyping techniques to measure them, may facilitate the integration of root traits in breeding schemes.

A large number of root phenotyping techniques in laboratory, greenhouse, or field conditions have been developed recently (for reviews see Atkinson et al., 2019; Tracy et al., 2020; Wasaya et al., 2018; Watt et al., 2020). Here, we specifically describe recent advances in low- and high-throughput techniques that can be easily deployed in field conditions for root observation, imaging, sampling, and further trait characterization. Some of these techniques can be used to identify the genetic determinants controlling root traits that are beneficial for crop adaptation to drought, as illustrated in a case study describing high-throughput phenotyping of pearl millet root architectural and anatomical traits in field trials in Senegal. These techniques may also be of interest for breeders seeking direct selection of desirable root traits in their breeding program.

Root Phenotyping in Agronomic Conditions

1. Architectural Traits

Trenches – The trench method predicts root length density from root intersections counted on a vertical soil surface (trench). This method requires a calibration step where the relationship between root intersection density (RID) and root length density (RLD) is modeled (Chopart & Siband, 1999; Tennant, 1975). The model is relatively robust within one species grown in one soil type; new calibration steps would be required when phenotyping in other soil composition and organization (Faye et al., 2019b). Once the model is created, the software Racine 2.2 calculates RLD and generates 2D maps along a soil profile (Faye et al., 2019a). These maps provide agronomically meaningful information to estimate water or nutrient acquisition in different soil horizons.

This method is not high-throughput but allows easy and low-cost analysis of root system response to management practices or environmental factors. Models for RID conversion to RLD exist for maize, sorghum, sugarcane, rice, and pearl millet (Chopart & Siband, 1999; Chopart et al., 2008a, 2008b; Dusserre et al., 2009; Faye et al., 2019b). In pearl millet, the model was used to study root drought-responses of a drought-sensitive dual-purpose variety and a less drought-sensitive inbred line in typical Sahelian soils (Faye et al., 2019b). This approach revealed a reallocation of carbon for root growth, combined with a reduction of RLD in topsoil layers under drought, which is hypothesized to be beneficial for water capture (Faye et al., 2019b).

Minirhizotron imaging – Field minirhizotron imaging is a nondestructive method for dynamic visualization of root growth *in situ* (Vamerali et al., 2012). It involves installing a transparent glass or plastic tube inside the rooting zone of a plant and inserting a camera inside the tube to visualize the roots coming into contact with the tube. Tubes can be of different lenghts and installed within the soil horizontally, vertically, or at an angle (usually between 30° and 60°) without excessive soil disturbance and with good soil-to-tube contact (Vamerali et al., 2012). Angled tubes are useful to obtain information about root vertical distribution; horizontal tubes installed at different depths provide information about root depth distribution (Johnson et al., 2001). Recently, an ingenious minirhizotron imaging facility, where plants were sown directly on top of 5.5 m tubes inserted into the soil with an angle close to the horizontal (15.8° and 23.5°), allowed a larger observation area per unit of soil depth covered (Svane et al., 2019b). Root images are usually performed using commercially available digital cameras (Arnaud et al., 2019; Ohashi et al., 2015), although improved root detection in soil was recently obtained using visible to near-infrared images (Svane et al., 2019a). Images are used to extract root traits, such as root intensity by counting root intersections on a grid superimposed on the image (Chen et al., 2019). Open-source or commercially available sofware such as RootFly (Zeng et al., 2008) or RootSnap (Ohashi et al., 2015) can also be used to extract root length, root diameter, and root area from the images.

Minirhizotron imaging could be considered high-throughput because imaging can take from 90 seconds to 5 minutes depending on the imaging system and image resolution (Arnaud et al., 2019), although to date it has not been used in such fashion in field experiments. In semifield experiments (i.e., recontructed field rather than open field), minirhizotron were used to study root depth in spring barley genotypes (Svane et al., 2019b) and the relationship between root depth and nitrate uptake in winter wheat (Chen et al., 2019; Wacker et al., 2022). The later studies demontrated that deep root traits can predict deep nitrate uptake, which could be exploited to measure deep root growth and function using ^{15}N tracer.

Soil coring – Soil coring involves the insertion of a core sampler to a defined depth at the proximity of a plant, followed by soil core breaks and soil collection at different depths for root washing, scanning, and RLD calculation (Böhm, 1979; Schroth & Kolbe, 1994; Shashidhar et al., 2012). The core sampler is usually made of steel pipes (10 cm to 45 cm in diameter and 60 cm to 2 m in length), with a sharpened end that enters the soil and a hinged opening to aid soil core removal (Henry et al., 2015; Wasson et al., 2014). The core size, number of cores taken, and location of core sampling varies between studies (Bengough et al., 2000). This technique is intrinsically prone to error and the significance of the results much depends on the location and the number of samples (Rossi & Nuutinen, 2004). Indeed, significant variations among soil coring locations within a plot have been observed. It is generally accepted that RLD variance decreases as the sample number increases. Virtual RLD measurements using the CRootBox model estimated that between 10 and 50 core samples per plot would be required to reach a 10% standard error in wheat and maize, respectively (Morandage et al., 2019; Schnepf et al., 2018). More recently, similar approaches comparing virtual soil coring using the OpenSimRoot model and actual field soil coring clarified the location (5 cm from the plant base between rows) and the sampling number (five) to best estimate RLD in maize and common bean (Burridge et al., 2020; Postma et al., 2017). Nonetheless, sampling at three locations around the plant within a plot, within four different plots, showed differences in RLD along the soil profile in rice (Grondin et al., 2018), while a single sample per plot, within four plots, differentiated lines for RLD and maximum depth in wheat (Wasson et al., 2014).

Although soil coring cannot be considered high-throughput because of its labor-intensive characteristics, it was deployed to identify Quantitative Trait Loci (QTL) controlling root mass at different depths in a BC_2F_3-population, derived from a cross between Moroberekan and Swarna rice cultivars. Some of these QTL collocated with QTL controlling yield component-related traits (Dixit et al., 2015). However, the validity of these QTL remains to be demonstrated. To increase the throughput of soil coring for QTL identification, a new methodology was developed where coring was facilitated using a tractor-mounted hydraulic soil corer (Wasson et al., 2016). Root washing and scanning were replaced by automated counts of root impacts on both sides of soil-core breaks using UV illumination and fluorescence spectroscopy, allowing for RLD calculation directly in the field (Wasson et al., 2016).

Shovelomics – Shovelomics consists of manually excavating the crown root system using a shovel. The soil around the root system is then gently cleaned to manually measure root angle; to count crown roots number; or to take images to automatically extract numerous architectural traits, such as root angle, root width, lateral root length, and branching frequency using image analysis software such as Digital Imaging of Root Traits (DIRT) or Root Estimator for Shovelomics Traits (REST; Bucksch et al., 2014; Colombi et al., 2015). This method was developed on maize and used to successfully quantify root architectural traits in other crops, including common bean, cowpea, and wheat (Burridge et al., 2016; Das et al., 2015; Trachsel et al., 2011; York et al., 2018).

When combined with digital imaging, shovelomics is high-throughput and has been used to identify QTL controlling root length density or width in cowpea (Burridge et al., 2017). In maize, the deployment of this method on a panel of 400 sequenced genotypes, grown in different environments under irrigated and drought-stress conditions, allowed for better understanding of the interactions between the architectural traits associated with drought tolerance and the genetic determinants controlling architectural plasticity (Klein et al., 2020; Schneider et al., 2020b).

2. Anatomical Traits

Hand & microtome sectioning – Root anatomy is traditionally studied using histological approaches consisting in transverse sections of fixed or fresh tissue that can be observed under an optical microscope (usually 50x to 100x magnification) equipped with a digital camera for image capture (Ruzin, 1999). Fresh materials are often conserved in ethanol or methanol (usually 50% v/v or above), and sections are obtained by hand or by using a vibrating microtome. Hand sectioning requires a high level of skill obtaining fine sections without damaging samples, especially in the case of thin roots (Lhotáková et al., 2008). Microtome sectioning requires a prior time-consuming step of paraffin wax or resin embedding, although simpler root embedding protocols in agarose without fixation have been successfully developed (Zelko et al., 2012). Recently, an updated protocol increasing throughput of sectioning using a vibrating microtome on fresh, nonfixed root samples conserved in ethanol and embedded in agarose has been developed (Atkinson & Wells, 2017). The main upgrade in the method consists of using custom designed, 3D-printed molds to embed five to 15 roots in a block that can be sectioned in a single cut. It should be noted, however, that fixation or embedding can cause deformations in the tissue structure due to softening or shrinking, which requires taking multiple images per sample to increase the likelihood of quality images.

Anatomical features can be quantified from the acquired image by using simple software image analyses such as ImageJ (Schneider et al., 2012), or more automated software such as RootScan (Burton et al., 2012), PHIV-RootCell (Lartaud et al., 2015), or RootAnalyzer (Chopin et al., 2015). Although these methods are not considered high-throughput, sectioning was used to study the anatomical features in a panel of sequenced 274 rice genotypes under both irrigated and drought-stress conditions to identify genetic determinants controlling six anatomical traits (root diameter; cortex diameter; stele diameter; metaxylem diameter; and number and stele diameter in proportion of root diameter) and their plasticity (Kadam et al., 2017).

Laser ablation tomography (LAT) – LAT is a novel imaging technology used for rapid and simultaneous sectioning and imaging of roots at spatial scales, (e.g., from 0.1 mm to 1 cm) with micron-level resolution (Hall & Lanba, 2019;

Strock et al., 2019). The fresh root segments are often preserved in ethanol (50% v/v or above), dehydrated using graded ethanol series (e.g., 75%, 85%, 95% and 100%), and then dried in a critical point dryer to preserve their cellular structure. Methanol can also be used for preservation before transfer to 100% ethanol prior to critical drying point. LAT also is frequently conducted on fresh samples without the critical drying point step.

The LAT imaging system consists of three components: an ultrafast pulsed UV laser source, a motorized linear stage to which the root sample is mounted, and a DSLR camera or machine vision camera with infinity-corrected long working distance objectives. The beam from the laser source is deflected through a galvanometer along a rapidly scanned line, which is used as a cutting sheet to ablate the root sample by moving it into the beam path using a high-precision motorized linear stage. Autofluorescence from the ablation of the sample by UV wavelengths is simultaneously captured using the camera system. A 3D stack of the cellular structure of the sample can be generated by feeding the sample into the ablation beam at fixed increments using the motorized sample stage.

Anatomical parameters can be qualified from LAT image stacks using semiautomated software such as RootScan or MiPAR (Burton et al., 2012; Schneider et al., 2020a; Strock et al., 2019) or highly automated, next generation machine-learning and deep-learning imaging software (Hall & Lanba, 2019). This method is high-throughput (each root sample takes between 2 minutes and 5 minutes to process). LAT has been recently used to measure root anatomical traits such as root cortical aerenchyma area, cortical cell file number, and cortical cell size in 641 maize genotypes grown in the field under irrigated and water-deficit conditions in different environments (Schneider et al., 2020a). The heritability of these traits was compatible with genetic association analyses and allowed the identification of QTLs and genes possibly involved in the control of root anatomical plasticity in response to drought (Schneider et al., 2020a). LAT has also been used to visualize root colonization by arbuscular mycorrhizal fungi (Strock et al., 2019) or more recently lignification in maize (Schneider et al., 2021b).

Case Study: High-throughput Pearl Millet Root Architectural and Anatomical Phenotyping in West African Soils

To better identify the root architectural and anatomical traits that are beneficial for drought tolerance in pearl millet and the genetic determinants that control these traits, an experiment was set up where 160 genotypes from the Pearl Millet inbred Germplasm Association Panel (PMiGAP) were grown in field conditions in the Centre National de la Recherche Agronomique (CNRA) of the Institut Sénégalais des Recherches Agricoles (ISRA) in Bambey, Senegal (14.42°N, 16.28°W). The PMiGAP panel includes inbred lines from Africa and Asia that are fully sequenced, allowing the identification of 29,542,173 Single-Nucleotide Polymorphisms (SNPs) that can be used for association genetics (Varshney et al., 2017). In our study, plants were grown during the dry season (March to June, which allowed for full irrigation control) under two treatments: irrigated, where plants received 30 mm of water twice a week; and drought stressed, where irrigation was stopped from 21 days to 42 days after sowing (DAS) to allow field dry down. The experiment was set up in an alpha-lattice design with four replications in each treatment, one plot being comprised of three rows of 10 plants with 90 cm between rows and 30 cm between plants within the row. At 42 DAS, three plants per plot with their main tiller tagged were harvested for root phenotyping (shovelomics and anatomics using LAT; see Figure 2) while the remaining plants were kept intact for morphological, yield, and yield components measurements at maturity.

Figure 2

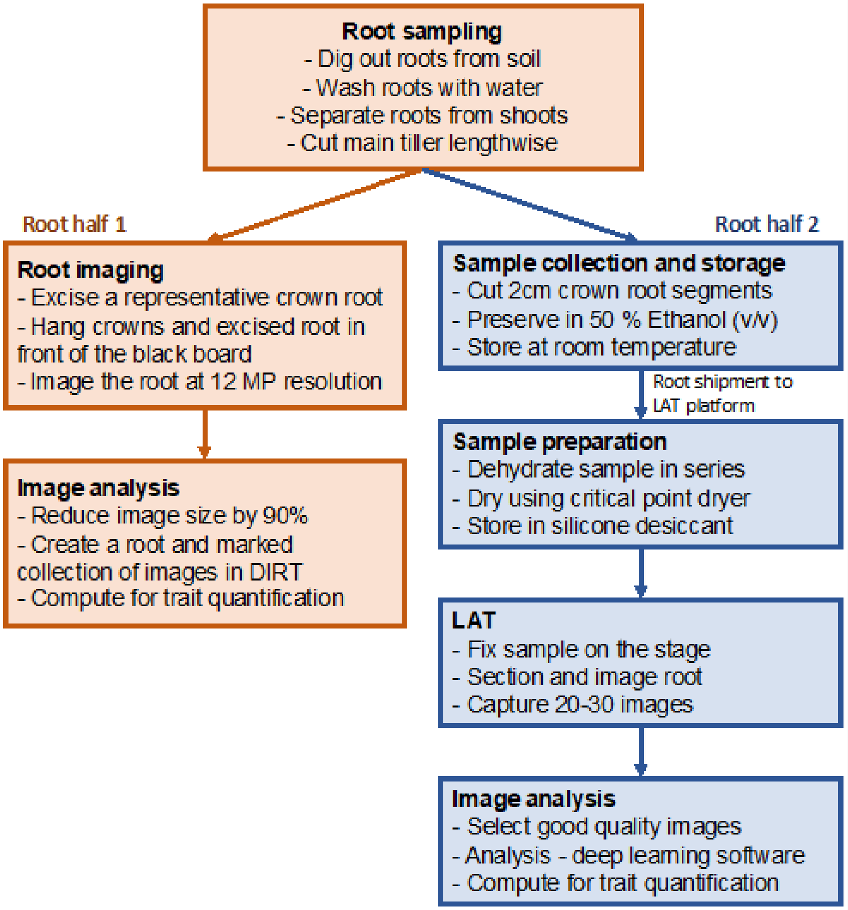

Figure 2 – High-throughput Root Field Phenotyping Process

3. Shovelomics

Root sampling and washing – At 42 DAS, the crown root system over a depth of 15 cm to 20 cm was sampled on three plants from the middle row using a shovel (see Figure 3a). The root system was initially washed in buckets filled with water and the shoot part was separated from the root system at around 10 cm above the main stem (see Figure 3b). The number of tillers per plant was counted and the shoots were placed in bags for measurement of aerial dry weight. The root system was further separated in half by cutting the main stem lengthwise. Half of the root system was used for imaging while the other was used for root sampling and anatomical measurements.

Root imaging – One representative crown root was excised from the half root system used for imaging and both were installed in the imaging chamber. The chamber consists of a black board in front of which the roots were hung, protected from direct sunlight by a white cloth. All hanging elements were of dark color so as not to be recognized as root material. Only a scale marker and the tag identifier were white in color. A digital camera was installed on a tripod approximately 1 m away from the black board and images were taken at a resolution of 12 megapixels. The shutter speed of the camera can be adjusted in case of root movement (due to wind, for instance) as well as the focal length in case of large changes in light intensity across the day. Low and homogenous light reflectance from the black board is important for further correct root segmentation by image analyses software.

Figure 3

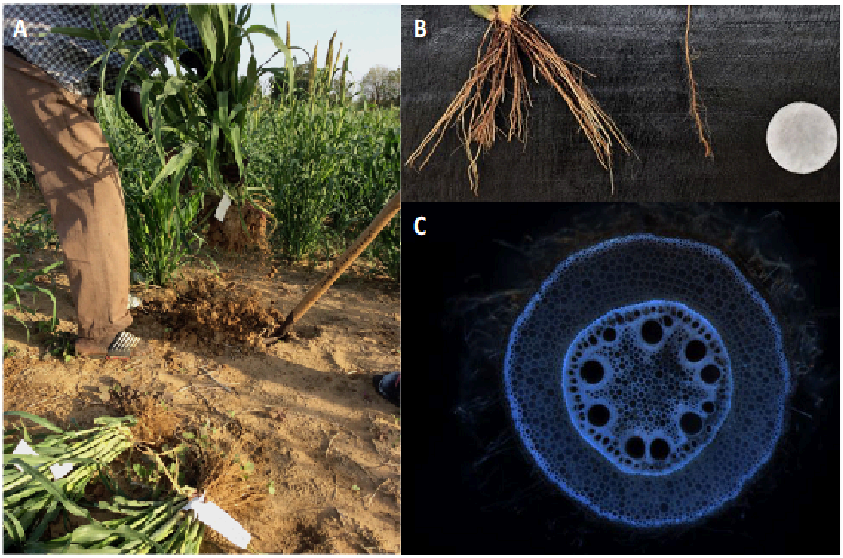

Figure 3 – Pearl Millet Root Phenotyping in Field Conditions

Notes. (A) Root sampling using the shovelomics method (photo by J. Burridge). (B) Image of the shallow root system from a single plant after washing. The root system was cut in half and one crown root was excised (photo by A. Grondin). (C) Image of the anatomy of a root emerging from the fourth whorl using laser ablation tomography (photo by D. Wells).

Architectural traits extraction – The automated DIRT software was used to measure the architectural traits according to Bucksch et al. (2014) and Das et al. (2015). Briefly, before being submitted to DIRT, the size of the images was reduced by 90% and bulk analyses of more than 100 images were performed at once. Although DIRT output provides 78 traits in total (among which 28 traits are specifically for monocotyledons roots), data analysis focused on the following traits:

- crown roots: root angle (top and bottom), root width (top, bottom, and accumulated over 10% to 90% depth), projected root area and averaged root density.
- excised roots: average lateral root length, distance to the first lateral root from the root apex, lateral branching frequency.

The presence of tillers makes more difficult the homogeneous root cutting into half and root hanging in a perfectly vertical position. Therefore, for tillering plants, root angle measurements using DIRT may be prone to errors. Alternatively, manual root angle measurements using the ObjectJ plugin in ImageJ can be performed (methods can be found at https://plantscience.psu.edu/research/labs/roots/methods/computer/rsaj).

Materials and equipment needed for shovelomics:

- Shovels for root sampling
- Buckets for root washing
- Paper bags for shoot harvesting and drying
- Table and cutter for stem dissection
- Black board, nails, and clamps to hang the roots
- White cloth to cover the black board
- Digital camera (Nikon D5600—other models are available) and tripod
- Hard drives for images storing
- Computer with internet access for DIRT analyses

4. Anatomics

Root sampling and storage – On the root half that was conserved for anatomical sampling (see section *Shovelomics/Root sampling and washing*), roots emerging from whorl four (of the layer of crown roots 1 and 8 in Figure 1) were identified. Two root segments of around 2 cm from the stem base were sampled and placed in a labeled 2 ml tube containing 50% ethanol (v/v) for conservation (roots can be conserved in higher ethanol concentration for several years) and transported to the analysis facility. Samples were then taken through an ethanol dehydration series from 50% to 100% (v/v) in 10% increments. Roots were left to rest at each dehydration stage for a minimum of 60 minutes. Following ethanol dehydration, samples were dried using a critical point dryer. This process removes all liquid from the sample while keeping the cellular structure intact, allowing samples to be stored indefinitely in sealed containers with silica gel desiccant.

Laser ablation tomography – LAT was conducted on a single sample at a time. Each dried sample is fixed in position on the sample stage using a magnetic clamp. Anatomical sections were then captured using the LAT at 30 µm intervals from the middle 1 cm of each root sample. In most cases, between 10 images and 20 images were captured per sample (see Figure 3c). However, when the section of sample being imaged was damaged, either from initial harvesting in the field or during the drying process, further images were captured. Anatomical traits were extracted using a deep-learning approach trained on ground truth sections that were hand annotated using CellSeT software (Pound et al., 2012).

Materials and equipment needed for anatomics:

- Razor blades for root sampling on the fourth whorl
- 2 ml plastic tubes labeled with ethanol resistant stickers for storing root samples
- Ethanol 50 % v/v for conserving root samples
- Boxes for storing the 2 ml tubes
- Absolute ethanol for sample dehydration in series
- Critical point dryer (Leica EM CPD300—other models are available)
- Sealed containers and silicone desiccant for dry sample storage
- Laser ablation tomograph (LatScan 2.0, L4IS)
- Data storage device and computer for image analysis

Prospects/Opportunities

Recent developments in image-based root phenotyping techniques now allow quantification of a number of root traits in field conditions with a throughput that is compatible with genetic approaches (Atkinson et al., 2019; Tracy et al., 2020). In fact, an increasing number of studies using these techniques (especially shovelomics and LAT) in genetic association approaches to identify QTLs controlling root traits have been published recently. Characterization of root diversity in large panels opens opportunities for breeding as it accelerates the identification of heterotic parents that can be used in conventional breeding approaches to validate and introgress these QTLs in popular varieties. In common bean for instance, germplasm identified with increased root length density in shallow soil were crossed with traditional varieties with deeper root system (Burridge et al., 2016; Burridge et al., 2019). This approach allowed the release of new varieties with shallower root systems that are more tolerant to low P stress in Mozambique (Lynch, 2022; Ndoye et al., 2022).

Large-scale phenotyping leads to the identification of haplotypes at the QTL regions of interest and ultimately of the genes underlying these QTLs. Candidate genes can be found through transcriptomics for the identification of differentially expressed genes between contrasted haplotypes and validated through reverse genetics. In maize, such approaches allowed the identification of a CBL-interacting serine/threonine-protein kinase 15 (*ZmCIPK15*) controlling root angle (Schneider et al., 2021a). The maize *cipk* mutant showed a 10° steeper root angle in some nodal specific positions, 18% greater shoot biomass, and 29% greater shoot nitrogen accumulation under suboptimal nitrogen availability as compared to the wild type. Haplotypes can also be used for functional analyses aimed at characterizing the physiological significance of the considered root trait. The use of contrasted maize genotypes for root multiseriate cortical sclerenchyma (lignin accumulation in walls of outer cortex cells) showed that roots with larger sclerenchyma had increased penetration ability in compacted soils (Schneider et al., 2021b).

The architectural, anatomical, and functional characterization of specific root traits is useful for improving root structural and functional models that provide a better view of root growth, development, and functional complexity in the soil. For instance, OpenSimRoot simulates how root traits dynamically interact with the soil environment and how this interaction influences resources acquisition in the soil and plant growth (Postma et al., 2017). The integration of root models into crop and climatic models will be important to define the right root system for the right environment, and the inclusion of root traits into the definition of breeding product profiles for development of future varieties best adapted to the conditions they will be subjected to (Lynch, 2018; Windhausen et al., 2012).

Despite these recent intense prebreeding efforts, examples of deployment of root traits in breeding schemes remain scarce. In this context, continuing the efforts to develop root phenotyping in field conditions and making these techniques usable by breeders remain of major importance. Identifying shoot traits that represent proxies for the expression of root traits are of particular interest too. However, providing breeders with genetic markers for root traits and phenotyping tools may not be enough to ensure the benefits of root traits because of their high degree of plasticity (Dwivedi et al., 2020). When a root trait is identified as beneficial in one environment, it is important to better apprehend how the expression of this trait, and its benefits, may change in other environments (Schneider & Lynch, 2020). Controlling the genotype by environment interaction affecting root traits is arguably the next biggest challenge in root research.

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11. Using Root-Soil Interactions in the Rhizosphere as Valuable Traits for Selection Against Drought

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Abstract

The rhizosphere, meaning the soil volume influenced by the living roots, hosts several important ecological processes implicating the soil, the root system and active microbiota. These various interactions often impact soil carbon (C) content and nutrient dynamics, as well as soil water retention, by modifying its biological and physico-chemical properties. Well-known root adaptive traits for drought tolerance include deep rooting and increased root development, both of which ensure better exploration of the soil volume required for greater water uptake. However, the intensity of root-soil-microbiota interactions shape the size of the rhizosheath (i.e., the soil mass that remains attached to roots after plant excavation), which could modulate the water retention capacity of soil. Indeed, genotypes with larger rhizosheath respond better to drought stress than those with a smaller rhizosheath in several plant species. From a breeding perspective, intra-specific variation in rhizosheath size has recently been demonstrated in two important crops in West Africa: pearl millet and maize. Therefore, genotypes with large rhizosheath could be considered for varietal selection for adaptation to drought. Ongoing genome wide association studies (GWAS) should confirm genetic control of rhizosheath size and map candidate genes and investigations should be performed on the mechanisms that support this genetically complex trait.

Keywords: Rhizosphere, Rhizosheath, Root-adhering soil, Drought, Root phenotyping

Introduction

West Africa faces many challenges to secure sufficient and sustainable food production. Indeed, water scarcity and soil nutrient deficiency are among the main constraints limiting crop production. Drought stress is considered one of the most harmful abiotic stresses limiting crop yields (Fang et al., 2017; Praba et al., 2009; Wang et al., 2017). Moreover, drought events are projected to be exacerbated by climate change in much of the world including West-African countries (IPCC, 2018).

Plants explore the soil for water and for various nutrients they need for growth through their roots. They can then develop their root system architecture, associate with a beneficial microbiota, and improve the biological and physico-chemical conditions of the rhizosphere to face drought stress (White et al., 2013a, 2013b). Therefore, it may be possible to cope with drought by selecting crop varieties that can better exploit/use the soil water for sustainable production. The interactions between plant roots and soil that occur in the rhizosphere, defined as the volume of soil affected by the exudates secreted by plant roots and colonized by soil microbiota (Pinton et al., 2007), are very important to explore.

An important manifestation of the interactions between plant roots, soil, and root-associated microbiota, is the formation of the rhizosheath, or the aggregation of soil particles around the root after plant excavation (Brown et al., 2017; George et al., 2014; Pang et al., 2017). The rhizosheath is also the part of the rhizosphere where the root-soil-microbiota interactions are more intense and therefore it presents optimized physico-chemical conditions for water and mineral acquisition compared to bulk soil. Many factors contribute to its formation, including root physiology (e.g., exudation, association with soil microbiota), or morphology (e.g., root architecture, length, and density of root hair) (Ndour et al., 2020; Pang et al., 2017). Because of its role in plant growth under abiotic stress (including drought), this trait is now gaining attention of plant biologists, especially by those exploring the possibility of developing genetic tools for plant breeding, a now widely discussed topic regarding various crop species. Importantly, the formation of rhizosheath has been studied in pearl millet, the main cereal crop cultivated in West Africa (Ndour et al., 2017).

In this chapter, we will (1) discuss the relationship between plant rhizosphere functioning and drought stress; (2) analyse the intra-specific variability of the interactions in the rhizosphere for some important crops in West Africa and; (3) discuss the opportunity to integrate these root traits in plant breeding programs.

Response of the Rhizosphere to Drought Stress

Water is a crucial resource for plant development, and drought stress is the most damaging constraint for plant productivity (Leng & Hall, 2019). Through their roots, plants acquire water and minerals directly from the soil. The root system is of great importance in the interaction between crop and soil fertility as they are the main interface between the plant and the soil (Mommer et al., 2016). Moreover, water uptake depends on the soil's physico-chemical characteristics, the physiology of plant roots and their morphological characteristics, as well as on the interactions between soil components and plant roots. Drought has several immediate consequences on plant physiology, including reduced seed germination rate, stomatal closure, reduced relative leaf water content and cell membrane stability, increased formation of reactive oxygen species, increased susceptibility to diseases, and reduced grain yield and quality (Zia et al., 2021). In the long term, plants develop various adaptation mechanisms to access water more efficiently. These include the development of several architectural and anatomical root traits such as root depth and aerenchyma formation (see Chapter 10, by Grondin et al. in this book), but also very interesting physiological traits which involve the soil matrix and its hosted microbiota (Grover et al., 2011; Lynch, 2011, 2019; Rodriguez et al., 2004).

The different interactions that take place in the plant-soil-microbe interface define rhizosphere functioning. These interactions are mediated by the root exudation (i.e., the deposition of organic compounds in the soil by plant roots). Root exudates are defined as the substances actively released by root in the soil from various mechanisms (Haichar et al., 2014; Nguyen, 2009; Sasse et al., 2018) and have a strong impact on the functioning of the rhizosphere (Cantó et al., 2020). Indeed, several studies have reported the influence of root exudation on the microbial composition of the rhizosphere in various crop species (Carvalhais et al., 2015; Ge et al., 2017; Haichar et al., 2008; Iannucci et al., 2021; Ma et al., 2018; Micallef et al., 2009; Neumann et al., 2014). Moreover, plant root exudation can be modulated in return by the rhizosphere microbiota (Canarini et al., 2019; Korenblum et al., 2020). Importantly, these interactions help plants to better withstand the various adverse effects of drought stress.

1. Plant Growth-promoting Microbiota

Microbial communities in the rhizosphere may be involved in plant response to drought. Under drought conditions, plant growth can be promoted by the direct response of soil microbiota as well as by indirect effects resulting from modification of root exudation (Vries et al., 2020). For instance, drought leads to a modification of the microbial community in the rhizosphere, including an increase in the relative abundance of *Actinobacteria* and *Firmicutes*, and a decrease of *Proteobacteria* and *Bacteroidetes* (Naylor & Coleman-Derr, 2018). In particular, a study on 30 species of angiosperms showed a significant correlation between the relative abundance of the root-colonizing *Streptomyces* and the drought tolerance of the host plant (Fitzpatrick et al., 2018). In this sense, a recent study on sorghum showed that drought stress increased the colonization of *Streptomyces* within the root and the rhizosphere, and that this colonization increases root development during drought (Xu et al., 2018). Recently, strains of *Acinetobacter calcoaceticus* and *Penicillium sp* isolated for their P-solubilization potential have been shown to mitigate the adverse effects of drought stress in foxtail millet (Kour et al., 2020). It will therefore be interesting to test on crop species cultivated in West Africa and their wild relatives, and to verify whether there is a genetic variation of rhizosphere and endosphere oligotrophic microbial communities that could help plants to better withstand drought conditions.

2. Arbuscular Mycorrhizal Fungi (AMF)

The association between plant roots and arbuscular mycorrhizal fungi is one of the most important plant symbiosis with soil microbiota (Cantó et al., 2020). It is widely recognised that plants associated with AMF have a greater water uptake capacity related to increased soil volume explored through the hyphal network. The positive effect of AMF on plant water uptake and plant drought tolerance was reported in both cereals and legumes. For example, inoculation of cowpea with the mycorrhizal fungus *Glomus deserticola* enabled the plant to withstand water stress and produced increased yield compared to the uninoculated control treatment (Oyewole et al., 2017). This positive effect was also observed in drought-stressed maize after inoculation with *Glomus versiforme* due to an improvement in the deleterious effects of drought-induced oxidative damage (Begum et al., 2019). In the case of pearl millet, mycorrhizal inoculation mitigated the effects of water deficit and helped the plants to maintain their biomass production (Fabbrin et al., 2015). So, these symbiotic associations are reliable opportunities and should be better explored for crop adaptation against drought in the West-African context.

3. Root Exudation and Rhizosheath Formation

Another striking and complex example of the physiological response of roots to drought is the formation of the rhizosheath around the root system. The rhizosheath is considered the most active compartment of the rhizosphere. The formation of the rhizosheath is an aggregation process responding to many factors including root exudation and production of bacterial exopolysaccharides (Ndour et al., 2020). Recently, it has been related to carbon exudation and dynamics in the rhizosphere at the early stages of development in pearl millet (Ndour et al., 2022). Price (1911) first hypothesized that plants developed rhizosheath formation as a mechanism to improve drought tolerance and root protection under arid conditions, a hypothesis that was recently confirmed (Alami et al., 2000; Benard et al., 2016; Pate & Dixon, 1996). Several other studies have reported a positive effect of a large rhizosheath in the growth of plants subjected to drought, such as foxtail millet and wheat (Basirat et al., 2019; T.-Y. Liu et al., 2018). A similar result was also obtained for a drought-tolerant chickpea in which Rabbi et al. (2018) showed greater water storage in the rhizosphere soil linked to a larger rhizosheath and greater exudation of root mucilage. Indeed, some of the factors affecting the rhizosheath, such as root exudation (mainly C exudation) and the associated exopolysaccharide production by rhizobacteria, increase organic matter content as well as soil aggregation in the rhizosphere (Alami et al., 2000; Berge et al., 2009). A recent study shows that moderate water stress leads to the formation of rhizsosheath in rice, and increased soil porosity and water content in the root-adhering soil volume compared to bulk soil (Zhang et al., 2020).

Overall, various studies have shown that the rhizosheath trait increased plant fitness, particularly under drought stress conditions. It can be assumed that the combination of better water retention due to the increase in organic matter content, particularly microbial polysaccharides, and improved soil structuration, which both occur in the rhizosheath, contributes to better water storage and availability in the immediate root periphery. Thus, genetic variability of these physiological traits on crop species could be very interesting from a plant breeding perspective to improve crop management, especially in arid regions. The various interactions taking place in the rhizosphere and contributing to drought stress tolerance are summarized in figure 1.

Figure 1

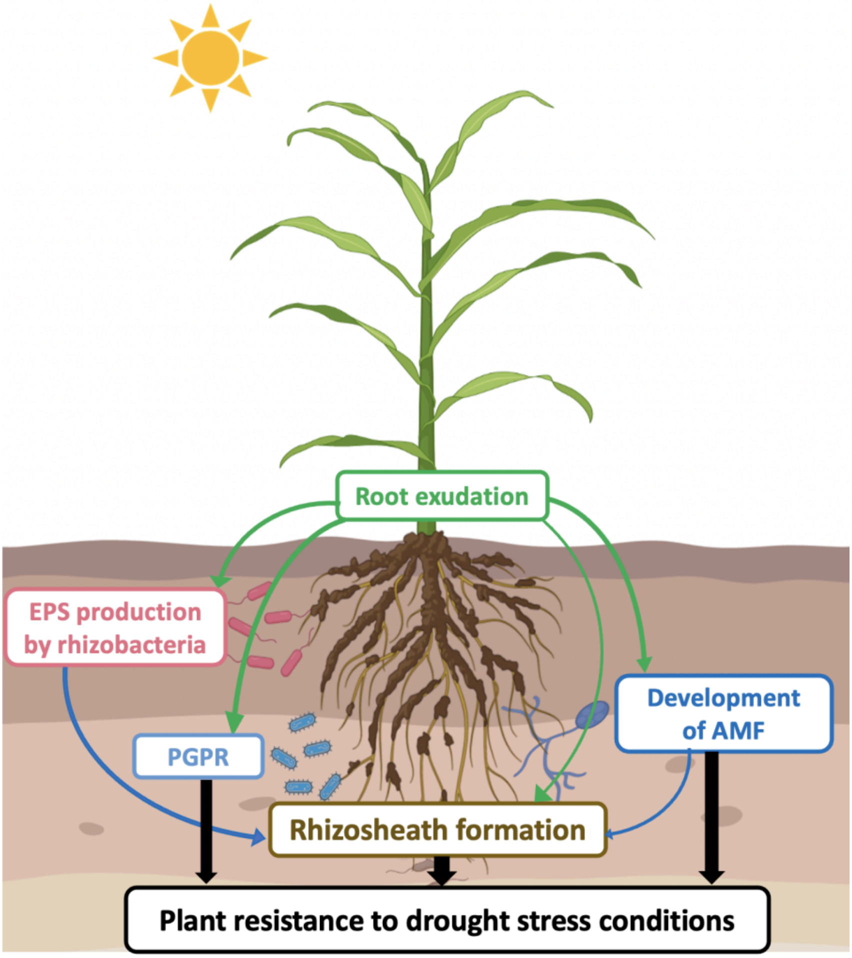

Figure 1 – Interactions Between Roots, Soil & Microbiota, which Occur in Rhizosphere to Help Plants Cope with Drought Stress

Note: EPS = Exopolysaccharide, PGPR = Plant Growth Promoting Rhizobacteria, AMF = Arbuscular Mycorrhizal Fungi

Genetic Variation of Rhizosphere Interactions in Crops: Example of the Rhizosheath

It is widely recognized that interactions in the rhizosphere play an important role in the response of plants to abiotic stresses and in particular in plant drought tolerance (Cantó et al. 2020). However, the relevant plant traits that characterize these interactions are often difficult to define due to their complexity. Consequently, intra-specific variations in these interactions are difficult to demonstrate. Nevertheless, the size of the rhizosheath has been used to test the genetic variability of the intensity of rhizosphere interactions in various species.

1. The Specific Rhizosheath Weight as a Proxy to Phenotype Rhizosphere Interactions

Different methods have been used to phenotype for rhizosheath size (reviewed in Ndour et al., 2020). The specific rhizosheath weight (i.e., the relative mass of dry soil that adheres firmly to the roots after plant has been excavated and roots have been shaken) is now widely considered as a reliable proxy to evaluate the rhizosheath size (Ndour et al., 2020). Operationally, it is defined as the ratio between the mass of dry root-adhering soil and the mass of dry root (RAS/RT). This emerging parameter was used to estimate the rhizosheath size on wheat (Amellal et al., 1998; Gouzou et al., 1993), sunflower (Alami et al., 2000; Sandhya et al., 2009), durum wheat (Kaci et al. 2005), barley (George et al. 2014) and on pearl millet (Ndour et al., 2017). Another parameter used to estimate the rhizosheath size is the ratio between the RAS dry mass and the total root length (RAS/RL), the latter of which was reported to be strongly correlated with the RAS/RT ratio (Adu et al., 2017). This method of estimating rhizosheath size by calculating the RAS/RT or the RAS/RL ratio seems to be effective for high-throughput phenotyping as it was used in numerous studies that aim to highlight its genetic determinants.

2. Case Study of the Phenotyping of Plant Rhizosphere Using the Rhizosheath Size

The rhizosheath size (RAS/RT or RAS/RL) would be genetically determined in many cereal species. First, phenotypic variation has been demonstrated in wheat (Delhaize et al., 2012; Haling et al., 2010; James et al., 2016), in barley (George et al., 2014; Gong & McDonald, 2017) and maize (Adu et al., 2017).

Our preliminary phenotyping study evaluated the impact of pearl millet genotypic variation on rhizosheath size using the RAS/RT ratio. Briefly, we grew 86 different inbred lines of pearl millet in MW pots filled with an arenosol sampled at the Centre National de Recherches Agronomiques (CNRA) of Bambey (Senegal), and each pot watered to its water holding capacity. After 28 days of growth, the plants were harvested and the root-adhering soil mass (RAS) and the root biomass (RT) were weighted and used to calculate the RAS/RT ratio, which was used as an estimator of rhizosheath size (Ndour et al., 2017). The results showed genotypic differences in pearl millet rhizosheath size. Subsequently, we replicated this experiment using the same protocol with a larger panel comprising 181 pearl millet lines for GWAS purposes. The results confirmed the genetic control of this trait within this larger panel of pearl millet lines with a 3-fold variation of the RAS/RT ratio between the more contrasting phenotypes (Ndour et al., 2021) and a broad heritability of 0.72 (Fig. 2).

Figure 2

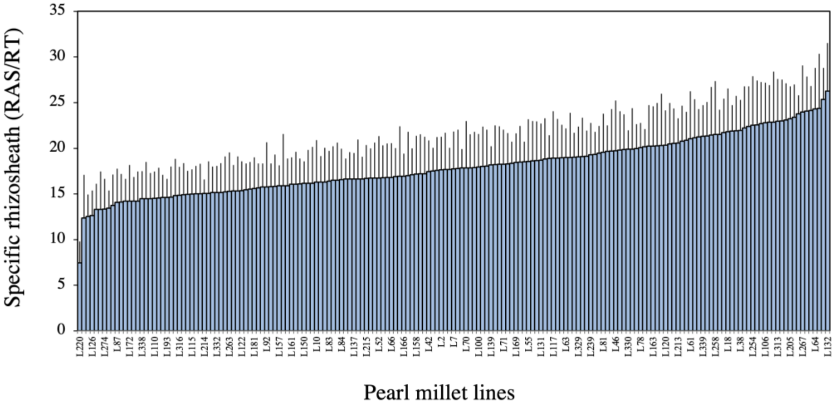

Figure 2 – Rhizosheath Size (RASRT Ratio) of 181 Pearl Millet Lines Grown in Greenhouse Conditions. n = 8 repetitions for each line.

3. Microbial Diversity Phenotyping in the Rhizosphere of Pearl Millet

As mentioned above, this rhizosheath size variation can be explained by many factors. However, in a study we conducted in a set of 9 pearl millet inbred lines selected for their contrasting rhizosheath size (RAS/RT), we focused on the microbiota component and compared the diversity of bacterial communities in the rhizosphere. This study concluded that the size of this rhizosheath was related with bacterial diversity since, based on 16S rDNA sequences data, the relative abundances of some taxa including *Proteobacteria* and *Firmicutes* varied significantly between lines characterized by small and large rhizosheath (Fig. 3). Moreover, the -diversity indices (e.g., Shannon, Chao1, Richness) calculated from these sequences are higher for large rhizosheath lines compared to those with small rhizosheath. This finding confirmed the response of this trait to rhizosphere microbiota (Alami et al., 2000; Bezzate et al., 2000; Fernández Bidondo et al., 2012) and suggested its genetic control by the host plant, probably through root exudation, and its effect on root-soil-microbiota interaction.

Figure 3

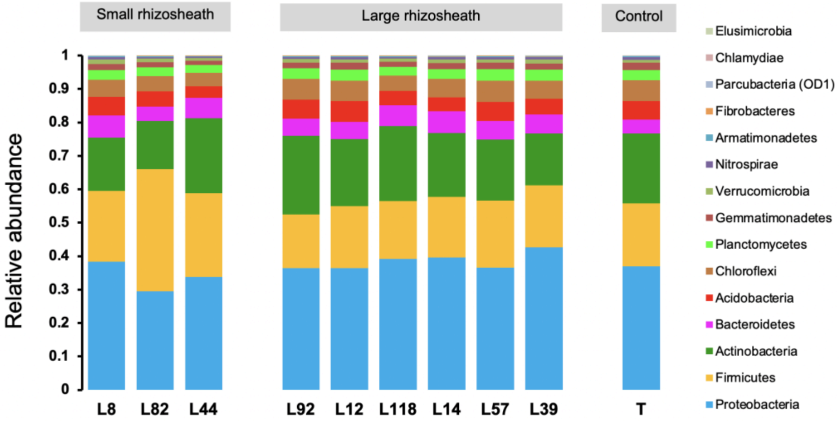

Figure 3 – Relative Abundance of 15 Major Bacterial Phyla in Rhizosphere of 9 Contrasted Pearl Millet Lines and in Unplanted Control Soil (T) (Ndour et al., 2017)

Another study we performed with contrasting rhizosheath pearl millet lines grown in the field showed that some enzymatic activities (e.g., chitinase, acid phosphomonoesterase, FDA hydrolysis) were higher in the root-adhering soil of the large rhizosheath lines compared to that of small rhizosheath lines (Ndour et al., 2021), suggesting that plant genetics (through root exudation variation) control not only the structure of the microbial community but also their enzymatic activities. This finding confirms the importance of root-soil-microbiota interactions, notably the importance of rhizosheath formation in C, nutrient dynamics in the rhizosphere, and consequently in plant nutrition under abiotic stress such as drought.

Opportunities for Plant Breeding for Drought Stress Tolerance

The potential of targeting root functioning for plant improvement against abiotic stress is well documented (Cantó et al., 2020; Lynch, 2019). This is particularly relevant in arid and semi-arid regions of West Africa where plants face multiple constraints including drought stress (Dossa et al., 2017; Drabo et al., 2019). Genetic variations in these root traits could be studied for the major crops of the region in order to ensure sustainable crop production.

For the rhizosheath trait for which genetic variations have been found in various crops, QTLs have been already detected in wheat (Delhaize et al., 2012; James et al., 2016; M. Liu et al., 2017) and barley (George et al., 2014; Gong & McDonald, 2017), although the molecular mechanisms explaining these phenotypes remain unknown. Adu et al. (2017) showed that rhizosheath was larger in maize improved varieties compared to landraces; based on these results, one may hypothesize that GWAS with a larger collection could therefore be used to detect QTLs and controlling genes in this important cereal for West-African countries. This trait should be further investigated for the other common cereals in West Africa such as sorghum. For pearl millet, the QTLs controlling this rhizosheath trait remain to be detected. However, the availibity of a reference pearl millet genome which was recently sequenced (Varshney et al., 2017) should make possible the rapid determination of the candidate genes related to this trait.

Conclusion

Drought is the main abiotic stress negatively affecting crop yield via plant growth, health, and reproduction (Fahad et al., 2017; Lamaoui et al., 2018; Leng & Hall, 2019). In response to this constraint, plants adapt their root morphology but also develop complex interactions with the soil and the root-associated microbiota. In the case of root interactions, the formation of rhizosheath improves plant drought tolerance through the combination of (1) exploration of a larger soil volume and (2) better water retention capacity due to increased organic matter content. The genetic variability of these root traits observed in pearl millet opens new opportunities for genetic selection to support crop and food production resilience in West Africa.

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12. Designing Dual-purpose Sorghum Ideotypes for High Grain and Biomass Yields Suitable for Various Target Environments in Senegal

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Abstract

Sorghum is a water-efficient crop and an important cereal in semiarid and arid environments where water availability limits production. Providing farmers with sorghum genotypes with specific agro-morphological characteristics of high double production (grains and biomass) would help to maintain or obtain high yields in these environments. The SAMARA model was used to define dual-purpose sorghum ideotypes for different target environments. Model calibration and evaluation were carried out with experimental data collected in Nioro du Rip in 2015 and Sinthiou Malem from 2013 to 2016 on 10 contrasting sorghum genotypes. Daily weather conditions from 1950 to 2016 were used for the simulations. Also considered were the different environmental (soil and climate) conditions of Bambey, Nioro du Rip, and Sinthiou Malem (Senegal). Simulations for the identification of optimal genotypic parameters in these target environments highlighted three ideotypes showing performances for a dual-purpose (grain and fodder) production superior to the reference genotype Nieleni. This was thanks to their strong capacity to colonize the soil (long roots) and to maintain green leaves (stay-green) throughout the cycle. Hence, long roots and stay-green trait should be strongly considered while selecting or developing dual-purpose genotypes of sorghum for the target environments, especially in less-watered areas like Bambey.

Keywords: Sorghum, dual-purpose, SAMARA, ideotype, target environment, Senegal

Introduction

Food security has become a major issue given the need to increase the global food supply by about 70% in 2050 (FAO, 2009). However, given the increasing limits to the expansion of cultivated areas in developing countries (land saturation linked to demographic changes), a significant increase in crop productivity seems necessary to achieve this objective. Sorghum is the fifth most important cereal crop in the world and is the staple food of more than 500 million people in more than 30 countries (ICRISAT, 2009). It is a water-efficient crop, making it an important cereal in semiarid and arid environments where water is the main limiting factor in production. Despite its high-yield potential in terms of grains and biomass, sorghum production is very sensitive to environmental conditions. In Senegal, the average yield of sorghum, the third most important rainfed cereal after millet and maize, remains low (1020 Kg.ha^{-1}; ANSD, 2018) with an estimated total area of more than 221,329 ha for a national production of 225,865 tons. Indeed, its cultivation faces several constraints including low soil fertility (Vanlauwe et al., 2010) and the lack of or low use of agricultural inputs (i.e., fertilizers, seeds of improved varieties; Gerstenmier & Choho, 2015). In addition, rainfall has inter- and intra-annual variabilities (Hansen, 2002).

To boost sorghum and other cereal crop production, farmers must be provided with genotypes that are more efficient and better adapted to their growing conditions. Thus, new sorghum genotypes with specific agro-morphological characteristics that result in a high double production (grains and biomass) in the target environments should be prioritized given the emergency to increase sorghum yields. Several traits have been identified because of their potential to develop sorghum ideotypes with high grain and biomass yields: internode length, stem diameter, leaf number and size, and number of grains per panicle (Ndiaye, 2019).

Donald (1968) was one of the first to propose an "ideotype selection" approach to underpin varietal improvement programs, which until then had been based on two selection philosophies: "elimination of defects" and "selection for yield" (Chantereau & Nicou, 1991). He defined *varietal ideotype* as an idealized plant, or plant model (not yet in the sense of a mathematical model), that should yield a greater quantity or quality when grown as a cultivar. On the other hand, *selection for yield* is limited by the fact that the desirable combination of traits is usually achieved by chance.

Reynolds et al. (2011) emphasized the importance of mathematical modeling as a powerful tool for elucidating optimal combinations including tradeoffs between traits for the creation of varietal ideotypes. Cultivation models based on ecophysiological processes are commonly used in basic and applied research in plant science and natural resource management (Hammer et al., 2002; Passioura, 1996; Rötter et al., 2011; Sinclair & Seligman, 1996; White et al., 2011) because they provide the best-known framework for understanding complex plant processes and their interactions with climate and the environment. These models play an increasing role in guiding basic research by providing quantitative predictions and highlighting knowledge gaps (Hammer et al., 2006, 2010; Semenov & Halford, 2009; Semenov & Shewry, 2011; Tardieu, 2003). Modeling can thus provide a rational approach to design and test *in silico* new sorghum ideotypes optimized for given environments (Hammer et al., 2006; Quilot-Turion et al., 2012; Semenov & Halford, 2009; Semenov & Shewry, 2011; Tardieu & Tuberosa, 2010).

Therefore, this study aims to illustrate the capacity of modeling in the design of sorghum ideotypes with high yields of both grain and biomass for target environments in Senegal using the SAMARA crop model that simulates crop growth and development at a daily time step.

Materials and Methods

1. Model Description

The SAMARA model (Simulator of crop trait Assembly, MAnagement Response and Adaptation) was initially implemented on the EcoTrop platform (programmed in Delphi language, Kouressy et al., 2008), a model development and simulation platform. This platform integrates a series of tools and interfaces: a library of simulation modules, a simulation engine, a user interface with graphical and numerical outputs, simulation scenarios that can be run in bulk, and a database for observed and simulated data among them. A description and commented source code of the model, the definition of all parameters (e.g., crop, plot, soil, and cropping practices), and all input and output variables are available at https://umr-agap.cirad.fr/nos-recherches/equipes-scientifiques/modele-samara. Only the principles and processes relevant to this study are described here. The version used for this study has been recoded under R version 3.2 (R Development Core Team, 2015) to facilitate the link with parameter optimization software and to make it more flexible within the developer community.

SAMARA is a deterministic crop model. Its objective is to simulate the growth of monocotyledons such as tropical cereals, rice, and sorghum. SAMARA simulates—according to radiation, temperature, water, and CO2—the growth and yield of cereals at the canopy scale at daily time steps. Input data for the model includes:

- Standard daily meteorological data (i.e., solar radiation or possibly insolation, minimum and maximum temperatures, mean wind speed, minimum and maximum relative humidity, potential evapotranspiration [Food and Agriculture Organization, FAO], and precipitation);
- Hydrodynamic properties of the soil (i.e., volumetric water content at wilting point, field capacity, and saturation); and
- Technical itineraries (especially sowing date and density).

Simple concepts described by Kouressy et al. (2008) are used to simulate biomass gain using the Big-Leaf approach, Lambert-Beer's law for the interception of photosynthetically active radiation, and radiation use efficiency for carbon assimilation.

2. Model Calibration and Evaluation

2.1 Experimental Data

The modeling work (calibration and evaluation) was based on data from 11 trials conducted during the rainy seasons of 20132016 at three research stations of the Institut Sénégalais de Recherches Agricoles (ISRA), namely Sinthiou Malem (in 2013, 2014, 2015, and 2016), Bambey (in 2013), and Nioro du Rip (in 2015; see Table 1). The environmental conditions at the different sites are given in Table 2. The main characteristics of these trials (soil type, agronomic management, and standard daily climate data—minimum, maximum, and average temperature; minimum, maximum, and average relative humidity; global radiation; average wind speeds at 2 m from the ground; and rainfall height) that served as inputs for the model were described in detail by Ndiaye et al. (2019).

Table 1
List of Trials Used for the Calibration and Evaluation of the Model

Trial	Zone	Code	Soil Type*	Sowing Date	Previous Crop	Calibration	Evaluation
Sowing 1/2013	BBY	B13D1	Sandy	17/07/2013	Fallow		
Sowing 2/2013	BBY	B13D2	Sandy	31/07/2013	Fallow		
Sowing 1/2013	SIN	S13D1	Sandy loamy	25/07/2013	Fallow		1
Sowing 2/2013	SIN	S13D2	Sandy loamy	6/8/2013	Fallow		1
Sowing 1/2014	SIN	S14D1	Sandy	17/07/2014	Peanut	1	
Sowing 2/2014	SIN	S14D2	Sandy	6/8/2014	Peanut	1	
Sowing 1/2015	SIN	S15D1	Sandy	9/7/2015	Peanut		
Sowing	SIN	S15D2	Sandy	8/8/	Peanut		1

Trial	Zone	Code	Soil Type*	Sowing Date	Previous Crop	Calibration	Evaluation
2/2015				2015			
Sowing 1/2015	SIN	S16D1	Sandy loamy	25/07/ 2016	Fallow	1	
Sowing 1/2015	NIO	N15D1	Sandy	16/07/ 2015	Cowpea		
Sowing 2/2015	NIO	N15D2	Sandy loamy	13/08/ 2015	Fallow		1

Note. BBY = Bambey; SIN = Sinthiou Malem; NIO = Nioro du Rip. *Classification according to the USDA method based on average data over the 0–30 cm horizon.

Table 2a
Environmental Conditions of the Different Trial Sites

Code	Coordinates	Alt (m)	*SAN (%)	CS (%)	N (%)	OM (%)	Rain (mm)	R0-30 (mm)
B13D1	14°42’N	20	94.2	6.6	0.15	3.1	644	180
B13D2	16°29’W		94.2	6.6	0.15	3.1	566	253
S13D1	13°49′ N	23	89.4	11.6	0.21	4.3	575	146
S13D2	13°55′ W		89.4	11.6	0.21	4.3	536	183
S14D1			91.2	10.2	0.17	5.7	488	158
S14D2			90.9	9.7	0.17	4.5	377	190
S15D1			93.7	6.3	0.32	3.5	505	52
S15D2			93.2	6.8	0.33	3.8	455	259
S16D1			84.1	15.9	0.55	10.6	447	230
N15D1	13°45′ N	45	92.4	7.6	0.31	3.5	943	196
N15D2	15°45′ W		87.0	13.0	0.43	6.1	747	329

Table 2b

Code	Coordinates	Alt (m)	R30-60 (mm)	R60-90 (mm)	R90-120 (mm)	Tmin (°C)	Tmax (°C)	**Healthy
B13D1	14°42’N	20	352	110	3	23	33.9	2
B13D2	16°29’W		256	56	1	22.8	33.9	3
S13D1	13°49′ N	23	365	59	6	21.4	35.3	5
S13D2	13°55′ W		306	46	1	21.2	35.4	5

Code	Coordinates	Alt (m)	R30-60 (mm)	R60-90 (mm)	R90-120 (mm)	Tmin (°C)	Tmax (°C)	**Healthy
S14D1			213	88	31	22.2	35.7	4
S14D2			156	31	1	22.1	35.6	5
S15D1			259	153	43	21.8	34.7	2
S15D2			155	44	2	21.2	34.9	4
S16D1			155	24	38	22.5	35.6	5
N15D1	13°45′ N	45	361	261	126	20.6	33.8	3
N15D2	15°45′ W		273	145	0	19.7	33.8	4

Notes: BBY = Bambey, SIN = Sinthiou Malem, NIO = Nioro du Rip, Alt = Altitude, SAN = Sand, CS = Clay + Silt, * = classification according to the USDA method based on average data over the 0–30 cm horizon, R_{030} = total rainfall between 0 and 30 days after sowing, R_{3060} total rainfall between 30 and 60 days after sowing, R_{6090} = total rainfall between 60 and 90 days after sowing, R_{90120} = total rainfall between 90 and 120 days after sowing, ** = score given to a given environment according to disease level: The favorable situation takes the score 5 (absence of disease) and the unfavorable situation the score 1 (strong presence of disease), Rain = total rainfall during the trial.

The plant material consisted of 10 genotypes from various regions of West and Central Africa that are known to perform well in their respective zones of distribution: Fadda, Nieleni, Pablo, Soumba, F2-20, 621B, SK5912, IS15401, Grinkan, and CSM63E. These genotypes have been selected to constitute a contrasting sample in terms of cycle duration, plant architecture (height, stem diameter in particular), structural characteristics (lignin, cellulose), and grain and biomass production. The characteristics of these 10 genotypes were described by Ndiaye et al. (2019). In these trials, observations on flowering and maturity dates, leaf area indices (LAI), biomass and plant height dynamics, yields (grain and biomass), and yield components were used for model calibration and evaluation. Total aboveground biomass and its distribution among stems, leaves and panicles, LAI, and leaf area numbers were monitored weekly in 2013 and 2014 and every 12 days in 2015 and 2016 for up to 10 days after flowering.

2.2 Calibration and Evaluation

The calibration of a model should in principle be carried out using data from trials conducted in well-controlled agronomic situations so that factors not considered by the model (e.g., diseases and weeds) do not sway data. Then the calibration of the model must be evaluated using data that are different and independent from those of the calibration and that come from trials also conducted under good agronomic conditions, if possible. Thus, the data from the three trials conducted in 2014 and 2016 at Sinthiou Malem (S14D1, S14D2, and S16D1) were used to calibrate the phenology, the dynamics of plant biomass, the height, the number of leaves appeared, and the final yields. The LAI was only calibrated on trial S16D1 because of the lack of LAI data in 2014 and because S16D1 was the best trial of all of the experiments with a very good soil fertility, an absence of disease, and low overall rainfall. Therefore, the LAI data from this trial are assumed to be the best. In addition to their good agronomic conditions, S14D1 and S14D2 had a 20-day delay between sowing dates, which is important for the calibration of the phenology. The evaluation of the model was done with trials conducted in 2013 and 2015 at Sinthiou Malem (S13D1, S13D2, and S15D2) and in 2015 at Nioro du Rip (N15D2; see Table 1). These trials had relatively good agronomic conditions (i.e., absence of diseases for S13D1 and S13D2; and less diseases for S15D2 and N15D2; overall more or less good fertility; see Table 2). The S13D1 and S13D2 assays were used for the evaluation of phenology, dynamics of plant biomass, height, number of leaves, yield, and yield components; S15D2 and N15D2 were used only for phenology, yield, and yield components. The dynamic measurements on these trials had been abandoned because of a weak development and heterogeneities observed on some plots. Parameterization was done as described by Ndiaye (2019). Details of further model parameters and their function and default values are provided in https://umr-agap.cirad.fr/nos-recherches/equipes-scientifiques/modele-samara.

2.3 Choice of Traits of Interest and Genotypic Parameters Used for Optimization

SAMARA, like most crop models, involves many parameters whose values need to be known or estimated so that the model can function correctly. There are 76 such parameters in SAMARA (Dingkuhn et al., 2013). Some have little influence; others are relatively well-known and not very variable, so that it is not necessary to optimize all of them. A choice must therefore be made for ideotype design based on the characteristics of interest (i.e., the output variables of the model) to be optimized and the sensitivity of these variables to the parameters that influence them. Thus, the choice of the parameters on which optimization for ideotype design must be done is determined either by expert opinion or based on field and modeling studies carried out beforehand for the identification of the model parameters to which the traits of interest are sensitive, in this case, grain and biomass yields.

Our previous study on the associations and plasticity of traits contributing to both grain and biomass yields (Ndiaye, 2019) highlighted four traits that could improve the yield potential of dual-purpose sorghum thanks to their strong correlation with grain and biomass yields. These traits are the number of green leaves, stem diameter, internode length, and number of grains per panicle (strongly correlated to grain yield). We defined the parameters of the SAMARA model that correspond to these traits of interest and whose values affect the output variables of interest (i.e., grain yield and biomass yield). For the optimization, the genotypic parameters of the model used were similar to the traits explained above. They are coefficient of sensitivity to leaf mortality (CoeffLeafDeath) for the number of green leaves, structural mass of the internode (CoeffInternodeMass) for the stem diameter, maximum length of the internode (InternodeLengthMax) for the internode length, and structural mass of the panicle (CoeffPanicleMass) for the number of grains per panicle. Additionally, the maximum root length (RootFrontMax) was considered because of its importance in the studied environments, which are often confronted with water stress. The range of values of these parameters (minimum and maximum values) based on the minimum and maximum values observed during the experiments or on the range of values of the parameters derived from the genotype calibration is given in Table 3.

Table 3
Genotypic Parameters Used for Ideotype Optimization and their Range of Variation

Parameter	Definition	Unit	Range of variation
RootFrontMax	Maximum root length	mm	200–2000*
CoeffLeafDeath	Coefficient of sensitivity to leaf mortality	–	0-0,03
CoeffInternodeMass	Structural mass of the internode	g.mm-1	0.005–0,1
InternodeLengthMax	Maximum length of the internode	mm	80-500
CoeffPanicleMass	Structural mass of the panicle	fraction	0,12–0,3

Note. *Range of variation given in the SAMARA model

2.4 Optimization Method to Define Dual-Purpose Sorghum Ideotypes

All three experimental sites were used as target environments for the optimization of dual-use sorghum ideotypes. For each environment, 67 years of site-specific daily weather conditions were used for the simulations: official data of the national meteorological division over the period 19502016 cleaned by ISRA-CERAAS and comprising average rainfall, maximum and minimum temperatures, solar radiation and insolation, minimum and maximum humidities, wind speed at 2 m from the ground, and potential evapotranspiration (FAO method). Each environment is also characterized by its soil type, its technical itinerary (resulting from our experiments), and by a sowing date based on the rainfall criterion used by Sambakhé (2018), for example, a cumulative rainfall of 30 mm over 3 consecutive days. This criterion is an adaptation of the 20 *mm over* 3 *days* criterion usually used in West Africa (Balme et al., 2005) to secure sorghum emergence. Indeed, in the target environments, and in general in West Africa, increasing instability in the start dates of the rainy seasons with dry sequences often necessitates reseeding.

Given its dual-use capabilities, the genotype Nieleni was considered as our reference and used to define the initial genotypic parameters required for the SAMARA model (Ndiaye et al., 2019). The values from the calibration were used. Then we optimized for each target environment the five genotypic parameters that were described in the previous section to define the typical ideotype of each of these environments. For this optimization, the minimum and maximum values (range of variation for optimization) were defined according to the minimum and maximum values observed in all our experiments for the Nieleni genotype (see Table 3).

For this purpose, the Rgenoud genetic optimization algorithm (Package R) was coupled to the SAMARA model (Sambakhé, 2018) to determine the optimal values of the genotypic parameters for the best performances (maximum grain and straw biomass yields) of sorghum ideotypes in a target environment. We optimized the five parameters chosen over the 67 years of climate in each target environment. This made it possible to define the ideotype, per target environment, with the highest average yield (grain and biomass) over 67 years and the lowest coefficient of variation. Thus, we obtain one ideotype per target environment with a high and stable grain and biomass yield. The P function to be optimized parameter was defined as follows:

P = *max {Simulated average yield of* 67 *years for a Minimum coefficient of variation}* (1)

2.5 Analysis of Ideotype Performance

A scatterplot was performed to compare the reference genotype Nieleni and the ideotype resulting from the model optimization across the target environments. For this, the reference genotype and the reference ideotype for each target environment over the 67 years were first simulated. Then, to compare the performance of Nieleni and the ideotype in terms of grain and straw biomass production, a potential index (I_{PO}) for grain (or straw biomass) production for a given target environment was used

$$I_{PO} = \frac{Y_{ij} - \bar{Y}}{\bar{Y}} \qquad (2)$$

where I_{PO} = potential index of a given genotype or ideotype i for the production of grain or straw biomass for a given target environment j; Y_{ij} = grain (or biomass) yield of a given genotype or ideotype i in a given environment j over the 67 years; $\bar{Y}$ = overall average grain (or straw biomass) yield of the two genotypes over the same period across the different target environments.

Thus, for a given target environment j, a positive I_{PO} (I_{PO}>0) of a given genotype or ideotype i for grain (or for straw biomass) indicates a good aptitude of this genotype or ideotype i for grain (or for straw biomass) production for this target environment j (and conversely if the I_{PO} is negative). A positive (or negative) I_{PO} for both grain and straw biomass will therefore indicate a good (or poor) dual-production ability (grain and straw biomass) for the genotype or ideotype i for the given target environment j.

Results

1. Genotypic Parameters of Ideotypes for Dual Purpose

Simulation results for the identification of optimal genotypic parameters for the new ideotypes in the three target environments are presented in Table 4. To obtain a high and stable dual production, regardless of the target environment, the following traits are key: the stay-green of the leaves must be increased with a decreasing coefficient of leaf mortality value; the structural mass (stem reserve); and maximum stem length with increasing structural mass of the internodes and the maximum internode length and the grain yield potential with increasing structural mass of the panicle. An increase in leaf greenness, stem reserve, and structural mass of panicles is therefore necessary at Bambey, Sinthiou Malem, and Nioro du Rip to obtain high and stable yields.

Genotypic parameters optimized for the three ideotypes ranged from zero to 0.0001 for the sensitivity coefficient of leaf mortality (CoeffLeafDeath), between 0.078 $g.mm^{-1}$ and 0.092 $g. mm^{-1}$ for the structural mass of the internodes (CoeffInternodeMass), between 222.5 mm and 275.6 mm for the maximum internode length (InternodeLengthMax), and between 1300 mm and 1775 mm for the maximum root length (RootFrontMax). The structural mass of the panicle (CoeffPanicleMass) was 0.3 for all three ideotypes. And the coefficient of leaf mortality remained close to zero for all the ideotypes designed.

Importantly, to achieve high and stable double yields at Bambey—the environment receiving the least rainfall—it is necessary to maintain the stay-green character and maximum root length to minimize the effects of water stress. It is also important to note that the structural mass of the panicle has remained constant regardless of the environment and that the more unfavorable the environment, the thicker but shorter the stems are.

Table 4
Optimized Genotypic Parameters of the Ideotype Designed for Each of the Target Environments using the SAMARA Model

Parameter	Root Front Max	Coeff Leaf Death	Coeff Internode Mass	Internode Length Max	Coeff Panicle Mass
Nieleni	1500	0,0054	0,068	196,0	0,25
Id_Sinthiou_Malem	1300	0,0001	0,078	275,6	0,3
Id_Nioro_du_Rip	1402	0,0001	0,08	245,0	0,3
Id_Bambey	1775	0	0,092	222,5	0,3

Note. Id = Ideotype

2. Agronomic Performance of Sorghum Ideotypes and Suitability for Dual Purpose

The average grain and straw biomass yields of the ideotypes and the reference genotype (Nieleni) are presented in Table 5. In general, ideotype yields are higher at Sinthiou Malem and Nioro du Rip compared to Bambey. Simulated grain yields were 4345 $Kg.ha^{-1}$, 4282 $Kg.ha^{-1}$, and 3339 $Kg.ha^{-1}$ for the ideotype in Nioro du Rip, Sinthiou Malem, and Bambey, respectively compared to 2996 $Kg.ha^{-1}$, 3173 $Kg.ha^{-1}$, and 2292 $Kg.ha^{-1}$ for the reference genotype. Thus, the optimized ideotype can potentially produce 29%, 45%, and 46% more grains respectively than the reference genotype in these different environments. For straw biomass, the simulated yields for the ideotype and the reference genotype were of the same order of magnitude in each target environment. It varied, depending on the environment, between 19725 $Kg.ha^{-1}$ and 28670 $Kg.ha^{-1}$ for the ideotype and between 19893 $Kg.ha^{-1}$ and 28343 $Kg.ha^{-1}$ for the reference genotype. The optimization of the ideotypes was mainly in the direction of grain improvement.

Figure 1 presents its indices of aptitude for grain and straw biomass production in the three target environments for each genotype. It can be noted that in Sinthiou Malem, the optimization was favorable for the double production (much improvement for grain and a little for biomass compared to Nieleni); in Nioro du Rip, it played on grain only (but very strongly); and in Bambey, it also strongly focused on grain yield but to the detriment of the biomass.

Table 5
Average Grain and Biomass Yields of the Reference Genotype and Designed ideotype in each Target Environment

Environment	Genotype	Straw biomass yield (Kg.ha-1)	Grain yield (Kg.ha-1)
Bambey	Ideotype	19725 ± 3894	3339 ±1090
Bambey	Nieleni	19893 ± 4369	2292 ± 1479
Nioro_du_Rip	Ideotype	24858 ± 3391	4345 ± 526
Nioro_du_Rip	Nieleni	24824 ± 3866	2996 ± 727
Sinthiou_Malem	Ideotype	28670 ± 3242	4282 ± 288
Sinthiou_Malem	Nieleni	28343 ± 3725	3173 ± 425

Figure 1

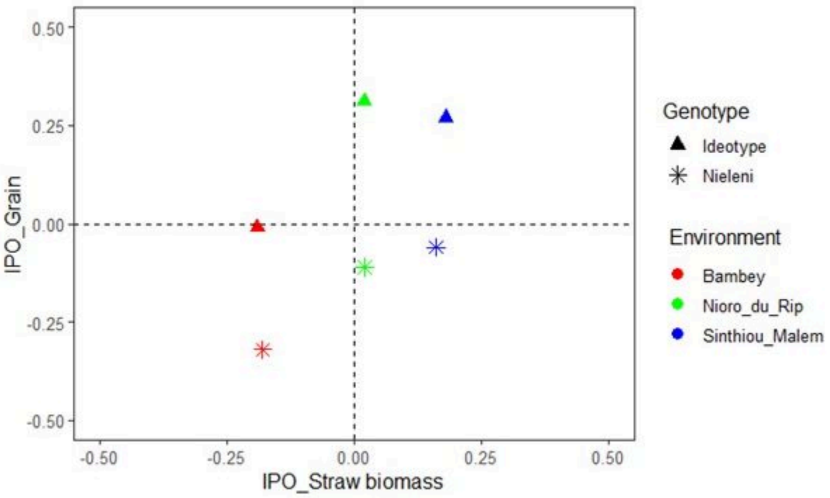

Figure 1 – Comparisons of the Dual-Purpose Abilities of the Three Ideotypes and the Reference Genotype Nieleni in the Three Target Environments Based on the IPO Indices

Discussion

Crop growth modeling can guide breeding line selection by studying *in silico* the performance of trait combinations and by identifying the best combinations and the optimal candidate genotypes for a target environment. Our results at Bambey, Sinthiou Malem, and Nioro du Rip using the SAMARA model show that a substantial increase in dual production, especially for grain, is possible for a given genotype and environment by optimizing its genotypic parameters through a combination of optimization rules and simulations of the crop model based on the historical data of this environment. The SAMARA model confirms that traits such as maximum root length, stay-green, internode length, stem structural mass, and panicle structural mass should be considered in the identification of dual-purpose ideotypes for the environments targeted. Additionally, the range of optimal values for each of these traits was determined for each environment.

1. Importance of the Genotypic Parameters of Optimized Ideotypes

This study showed that dual-purpose sorghum ideotypes should have a deeper maximum root length, especially in environments subject to water stress at the end of the growth cycle and/or with deep, sandy-dominated soils such as those of Bambey. In this study, the maximum root lengths of the designed ideotypes ranged from 1300 mm to 1775 mm. These values are greater than those reported by Chopart (1980) who showed, while studying the sorghum root system in Senegal, that the maximum root length varied between 1100 mm and 1300 mm. Such difference could be explained by the type of variety used, as dual-purpose varieties require more resources from the substrate, especially water, but also by the shortening of the rainy season observed in the past few years. This rainfall decrease that is accentuated by the climatic changes requires plants to develop more robust root systems (deep) for a better adaptation to dry environments. Chopart (1980) also emphasized that the new genotypes that are more efficient in terms of yield potential should not have root systems that are less well-developed than the existing varieties. Similarly, Sambakhé (2018), in defining grain sorghum ideotypes in Senegal, showed the importance of long roots for stabilizing yields in different target environments—Bambey in particular. In our environments affected by a low level of soil fertility and irregular rainfalls, the speed of progression of the root front and the degree of soil colonization by the roots are two important traits that also should be considered (Chopart, 1980).

It also appeared that dual-purpose sorghum ideotypes should have a high number of green leaves that are maintained as long as possible. This trait of interest depends on the total number of leaves—which is conditioned by the speed of leaf production (the phyllochrone)—and on the capacity of the plant to maintain its leaves green (stay-green character), especially during grain filling. Thus, the yield improvements observed in the ideotypes we have designed could be due to the improvement in the efficiency of light interception and conversion (because of the maintenance of the leaves in a green state), which makes it possible to maintain significant assimilate production for a longer period of time and consequently to cope more easily with water stress at the end of the season (Kamal et al., 2019), given that transpiration is well controlled. Consequently, to have sorghum with a good double production (grain and straw biomass) at Bambey, maintenance of a significant number of leaves in the stay-green state is essential (coefficient of leaf mortality equal to 0). The importance of keeping sorghum leaves photosynthetically active during the grain filling period has been reported as an adaptation factor to water-limiting environments (Borrell et al., 1999, 2000; Haussmann et al., 2002; Jordan et al., 2003). Additionally, all ideotypes developed had very high panicle structural mass (high potential kernel count) of 0.30 (see Table 4), which predicts a high yield potential as reported by Hassan and Mohammed (2015), who found that large panicles were associated with a high potential for grain number and grain yield. Hence, a high structural mass is advantageous in arid environments (Bambey) or in environments where fungal diseases are prevalent (Nioro du Rip). In addition, a long stem internode length should be favored, particularly in environments with good soil fertility (predominantly clay) and good rainfall distribution, such as those in Sinthiou Malem. Indeed, a positive association between plant height and grain yield has been reported for sorghum (Jordan et al., 2003), probably because of a greater efficiency in the use of radiation (George-Jaeggli et al., 2004). In addition, if the demand for grain assimilates exceeds the production through photosynthesis, an accelerated translocation of assimilates from stems and leaves occurs (Triboi & Triboi-Blondel, 2002).

2. Involvement for Adaptation in our Target Environments for Breeders and Agronomists

This study shows that the double production of sorghum (grain and fodder) could be significantly increased in these target environments if new ideotypes, superior to Nieleni (especially for grain production), are developed and implemented. Rötter et al. (2011) suggested that to cope with adaptation in the current environments, only new genotypes aimed at increasing yield potential and drought tolerance, combined with adapted agronomic practices, such as the modification of sowing dates, adequate management of nitrogen fertilizers, and plant protection, would allow yield levels to be maintained and losses avoided.

The use of new breeding methods—such as ideotype definition through modeling to create more appropriate genotypes—should allow better adaptation in the target environments (Dawson et al., 2015). This ideotyping requires an *in silico* approach to design ideotypes for specific uses in a given context. Thus, this study for the design of varietal ideotypes for the three environments targeted based on traits of interest for sorghum double production, historical meteorological data, and research recommendations (technical itinerary) is only one typical example that applies for our specific environments. This simulation approach can be pursued by varying other input variables (e.g., elements of the technical itinerary, soil, or climate) for the definition of varietal and crop ideotypes (technical combinations that affect the traits of the ideotypes). Thus, this study highlights an innovative approach that appears judicious to accelerate the collaboration between crop modelers, agronomists (ecophysiologists), and breeders. More comprehensive breeding programs that would combine the definition of ideotype by simulation and current selection methods could undoubtedly shorten the time required to create new sorghum genotypes better adapted to our different environments.

3. Limits of the Study

Limitations due to some uncertainties are noted, either in the structure of the model or in the approach used. Indeed, the target environments are considered as limited only by physical pedoclimatic conditions (climate, soil water reserve). We do not know the response of our ideotypes to other constraints, such as limited nitrogen (N) contents. In SAMARA, a module dedicated to nitrogen has not yet been integrated. Thus, we have been unable to consider the N limitation in the design of the ideotypes. N uptake and redistribution of N during the post-anthesis phase could be an important constraint to consider in order to achieve a higher sorghum yield potential. Indeed, as noted in this study, maintaining the green leaf biomass during grain filling can increase the grain yield of sorghum grown under water limiting conditions at the end of the cycle (Kamal et al., 2019). However, the effect of this stay-green trait can be limited by nitrogen deficiency (Borrell et al., 1999; Muchow & Sinclair, 1994; Peng et al., 1995).

In this study, we optimized our ideotypes using the genotype Nieleni as a reference. It is a caudatum type and a very efficient genotype in both grain and biomass production. Optimization could be done with a guinea-type genotype as a reference or guinea and caudatum genotypes simultaneously because the guinea types, although with low harvest indexes, are robust, generally tall, and better adapted to the constraints of the target environments compared to the caudatum types, which are rather sensitive (Ndiaye et al., 2019).

In this study, too, we have optimized our ideotypes based on the available history of meteorological data for the target environments, whereas it might be more judicious to use future climate data from climate scenarios for the design of ideotypes given the threats related to climate change in the target environments we considered. Future research also may use data from a shorter and particular climatic period, such as that from the dry period of 19701990 that affected the Sahel or from the recent period of gradual return of rainfall of 19902010 (Salack et al., 2011).

Finally, another limitation of the study lies in the technical itinerary used in the ideotype design. Indeed, this itinerary being the one recommended by the research, we did not take into account some yield reduction factors that producers face (e.g., constraint of sowing date, limited inputs, etc.). Thus, it might be interesting to conduct the study with an itinerary that considers constraints farmers face when designing ideotypes for target environments and contexts to increase efficiency.

All of these limitations reveal the importance of interdisciplinarity (crop modeling, agronomy, ecophysiology, and breeding) in the design of sorghum ideotypes that perfectly fit a defined use in a given context, and they show the importance of crop modeling as a powerful integrative tool for these explorations. This study is a proof of concept on the potentialities of crop modeling for ideotype explorations. Further simulations are required to cover the diversity of situations encountered in farmers' fields.

Conclusion

This study aimed to use a crop model to design high-performance and stable dual-production (grain and straw biomass) sorghum ideotypes for the target environments of Bambey, Sinthiou Malem, and Nioro du Rip. The results revealed that under our current soil and climate conditions, sorghum ideotypes for dual purpose (grain and fodder) should have a thick stem, large panicles, and a high capacity for deep soil colonization by roots, especially in water-stressed environments such as in Bambey. This study also emphasized the importance of stay-green, especially in the least-watered areas such as Bambey, where the coefficient of leaf mortality is 0. Additionally, this study allowed us to quantify the optimal range of the traits considered for each environment targeted, which can greatly facilitate varietal choice.

Thus, our designed ideotypes can be a decision support tool for increasing productivity in these target environments. The conclusions of the study are potentially interesting for sorghum breeding programs, as they are part of the first step in the design of genotypes adapted to a target environment, namely the definition of the ideotypic traits to be favored. Thus, we recommend that the optimal range of values for these traits are taken into account when identifying appropriate genotypes in sorghum breeding programs for the target environments considered.

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PART III

GENETIC DIVERSITY AND IMPROVEMENT OF DRYLAND CROPS

13. Biodiversity as a Cornerstone of Agrosystems' Sustainability in West Africa

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Highlights box

- Agrobiodiversity is an asset for resilience and sustainability at different scales (species and intra-specific).
- Crop wild relatives and landraces extend the gene pool, providing a functional reservoir of genetic diversity.
- Approaches and methodologies in population genetics can help identify interesting diversity.
- Tapping genetic diversity toward the creation of large populations for breeding schemes is essential in breeding strategies.
- Agrobiodiversity management and use are central under erratic environments.

Abstract

Agrobiodiversity, encompassing crop diversity and the biodiversity that supports agricultural system functioning, plays a major role in agriculture in the context of climate change. This is all the more true in regions like West Africa, where population growth is strong and economic resources are limited. Global models predict average yield loss for major crops of 11% in West Africa by the 2050s. Moreover, climate niches of African crops are expected to shift significantly, reinforcing the need to adapt agricultural diversity and practices. A better use of agrobiodiversity, relying on improved understanding and knowledge of its characteristics, would support greater adaptation and resilience of African agrosystems and food security. Agrobiodiversity, from gene to landscape, is key to achieving food security in the face of the erratic effects of climate change. This chapter highlights novel strategies for agrobiodiversity management and use, while building sustainable and resilient agrosystems for the future of West Africa.

Keywords: Agrobiodiversity, agrosystems, crop wild relatives, resilience, climate change, food security

Introduction

Agriculture in West Africa, which relies primarily on rainfall, is highly vulnerable to climatic events that are particularly extreme and erratic under the influence of the African monsoon. The Sahel and West Africa are considered today as “climate change hotspots” (Intergovernmental Panel on Climate Change, p 1209, 2014). Data indicate long-term changes in the seasonality of rainfall (Nicholson et al., 2018) and increased variability in precipitation (Cornforth et al., 2019). Deep changes are expected in climate suitability, leading to geographic or temporal redistribution of cultivated species (Egbebiyi et al., 2020; Pironon et al., 2019).

Considering the high spatiotemporal variability of West Africa, it is essential to focus not only on agrosystems’ productivity but also on agrosystems’ resilience and sustainability. The concept of resilience, embedding ecological and social-ecological definitions, refers to the capacity of agrosystems to buffer, resist, adapt, or transform to continue feeding the population (Berkes, 2008; Holling, 1973; Walker et al., 2004).

Decades of research in empirical and theoretical ecology have shown that biodiversity, in a broad sense, drives systems resilience. Regarding agrosystems, biodiversity is key to establishing resilient and sustainable food production and improving livelihood (Félix et al., 2018; Lin, 2011). Crop intraspecific diversification or change in the crop portfolio is often the first adjustment chosen by smallholder farmers facing climate change impacts (Fahad & Wang, 2018; Kassie et al., 2013; Shinbrot et al., 2019). However, the nature of crop diversity changes is essential: In a recent review, Labeyrie et al. (2021) showed that farmers' decisions in response to ongoing climatic events may not be adapted to long-term climate predictions. More research is needed to make the best possible use of biodiversity in agrosystems.

Until now, the valorization of diversity was based on a vision in which the environment was relatively controlled and stable, which made it possible to respond to each constraint by optimizing a few genes within varieties for a single objective. The plurality of values (socio-agro-ecological) and the plurality of environments due to their uncertainties, force researchers and farmers to think of biodiversity as an integrated response of agrosystems and not as a reservoir of solutions. To do this, it is important to consider diversity not as a static element of ecosystems but to understand its dynamics from genes to species, functions and ecosystems, and spatial and temporal scales.

This chapter explores why and how biodiversity in agrosystems (i.e., agrobiodiversity) can participate in resilience and sustainability in West Africa. First, researchers present the role of agrobiodiversity at the agrosystems' scale and explain how it can help improve yield and stability. Second, researchers underline the importance of understanding the dynamics of diversity at its finest scale to make a better use of agrobiodiversity to face environmental constraints. Finally, researchers highlight that agrobiodiversity management and use is central to building sustainable and resilient agrosystems for the future of West Africa.

The Role of Agrobiodiversity in Agrosystems

1. How Does It Work?

Agrobiodiversity includes domesticated plants and animals, wild fauna, flora, and microbiota, as well as people's knowledge that supports food production and agriculture (Qualset et al., 1995). It is a pillar of agroecology, ecological engineering, or "nature-based solution," frameworks that all seek to promote and pilot ecological processes to produce food in a sustainable and resilient way.

The impact of biodiversity on ecosystem services was first studied in natural ecosystems (Gross et al., 2014; Isbell et al., 2015, Tilman & Downing, 1994). Different mechanisms have been identified and have been proven to function in agroecosystems: the insurance effect, the selection effect, and the complementary effect. The insurance effect principle states that in a diversified system, one species—or variety at the species level—may fail, but multiple failures are less likely (Yachi & Loreau, 1999). Different plants exhibit different responses to temperature, precipitation, pests, and diseases. Fluctuations in yield among plants can compensate for each other and stabilize the total biomass production through time. The selection effect principle outlines that the more species or varieties there are in an ecosystem, the greater the chance that the best performing crop will be included. Because one species will find the environmental conditions to be favorable, total biomass production stays stable from year to year. However, an important condition for the selection effect to happen is that the best-performing species or variety in the given year must be dominant. The complementary effect entails direct ecological interactions between plants. Functional differences between species (Hector, 1998; Loreau & Hector, 2001) can lead to reduced interspecific competition, facilitative interactions, and exploitation of different resources (i.e., soil nutrients). Plant height differences, for example, can buffer the impact of extreme climate events (Philpott et al., 2008) or create microclimates that can help control diseases and pests (Zhu et al., 2000).

2. Agrobiodiversity to Improve Yields

Increasing agrobiodiversity through the addition of crops varieties, species, or functional groups (e.g., cereals versus legumes) can be achieved at multiple spatial and temporal scales. Within the same fields, practices include rotations of crops within 1 year (with no temporal overlap) or year after year; inter cropping (i.e., cultivation of more than one crop species); and cultivar mixtures (i.e., cultivation of more than one cultivar of the same species; Smith & McSorley, 2000). Agrobiodiversity also entails management practices promoting noncrop species—including habitat within or around fields (e.g., hedgerows)—or soil biodiversity (i.e., inoculation of beneficial organisms, organic amendments, etc.).

Recently, research on the benefits of diversification practices bloomed worldwide (Beillouin et al., 2019), showing that promoting agrobiodiversity can create multiple benefits simultaneously. In one of the largest-scale field trials across Malawi. Snapp et al. (2010) showed that rotations involving maize and long-lived legumes, at moderate levels of nitrogen fertilizer, had similar yet more stable yields, compared with monoculture maize. In addition, these rotations provided substantial nutritional benefits (i.e., increase in protein yield), greater fertilizer-use efficiency (e.g., >100% more grain yield with the same amount of nitrogen input), and acceptability to farmers. Himmelstein et al. (2017) found that intercropping practices across Africa benefitted both yields (e.g., increase of 23% on average) and growers' incomes compared with monocropping systems. However, authors noted that the management of leguminous intercrop systems could still be optimized to reach their full potential. Until now, cultivar mixtures have been used mainly for disease and weed management (Beillouin et al., 2019). However, meta-analyses have demonstrated that mixtures significantly improved yield compared with monoculture (Reiss & Drinkwater, 2018; Smithson & Lenné 1996). They also found that yield benefits were much greater in tropical areas and where plants grow in soil stressful conditions (i.e., low soil organic content and in acidic soils).

3. Agrobiodiversity to Face Climate Variability

The potential for agrobiodiversity to buffer agricultural impacts of climate shocks is less researched. Among the few empirical studies assessing yield stability, results supported the positive effect of the diversity of crop species (Gaudin et al., 2015; Smith et al., 2008) on the temporal stability of yield and income (Auffhammer & Carleton, 2018; Di Falco & Chavas, 2008). To date, only two meta-analyses synthesized results on the stabilizing effect of diversity. Research showed that yield stability of cereal-grain legume intercropping systems in tropical regions is greater than both cereal and legume cultivated as sole crops (Raseduzzaman & Jensen, 2017; Reiss & Drinkwater, 2018) Facilitation mechanisms leading to greater productivity and stability within fields may be stronger under more stressful conditions (Maestre et al., 2009; Prieto et al., 2015).

Renard & Tilman (2019) investigated whether crops' diversity increases year-to-year stability of crops production in the context of climate change at the national scale over 5 decades (19612011) and 91 nations. Results showed that greater crop species and functional group diversity increased the stability of food supply and resilience to interannual variability of precipitation at the national level. Although agrobiodiversity can contribute to sustainable agriculture in diverse ways, how to pilot it for greater resilience deserves more research, notably in West Africa with its strong climate constraints.

From Landscapes to Genes

1. A New Perspective on Selection Schemes

At the scale of varieties, the same principles may apply. The insurance strategy guides farmers' choices in regions with high variability: They prefer to have varieties that produce a lower yield under a multitude of conditions than varieties that perform extremely well only under very specific conditions (Van Oosterom et al., 1996; Weltzien et al., 1998). At the agrosystems level, more research is needed to identify combinations of species and traits that can optimize yield stability through an insurance or a complementary effect. Achieving production stability under all climatic conditions could also rely on the valorization of intraspecific diversity. As Haussmann et al. (2012) stated, the scale of varieties should consider two levels: individual buffering and population buffering. Individual buffering is the variance of the individual's phenotype, which is expressed as a function of environmental conditions. This buffering may be accentuated by the presence of different alleles for the locus of interest. Population buffering is the variance across all individuals in the population and therefore of the intra-population diversity (see Figure 1).

Figure 1

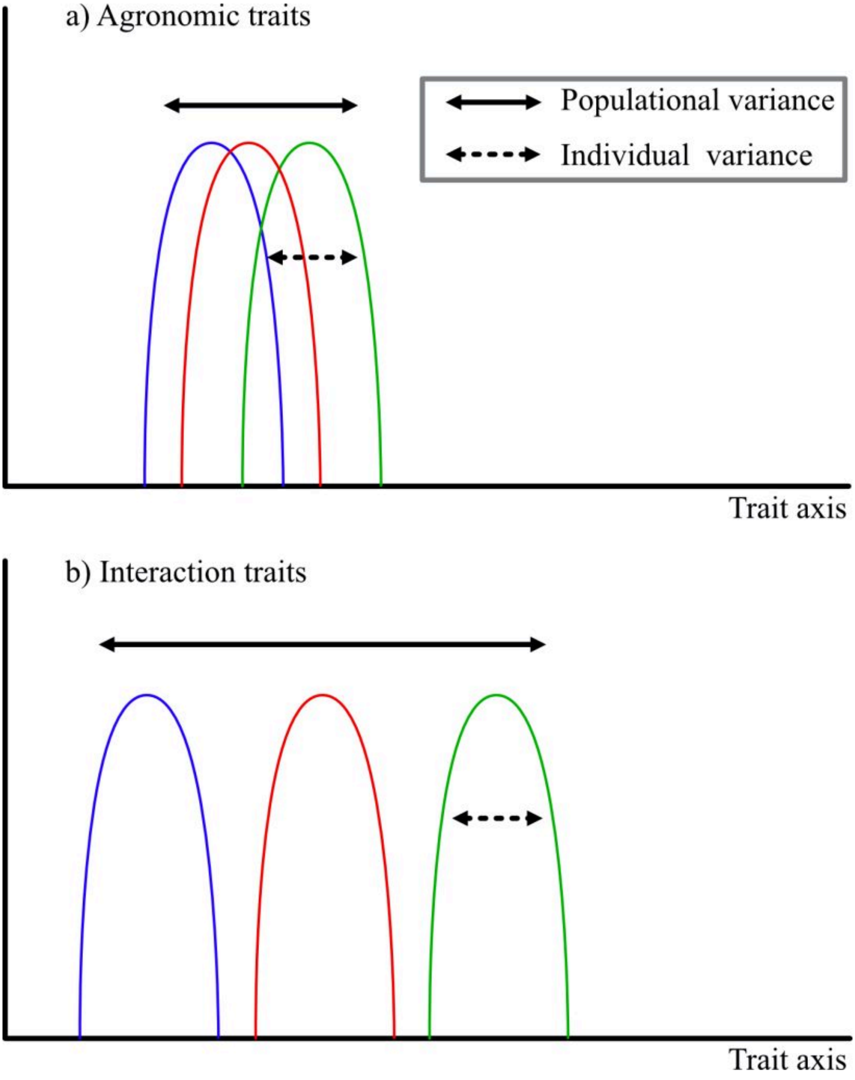

Figure 1 – Population buffering is the variance across all individuals in population & therefore of intra-population diversity

The idea of highlighting variances within individuals and populations to improve agrosystems' performance is recognized in ecology for natural ecosystems (Violle et al., 2012) and has been further developed for agrosystems by rethinking selection schemes (Litrico & Violle, 2015). The authors break functional traits into two types: traits of agronomic interest, often related to productivity (i.e., grain number and weight) and interaction traits (i.e., rooting depth, vegetative architecture, and phenology). Thus, Litrico and Violle (2015) proposed that the variance be considered according to the two types of traits. Agronomic traits should have a very small variance of the trait at the individual level and the population level, so that all individuals tend toward the same optimum. Conversely, interaction traits should minimize the individual variance and maximize the population variance, so that the population covers a wide range of conditions. Thus, it is rather a question of thinking of an "ideomix" than an ideotype.

Variance, at the individual and population scales, is governed by genes involved in the trait under consideration. Flowering earliness, for instance, is highly regarded as adaptive to drought. It allows escape from the midseason rainfall breaks which are characteristic of Sahelian Africa. Many studies seek to identify the major genes involved in earliness. Fewer studies focus on the variance within the cycle, but a variance of a few weeks may allow some plants to survive while others do not. In pearl millet, PhyC (PHYTOCRHOME C) has been identified as a major gene involved in precocity (Saïdou et al., 2014; Vigouroux et al., 2011). Nevertheless, a gap of more than 15 days may exist between the first plant to flower and the last. Such gaps are even observed within full-sib families. Faye et al. (2022) confirmed the importance of the PgPhyC gene with the T allele of the SNP (Single Nucleotide Polymorphism) chr2_11155563 almost fixed in early varieties and the alternative allele in late varieties. In addition, they identified a second gene, FRS12 (FAR1-RELATED SEQUENCE 12) for which four SNPs were identified, some with more subtle frequency differences between the two varieties. In addition to these two genes, which seem to have major effects, a number of other genes have also been detected and present a great interest in breeding to target individual or population buffering in breeding programs.

2. Sources of Interesting Genetic Diversity

The described example on flowering earliness highlights the necessity to identify reservoirs of genetic diversity, the importance of understanding genes' involvement in traits, interactions, and the relationship between genes and environment. This study presents functional reservoirs of diversity and describes why this diversity could be interesting in an integrated way of valorization. Neglected crops will not be included here but rather detailed in a companion paper.

2.1 Wild Relatives as a Source of "Ready-to-Use" Genes for Crop Adaptation

Since the first domestication of wild plants some 12,000 years ago, cultivated crops have shared a complex and long history with humans, the environment, and their wild relatives. Despite the reduction of habitats because of evolving environmental conditions and human spread, Crop Wild Relatives (CWR) remain interesting reservoirs of diversity and may conceal useful alleles in view of crop improvement and adaptation (Guarino & Lobell, 2011). Wild relatives still exchanging genes with the cultivated pool refuels the cultivated diversity. In yam, for example, constant inclusion of wild individuals in the cultivated pool in Benin is a factor of enrichment of the cultivated diversity (Scarcelli et al., 2006). A genomic study on pearl millet provided evidence that wild-to-crop gene flow increased cultivated genetic diversity leading to adaptive introgression (Burgarella et al., 2018). Such cases may be an effective strategy for informing new breeding directions and for uncovering ready-to-use wild diversity relevant for crop adaptation to current environmental changes (Burgarella et al., 2019).

Populations of African CWR are also found outside the geographical range of their cultivated counterparts, and therefore they experience different environmental conditions. For instance, the wild rice *Oryza barthii* shows a much wider distribution than the domesticated species it gave birth to, the cultivated African rice *O. glaberrima* (Lu et al., 2010). The wild ancestor of pearl millet is found in more extreme northern latitudes than the cultivated populations (i.e., in drier environments, see Figure 2). In these populations, Berthouly-Salazar et al. (2016) identified genetic variation linked to abiotic and biotic stress responses, and Ousseini et al. (2017) revealed a gene implicated in the number of flowers, both covarying with the gradient of rainfall. This pristine natural variation linked to local adaptation can be an asset for crop improvement.

Figure 2

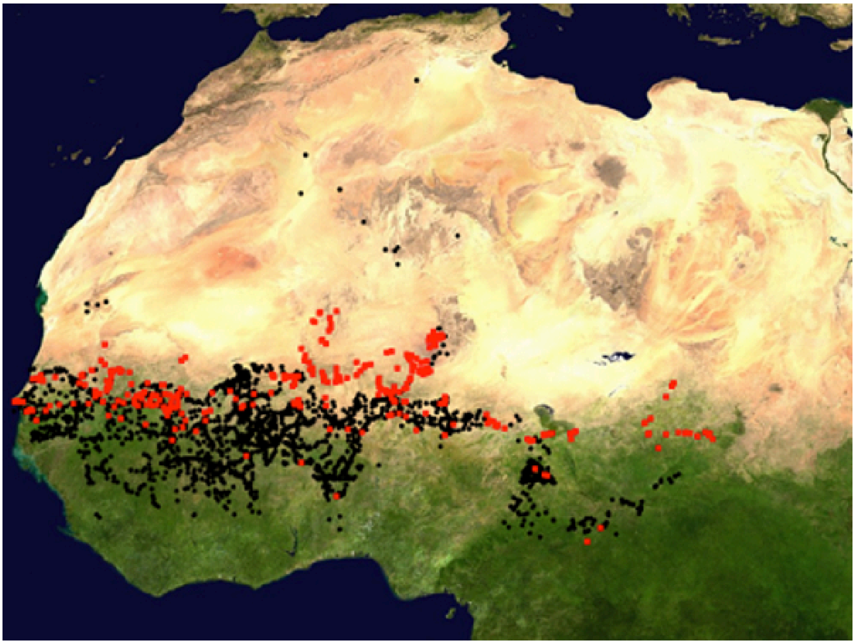

Figure 2 – Wild Ancestor of Pearl Millet is Found in More Extreme Northern Latitudes than the Cultivated Populations

2.2 Landraces, Genetic Load, Local Adaptation, and Cryptic Variation

Despite the well-known bottleneck effect that makes the wild compartment of landraces a complementary source of diversity, a lesser-known effect of the domestication process is the existence of a deleterious load within cultivated populations (Moyers et al., 2018). This possible "cost of domestication" refers to the increase in frequency of deleterious alleles segregating in the domesticated species as compared to the wild compartment. The existence of this genetic load implies an extended linkage and reduced genetic diversity. Intensive breeding programs would also strongly increase the number of deleterious mutations in domesticated species (Frantz et al., 2020). The study of these deleterious alleles, and of their frequency in different populations, may help orientate breeding strategies and diversity valorization, as their existence may limit the efficacy of selection and impact breeding efficacy.

From their domestication, each crop settled in new locations and colonized new environments through farmers or seed exchanges. These landraces now significantly contribute to the important genetic resources at the disposal of farmers and breeders. Two specific kinds of genetic diversity (i.e., allelic variations) may be of particular interest for crop adaptation and sustainable use in breeding while ensuring diversity conservation.

First, the variability of environmental conditions across a species range drives differential adaptation of populations, resulting in local adaptation. Local adaptation is the difference in relative fitness between a native genotype in a given environment and a nonnative genotype in the same environment (Kawecki & Ebert, 2004). A meta-analysis of 74 studies revealed that local adaptation is common among species and that a local population has on average 45% greater fitness than a foreign population (Hereford, 2009). This statement might not stand when population environments are drastically different or when selective factors are different at opposite ends of the gradient (Hereford, 2009; Popovic & Lowry, 2020). Local adaptations are critical for species survival in diversified and variable environments and thus may enable crop populations, if incorporated in their genetic background, to withstand impacts of climate changes (Razgour et al., 2019; Vargas et al., 2017).

Cryptic variations are a second source that can be just as important in coping with environmental changes, especially when environmental changes are highly contrasted and rapid (Bitter et al., 2019). Cryptic genetic variation has been reported in wild progenitors of crop species and landraces (Lauter & Doebley, 2002; Von Wettberg et al., 2018). Cryptic genetic variation is defined as standing genetic variation that does not contribute to the normal range of phenotypes observed in a population but that can bring forth phenotypic variation after environmental change (Gibson & Dworkin, 2004). Cryptic variation allows large phenotypic shifts outside the normal boundaries of phenotypic variation of a population, (i.e., when a variation in environmental conditions substantially changes the optimal phenotype). These shifts require important genetic stepping-stones that would be possible to reach only if cryptic variation precedes the change in environmental conditions. (Zheng et al., 2019). Given the current pace of environmental changes, exploring and conserving cryptic diversity should be of primary focus.

3. Population Genomics Can Identify Interesting Diversity: Approaches and Methodologies

The potential of this available diversity to improve agriculture in the face of climate change is huge. However, its use is far from being obvious to valorize. Population genetics is the study of allele frequency changes in a group of individuals exchanging genes (i.e., a population). Its concepts and tools are used to study microevolution, population dynamics, and conservation genetics. While broadly applied in natural conditions, population genetics approaches are also relevant in agriculture. When accessing the genetic composition of a population, several parameters can be studied: genotype frequencies, allelic frequencies, gene flows, heritability, genetic correlations, heterozygosity, and other indicators that allow an understanding of the genetic dynamics of the population under study. Using such approaches may help identify the historical effects of evolutionary forces that have shaped current diversity and reveal interesting alleles directly related to the environmental conditions to which they respond. This knowledge and understanding are essential to make an integrated use of agrobiodiversity and to ensure that it is a factor of resilience in agrosystems.

3.1 Detecting Footprints of Selection

The identification of selection, phenotype-genotype links, and candidate genes is possible through the study of allelic frequencies at the whole genome scale. In this paragraph, a synthetic and theoretical way the genomic footprints left by selection in the case of a strong and recent selection by an environmental pressure is presented. The cases of polygenic selection or soft selection are more complex and harder to detect, although surely more frequent and often linked to local adaptation and rapid evolution (Hermisson & Pennings, 2017).

In case an ideal unique population at equilibrium and a recent mutation under strong positive selection is considered, the haplotype(s) carrying a beneficial mutation will increase rapidly in frequency in the population. This selection of a small number of haplotypes will lead to a reduction in diversity around the adaptive allele because polymorphisms physically linked to it will be swept along (referred to as hitchhiking effect). This binding strength will depend on the rate of recombination and the time it takes for it to act. In other words, the lower the recombination rate, the greater the size of the haplotype will be, with a loss of diversity that will expand far away from the causative allele. Similarly, the older the selection pressure is and the more time the recombination has had to break the linkage, the smaller the region affected by the loss of diversity. Because it is this difference in diversity relative to the rest of the genome that can be used to identify the presence of adaptive alleles, it is easy to understand that it will be easier to identify adaptive alleles that have been selected recently or in regions/genomes with low recombination rates.

The loss of diversity around the adaptive allele can be measured either by classical diversity tests, such as Tajima's D, and across the spectrum of allelic frequencies, also called site frequencies spectrum (SFS). In case of neutrality, this spectrum follows a distribution of the form $y = 1/x$. In case of selection, the intermediate classes are very little represented or even absent, and the extreme frequencies (i.e., very rare or very frequent alleles), increase in frequency. A third pattern that appears around the adaptive allele, in addition to the reduction of diversity and the SFS change, concerns the linkage disequilibrium (LD). Within a selected haplotype, the LD is high among polymorphisms located on the same side of the adaptive allele but low between SNPs located on either side of the allele. The w-statistic has been proposed to measure this pattern.

Analyses can be performed at the metapopulation level by comparing populations. If the adaptive allele is selected in a specific population, the difference in frequencies of the adaptive allele and those physically linked to it compared to their frequencies in the other populations will be very strong. This phenomenon creates a pattern along the genome where genomic zones involved in adaptation will exhibit more differentiation between populations than the rest of the genome. This differentiation is often measured by the fixation index (F_{ST} parameter), estimated from allelic frequencies. The study of F_{ST} values, along the chromosomes between two populations, allows the identification of particularly high values of F_{ST}, which highlight candidate regions of the genome for selection, including genes involved in adaptation in one of the compared populations.

Approaches based on diversity indices, SFS or LD, are highly dependent on the number and density of SNPs identified. Consequently, these methods are adapted to Whole Genome or capture sequencing technologies, allowing regions spanning a minimum of several dozens to several hundreds of kilobases. The GBS (Elshire et al., 2011), RADSeq (Hohenlohe et al., 2010), or small area capture approaches (Mariac et al., 2018) are more adapted for approaches based on population differentiation. When these types of methods based on F_{ST}/genetic differentiation are targeted, the choice of populations (i.e., spatial sampling protocol) is crucial (De Mita et al., 2013). Table 1 presents a synthesis of the different methods to detect selection and associated software.

Table 1
Synthesis of Methods to Detect Selection

Sequencing methodology leads to	**Number of populations needed**	**Types of footprint**	**Softwares**	**References**
genomic regions > 50,000 kb	1	Diversity indices	ANGSD	Korneliussen et al., 2014
		(Tajima's D)		
		SFS	SweepFinder, SweeD	Nielsen et al., 2005 ; Pavlidis et al., 2013
		LD	OmegaPlus (2012)	Alachiotis et al., 2012
genomic regions < 1000 kb	>2	Genetic differentiation	PCAdapt, BayeScan	Luu et al., 2017 ; Foll & Gaggiotti, 2008

3.2 Association Methods

Genomic scans looking for adaptive alleles can be complemented by approaches revealing significant correlations between allelic frequencies and phenotypic traits (genotype-phenotype association [GPA]) or environmental variables (genotype-environment association [GEA]). These methods are tailored to help understand the genetic basis of phenotypic variation (GPA) or adaptation to the environment (GEA). The association between phenotypic/environment and genomic variability can be examined through Genome Wide Association Studies (GWAS) and helps decipher metabolic pathways for a better understanding of functional processes. These methods are necessarily sensitive to the number of points to estimate the relationship (>100) and the kinship within the sampling. A review of tests and study of their limitations for GEA and GPA can be found in Rellstab et al. (2015) and Tam et al. (2019), respectively.

Studying adaptation to drought or other stresses on classical inbred lines or more complex ones such as RILS or NAMs is a good start but it is not enough. The diversity represented in these synthetic panels is reduced, and creating these resources is time consuming and costly—they generally require several generations of inbreeding of a rather large number of individuals. Whenever possible, CWRs and landraces should be included in adaptation studies because they are functional reservoirs of a genetic diversity that are essential for the resilience of varieties. Then, if researchers want to extract information from them, they must use population genomics methods that are adapted to heterogeneous populations and that allow the detection of local adaptations (Hoban et al., 2016).

3.3 Correlation Between Genetic Diversity and Environmental Variability

Another emerging set of methods seeks to infer the current populations' vulnerabilities to future climatic conditions, including increased drought events. In contrast with well-known niche-modelling approaches that use the extent of species distribution to draw suitable areas at the species level, these approaches use the available genetic diversity to give a finer-scale view of the effect of future climates on local populations (i.e., landraces). These approaches largely rely on newly developed Machine Learning approaches to link the variations of genetic diversity and the climate that should have modelled it. If these approaches were initially developed and applied to natural populations of plants or animals (Bay et al., 2018; Fitzpatrick & Keller, 2015), there is a growing interest in applying them to cultivated plants (Capblancq et al., 2020; Rhoné et al., 2020). A detailed example is reported in Box 1.

Altogether, population genetics theory and its application to the study of agrobiodiversity's history and contemporary evolution in the face of current environmental constraints is a powerful tool to better understand populations' dynamics and identify how to make a reasonable and integrated use of their genetic diversity.

Box 1: A study of genomic vulnerability

A recent study has focused on estimating the local adaptation of traditional landraces of pearl millet to environmental variations in West Africa (Rhoné et al, 2020). Using a fine-scale climatic dataset and climatic variables calculated to match the growing season of the crop (Sultan et al, 2019), researchers have investigated how genetic diversity has been shaped by variation in climate conditions. Using a machine learning algorithm that monitors shifts in allele frequencies toward environmental gradients, this first step of the study determined that the impact of climate on genetic structure is important. Using the relationships established between climate variables and allelic variations, a second step of the study consisted in predicting the allelic composition that will be required to fit future

climate conditions estimated under a climate change model. By calculating a genetic distance between the current allelic composition of a landrace and the future one at the same location under climate change, researchers computed a so-called genomic vulnerability (GV, aka genetic offset). This GV informs on the magnitude of evolution needed to cope with future climate for a given landrace. For pearl millet, researchers observed a particular pattern of GV that was subsequently linked to a variation in flowering time using a GWAS approach.

To validate that the GV can efficiently predict a biological impact of climate change, researchers used a common garden experiment. Using a field in Niger as a common environment for several landraces coming from all West Africa, researchers computed for these test landraces a GV between their original location and the common garden. They evaluated performance of the landraces by monitoring the growth and several key phenotypic traits linked to the yield. They then tested if a greater GV ended up with a lower yield. The obtained negative correlation between GV and yield estimators was highly significant, with a Pearson's r ranging from -0.31 to -0.42 depending on the considered parameter, validating the predictive power of the GV approach for the first time in a crop plant.

A last work performed under this study was to evaluate if material exchange throughout West Africa could locally reduce GV, using a newly developed measure of the remaining GV after a migration event. This investigation led to the outcome that within-country migrations would not be efficient in significantly reducing the GV but larger, regional-scale migrations should help reduce the risk of yield loss due to adverse climatic conditions.

Management and Uses of Agrobiodiversity

1. Conservation Strategies

The importance of agrobiodiversity, defended in this chapter, brings another perspective on the conservation of genetic resources. While it is recognized that in situ conservation—in addition to ex-situ collections of diversity—is crucial to maintain evolutionary forces under work in populations, the question of the genetic erosion arises in debates on climate change. The pace imposed by this environmental perturbation begs the question: Can populations adapt quickly enough while not losing all important genetic variation if the selection pressure is too strong? In the face of climatic change, it becomes important to maintain evolutionary forces at work and to ensure that these evolutionary forces will be able to maintain a dynamic state that continues creating diversity. Evolution models must therefore be developed to thoroughly understand how diversity will behave in the face of climate change and to make recommendations on practices that would promote a dynamic in favor of maintaining diversity, and against undesired genetic erosion. In that, the role of so-called de-facto conservation, through agricultural practices oriented toward more inclusion of agrobiodiversity is primordial, local actors are guarantors of the genetic richness present on their territory.

2. Genetic Resources Access

Despite the key role that agrobiodiversity is expected to play to build a sustainable agriculture resilient to climate change, a paradoxical situation prevails today. On the one hand, new genomics, phenotyping, and information technologies promote a more rapid development of knowledge and an increased and accelerated exploitation of genetic resources in the public and private sectors. On the other hand, international regulations tend to make access to and exchange of genetic resources more complex, although underpinned by the laudable goal of equity. These instruments (the International Treaty on Plant Genetic Resources [ITPGRFA] and the Nagoya Protocol [NP] of the Convention on Biological Diversity [CBD]) aim to guarantee access to genetic resources and the fair and equitable sharing of the benefits stemming from their use. Better uses of this diversity will require improved mechanisms for exchanging information and resources rapidly and effectively, considering the diversity in value systems at work among stakeholders who often have different visions and objectives for the exchange of genetic resources (Jankowski et al., 2020).

These challenges will require coordinated transdisciplinary projects across research disciplines (e.g., agronomy, anthropology, sociology, economics, breeding and genetics) involving actors beyond research. Access to this biodiversity must be preserved in itself for the functions and services rendered within agro-ecosystems, which does not prohibit the use of the genetic resources offered (i.e., genetic improvement). It must be done in a sustainable manner and in a logic of common goodness at different scales and for multiple actors. To meet the current challenges of crop adaptation and improvement under dry environment, the authors advocate for a broad understanding of innovation, which requires the involvement of new diversity and new actors in the knowledge production process.

Perspectives

The identification of genes or genomic regions involved in adaptation or in the past evolution of populations significantly enriched the knowledge of the variability existing in populations and its potential usefulness, in particular through the study of the links with the environment. It also appears that a classical view, where one crop improvement need can be addressed by one appropriate allele, does not respond properly to the specific constraints imposed by the local context of West Africa or to the perspective of the ongoing rapidly changing climate. Moreover, such approaches would fail in establishing long-term sustainable and resilient agrosystems. On the contrary, the maintenance of numerous alleles in a diversity of crops seems more likely to ensure agrosystems' stability at the level of crops populations. Similarly, maintaining a diversity of crop species within and outside fields holds the potential to promote stability of food production and livelihoods.

CWR and landraces are thus potentially valuable sources of alleles of interest, especially in the context of climatic unpredictability and of needed resilient strategies. A classical view regarding biodiversity valorization relies on a triptych conservation-characterization-use in prebreeding. However, this approach is far from simple. The characterization and use of genetic resources requires tremendous investments and precedent knowledge regarding the genetic complexity of adaptive traits. As a result, biodiversity valorization in breeding programs has been recognized as essential for a long time but scarcely led to concrete successful examples, regarding the huge potential offered by the total conserved diversity. In addition, it remains a tit-for-tat strategy that may encounter limits when it comes to adapting populations to important and erratic changes in the environment.

Conclusion

Agrobiodiversity should be an integrated input at several scales—landscapes, species, individual genotypes, and genes—to contribute to more stable food systems in the face of erratic effects of climate and global changes. Allowing a broader and more efficient use of agrobiodiversity, (i.e., the study of the finest level of diversity in its dynamic state, as population genetics and genomics approaches), is essential for a better understanding and knowledge of the characters of interest to significantly improve agrosystems' functioning. Through their role, breeders and farmers are the guarantors of this agrobiodiversity. They can greatly influence its conservation by integrating the concept of diversity into their strategies. If improvement is still considered a factor of erosion in intensive agricultural systems, an inverted paradigm is possible through an approach based on an objective of stability and resilience of agrosystems.

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14. Management of Cowpea [Vigna unguiculata L. (Walp)] Germplasm Diversity in Senegal: A Crucial Asset for Breeding Programs

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Abstract

Cowpea is a legume of nutritional, socioeconomic, and therapeutic importance in Senegal, as in other West African countries. However, biotic and abiotic constraints affect its production. To mitigate those constraints and enhance its productivity in Senegal, the management of cowpea genetic resources is a priority. Managing these resources involves extensive collection to cover maximum cowpea diversity, standard characterization, and sustainable conservation of the local germplasm. A review of the diversity management of the local cowpea germplasm and results from a study conducted between 2015 and 2021 are presented in this chapter. Many cowpea prospections and collections have been done since 1953, but they only covered a few cowpea growing areas.

Moreover, many collected accessions have been lost due to a lack of adequate conservation. This deprived cowpea breeding programs of great germplasm diversity. Therefore, in 2015, a cowpea collection was made, covering more production regions, including cultivated cowpea, hybrids, and wild accessions. The molecular characterization of this collection showed that the genetic diversity is higher in hybrids and wild accessions than in the cultivated species. These results will be used for a better valorization of cowpea genetic resources to overcome constraints encountered in the production of this crop.

Keywords: cowpea, local germplasm, diversity, breeding program, Senegal

Introduction

African agriculture faces major challenges to crop productivity in family farms. These challenges are in combination with climate change, which worsens soil degradation, drought, and heatwaves. Food demands are increasing due to the growing population and continual decrease in arable lands due to urbanization and industrialization. This requires a sustainable intensification of agricultural production based on resilient crops, such as cowpea, that can generate income and balance the diet of populations without degrading the ecosystem. Cowpea [V*igna unguiculata* (L.) Walp] is mainly a self-pollinating plant. This important staple food crop, well-adapted to dry tropical regions and offering considerable economic, nutritional, and agronomic benefits (Agbicodoet al., 2009) in the tropical savanna areas of Africa, deserves special attention. Cowpea provides more than half of the vegetable proteins in the diet of populations in many developing countries, especially in sub-Saharan Africa (Aliyu &Wachap, 2014; Bhattarai et al., 2017; Boukaret al., 2016). It also contains a significant amount of minerals and vitamins. Moreover, cowpea has a short growing cycle, making it a reliable lean food for populations, especially during mid-season (around September in Senegal), when other crops have not reached maturity. It has economic importance because large quantities of its products (green pods, seeds, and haulms) can be marketed, providing a significant additional income to rural populations (both men and women). Cowpea is also processed into many popular food items such as couscous, *thiakry*, coffee, etc., representing another source of income for women processors. The crop is a legume adapted to drought conditions. It plays an important role as a source of nitrogen for other crops, such as cereal crops, especially in low soil fertility areas. Indeed, it fixes atmospheric nitrogen through its symbiotic associations with bacteria of the *Bradyrhizobium*genus, thus reducing the demand for nitrogen fertilizer and agricultural production costs (Asiwe et al., 2009; Dugje et al., 2008).

According to Ng and Maréchal (1985), the crop has been cultivated in Senegal for centuries. Séne (1966) hypothesized that local early maturity varieties were introduced from Nigeria for recession cultivation in the Senegal River valley in the northern part of the country. In contrast, the late maturity varieties were introduced from Mali. They were cultivated in association with millet in the wetter areas of Senegal and spread out all over the country, favored by trade and migration. Despite its importance, cowpea yields are relatively low in Africa, particularly in Senegal, at less than 700 kg/ha, according to a recent report released by the "Agence Nationale de la Statistique et de la Démographie" (ANSD, 2021). The low yields may be due to several abiotic (cold, heat, drought, low soil fertility, salinity, etc.), biotic (diseases, pests, parasitic plants, etc.), and socioeconomic constraints (Obilana, 1987; Singh & Sharma, 1996). Therefore, breeding programs in Senegal have been focused on developing high-yielding varieties adapted to different growing areas. Diverse, available, and accessible crop collections are crucial for the success of such crop improvement programs. According to the breeding objectives, new traits can be tapped from crop germplasm diversity, using advanced tools such as marker-assisted selection to speed up cowpea breeding.

Moreover, wild relatives can be an abundant source of interesting and exploitable genes for crop improvement (Feldman & Sears, 1981). However, lack of genetic diversity, information on a genetic marker, and knowledge of agronomic traits of interest constitute many limiting factors to cowpea breeding programs. This justified all cowpea prospection missions around the country that happened in the past, which were unfortunately not always sustainably managed and conserved for future use.

Herein, we review the work carried out in Senegal on the genetic diversity management of the local cowpea germplasm and present the results of a five-year study completed in 2021.

Cowpea Biodiversity Management in Senegal Before 2015

According to previous reports, cowpea biodiversity management started around 1950 in Podor (the northern part of Senegal) and allowed the selection of a local variety called 58-57. This variety is resistant to drought, reaches maturity 75 days after sowing, has a prostrate stand, and produces a significant number of seeds and haulms. In the same period, several prospecting missions were made in Senegal and beyond (in West Africa), which allowed the collection of 74 accessions (Séne, 1966). Between 1964 and 1967, germplasm evaluation work permitted the identification of cowpea varieties adapted to many production zones in Senegal.

In 1979, American varieties selected for drought and high temperatures tolerance were introduced in various Senegalese agro-ecological zones and compared with local varieties (Cissé et al., 1984). Most promising varieties showing the best adaptability were evaluated in larger trials before diffusion. Furthermore, they have been crossed with local varieties for transferring drought and heat tolerance and pests and disease resistance traits (Hall, 1982, 1984). Then, the breeding program prioritized crosses between the best local and introduced materials, focusing on the ones with promising drought tolerance and high yielding traits. Several cowpea varieties developed in Senegal (Ndiambour, Mougne, Bambey 21, Diongoma, Melakh, Mouride, Yacine, and Pakau) came from those crosses. In 1983, the Senegalese cowpea germplasm collection consisted of 535 accessions, including 347 early maturing lines (not photosensitive), 72 late (photosensitive), and 31 irradiated lines from different origins. The same year, new collections were carried out in the Center and the South of Senegal to complement the existing collection. A total of 85 samples were collected (Ndiaye, 1986).

In 2002 and 2014, the inventory of the national cowpea collection revealed that several accessions were lost due to conservation issues. In 2002, the number of accessions available in the "Centre National de RecherchesAgronomiques" (in Bambey) of "InstitutSénégalais de

RecherchesAgricoles" (ISRA) was 247. This prompted a collection mission that resulted in the acquisition of 58 cowpea accessions collected in the Louga, Thies, and Diourbel regions of Senegal (North and Center-North) (Kouakouet al., 2007) and molecular and agro-morphological characterization of the germplasm. Unfortunately, in 2014, most of those accessions were lost again. This loss concerned all accessions collected in the main cowpea growing areas in the North and Center-North regions and the Center-South, the East, and the South of the country. Moreover, before 2015 no cowpea collection or prospection carried out in Senegal included wild cowpea relatives.

Cowpea Biodiversity Management in Senegal Between 2015 and 2021

Between 2015 and 2017, a new national cowpea collection was set up in the framework of a project funded by the West African Agricultural Productivity Program (WAAPP). The overall objective of this project was to contribute to the fight against poverty and food insecurity through better management of cowpea genetic resources. The aim was to set up, conserve and characterize a national cowpea collection for Senegal.

1. Germplasm Collection

Regarding the cultivated cowpea accessions, surveys and collections were carried out between September 2015 and March 2016 in the main cowpea growing regions of Senegal (Louga, Thies, Fatick, Diourbel) and additional regions such as Saint Louis (North), Sédhiou, Kolda (South) and Kédougou (Southeast). The villages covered during the collection were selected in consultation with rural development services (Division Régionale de Développement Rural, DRDR), allowing easier access to cowpea production villages. For optimal coverage, three departments were visited in each region, and four to six villages were visited in each department. An average of 10 farmers were interviewed per village, and seed samples were collected from the fields or granaries. Accessions of wild cowpea relatives were collected between November and December 2016 in six regions (Louga, Thiès, Diourbel, Fatick, Sédhiou, Kolda). Seven hundred thirty-one cultivated accessions and 82 wild relatives were collected across all the regions surveyed (Figure 1, Table 1).

Figure 1

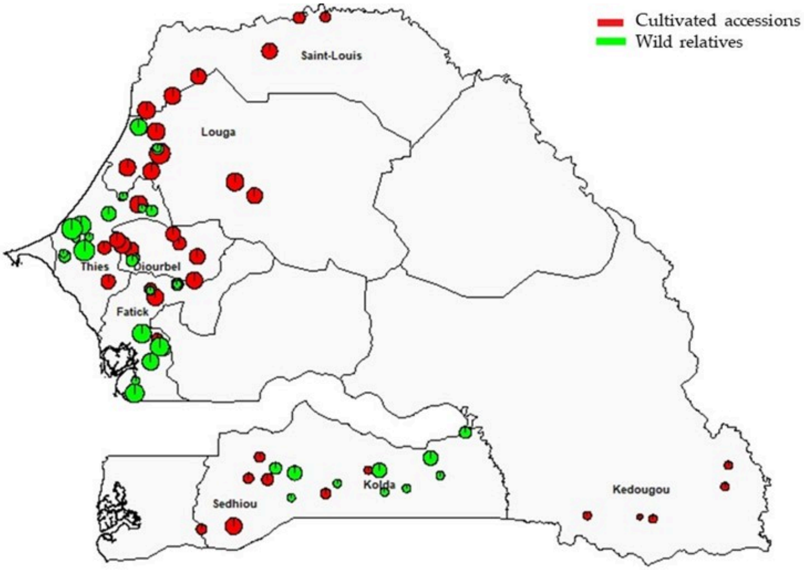

Figure 1 – Map Showing the Villages Where Cultivated and Wild Relative Accessions were Collected (Sarr et al., 2020)

Table 1
Number and Type of Cowpea Accessions Collected Per Region in Senegal

	Louga	Diourbel	Thiès	Fatick	Saint Louis	Sédhiou	Kédougou	Kolda
Cultivated cowpea	152	158	89	90	122	79	35	6
Hybrids	14	2	0	4	0	0	0	1
Wild accessions	0	2	22	21	0	3	0	13
Total	166	162	111	115	122	82	35	20

Among the 82 accessions initially considered wild relatives, 21 were actually spontaneous hybrids between wild and cultivated cowpea (weedy). The hybrids included 20 accessions from the Senegalese Midwest area (Louga, Diourbel, Fatick) called Kodj (spontaneous germination accessions) and one from Kolda. The wild accessions belonged to 2 species: *Vigna unguiculata* var. *spontanea* and *Vigna racemosa*. All *Vigna unguiculata* var. *spontanea* (45) originated from the Midwest, and all *Vigna racemosa* (16) were from the South of Senegal (Sédhiou and Kolda). The cultivated, hybrid, and wild accessions represent the national cowpea collection and represent the local cowpea germplasm. In this chapter, *Vigna unguiculata* var. *spontanea* and *Vigna racemosa* are considered wilds, and both hybrids and wilds are considered wild relatives.

2. Genetic Characterization of the Collection

The collection of cultivated cowpea and wild relatives was sown in the screenhouse at the "Centre d'Etude Régional pour l'Amélioration de l'Adaptation à la Sécheresse" (CERAAS). Among the 731 cultivated accessions, only 671 germinated and were genotyped. However, all the 82 collected samples grew and were genotyped for the wild cowpea relatives. DNA has been extracted on fresh leaves of 21-day-old plants, and genotyping was done with fifteen (15) simple sequence repeat (SSR) markers (Table 2) selected from a previous screening of cowpea markers available at CERAAS. The genetic diversity of the national cowpea germplasm was then compared with that of 25 accessions from 5 countries (Nigeria, Niger, Burkina Faso, India, USA), kindly shared by the Genetic Resources Center (GRC) of the International Institute of Tropical Agriculture (IITA). The data were analyzed using R, GenAlex, STRUCTURE, and Darwin software to calculate genetic parameters, determine the genetic structure, and build dendrograms.

Table 2
SSR Primers Used in the Genetic Study and Their Hybridization Temperature (Tm)

Primer code	Sequence (5′-3′)	Tm (°C)
SSR6671-MF	CACGACGTTGTAAAACGACCAAACTTTGATATCGATCCTTG	79.5
SSR6671-R	GTTCTCTCATGCCATGATG	59.2
SSR6418-MF	CACGACGTTGTAAAACGACCAAATTCCCAAAGACATGTAA	79.4
SSR6418-R	CATGCAATGGCTAAAGGACA	63.6
SSR6777-MF	CACGACGTTGTAAAACGACGTTATCATATATGACAGTCTTTAATC	75.2
SSR6777-R	CATTTGATGCGGTTGATGGG	68.3

Primer code	Sequence (5′-3′)	Tm (°C)
SSR6311-MF	CACGACGTTGTAAAACGACATGCCATTGTTGAGTTGCTTT	81.5
SSR6311R	AGGATGTTGTAGCAGGCTAATTG	63.1
SSR6800-MF	CACGCGTTGTAAAACGACTGACTCTTTCTCTCAAGTTA	75.5
SSR6800-R	GATGGGTTGTTGAAAATAAA	56.5
SSR6807-MF	CACGACGTTGTAAAACGACGAACTATTATACAATCATGCACGA	79.2
SSR6807-R	GTAGCTTACTTCAATGATTAG	50.1
SSR6289-MF	CACGACGTTGTAAAACGACCCCCCAAAGTTGATGAACAC	82.5
SSR6289-R	TTGATGGAGTTCGCATCTTCT	63.7
SSR6243-MF	CACGACGTTGTAAAACGACGTAGGGAGTTGGCCACGATA	82.7
SSR6243-R	CAACCGATGTAAAAAGTGGACA	63.5
SSR6304-MF	CACGACGTTGTAAAACGACCTCTCACATGCAATCCTAAATGGC	82.9
SSR6304-R	CTACGATAATGAGGATAACCATC	58.1
SSR6323-MF	CACGACGTTGTAAAACGACCAAAGGGTCATCAGGATTGG	82.6
SSR6323-R	TTTAAGCAGCCAAGCAGTTGT	63.7
MA113-MF	CACGACGTTGTAAAACGACTCGCACACAGATCCAACATT	81.9
MA113-R	CCTTATTTCTGGTGGGAGCA	63.9
SSR6241-MF	CACGACGTTGTAAAACGACGGGCAGAATGGAGATGAGAA	83.3
SSR6241-R	TTGATGGAGTTCGCATCTTCT	63.7
SSR6819-MF	CACGACGTTGTAAAACGCGCAACATGGAGGAAGATGCAAAG	84.4
SSR6819-R	CAAAAGAAATCATGATCTAACTTC	57.6
SSR6425-MF	CACGACGTTGTAAAACGACTGCTCAGTTCTGTGGTCCTG	82.1
SSR6425-R	TGGTTTATTCATCCAACATAGCA	62.9
SSR6217-MF	CACGACGTTGTAAAACGACGGGAGTGCTCCGGAAAGT	83.6
SSR6217-R	TTCCCTATGAACTGGGAGATCTAT	62.7
M13-tailed primer	CACGACGTTGTAAAACGAC	

2.1 Genetic Diversity of cultivated cowpea accessions

The genetic similarity values of the accessions collected from different regions ranged from 0.971 (Sédhiou and Diourbel) to 0.732 (Louga and Kolda) (Table 3). These results mean that the accessions from Sedhiou and Diourbel were genetically closer, while those from Louga and Kolda were the most distant ones. In general, the genetic diversity is low in the cultivated cowpea accessions. This low genetic diversity was found in many cowpea molecular studies using different technics (Asare et al., 2010; Badiane et al., 2012; Diouf & Hilu, 2005; Fatakun et al., 2018; Kouakou et al., 2007; Sarr et al., 2020; Sarr et al., 2021). This can be explained by the cowpea's mode of reproduction, a self-pollinating plant.

Table 3
Genetic Similarity Values Between the Cultivated Cowpea Accessions Collected from Different Regions in Senegal

Thiès	Sédhiou	Kédougou	Saint Louis	Louga	Diourbel	Fatick	Kolda	
1.000								**Thiès**
0.916	1.000							**Sédhiou**
0.860	0.956	1.000						**Kédougou**
0.851	0.907	0.826	1.000					**Saint Louis**
0.912	0.945	0.861	0.882	1.000				**Louga**
0.866	**0.971**	0.917	0.897	0.948	1.000			**Diourbel**
0.954	0.912	0.830	0.891	0.922	0.906	1.000		**Fatick**
0.762	0.782	0.768	0.745	**0.732**	0.736	0.770	1.000	**Kolda**

The intra-regional variability was greater (79%) than the inter-regional variability (14%) (Table 4). These results agree with those of Sarret al.(2020) (75% versus 11%). The high intra-regional diversity could be linked to many different accessions in each region. In contrast, the low genetic diversity between regions could be partly explained by the distribution of the same cowpea seeds (same varieties found everywhere) in all the regions through donations, seed companies, or agricultural extension services.

Table 4
Analysis of Molecular Variance of Cultivated Cowpea Accessions

Source of variation	Variations (%)	Fst
Among Populations	14	0.141***
Among Individuals	79	
Within Individual	7	
Total	100	

Fst: Genetic differentiation Index; $^{***}p \leq 0.001$

The dendrogram showed three main genetic groups and several subgroups. The genetic structure of collected accessions was independent of geographical origin. However, cultivated cowpea accessions from floodplain recession areas were all in a single subgroup. This can be explained by the low gene flow between accessions cultivated in floodplain recession areas and the rainfed areas. They are cultivated in different growing systems and flower at different times (Figure 2).

Figure 2

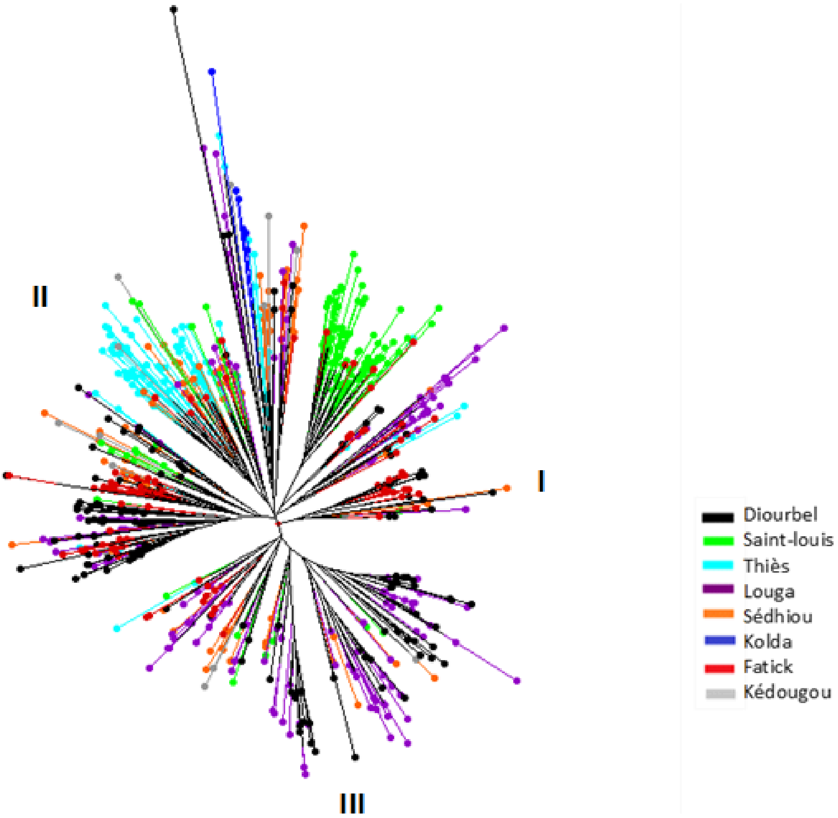

Figure 2 – Dendrogram Based on Genetic Dissimilarity Showing Genetic Relationships Between Cultivated Cowpea Accessions from Eight Regions of Senegal

2.2 Genetic Diversity of Wild Relatives Accessions (Hybrids and Wilds)

The dendrogram showed that hybrids and wilds were divided into three groups according to their type and origin (Figure 3). The first group contained the wild accessions from southern Senegal (Kolda and Sédhiou). The second group contained all the accessions from the Midwest (Louga, Thiès, Diourbel, and Fatick). This group was subdivided into two subgroups. The first subgroup comprises the 45 wild accessions described as *Vigna unguiculata* var. *spontanea* from Thiès, Fatick, and Diourbel. The second is the 20 accessions identified as hybrids (weedy) called “Kodj” in the local name from Louga, Fatick, and Diourbel. Usually, these hybrids germinate spontaneously in farmers’ fields. After harvest, farmers did not mix them with their seeds. They sort the seed of the hybrids and throw them away because they take a longer time to cook as their seed coat is harder than that of the cultivated. Moreover, the seed coat of the hybrids is smoother and the size smaller than that of the cultivated cowpea but larger than that of the wild species. The third group included only the one hybrid from Kolda.

Figure 3

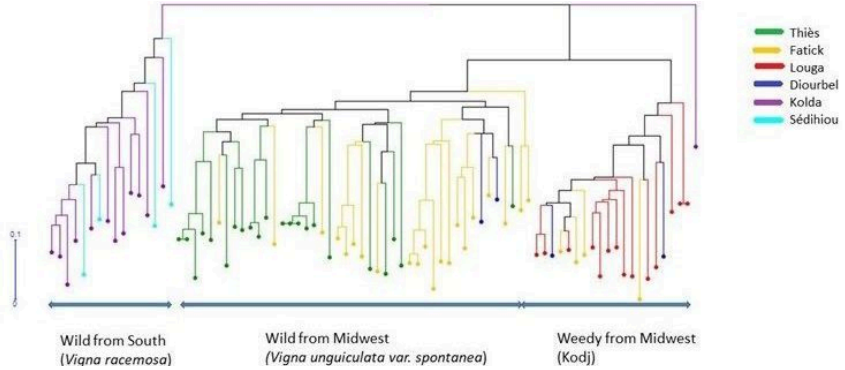

Figure 3 – Dendrogram Based on Genetic Dissimilarity Showing Genetic Relationships Between Cowpea Hybrid and Wild Accessions from Six Regions of Senegal

The genetic differentiation index (Fst) was high, reaching 0.169 between wild accessions from Midwest (*Vigna unguiculata* var. *spontanea*) and hybrids (weedy), 0.234 between those from Midwest and the South (*Vigna racemosa*), and 0.353 between hybrids and southern wild accessions (Table 5). Wilds from the South belong to the *Vigna racemosa* species. This species is different from *Vigna unguiculata var spontanea* from the Midwest. The speciation and the geographical difference could have limited the gene flow between these two species and explained the high genetic differentiation index.

Table 5
Genetic Differentiation Index (Fst) Between Hybrids and Wild Accessions

	Hybrids	**Wild from Midwest**	**Wild from South**
Hybrids	0.000		
Wild from Midwest	0.169	0.000	
Wild from South	0.353	0.234	0.000

****p-value*<0.001

2.3 Genetic Diversity of the Overall Collection (Cultivated, Hybrids, and Wilds)

Cluster analysis of the entire Senegalese cowpea collection (i.e., cultivated, hybrids, and wild accessions) showed two genetic groups with 1.3% admixture. The first one contained the hybrids and the wild accessions (V*igna unguiculata* var. *spontanea* and V*igna racemosa*). The second group included the cultivated accessions. The principal coordinate analysis (PCoA) showed the two distinct genetic groups (Figure 4). The dendrogram of the cultivated cowpea, hybrids, and wild accessions' genetic dissimilarity showed three major groups. The first and second were homogeneous and included only the cultivated accessions. The third group included mainly the wild accessions and the hybrids (Figure 5). The fact that hybrids were clustered with wilds could be explained by their genetic proximity revealed by the 15 SSSR used.

Figure 4a

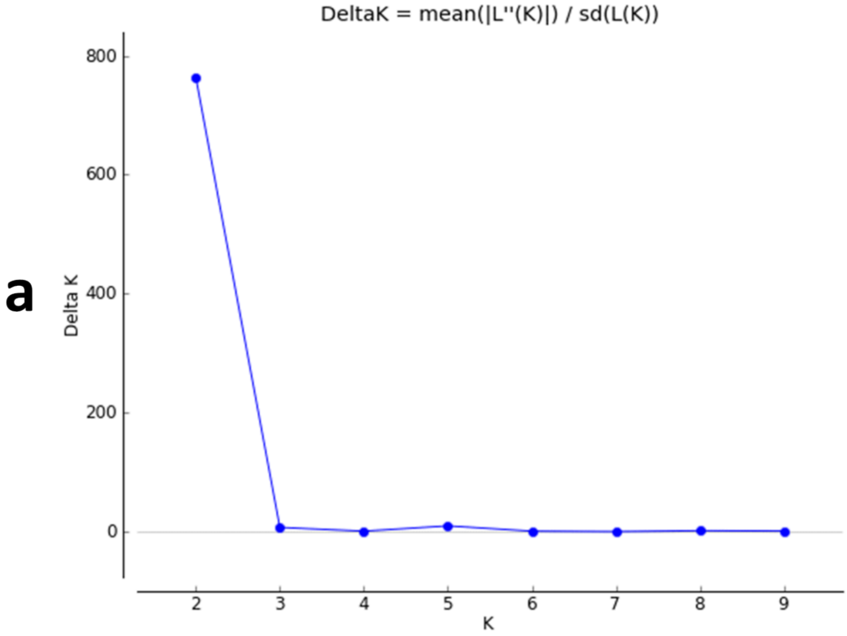

Figure 4a – STRUCTURE Analysis and Principal Coordinate Analysis (PCoA) of Cultivated Cowpea, Hybrids, and Wild Accessions

Figure 4b

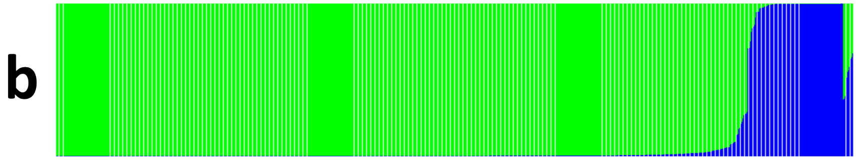

Figure 4b – STRUCTURE Analysis and Principal Coordinate Analysis (PCoA) of Cultivated Cowpea, Hybrids, and Wild Accessions

Figure 4c

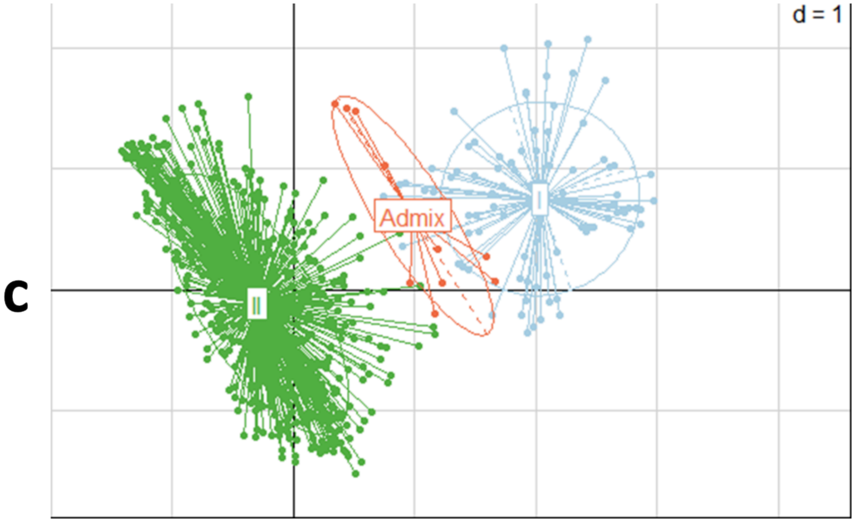

Figure 4c – STRUCTURE Analysis and Principal Coordinate Analysis (PCoA) of Cultivated Cowpea, Hybrids, and Wild Accessions

Figure 5

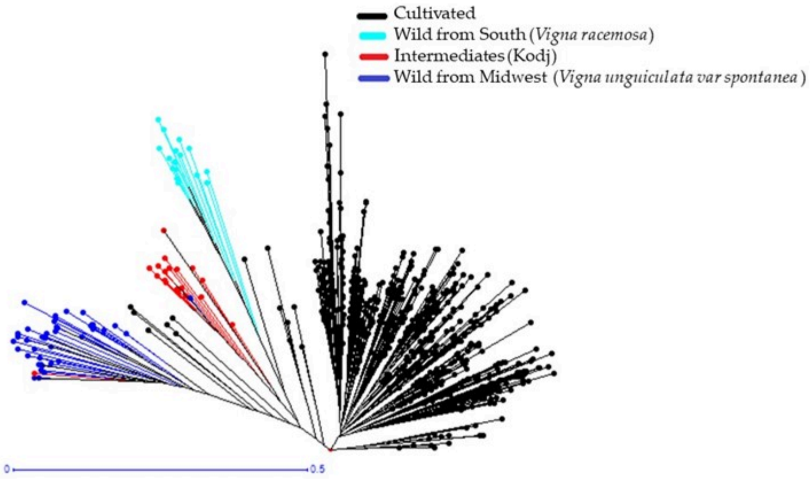

Figure 5 – Dendrogram Showing Genetic Dissimilarity Between Local Cowpea Germplasm (Cultivated Cowpea, Hybrids, and Wild Accessions) from Senegal

All the values of the diversity indices calculated for the two populations, the mean number of alleles (Na), expected heterozygosity (He), and fixation index (F), based on the allelic frequencies for the 15 loci tested, were higher for the hybrids and wilds than for the cultivated cowpea. The genetic differentiation index value (Fst) was 0.229, with the number of migrants (Nm) equal to 2.557 (Table 6).

Table 6
Genetic Diversity Between Cultivated Cowpea and Wild Relatives

Parameters	**Group II**	**Group I**
Sample size (N)	662	83
Mean number of alleles (Na)	5.4	6.267
Expected Heterozygosity (He)	0.382	0.552
Fixation Index (F)	0.834	0.869
Genetic differentiation Index (Fst)	0.229***	
Number of migrants (Nm)	2.557	

****p-value* < 0.001

2.4 Comparison of the Genetic Diversity of the Senegalese Cowpea Germplasm with the Reference Cowpea Collection from IITA

The average genetic diversity observed for the national cowpea germplasm was lower (0.457) than the average diversity of accessions from Nigeria (0.508). At the same time, it was comparable to those obtained for the accessions from India (0.430). These values were higher when compared with the values obtained for accessions from Niger (0.328), Burkina Faso (0.380), and the USA (0.385).

The highest genetic differentiation index was observed between Senegal and USA (Fst = 0.253, p-value = 0.002). So, the Senegalese accessions and those from the USA are the most distant. Important differentiations were also found between Senegal and India (Fst = 0.155), Senegal and Niger (Fst = 0.183), and Senegal and Burkina Faso (Fst = 0.147). The genetic differentiation index (Fst = 0.115) is moderate between Senegal and Nigeria. The ancient introduction could explain this in Senegal of accessions from Nigeria (Sène, 1966). The lowest Fst was noted between Indian and Nigerian accessions (0,101); it could mean that they are genetically closer (Table 7). This study represents accessions from Niger, Nigeria, Burkina Faso, India, and the USA by five samples each. Therefore, the comparison made in this part is only valid for this small number of samples.

Table 7
Genetic Differentiation Index (Fst) Between the Accessions From Different Countries

Senegal	USA	India	Niger	Nigeria	Burkina Faso	
0.000						**Senegal**
0.253	0.000					**USA**
0.155	0.149	0.000				**India**
0.183	0.253	0.198	0.000			**Niger**
0.115	0.171	0.101	0.133	0.000		**Nigeria**
0.147	0.209	0.188	0.119	0.117	0.000	**Burkina Faso**

The dendrogram showed three groups. The first and second groups were homogeneous and included only cultivated accessions from Senegal. The third was divided into two subgroups. The first subgroup enclosed all accessions from IITA, the hybrids, and wild relatives, and the second included some cultivated accessions from Senegal. The Senegalese hybrids and wild accessions have clustered well in the same subgroup regardless of geographical origin (Figure 6).

Figure 6

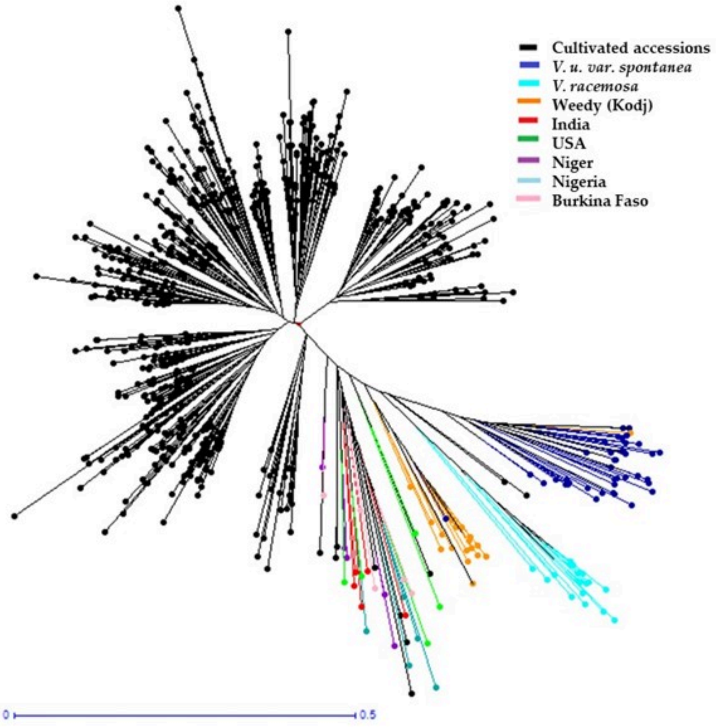

Figure 6 – Dendrogram Showing Genetic Dissimilarity Between the Accessions from Senegal and Those from IITA

Conclusion and Perspectives

Thanks to the important collection and characterization efforts, ISRA has assembled a wide collection of cowpea genetic resources that is representative of the local germplasm and combines old and new collections. The old collection consisted of only cultivated cowpea, while the new one consisted of cultivated hybrids and wild accessions. Besides, this new collection has been genotyped. Cowpea wild relatives, having higher genetic diversity than cultivated cowpea with moderate differentiation, can provide important genes for tolerance or resistance to various stresses that hinder production. Similarly, the five accessions from the USA that were most distant from those from Senegal could provide new genes for crop improvement. The good management of the local cowpea germplasm could improve crop productivity in Senegal in the context of climate change. This improvement will positively impact the livelihoods of both male and female farmers, both nutritionally and economically.

Following this work of collecting and characterizing local Senegalese germplasm, it would be interesting to evaluate the wild relatives for traits related to drought tolerance, *Striga*, and *Macrophomina* resistance which are major constraints to cowpea cultivation in Senegal.The most promising accessions could then be used to make crosses with cultivated cowpea to identify QTLs associated with the traits of interest and yield components.

Acknowledgements

We thank the West African Agricultural Productivity Program (WAAPP) for funding the study and the *International Institute of Tropical Agriculture* (IITA) for providing the global accession from Niger, Nigeria, Burkina Faso, India, and the USA. We also thank AblayeNgom and Rémy Pasquet for their help in identifying cowpea species.

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

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

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

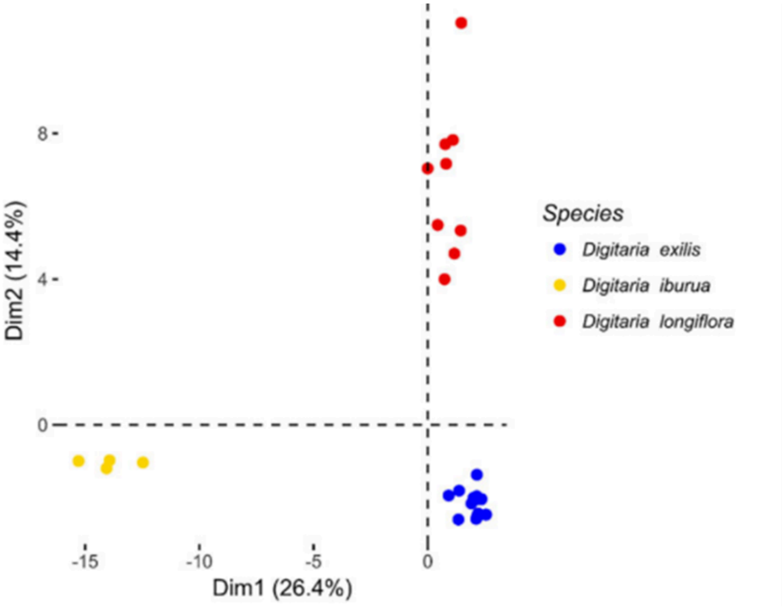

Figure 1 – Principal Component Analysis of the Pattern of Genetic Diversity among Digitaria Species- Digitaria Exilis (white fonio) Digitaria Uburua (black fonio) & Digitaria Longiflora (wild progenitors of white fonio)

Figure 2

Figure 2 – Digitaria Exilis, White Fonio, Plant

Figure 3a

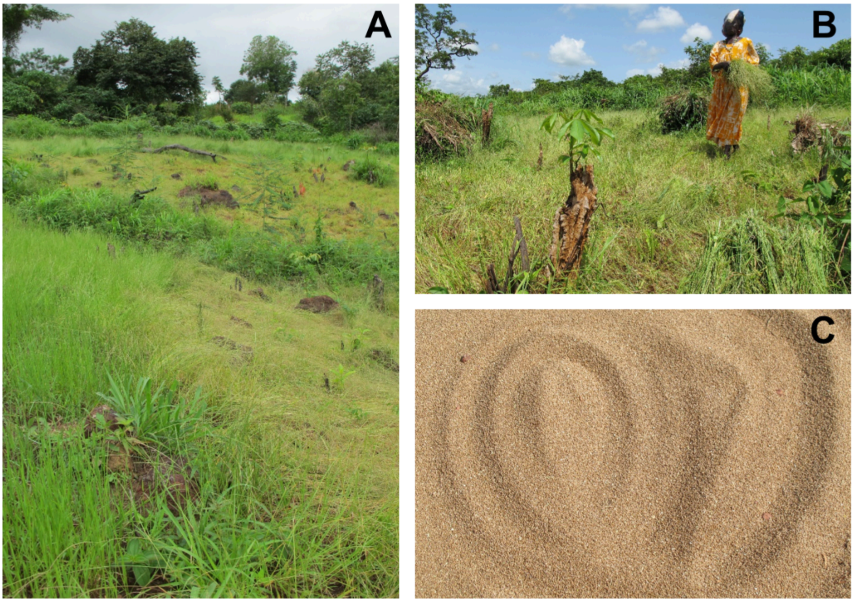

Figure 3a – Fonio, Digitaria exilis, an indigenous staple crop from Western Africa. A – Fonio fields growing short cycle and long cycle landraces; B – Fonio harvest; C – Fonio grains

Figure 3b

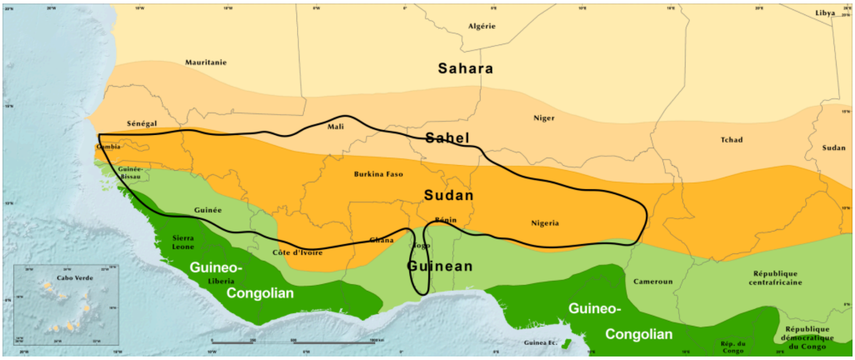

Figure 3b – Geographic distribution of fonio in the bioclimatic regions of West Africa (CILSS, 2016)

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

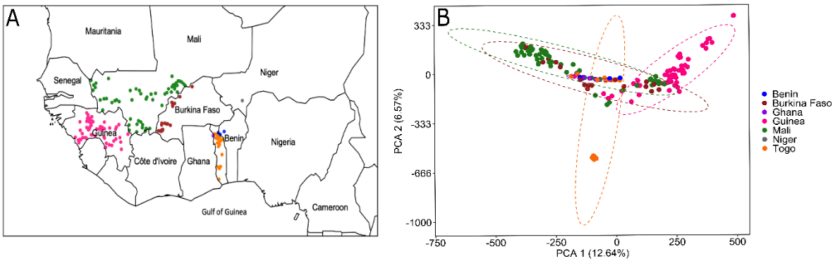

Figure 4 – Genomic Diversity of Fonio Landraces in West Africa

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.

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16. Past, Present, and Future of West African Sorghum Improvement: Building a Roadmap for Climate-adaptive, Farmer-adopted Varieties

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Abstract

Food security and sustainable economic prosperity are key goals for the countries of West Africa (WA). Sorghum (Sorghum bicolor) is among the most important staple crops in WA and has adapted to diverse environments and cultures over many years. However, the process of adaptation is not perfect, and the environment and stakeholder demand is changing, so further sorghum improvement is necessary. National and international sorghum breeding programs are working to improve yield, abiotic stress resilience, and biotic stress resilience. However, it has proved difficult to retain essential end-users' traits, such as grain quality, and adoption of new varieties has remained low throughout the region. The natural genetic variation within locally adapted and preferred cultivars is key to rapidly develop new climate-adaptive varieties by continuously changing allele frequency and directly selecting outstanding lines through efficient genomics-assisted breeding. It is critical to understand the genetic architecture of adaptive traits, develop genomic tools for marker-assisted and genomic selections, and establish effective data management systems

across the region. In this chapter, we describe the genetic diversity of the sorghum germplasm, as well as present an overview of sorghum improvement and perspectives for delivering rapidly and sustainably climate-adaptive breeding products in WA.

Keywords: sorghum, West Africa, breeding, adaptation, genetic diversity

The Sorghum Crop

Sorghum (*Sorghum bicolor* L. Moench), a C4 grass used mainly for grain and biomass production, is a staple crop for over 500 million people in Africa and Asia (National Research Council, 1996) and grown across various climates (Harlan & de Wet, 1972). Sorghum is a diploid species with 10 pairs of chromosomes and is a predominantly a self-pollinating crop, though it will readily cross-pollinate; gene flow is also commonly seen in sorghum (Barnaud et al., 2008b). The small size of the sorghum genome (about 730 Mbp) makes it a good model system among grass species (McCormick et al., 2018; Paterson et al., 2009) for genomic studies and genomics-assisted breeding.

Cultivated sorghums belong to *Sorghum bicolor* subspecies. *bicolor*, with their domestication estimated about 8,000 years ago in East Africa (around present-day Ethiopia and Sudan), followed by their diversification before diffusing south, east, and west (Harlan & de Wet, 1972; Wendorf et al., 1992). A second center of domestication was proposed in West Africa (WA) for guinea margaritiferum (Deu et al., 1994; Folkertsma et al., 2005). Five basic botanical types and ten intermediate types have been defined based on the spikelet and panicle morphology (Harlan & de Wet, 1972). These types—bicolor, durra, guinea, caudatum, and kafir—are originally distributed with respect to geographic regions across Sub-Saharan Africa. These types are used by sorghum breeders worldwide at different levels based on their agronomic importance.

Additionally, four wild races of sorghum have been defined: *virgatum*, *aethiopicum*, *arundinaceum*, and *verticilliflorum*; these predominate in northeastern Africa, the semi-arid, tropical, and savanna Sahelian regions of West Africa, respectively (de Wet, 1978). These races are grouped into S. *bicolor* subspecies *verticilliflorum* (Harlan & de Wet, 1972). In sorghum, wild relatives are rarely used for crop improvement (Ananda et al., 2020), perhaps due to the great diversity available in the domesticated gene pool, compared to crops such as wheat, where wild relatives are often used as donors of traits such as disease resistance (Gill et al., 2011). Still, West African wild, weedy, and admixed sorghums may be useful sources of favorable alleles for stress resilience traits if suitable alleles cannot be identified in the domesticated germplasm (Tesso et al., 2008).

Regardless of botanical type, almost all traditional varieties (landraces) of sorghum in West Africa are tall (2–4 m) and photoperiod-sensitive; that is, they require a critical minimum day-length to flower. Guineas, characterized by an open panicle and resistance to pathogen infection, are predominantly distributed in the humid savannas of West Africa. Caudatums are highly appreciated by breeders, mainly due to their high yield potential (ISRA, 2005), especially in Senegal. Durras, with a compact panicle and usually curved peduncle, are more adapted to the semi-arid Sahelian zone and usually used in breeding programs to contribute drought resilience traits.

Sorghum in West Africa

1. Cropping Systems and Uses

In West Africa, sorghum is mostly cultivated in environments characterized by limited soil fertility, drought, heavy bird attacks, and phosphorus- and aluminum-limited soils (Leiser et al., 2015), where other cereals such as maize and pearl millet can hardly survive. Almost all sorghum production in the region depends on rain-fed farming systems, along with lack of agricultural inputs and vulnerability to climate change, with drought acting as the most common climate factor that limits the production (Mundia et al., 2019). The diversity of farming systems and cultural influences, such as human consumption of sorghum grain for the preparation of meals, including couscous, *lakh*, *To*, *nieling*, *mony*, and local beer, are key factors for sorghum production (Barnaud et al., 2008a, 2008b). Grain quality for food consumption and farmers' preferences remain valuable parameters that determine the types of sorghum varieties grown by smallholder farmers. It has been suggested that locally focused studies need to be undertaken to plan for climate-adaptive varieties to meet the needs of the growing population (Mundia et al., 2019). However, the development of broadly adaptive and resilient varieties would contribute to sustainable food security globally.

2. Genetic Diversity

The genetic diversity of West African sorghum is extremely high and is structured by botanical type, with several ancestral populations within botanical type across countries (Deu et al., 2006; Deu et al., 2008; Faye et al., 2019, 2021b; Folkertsma et al., 2005; Maina et al., 2018; Olatoye et al., 2018). However, several gaps exist in the national and international ex situ collections of WA with untapped genetic diversity and less accessibility to the global sorghum community (Upadhyaya et al., 2017). The French colonial science agency ORSTOM (*Office de la recherche scientifique et technique outre-mer*), predecessor to the current IRD (Institut de Recherche pour le Développement) made collections of sorghum landraces in Senegal, Nigeria, Niger, and Mali in the 1970s (Borgel & Séquier, 1977; Clément & Houdiard, 1977). These collections exist in several genebanks (IRD, ICRISAT, USDA-NPGS, etc.) and constitute sources of adaptive traits for breeding programs. In national breeding programs, most of the duplicated seed lots of these collections have been lost due to poor conservation. More recent collections have been assembled to partly complete the existing gaps and are available to the global sorghum community as ex situ collections. The existing germplasm conservation must remain a key activity to limit the loss of diversity in small and young breeding programs.

Sorghum local varieties harbor genetic variation that should be favorable for developing climate-adaptive varieties (Meyer & Purugganan, 2013). Sorghum is one of the most genetically diverse crops due to its extensive diversification, local adaptation across multiple agroclimatic zones, and continuing wild-crop gene flow that occurred after its domestication (Sagnard et al., 2011). This diversity presents great opportunities, such as the identification of climate-resilient and biotic stress resistant sources (Faye et al., 2021a); however, the diversity of WA sorghum poses challenges such as understanding local adaptation and recovering adaptive traits across various environments. Advances in sequencing and high-throughput genotyping, such as genotyping-by-sequencing (Elshire et al., 2011; Poland et al., 2012) can generate cost-effective and high-density SNP (single nucleotide polymorphism) markers. The development of high-throughput genotyping, combined with large-scale phenotyping, helps to identify natural variants controlling adaptive traits (Faye et al., 2021a; b).

Sorghum Improvement in West Africa

West African smallholder farmers have selected and diffused adapted sorghum for thousands of years through mass selection and seed exchange. Unfortunately, this history of sorghum improvement by smallholders remains poorly understood. Early sorghum breeding in francophone West Africa, prior to independence, was conducted by IRAT (*Institut de recherches agronomiques tropicales et des cultures vivrières*), a French colonial institute. The sorghum improvement program was based in Bambey, Senegal but was part of a research network across French colonial West Africa for germplasm and multi-environment trials. After independence, the national breeding programs of francophone countries of West Africa, (Institut Sénégalais de Recherches Agricoles–ISRA in Senegal, Institut National de la Recherche Agronomique du Niger–INRAN in Niger, Institut d'Economie Rurale–IER in Mali, Institut Togolais de Recherche Agronomique–ITRA in Togo, and Institut de l'Environnement et de Recherches Agricoles–INERA in Burkina Faso) were established to continue the work of IRAT. These programs work in close collaboration with international breeding programs to develop or test varieties for diverse environments. In later sections, we will focus on the history of the formalized sorghum improvement programs in Senegal and Niger.

1. History of Sorghum Improvement in Senegal

Sorghum breeding in Senegal reflects sorghum breeding in WA and has yielded several good varieties that were developed for specific agro-ecological regions. Table 1 depicts the main sorghum varieties that were released and disseminated to farmers for the different agro-ecological zones of Senegal. However, considerable extension efforts must be made to disseminate these varieties in all smallholder farmers and cropping systems.

Table 1
The Sorghum Varieties Developed and Disseminated in Senegal

Varieties	Code	Year of Release	Maturity Cycle (days)	Seed Type	Grain Yield (ton ha-1)	Agro-ecological Zone
Payenne	ISRA-S-618-1	2015	85–90	White creamy Semi-vitreous	2.5–3.5	North peanut basin (300–600 mm)
Golobe	ISRA-S-618-2	2015	85–90	White creamy Semi-vitreous	2.5–3.5	North peanut basin (300–600 mm)
CE180-33	CE180-33	1983	90	White floury	2–3	Centre-north (300–600 mm)
CE151-262	CE151-262	1980	90	White creamy Semi-vitreous	4–5	Senegal river valley
CE196-7-2-1	CE196-7-2-1	1983	95–100	White creamy Semi-vitreous	3–3.5	Centre-west (Mbour area)
CE145-66	CE145-66	1980	100	White floury	2.5–3	Centre-north, Sine-Saloum, South-east
Darou	ISRA-S-622B	2011	105	White creamy Semi-vitreous	2.5–3	South peanut basin (600–800 mm)
Faourou	ISRA-S-621B	2011	105	White creamy Semi-vitreous	2.5–3	South peanut basin (600–800 mm)
F2-20	F2-20	1983	110	White creamy Semi-vitreous	3–3.5	Centre-south, South, and South-east
Nguinthe	ISRA-S-621A	2011	110	White creamy Semi-vitreous	2–3	South-east and North Casamance (800–1000mm)
Nganda	ISRA-S-622A	2011	110	White creamy Semi-vitreous	2 – 3	South-east and North Casamance (800–1000mm)

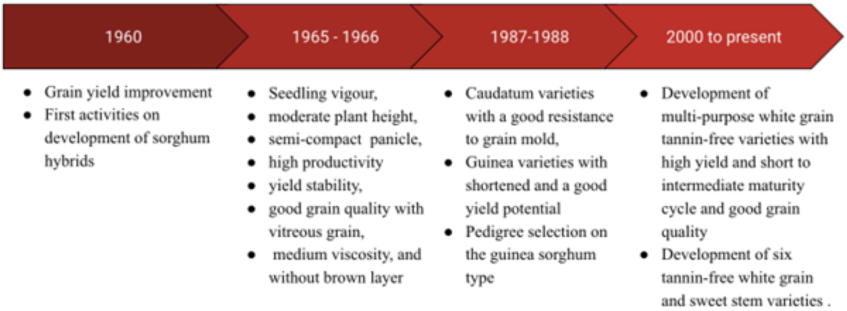
1.1 Senegalese Sorghum Cropping Systems

Sorghum is cultivated in Senegal in three different cropping systems. The most important, in terms of production, is rainfed cultivation (sowing in July) in the southern groundnut basin, eastern Senegal, and middle and upper Casamance. The two other production systems are flood recession cultivation (*décrue*) from November to April along the Senegal River valley (Roy, 2008) and irrigated cultivation during the rainy season (sowing in July) and cold off-season (sowing in October) in the Senegal River valley. Some varietal improvement efforts were carried out in each of the three different cropping systems. Three basic botanical types (guinea, caudatum, and durra) and their intermediate types are predominantly cultivated.

1.2 Beginning of Formal Sorghum Improvement Activities

There have been several phases of sorghum improvement in Senegal (Figure 1). Sorghum genetic improvement started in the 1950s, but it was not until 1960 that defined breeding targets were established for sorghum varietal improvement (Mauboussin et al., 1977). Before 1960, the objective was to focus on farmers' preferences by selecting sorghum lines phenotypically, similar to local cultivars, with better productivity and grain quality. Between 1960 and 1965, sorghum lines were selected more intensively. Breeding objectives were still focused on general grain yield improvement while obtaining varieties close to local cultivars. Short stature was not systematically sought, and trials were carried out without fertilizer inputs. A mass selection activity in the local cultivars of the flood recession and rainfall cropping systems was carried out on the Senegal River. This period also marked the beginning of the development of sorghum hybrids in Senegal. However, the hybrid program was not continued consistently, and no sorghum hybrids were released in Senegal (ISRA, 2005; FAO, 2012).

Figure 1



1960

- Grain yield improvement
- First activities on development of sorghum hybrids

1965 - 1966

- Seedling vigour,
- moderate plant height,
- semi-compact panicle,
- high productivity
- yield stability,
- good grain quality with vitreous grain,
- medium viscosity, and without brown layer

1987-1988

- Caudatum varieties with a good resistance to grain mold,
- Guinea varieties with shortened and a good yield potential
- Pedigree selection on the guinea sorghum type

2000 to present

- Development of multi-purpose white grain tannin-free varieties with high yield and short to intermediate maturity cycle and good grain quality
- Development of six tannin-free white grain and sweet stem varieties .

Figure 1 – The Different Phases of Sorghum Breeding in Senegal

1.3 1960s–1980s: Landrace Purification and Green Revolution-style Varieties

Starting in 1965–1966, several initiatives were undertaken, including the improvement of farming practices, the introduction of founder cultivars from the world collection, the addition of a section for diversification in the Senegal River area, and, above all, the definition of precise selection targets and objectives by the agro-ecological region (Mauboussin et al., 1977). Generally, common selection objectives were defined, then specific objectives were added for each area considered. These common objectives, which broadly correspond to "Green Revolution" style varieties (Swaminathan, 2006), included (a) moderate plant height (~1.8–2 m for rainfed system, ~1.5 m for irrigated system); (b) seedling vigor; (c) semi-compact and erect panicle with good exsertion; (d) high productivity and yield stability; (e) good grain quality with vitreous endosperm, medium viscosity of grain flour, and without brown layer, tannin, and anthocyanin. Specific objectives were also defined for different cropping zones: lines with short maturity cycles less than 90 days, good dryness, and resistance to grain mold for the central zone of the peanut basin; lines with intermediate maturity cycle between 100–110 days and resistance to grain mold for the south-central zone of the peanut basin; lines with late maturity cycle between 110–120 days and resistance to grain mold for the south-eastern Senegal and northern Casamance; and hybrids and lines with early maturity cycle between 80–90 days, very productive, and short stature of about 1.80m for the Senegal River zone.

Selection activities between 1970 to 1980 focused on development of early maturity lines and hybrids for the rainfed and irrigated systems (ISRA, 2005; Luce, 1988). Some of the key varieties that were developed during this period are presented in Table 1. Among them, IRAT 204 (also known as CE 151-262) was developed in 1980 from a cross between IRAT 11 (CE 90) and 73-71 (IS 12610), an Ethiopian line. This variety was developed particularly for the Soudano-Sahelian agro-climate zone (annual rainfall of 500–700 mm) and has been used in several breeding programs in WA because of its high tolerance to biotic and abiotic stresses, such as drought, leaf disease, and insect damage (Muleta et al., 2021).

1.4 1980s–1990s: Refocusing Breeding Targets for Caudatum and Guinea Pure lines

In 1987–1988, the breeding target was reoriented because of the difficulties of the dissemination and adoption of the improved caudatum varieties relative to traditional varieties belonging mainly to the guinea type (ISRA, 2005; Luce, 1995). A study conducted in 1987 and 1988 showed that local guinea cultivars were generally less susceptible to grain mold than improved caudatum varieties, had good adaptive traits, good resistance to diseases and insects, and good grain quality, but their productivity was generally low and their height high. It was therefore proposed to conduct two breeding targets for the Center-South and South zones, with the objectives to (a) emphasizing obtaining caudatum varieties with a good resistance to grain mold and (b) obtaining guinea varieties with short stature and good yield potential while maintaining the characteristics of traditional cultivars (FAO, 2012; ISRA, 2005; Luce, 1988). The year 1988 marked the beginning of pedigree selection on the guinea sorghum type. A recurrent selection program was also initiated for the creation of populations between guinea and caudatum types. In 1993, the selection program for the irrigated system in the Senegal river was stopped.

1.5 2000s–2010s: Focus on Multi-purpose Caudatum Varieties for Central Senegal

From 2000 to 2018, the program focused on the development of multi-purpose, white grain, tannin-free varieties with high yield potential, short to intermediate maturity cycle, and good grain quality that could be used for both food and feed. A cross between the varieties IRAT 204 and Sorvato-1, a line with good grain quality from Togo, resulted in the development and release of six pureline caudatum type varieties (Nguinthe, Faourou, Nganda, Darou, Payenne, and Golobe), all tannin-free, white grain, and sweet stems (FAO, 2012). These varieties were successfully used in bread making to produce compound bread (20% sorghum flour and 80% wheat flour). Their vegetative part, highly prized by animals, is stored after harvest and used as fodder during the dry season. The average adoption rate of the improved varieties in Senegal has increased from low (5%) for the varieties released in the 1980s (Trouche et al., 1999) to moderate (25%) for varieties released in the 2010s (Ndiaga Cisse, personal communication, March 2018). This current adoption rate is comparable to the 27.4% average adoption rate of improved sorghum cultivars in Sub-Saharan Africa (Walker & Alwang, 2015). Two of the major factors limiting the adoption of improved varieties is the lack of financial resources and material to apply the full technology package, as well as the fact that improved varieties do not meet farmers' grain quality preferences. The hybrid program initiated in the 1960s was also resumed in 2012. Recently, ten hybrids were developed, five for the south peanut basin zone and five for the north zone, all of which are in the registration process (Diatta et al., 2019, 2021).

1.6 2020s–Onward: Focus on Breeding Adaptive Varieties for Particular Agro-climates

Since 2018, emphasis has been put on defining and using breeding product profiles (BPPs) based on end-users' preferences and adaptation criteria to guide breeding program objectives.

In the Senegal River, farmers preferred traits consist of short stature, more precocity (<90 d) than the elite improved varieties, and the presence of awn on the panicle to prevent bird attacks (Bullard, 1988; Perumal &

Subramaniam, 1973). The current varieties, Golobe and Payenne, are medium-stature and early-maturing. The first breeding target is to improve the presence of awn on the panicle. The second target is to develop varieties that are insensitive to the cool-off season because high stature varieties tend to reduce their height during the cool season.

In the central and south agro-ecological zones, the main challenges are related to crop management practices; thus, the goal is to deliver varieties that are adapted to the length of the growing season (e.g., moderate photosensitive varieties), or early (< 90 d), medium (95-105 d), and late (> 110 d) maturing varieties for a given zone. Photoperiod sensitivity is an adaptive trait where cycle durations of sensitive varieties coincide with growing season lengths, allowing for local adaptation to abiotic (water limitation) and biotic (grain mold and bird attacks) constraints (Curtis, 1968; Kouressy et al., 2008). In addition, the open panicle trait and grain hardness are targeted as proxies to reduce grain mold damage in caudatum varieties in the central and southern regions. The variety Grinkan from the Mali breeding program is used to bring semi-open panicle, seedling vigor, and moderate photoperiod sensitive traits into elite varieties. In parallel, more efforts are being put into guinea sorghum types for the sorghum growing regions with annual rainfall >800 mm by combining elite caudatum varieties and local guineas to develop varieties with vitreous and hard grains.

To increase the adoption rate of sorghum varieties, current breeding activities involve gathering farmers' preferences, starting with end-users' demands, and integrating farmers in the process of varietal selection (Aissata, 2018; Sissoko et al., 2019). These demands are formulated as BPPs for the different agro-ecological zones. To develop new versions of farmers' preferred cultivars, backcross populations are being developed to introgress the *lgs-1* striga resistance allele from the donor line SRN39 (Gobena et al., 2017), staygreen alleles from the donor line B35, grain mold resistance, and high grain protein digestibility into elite varieties using marker-assisted backcross (MABC).

2. History of the Nigerien Sorghum Breeding Program

2.1 Role of Niger within the French Colonial System

Sorghum breeding activities started earlier with the French institute IRAT in the 1960s across WA through screening and evaluations of local varieties in Niger. Promising varieties were selected for yield improvement and varietal purification for broad adaptation using either mass selection or pure line selection (Chantereau et al., 2002). The French institute, Office de la Recherche Scientifique et technique Outre-mer (ORSTOM), which become the Institute of Research for Development (IRD) collected also sorghum landraces, across Niger in 1976 and 2003 with national partners (Bezançon et al., 2009). Local varieties such as Jan Jare, Bogoba, Babadia Fara, and Babadia Ja were used as screening material from Niger. The objectives were to develop high yielding varieties with medium height and adapted to semi-arid regions. The variety IRAT 204 (early maturing at 90 days) was among the promising varieties developed for WA, which represents 2.74% of the total sorghum cultivated area in Niger. Moreover, IRAT 11 (known as L30, derived from line 137-62 and Jan Jare) was selected for medium maturity (110 days) in the 1970s. However, L30 was not adopted by farmers due to its low food quality.

2.2 Launching of the INRAN National Program

INRAN was created in 1975 following IRAT programs in Niger with four regional research centers in the country based at Kollo, Maradi, Niamey, and Tahoua. The objectives were to contribute to food security and rural development in Niger under the ministry of agriculture. Sorghum breeding is among the earlier programs of other crops in Niger attempting to develop high yielding varieties tolerant to stresses. Major targeted traits were early maturity, acceptable food quality, and good nutritional value. Caudatum and durra-caudatum were the types adapted for semi-arid regions.

2.3 1980s–2010s: INRAN Collaborations with INTSORMIL and ICRISAT

Sorghum breeding in Niger started with germplasm exchange through international programs. Early generations and advanced generations from existing US parents were introduced. Several breeding nurseries were conducted and germplasm exchanged during the International Sorghum and Millet Collaborative Research Support Program (INTSORMIL) to establish strong and durable selection programs in Niger. Sorghum hybrid production started with germplasm from international collaborations for joint evaluations with breeding programs from Purdue University and the International Crops Research Institut for the Semi-Arid Tropics (ICRISAT). Progenies developed by ICRISAT were evaluated in Niger through the Sorghum Elite Progeny Observation Nursery (SEPON). From 1991 to 1995, two sorghum varieties were released: the variety SEPON 82 (M 90038) and SRN39 (ICSV 1007 BF) (Bantilan et al., 2004). Moreover, germplasm exchanges with international partnerships lead to the development of hybrid varieties, such as the NAD1 hybrid (ATx623 x MR732), which was released for the Sahelian agro-climatic zone in 1991 (Ministère de l'Agriculture du Niger, 2012). The NAD1 hybrid is a white seeded and medium-maturity line that yields over two tons per hectare, higher than the local check Mota Maradi (Kapran et al., 1997, 2007). However, the developed varieties were either not broadly adapted or less appreciated by end-users especially during food preparation. NAD1, SRN39, and SEPON 82 represent 0.45%, 0.07%, and 4.95% respectively of the total sorghum cultivated area in Niger in 2009 (Walker & Alwang, 2015).

2.4 2020s–Onward

Nowadays, the Niger breeding program aims to focus more on understanding the needs of end-users through Participatory Rural Appraisal (PRA) and market needs, while accelerating breeding cycles to deliver new varieties with better appreciation (Aissata, 2018). The current breeding targets are defined as BPPs to release adapted lines for different regions across the country. The main breeding targets involve breeding for high yielding varieties with tolerance to drought stress; resistance to striga, downy mildew, midge, and long smut; early maturing; and high grain and forage quality.

Genetic and Genomic Resources for West African Sorghum Breeding

The sorghum germplasm in WA, including landraces, were (and are still being) adapted to various environmental variations and farming practices for many generations; thus, selection must have favored the fixation of adaptive loci (Orr, 1998) useful for breeding (Leiser et al., 2014). The majority of elite varieties in breeding programs of WA were developed over 30 years ago. Though some of these varieties might be obsolete, several of them are still adapted to different environments across WA. For example, IRAT 204, SEPON 82, Sorvato-1, Sariaso 11, Sariaso 15, Grinkan, Mota Maradi, and SRN39 are key elite breeding lines. These key varieties have been extensively used to generate crosses across breeding programs, and it is expected that the presence of shared common haplotypes across diverse breeding populations may facilitate deciphering the genetic control of key traits and their pyramiding in improved varieties.

1. Genome-wide Genotyping of Genebank Collections

The thousands of West African sorghum accessions available in genebanks are potentially useful sources of trait donors for pre-breeding (Kimber et al., 2013; Upadhyaya et al., 2017). Recently, using sequencing technologies, several genebank collections have been characterized, providing useful resources for breeding programs of the region (Bellis et al., 2020; Billot et al., 2013; Faye et al., 2019; Lasky et al., 2015; Maina et al., 2018; Olatoye et al., 2018). In WA, national and international sorghum collections were genotyped using high-density SNP markers that are publicly available to the global scientific community (Faye et al., 2019, 2021b; Maina et al., 2018; Olatoye et al., 2018). Genomic analyses showed several ancestral populations structured hierarchically with respect to botanical types and agro-climatic zones across countries.

A West African sorghum association panel (WASAP) was assembled by breeders, physiologists, and geneticists in Senegal, Niger, Togo, and Mali and genotyped using GBS (Faye et al., 2021b). Based on 159,101 high-quality biallelic SNPs obtained for this panel, genetic characterization showed that high genetic diversity exists in sorghum across WA where 8 ancestral populations are found in Senegal, Niger, Mali, and Togo germplasms. The genetic characterization of the WASAP and different collections, *ex-situ*, allowed to better understand the genetic diversity, population structure, putative alleles for local adaptation, and farmer selections existing in WA. These genomic resources for WA sorghum germplasm would contribute to the genetic dissection of adaptive traits and development of new varieties adapted to the current and future environmental conditions.

2. The Potential of Genome-wide Association Studies for Trait Discovery

Cultivars harboring favorable alleles for local adaptation are potential donors of winning traits and can be used for pre-breeding through genomics-assisted breeding. Genome-wide association studies (GWAS) help to identify natural variations that control key traits in adapted cultivars and multi-parental populations. GWAS have been successfully applied in sorghum panels including WA cultivars, with the identification of known and novel loci associated with photoperiodic flowering, plant height, drought tolerance, grain pigmentation, farmer preferences, and climatic variables (Bellis et al., 2020; Faye et al., 2019, 2021b; Hu et al., 2019; Lasky et al., 2015; Maina et al., 2018; Olatoye et al., 2018). The Maturity genes, *Ma6*, *Sb*CN8, and *Sb*CN12, have been mapped several times using different sorghum panels of WA, suggesting the predominant role of these genes for photoperiodic flowering differences in the WA sorghums. However, the strong population structure observed in the germplasm suggests applying regional GWAS on specific populations or on multiparental populations with balanced gene pools.

The backcross-nested association mapping (BC-NAM) populations developed by the Mali breeding program (Teme, 2018), Australia breeding program (Jordan et al., 2011), and the sorghum MAGIC population from Purdue University (Ongom & Ejeta, 2017) were shown to segregate for key adaptive agronomic traits, including high yield, drought tolerance, early maturity, grain quality, high protein digestibility, and disease and pest resistance. These multiparental populations constitute useful genetic resources for GWAS and varietal improvement in WA (Teme, 2018). Also, following a similar strategy, nested-association mapping populations (NAM) were developed in Senegal and Niger to constitute useful genetic resources for breeding programs.

Perspectives on New Breeding Technologies for Sorghum in West Africa

1. Overview of Adoption of New Technology: Separating Fads from Solutions

Technology in plant breeding and genetics is constantly evolving. Crop improvement programs must carefully consider which new technologies they adopt or not (Bernardo, 2016b ; Simmonds, 1991). Some technologies may be useful for some programs and not for others, or for specific breeding targets within a program and not others. All breeding programs, from well-financed commercial breeding to small developing country NARS programs, must consider the breeding technology to use depending on the status of their breeding program and the genetic architecture of priority traits. For instance, a simulation of a Haitian sorghum breeding showed that genomic selection may, or may not, be more cost-effective than phenotypic selection depending on the underlying genetic architecture for yield variation (Muleta et al., 2019). This highlights the need to integrate effective selection methods for small NARS programs. Genomics-assisted breeding based on shared genetic and genomic resources can help to leverage limitations of field phenotyping for optimal selection in early generations across multiple environments (Cobb et al. 2018; Deshpande et al., 2016).

The development of genomic tools contributes to solving the roadblocks that limit or delay the process of achieving breeding product concepts using conventional breeding. Conventional breeding has yielded many elite varieties of important economic values. However, phenotypic selection in early generations for many adaptive traits, such as photoperiodic flowering and drought tolerance, is difficult for small and young breeding programs.

One of the reasons is that multiple field trials are generally required for optimum selection. Crop variety update is a slow process in small and young breeding programs and can take up to 10 years from first crossing to releasing new varieties to farmers and end-users. This process can take even longer when considering large-scale farmer diffusion and adoption, while a limited attention is given to most staple food crops such as sorghum in Africa. With advances in next-generation sequencing technologies and cost-effective genotyping platforms, there are opportunities to modernize small and young breeding programs to accelerate varietal development and continuously release new founder lines through genomics-assisted breeding (Poland, 2015). Figure 2 resumes the key local and elite germplasm useful for the development of climate-adaptive varieties for smallholder farmers and end-users using genomics-assisted breeding.

Figure 2

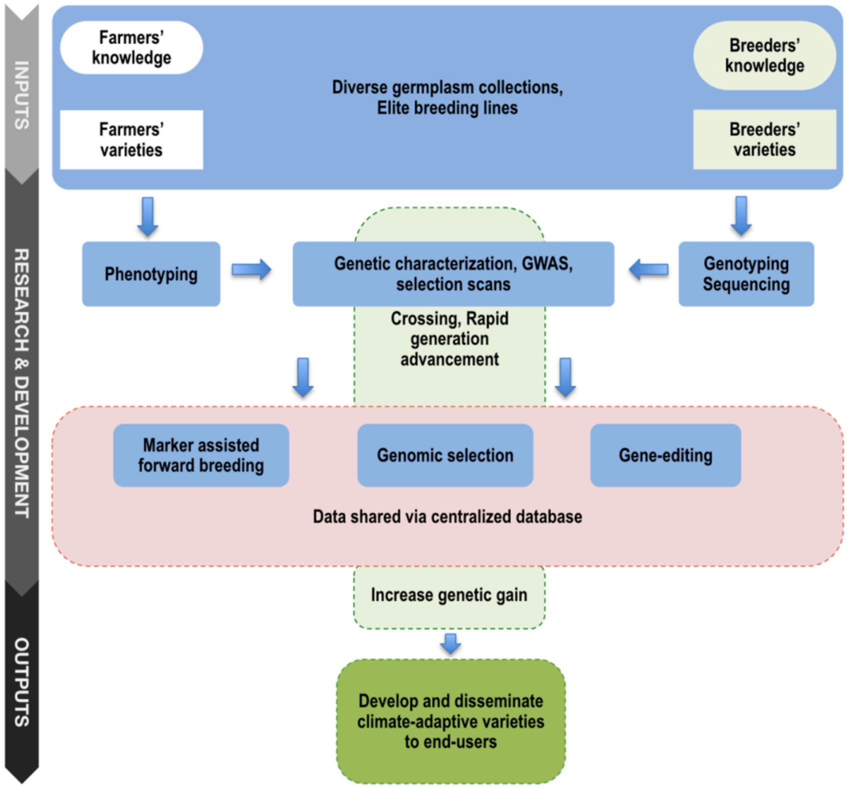


Figure 2 – Development of Climate-adaptive Varieties through Genomics-enabled Breeding Network Systems

2. Rapid Generation Advancement and Targeted Use of SNPs

Rapid generation advancement has been proposed to accelerate variety product profile development in the International Rice Research Institute (IRRI) breeding program (Collard et al., 2019). The method consists of rapidly fixing genotypes to homozygosity with 3.5 to 4 generations per year and starting yield trials with F_5-derived lines for seed increase instead of using F_7 lines. In this context, quality and uniformity control of seed lots and crosses can also contribute to establishing an efficient breeding product development. In the case of sorghum in WA, a defined set of several SNP markers can be used for quality control of any pair or multiple founder breeding lines. Having highly polymorphic markers will complement the available trait-associated cost-effective Kompetitive Allele Specific PCR (KASP) markers to establish an efficient marker-assisted selection (MAS) program for forward breeding of simply inherited traits. Quality control activities of WA breeding programs can be carried out at the regional facility established at ISRA/CERAAS. However, out-sourcing genotyping in specialized laboratories would be more effective for large-scale genotyping, especially for saving breeders' time and focusing on main breeding activities.

3. Systems for Data Management and Sharing

Enabling data sharing and developing a centralized database that stores phenotypes, genotypes, and pedigree breeding information will contribute to establishing an efficient genomics-assisted breeding pipeline in WA. Since 2014, the Breeding Management System (BMS) of the Integrated Breeding Platform (IBP) has actively helped the management of breeding activities of several crops, including sorghum, in several NARS in WA. Such a centralized database would be particularly beneficial for GS model training to improve prediction accuracy and have access to correlated phenotypic and genotypic data from different environments. These datasets would contain high frequency of common haplotypes shared across populations and a wide range of environmental trials. The more related data and larger training populations available to train GS models, the better the prediction accuracy as previously demonstrated in the International Maize and Wheat

Improvement Center (CIMMYT) wheat breeding (Battenfield et al., 2016). Accessible breeding and training populations will be potentially useful to develop climate resilient varieties because of the extensive agro-climate variation and local environment testing that were exercised by breeders in the region through the IAVAO network.

4. Genomic Selection

Genomic selection approach was first established in animal breeding and is an efficient method to accelerate breeding cycling and increase genetic gain (Jannink et al., 2010). Its usage in crop breeding programs is recent and has shown promising results, especially in crops such as maize, wheat, and barley (Michel et al., 2017; Pierre et al., 2016; Zhang et al., 2017). Simulations and empirical studies of GS have demonstrated a potential to increase genetic gain while reducing the number of breeding cycles in several food crops (Battenfield et al., 2016; Bernardo, 2016a). In GS, the whole performance of individuals is assessed regardless of interaction between positive and negative alleles by estimating the individual total performance based on individual genomic-estimated breeding values (GEBV), thus more efficient when dealing with polygenic traits. Both genomic selection and MAS provide advantages to more rapidly increasing genetic gain per unit time and unit cycle, and therefore can be integrated together in the breeding pipeline for more efficient breeding.

Applications of GS are currently limited in small breeding programs, including WA sorghum breeding. Most NARS breeding programs run elite by exotic breeding rather than elite by elite breeding compared to most advanced public or private international breeding programs. However, correlated genotypes exist in diverse West African sorghum populations because the genetic diversity is structured by botanical types and subpopulations within botanical type across countries (Faye et al., 2021b) and diverse key founder lines such as IRAT204, Sorvato-1, Grinkan, SEPON 82, and Sariaso 11 are shared among breeding programs. Continuous sharing of breeding materials across breeding programs will be useful for effective GS implementation.

5. Gene Editing

CRISPR/Cas9, Cas12a, and Cas13 gene editing systems are emerging technologies that hold opportunities to increase genetic gain in breeding. Integrating CRISPR-based gene editing with genomic-assisted selection may help to purge deleterious alleles while favoring rapid genetic gain. This system yields potential interest to deal with negative epistasis traits (Sackman & Rokyta, 2018). Important traits such as tannin content, which may be negatively associated with grain mold resistance (GMR) and grain quality, or grain yield with plant height could involve negative epistasis. The condensed tannin in the pigmented testa of sorghum seed is controlled by the presence of loss-of-function alleles at both *Tannin1* (*Tan1*) and *Tannin2* (*Tan2*) genes (Wu et al., 2012, 2019), and indirectly involved in GMR (Ackerman et al., 2021; Nida et al., 2021), which can be directly edited in tannin-free elite varieties. Other loci such as YELLO SEED1 (Y1) and Y3 genes have also shown to contribute to GMR (Nida et al., 2019) and thus can be edited to develop resistant varieties.

Conclusion

Important progress has been achieved in assembling and genetically characterizing the WA sorghum germplasm. High genetic diversity exists within and across breeding programs, with multiple ancestral populations shared across countries. To take advantage of the diverse sorghum germplasm, interdisciplinary researchers must work in synergy to understand sorghum adaptation to specific and across diverse environments. Genomics-assisted breeding through population genomics, GWAS in multiparental populations, MAS, GS, and gene-editing can offer the ability to directly trace the untapped diversity and introduce natural variation into locally preferred cultivars. However, a rigorous scientific approach, such as the GoHy method, must be employed to avoid wasting time, resources, or distracting breeding activities as a result of adopting new technologies without proper setting of development goals and rigorous hypotheses. The rigorous definition of BPPs and GoHy will not only allow testing hypotheses for functional causal variants for adaptive traits but also increase genetic gain to establish food security in West Africa. As phenotyping and genotyping platforms continue to be more and more sophisticated, it is urgent to enable continuous data sharing and management with a centralized database.

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17. Modern Approaches for Sorghum Breeding in Mali

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Abstract

Sorghum is an important and versatile food crop in the Sudan savannah environments of West Africa. Sorghum production doubled in the last 20 years and its yield remained stable and low in Mali. Molecular markers were used to dissect quantitative variation to increase efficiency of breeding programs. From 2009–2014, marker-assisted recurrent selection (MARS), an integrated process to identify favorable alleles and to monitor their pyramiding throughout the breeding course, was implemented. Two large bi-parental populations derived from complementary recent elite inbreds, Tiandougou, Keninkeni, and Lata-3, were developed to improve grain yield productivity and stability while maintaining traditional food processing quality. Populations were phenotyped multi-locally. Quantitative Trait Loci (QTL) analyses identified, in each genomic region, the most favorable morphologic, yield components, grain quality, and flowering time parental alleles. Marker-assisted recurrent selection approach is detailed for one of the populations. Several genotypic ideotypes corresponding to ideal recombination patterns between the parents were defined. Molecular marker-guided recurrent crossing allowed favorable QTL accumulation for a large range of traits. Three marker-assisted recurrent selection cycles were accomplished. Four stable and superior elite lines were identified, leading to their registration in 2018 in national and ECOWAS (Economic Community of West African States) catalogs.

Keywords: sorghum, marker assisted selection, photoperiod, Sahel

Introduction

Sorghum (*Sorghum bicolor*) is one of the most important staple crops in West Africa, especially in the Guinea and Sudan savannah environments. Sorghum production in West Africa doubled from 1980 to 2008 because of the increase in cultivated areas although the yield remained stable and low. Past breeding efforts on sorghum in West Africa, starting in the sixties, were essentially on increasing the harvest index by developing photoperiod insensitive varieties and reducing plant height and tiller number. However, this approach showed limited positive impact mainly because making the sorghum photoperiod insensitive removed a key component of adaptation to climatic conditions and cultural practices of the target environments (Kouressy et al., 2008a). Furthermore, new varieties showed poor grain quality because of unsuitable biochemical and physical properties or sensitivity to grain weathering. Recent approaches aim to maintain rusticity traits and grain quality of local cultivars (Vaksmann et al., 2008) with improved yield potential to support intensification.

This breeding strategy is particularly adapted to the Malian southern zone (>800 mm of annual rainfall) where better soil fertility, due to cotton cultivation, allows new sorghum varieties to express their yield potential. However, in the center zone of Mali (≥500 mm) where sorghum crop faces more severe drought constraints, early maturing varieties with a low level of photoperiod sensitivity are the main focus of breeders.

Sorghum has a wide range of use in food and feed industries, as well as in alcohol and renewable energy production. In Africa, particularly in Mali, sorghum is mainly used in traditional food and beverage (processing of main meals and traditional beer). Improved varieties are not widely adopted by end users mainly because of the poor seed quality. In Mali, one of the main traditional dishes prepared from sorghum flour is Tô, a thick porridge. The characteristics of a good Tô are firmness and retention of its firmness, water, color, and taste while stored at night. Biochemical and physical characteristics of grain and their interactions determine its quality for end users (Fliedel, 1995).

Molecular markers are useful tools to dissect highly polygenic traits into QTL, providing a way to improve breeding efficiency of polygenic traits. During the past 20 years, QTL studies have often relied on using segregating populations suitable for repeated or multi-environment characterization. However, such populations have the drawback of generally being disconnected from breeding materials because of the time needed to develop them. For this reason, QTL detected in such experimental populations are often not transferable and not applicable in breeding populations. On the contrary, QTL analyses that are integrated to the breeding process and specifically designed for target crosses should provide applicable tools to improve breeding efficiency.

Marker-assisted recurrent selection (MARS) has been proposed as an integrated process of breeding and detection of QTL of interest. In such approaches, molecular markers are used to identify key QTL involved in target traits and environments and to monitor and pyramid favorable alleles in subsequent generations through progenies crossing. The ideal genotype that can be obtained from a bi-parental cross can is a mosaic of chromosomal segments carrying favorable alleles from both parents.

MARS schemes involve several successive generations of crossing of superior individuals, based on their molecular marker genotypes, and the use of multi-trait selection indices. This approach could enable the achievement of an ideal genotype, which is unlikely to be realized with a classical breeding process within a population of realistic size (Peleman & van der Voort, 2003). The added value of using molecular markers is to track recombination towards the breeder's ideotypes and allow simultaneous detection of QTL for all traits that need consideration. QTL analysis can also be assessed in different environments to provide a basis for Genotype by Environment (GxE) interpretation.

For now, only a few examples have been published on the application of the MARS approach (Beyene et al., 2016; Eathington et al., 2007; Johnson, 2003; Rahman et al., 2020), and to our knowledge, its use on African sorghum has not been reported. However, the MARS approach has been successfully applied by the private sector, especially in maize (Ribaut & Ragot, 2007).

Integration of molecular markers requires significant modification in the organization of a breeding program, which becomes a more complex decision-making process involving more data analysis in a shorter timeframe. For this reason, the successful application of this approach must rely on a tight interaction between breeders, genotyping services, and geneticists in charge of data analysis and crossing schemes development.

Between 2008 and 2014, as part of the Generation Challenge Programme (GCP), a project called "Improving sorghum productivity in semi-arid environments of Mali through integrated MARS" was implemented within the national breeding program of Institut d'Economie Rurale (IER) with the collaboration of Syngenta and the Centre de coopération Internationale en Recherche Agronomique pour le Développement (CIRAD). This chapter summarizes the results obtained from that project and reflects on lessons learned from implementing marker-assisted and ideotype-driven selection in a national breeding program. Prospects for accelerating sorghum breeding under climate uncertainties and with better precision are also highlighted.

Population Development

1. Parents' Choice

The breeding product targeted an improved grain yield (>2 t/ha), photoperiod sensitivity that provides adaptation to local production environment, and acceptable grain quality for traditional food preparation. Three varieties were used as parents for the development of new breeding populations based on their complementary attributes. The first two varieties, Tiandougou and Keninkeni, were elite varieties from the IER breeding program, while Lata-3 was an improved variety from the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT). Tiandougou is a Caudatum type with a thick pericarp, large seed size, and chalky grains, while Keninkeni and Lata-3 are Guinea botanical types with a thin and glassy pericarp (vitreous endosperm) and medium seed size. The three parents are medium height (< 200 cm), well adapted to the Sudano-sahelian conditions, and photoperiod sensitive. From sowing to grain's physiological maturity, Tiandougou is slightly later (127 days) than Keninkeni and Lata-3 (120 days). Two populations, Tiandougou by Keninkeni (P114) and Tiandougou by Lata-3 (P118), were selected to pursue the recurrent cycle selection.

2. Crossing and Population Development

Hand emasculation was performed among varieties during the 2008 rainy season to generate F_1 seeds. During the crosses, male and female individual plants used in each cross were self-pollinated. The different crosses were harvested and sown during the first off-season (2008–2009) to produce F_2 seeds. Parental conformity and genetic variability tests were performed in an off-season F_2 production nursery on each F_1 plant and parental seed lot using molecular markers. The systematic control of F_1 plants allowed the identification and avoidance of several issues like self-pollinations or non-conformity to the expected cross. Thanks to this quality control, unique F_1 plants identified as conforming to the parents were selected to develop the F_2 generation, which ensured perfect homogeneity of the populations. The F_3 seeds were then produced during the same off-season (See Figure 1). The two populations, each made up of more than 400 F_3 families, were evaluated in the field in the 2009 cropping season. Rows of 10 F_3 individuals per family were planted in 2009 and a single F_3 plant was randomly taken in each row. Ten F_4 plants per family were then sown in the 2009 -2010 off-season, selfed, and bulked, leading to a total of 400 $F_{4:5}$ bulk family seeds, which were used for multi-location phenotyping experiments in the 2010 cropping season.

Figure 1

Figure 1 – Generation Advancement of Photoperiod-sensitive Sorghum Lines

Field Phenotyping

Multi-location phenotyping experiments were conducted during the cropping season, in 2010 for P114 and in 2011 for P118. Three experimental research stations were identified (See Figure 2) as having reliable and homogeneous field conditions to allow large populations phenotyping: Cinzana station (13°15′N, 5°58′E W, 265 m; Sudano-sahelian savannah), Sotuba station (12°39′N, 7°56W, 381 m; Sudano-sahelian savannah), and Farako station (11°13′N, 5°29′W, 375 m; Sudano-Guinean savannah). The three stations cover the main sorghum production areas in Mali. All three sites have a mono-modal pattern of rainfall in summer (May to November), accounting on average for 690 mm at Cinzana, 890 mm at Sotuba, and 1,060 mm at Farako. Average maximal/minimal monthly temperatures were 35.6 °C/19.3 °C at Cinzana, 34.7 °C/20.6 °C at Sotuba, and 33.7 °C/21.0 °C at Farako.

In order to increase the number of environmental conditions, phenotyping was conducted at two different sowing dates in each location. Each population was thus phenotyped in six environments. In Sotuba, a late sowing in October was conducted to complete a photoperiod-sensitivity study of the progenies. Each population was thus observed in long and intermediate day length (usual cropping season, sowing 19 June and 15 July 2011) and short-day length (off-season, sowing 3 October 2011). Maximum astronomical day length is 12.78 h at Cinzana, 12.75 h at Sotuba, and 12.66 h at Farako.

Figure 2

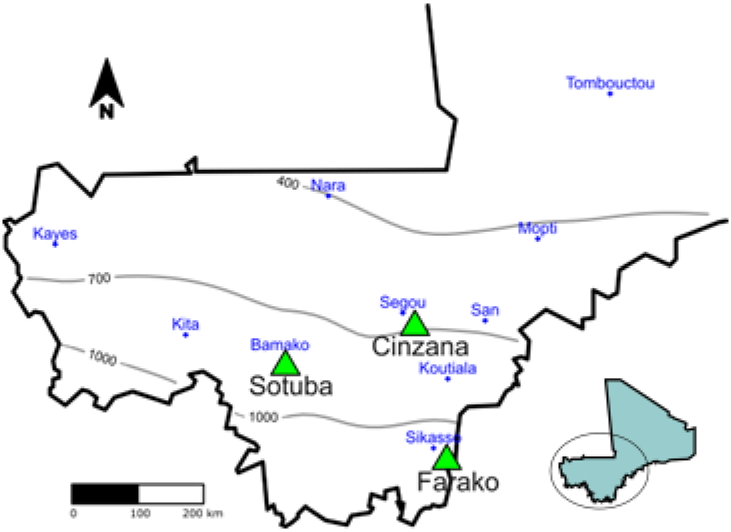

Figure 2 – Location of Phenotyping Sites in Mali and Isohyets Over the 1981–2010 Period

Experimental layouts for each population followed an augmented design. For P114, there were 447 entries with 2 rows of 4m per entry (spacing within rows: 0.4 m; spacing between rows: 0.75 m), 20 hills per plot, and 2 plants per hill. Each trial included a single replication of 401 progenies plus the two parental lines, used as checks (23 entries of each parent) regularly included in the design to control field heterogeneity. For P118 there were 464 entries with 29 blocks of 16 entries (14 progeny and 2 parents used as checks) with the same spacing and thinning as the P114. Traits recorded in the different locations were grain yield, yield components, flowering date, plant height, and panicle morphology. Some other traits, such as lodging, disease, and bird damage were recorded when relevant.

Grain quality was phenotyped in both populations using grain samples from a single environment that was selected after harvest based on the overall quality of the harvested grain (Guindo, 2016). The grain samples collected after harvest were analyzed in the agroclimatology laboratory of IER. Dehulling yield, the ratio of dehulled grain weight to total grain was measured. A mini-Tô was prepared from dehulled grain in the Food Technology Laboratory (LTA) of IER on which Tô consistency and Tô color were measured. In addition, a sample of harvested grain was sent to CIRAD, France where Near Infrared Spectroscopy (NIRS) analyses were performed on whole grain to obtain predictions for the total content of grain proteins, lipids, and amylose (Guindo et al., 2016). Endosperm texture and pericarp thickness were also measured by visual examination of grains. Finally, image analysis was conducted on a sample of grains to determine grain shape and color.

Genetic Maps Construction

Genotyping of P114 was completed in 2009/2010. DNA was produced from a bulk of 10 F_4 individuals from each F_3 family grown in the greenhouse at Montpellier. At the beginning of the project, and until 2010, single nucleotide polymorphism (SNP) markers were not commonly used in sorghum. A set of 79 simple-sequence repeat (SSR) markers was thus used at the early stages of the project for population construction. This map was then completed with SNP markers using the SNP information available in early 2010. A first experiment, using Illumina technology, was carried out using an array of 384 markers. Genotyping of the population was finally completed with an additional experiment using 100 well-distributed Kasp SNPs developed by the Integrated Breeding Platform (https://www.integratedbreeding.net/45/products-catalogue?id=330). A map using the most informative markers was derived with a total number of 200 loci (124 SNP, 76 SSR) (See Figure 3) that spanned a total genetic distance of 1,793 cM and was used for QTL detection.

Genotyping of P118 was carried out in early 2012. DNA extracts were produced from bulks of F_4 individual plants sampled from each family during seed multiplication in Sotuba in 2010. A total of 236 Kasp SNP markers were analyzed on 401 F_3 individuals. The genetic map was constructed from 224 reliable markers, spanning a total genetic distance of 1,340 cM.

Figure 3

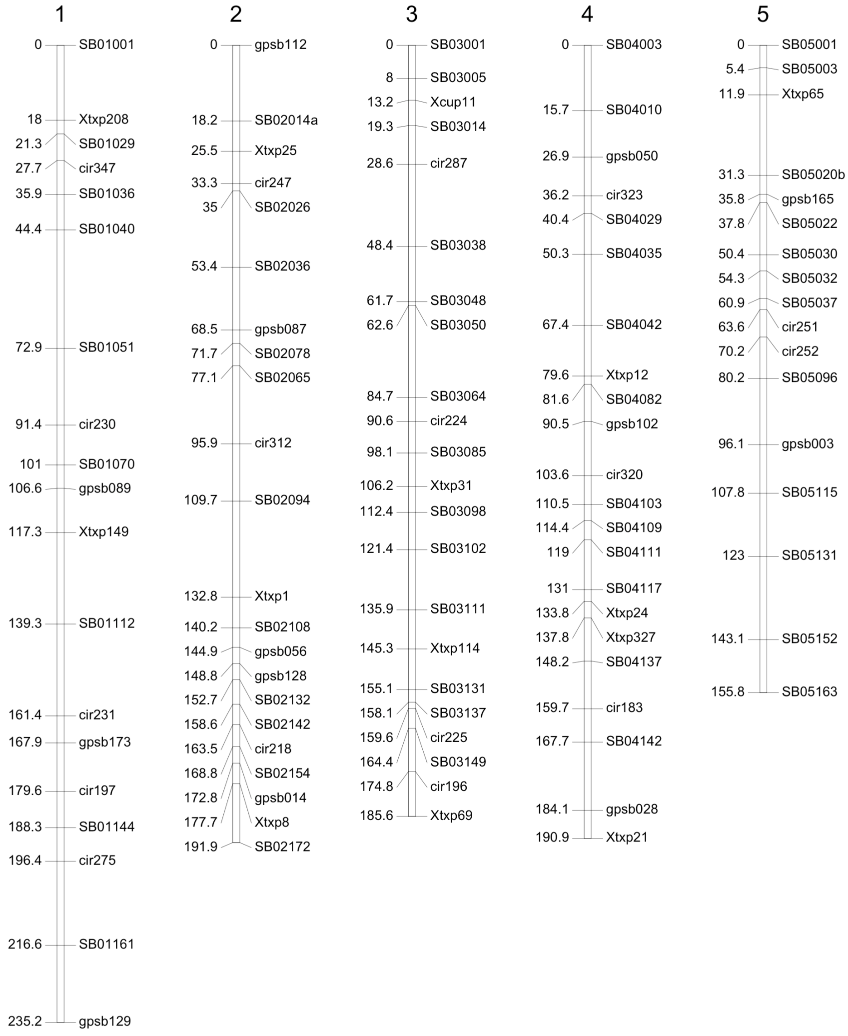

Figure 3 – Genetic Map with 200 Loci (124 SNP, 76 SSR) used for QTL Detection of P114

Figure 3 Continued

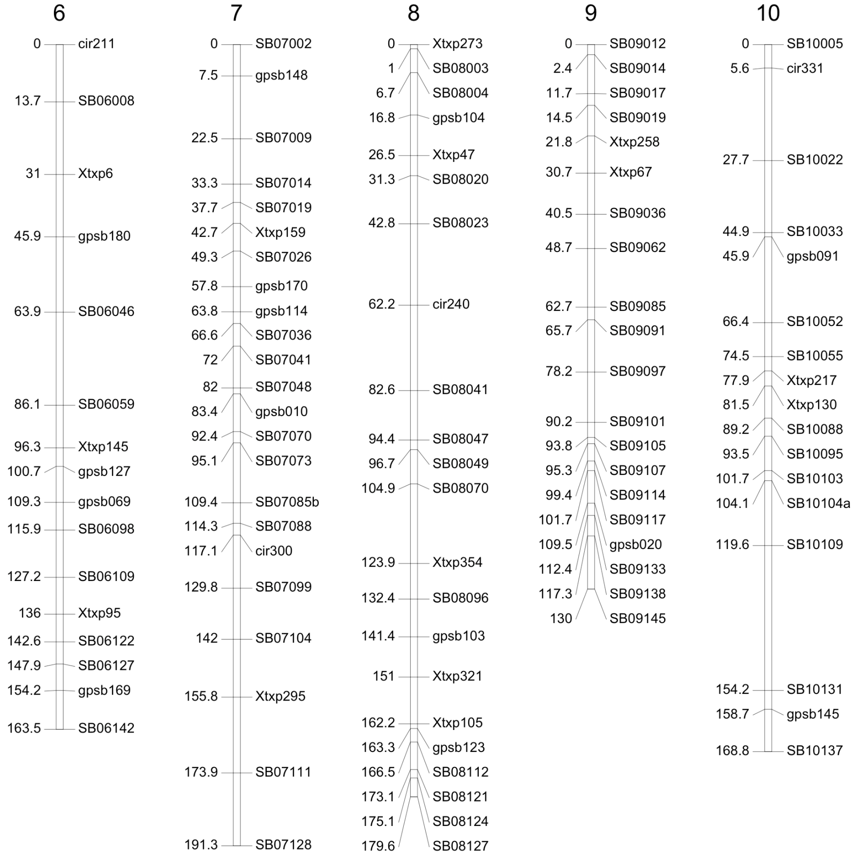

Figure 3 Continued – Genetic Map with 200 Loci (124 SNP, 76 SSR) used for QTL Detection of P114

Genetic Analysis

QTL analyses and modeling were conducted for all traits available across environments. For a given trait, independent QTL analyses were conducted in separate environments. QTL analyses were conducted using composite interval mapping with QTL Cartographer software (Basten et al., 2002). Several hundred QTL were globally detected for all traits in all environments to identify the most favorable parental allele in each region of the genome and to define several genotypic ideotypes to achieve breeding objectives.

Grain productivity was one of the main targeted traits, and the QTL detection allowed for the identification of several genomic regions that were involved in grain productivity and for the assessment of QTL effects' stability across the six environments. In addition, the genetic analysis performed in this context allowed the deciphering of relationships between traits and between environments, breaking possible antagonisms between traits, testing different hypotheses, and designing several ideotypes for various objectives or environments.

1. Large-effect QTL

Some major QTL with large effects have been detected in both populations for pericarp thickness, flowering date, plant anthocyanin (Guindo et al. 2019), and plant height (See Table 1):

- A major QTL for pericarp thickness, corresponding to the Z gene (Ayyangar, 1934), was located on chromosome 2 for which both guinea parents brought the Z (thin) allele.
- A major QTL for flowering date was detected on chromosome 3. In both populations, the allele brought by a Tiandougou parent on this QTL was responsible for later flowering (8 days on average).
- A major QTL for plant anthocyanin corresponding to the P gene (Ayyangar et al., 1933) was detected on chromosome 6 for which Tiandougou brought the recessive p (tan) allele.
- Finally, a major QTL for plant height was detected on chromosome 7, identified as the dwarfing gene Dw3 (Karper, 1932). Both guinea parents, Lata3 and Keninkeni, brought the Dw (tall) allele.

Table 1
List of Major QTLs Detected in Both Populations

Trait	**Known Gene**	**Chrom**	**Effect**		**Target Allele**	
			P114	**P118**	**P114**	**P118**
Pericarp thickness	Z	2	KK thin	Lata thin	KK	Lata
Flowering date		3	Tian late	Tian late	Tian	–
Anthocyanin	P	6	Tian Tan	Tian tan	Tian	Tian
Plant Height	Dw3	7	KK tall	Lata tall	KK	Lata

Grain yield and quality are closely related to flowering date because flowering is a complex trait that controls adaptation of the plant to its environment. In West Africa, most local sorghum varieties are photoperiodic short-day plants. The photoperiod sensitivity constitutes sorghum's main adaptation factor to climate and parasitic constraints in the Sahel zone (Kouressy et al., 2008b). Grouping flowering at the end of the rainy season ensures a balance between satisfaction of water needs and avoidance of many biotic constraints. Grain of early photoperiod insensitive maturing varieties is attacked by birds and altered by mold and insect complexes, while photoperiod sensitive and late varieties deplete soil moisture before the end of grain filling and escape their seeds' alteration. The reintroduction of photoperiodism in breeding programs in Mali is recent and plays a key role in sorghum improvement success in the Sahelian zone.

A major QTL for flowering time detected on chromosome 3 was only expressed under long day conditions, showing that it was related to photoperiod sensitivity. The allele brought by the Tiandougou parent was responsible for later flowering (8 days on average). These results were investigated further using a crop modeling approach (Guitton et al., 2018). The different parameters of the Crop Environmental Resource Synthesis (CERES) model corresponded to different chromosomal regions. The major QTL was related to the critical photoperiod parameter (P2O) of the CERES model, that represents, for a given genotype, the value of photoperiod under which the duration of the vegetative stage is constant. Knowledge of genetic control of flowering time now allows breeders to develop varieties specifically adapted to different Sudano-sahelian target environments.

Specifically, the modification of the critical photoperiod allowed for modification of the vegetative duration phase while preserving photoperiod sensitivity.

Ideotype Construction

QTL results were translated into genotypic ideotypes, which represent the target parental allele all along the genome that brings favorable contributions for key QTL. In each marker interval, the respective contributions of each parent were compared for all detected QTL, taking into consideration the effects of the QTL and the breeding objectives.

There were some trade-offs to be made that involved the large QTL effects (See Table 1). First, for the major QTL involved in pericarp thickness, the Z (thin) allele was selected as the target allele for both populations. Second, the large effect QTL involved in flowering time and critical photoperiod affected grain productivity, depending on the environment and the genetic background. In P114, late flowering was associated with a QTL for grain yield in all environments, and the late allele (Tiandougou) was selected as the target allele in this population. In P118, the late-flowering allele was also associated with a QTL for grain yield but only in the Farako location; the early flowering allele was associated with a major QTL for grain yield in the Sotuba and Cinzana locations. Two ideotypes were thus derived for both environments differing only on this major flowering time QTL. Third, on the P locus involved in plant anthocyanin, the p (tan) allele was the target allele for selection. Indeed, tan plants (no anthocyanin) are preferred because they generally produce whiter flour and whiter Tô.

Next, the major QTL for plant height was detected on chromosome 7 and identified as the Dw3 gene. Although the overall objective, in terms of plant height, was medium, the tall allele was selected in this region for both populations because it was associated with a QTL for panicle length and consequently with a QTL for grain yield. To compensate for the effect of this QTL on plant height, alleles that contributed to reducing plant height on all other QTL in the rest of the genome were selected (11 and 16 QTL detected in P118 and P114, respectively).

Finally, using only P114 as an example, three different genotypic ideotypes

(See Figure 4) were defined. The overall objective was to combine grain productivity (as defined by grain yield and yield components) and grain quality (vitreous endosperm, high amylose, and good Tô properties) with a medium plant height, a thin pericarp, and non-anthocyanin plants. A grain yield (GY) ideotype was constructed that gave priority to grain yield when a conflict was observed in any region between grain yield and grain quality. Additionally, a grain quality (GQ) ideotype was constructed that gave priority to grain quality. Lastly, a third ideotype (GYQ) tried to balance the contributions of both grain yield and grain quality.

Figure 4

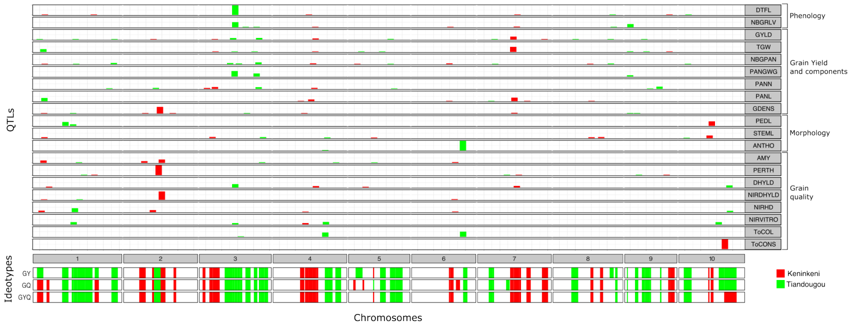

Figure 4 – QTLs and Ideotypes Along the 10 Chromosomes of the Genome of P114

QTL Pyramiding by Recurrent Selection

Cycles of three recurrent selection processes of P114, conducted from September 2011 to March 2013, were achieved (See Figure 5). At each cycle, approximately 700 plants were genotyped on the flanking markers of QTL that were included in genotypic ideotypes. Genotypic data were first analyzed to check for consistency across generations and to track pedigree errors from one cycle to the next. From the genotypic data produced at each cycle, genetic values were computed for all possible crosses between all available plants. The genetic values were computed for several QTL indices and for different ideotypes. All computations were performed by Syngenta (Toulouse, France) using proprietary software. A list of best candidate crosses was determined from these genetic values.

Each single selection cycle represented a great challenge because all operations (i.e., leaf sampling, DNA extraction, genotyping, and data analysis) needed completion before flowering. This required a harmonization of field, laboratory, and geneticist teams' efforts.

Figure 5

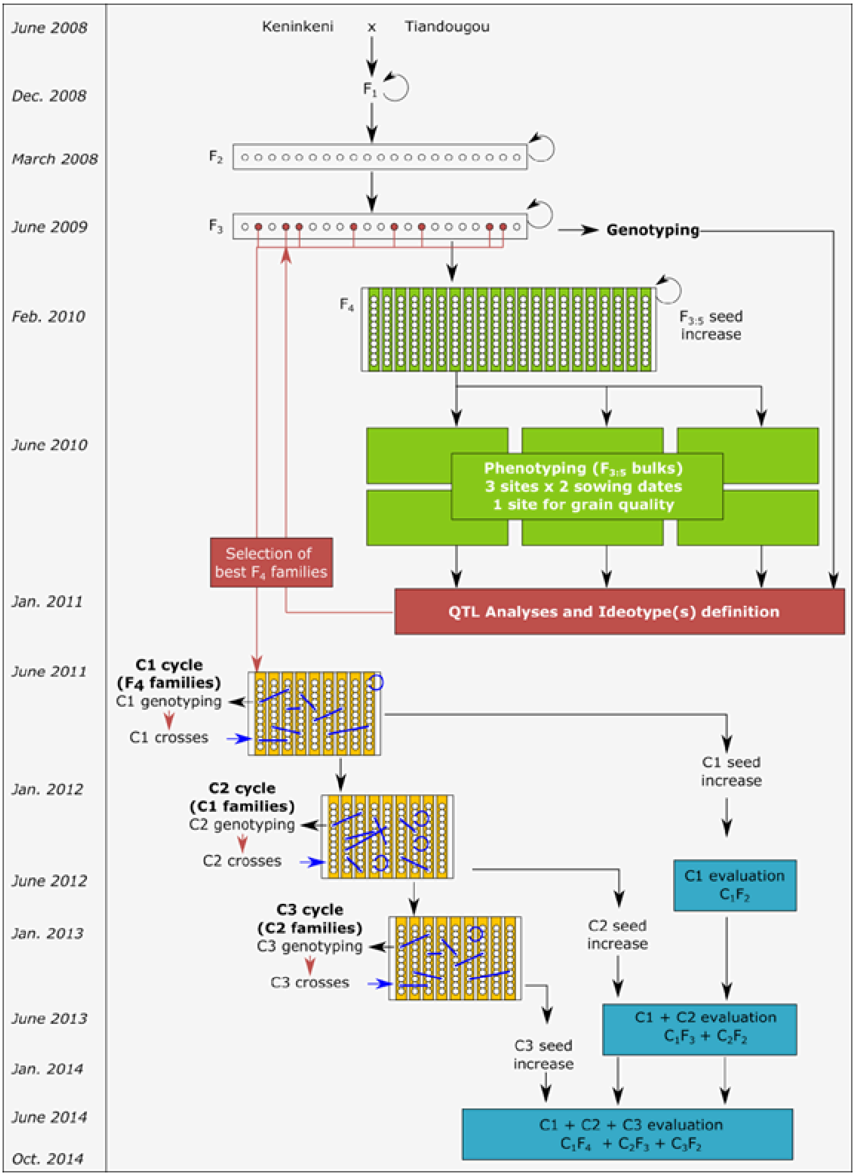

Figure 5 – MARS Project Population Development QTL Accumulation Process

Various numbers of crosses were produced in different selection cycles (See Table 2). Crosses made during the warm off-season (i.e., between March and June) struggled to obtain appropriate flowering time among parents. Globally, about 450 families were produced by MARS for P114, either by crossing or selfing progenies. Figure 6 shows the pedigree of the 20 C3 families produced after 3 cycles, illustrating the level of intercrossing that occurred during the whole process. At each cycle of recurrent selection, many more families were produced, but only those that contributed to the final cycle are represented here.

Table 2
Number of Progenies and SNPs Analyzed and Number of Crosses and Produced at Each Recurrent Cycle in P114

Cycle	Date	Nb of plants	Nb of SNPs	Nb of Crosses	Nb of Selfing
C1	09/ 2011	724 F4 (20 families)	140	130	105
C2	01/ 2012	647 C1 (23 families)	140	125	70
C3	03/ 2013	558 C2 + C1 (13 C1 + 19 C2 families)	150	20	60

Figure 6

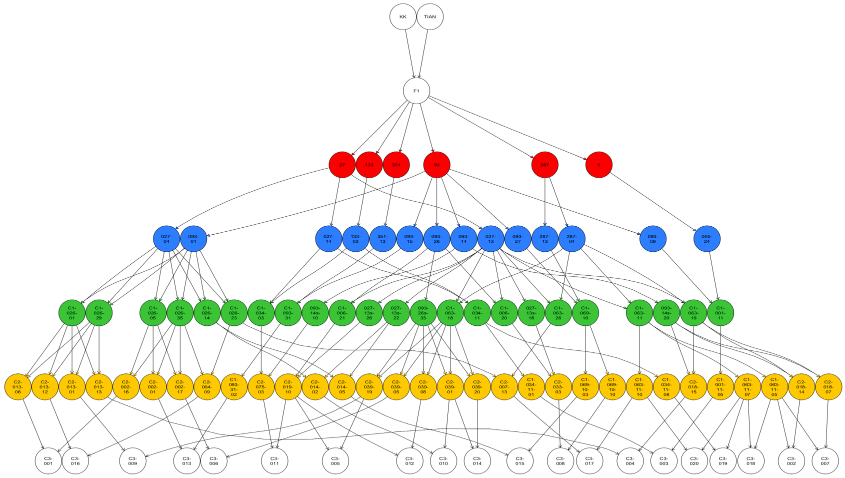

Figure 6 – Pedigree of the C3 Families of P114 MARS

The material obtained through MARS was considered as pre-breeding material enriched with favorable QTL. The QTL involved in this process represent genetic factors that were identified and evaluated in experimental conditions, during several years, and in varying locations. The set of QTL involved in the genotypic ideotypes can be considered as a "must-have". Whereas a significant part of the genetic variation was not explained by the QTL which was still segregating in the populations. For this reason, we developed many different families that accumulated positive alleles at QTL but that were globally very diverse. In addition, early MARS families consisted of non-fixed material (because they resulted from a cross) but needed to be fixed toward pure lines. These families were further field evaluated, and 21 lines that showed good and stable performance were selected.

Variety Registration

1. Agronomic Performances

Procedures for new variety registration in the Economic Community of West African States (ECOWAS), changed in 2009, were followed. The objectives were to guarantee users that every variety is perfectly identifiable and thus distinct, uniform, and stable (DUS) from other registered varieties. This DUS test was conducted in 2017 only at Sotuba. Variety must have a sufficient value for cultivation and use (VCU tests). VCU tests were conducted in Mali in 2016 and 2017, and a multi-location trial network was set up in collaboration with the National Committee for Plant-Based Seeds (CNSOV) at fifteen locations. The experiment included four MARS lines (C0-P114-160A-, C2_075-16, C2_075-15, and C2_007-03) and two registered elite checks (Grinkan and Tiandougou Coura). Sites chosen were between 750–950 mm isohyets in research stations and in farmer or seed companies' fields. Trials were conducted in randomized, complete block design (RCBD) with four-repetitions. The recommended sorghum population density was used (53,332 plants per hectare), and each plot comprised of 5 rows of 5 meters long, which corresponded to a net plot of 9 m^2. Chemical fertilizers (73 kg N/ha, 30 kg P/ha) were applied. Analysis of variance (ANOVA) was performed for each environment, and a combined ANOVA was undertaken for all environments. Before pooling trials, Bartlett's test was used to assess the equality of variance across locations for each variable. Three trials were eliminated because of inequality of variances. Genotype x Environment (GxE) interaction was studied using the Additive Main Effects and Multiplicative Interaction Model (AMMI) (package 'agricolae') in the R environment (R_Development_Core_Team, 2008) and by the Finlay-Wilkinson approach (Finlay & Wilkinson, 1963).

The model for the combined analysis across locations was:

Yijk = m + Ei + gj + (gE)ij + bik + eijk

- Yijk is the observation in the i^{th} environment of the j^{th} genotype, in the k^{th} block of the experimental design.
- m is the grand mean
- Ei is the effect of the i^{th} environment
- gj is the effect of the j^{th} genotype
- (gE)ij is the interaction of the j^{th} genotype with the i^{th} environment
- bik is the effect of k^{th} block in i^{th} environment
- eijk is the residual error

The GxE interaction (See Table 3) was not significant for grain yield, which means that despite very large environmental disparities, lines were similar across environments. In a previous study (Sissoko et al., 2018) comparing MARS short varieties with tall landraces, a very strong GxE interaction was detected. In their case, the strong GxE interaction was explained by the very great diversity among tested varieties. In the current variety registration trials, absence of GxE interaction meant that tested varieties were similar in morphology and maturity traits.

Table 3
Combined Analysis of Variance for Grain Yield of 6 Sorghum Lines Tested in 9 Environments in 2011 in Mali.

Source	Df	Sum of Squares	Mean Squares	F Value	P Value
Environment (E)	8	117861282	14732660	16.19	0.000
Block b(E)	27	24575733	910212	4.54	0.000
Genotype (G)	5	9351668	1870334	9.33	0.000

Source	Df	Sum of Squares	Mean Squares	F Value	P Value
Interaction (GxE)	40	8708531	217713	1.09	0.357
Residuals (e)	131	26273999	200565		

The Finlay-Wilkinson approach is designed to investigate the GxE interaction (See Figure 7). The method consists of fitting for each genotype, a regression of grain yield according to environmental average yield (i.e., the mean response of all varieties in each environment). As the GxE interaction was not significant, the regression lines corresponding to each variety were almost parallel. The regression slope, approximating to 1.0, indicates an average stability, except for C2_007-03 and C2_075-15, which have a significantly lower slope of 0.84.

Figure 7

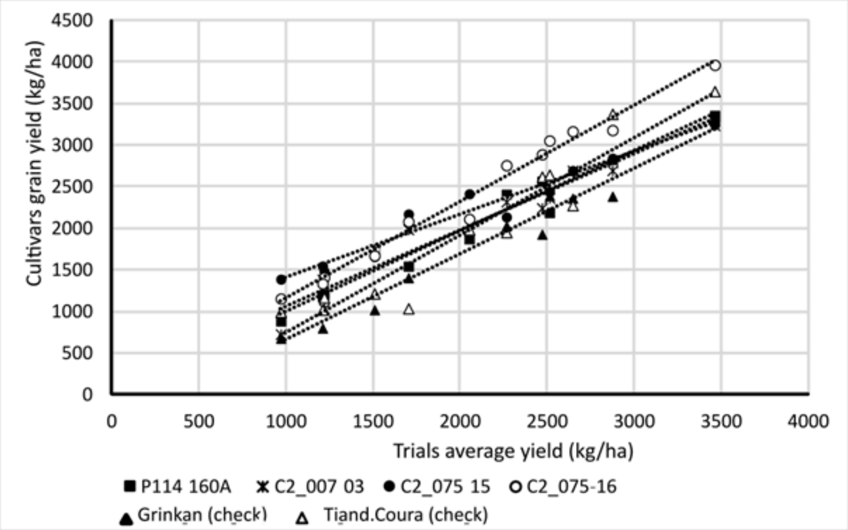

Figure 7 – Stability Analysis According to Finlay & Wilkinson (1963)

Yields ranged from 1,000 kg/ha to almost 3,500 kg/ha. Table 4 presents the mean grain yield comparison of the six varieties tested. Three homogenous groups were identified. The yield of C2_075-16 was significantly higher than other varieties, including the two checks. The other three MARS varieties have a significantly higher yield than that of the Grinkan check.

Table 4
Mean Yield of Multi-location Trials Realized in Mali in 2016 for VCU.

	Mean Yield (kg/ha)	**Homogeneous Groups**
Grinkan (check)	1809	c
Tiandougou Coura (check)	2039	b
C2_007-03	2150	b
C0_P114-160A-	2163	b
C2_075-15	2247	b
C2_075-16	2499	a

Note. The means followed by the same letter are not different by Fisher's least significant difference (LSD) procedure at the 5% threshold.

The technological quality of MARS lines was satisfactory. There were no significant differences among lines and controls in terms of Tô color and texture. The dehulling yield ranged from good (65%) to very good (> 75%). Additionally, MARS lines exhibited significantly lower vitreousness, only C0_P114-160A- showed a vitreousness comparable to checks. The 1,000-kernel weight of the highest-yielding variety (C2_075-16) was significantly less than those of the checks.

2. Climate Adaptation

Methodology for studying adaptation to climate change was presented by Sissoko et al. (2018) and Kouressy et al. (2020) using CERES approach. In this approach, a study of photoperiod sensitivity allowed the calculation of the model's phenological parameters. Then, the model's predicted areas where the varieties could be grown at minimal biotic and abiotic risks.

2.1 Phenological Study

A trial with three sowing dates was used for P114 derived lines/varieties and checks in the phenology study (See Figure 8) under different photoperiod conditions. Phenology was determined by the date of flag-leaf ligulation. In sorghum, this observation is more accurate and repeatable than the scoring of the average flowering date commonly practiced in agronomic experiments (Tarumoto et al., 2003). A split-plot design in two replicates was used. The main factor was the date of planting, and the secondary factor was variety. The sowing dates were June 21, July 20, and September 15. The first two sowing dates were used to determine lines behavior in a farmer's normal sowing period (i.e., long and intermediate photoperiod), while the third date (i.e., off-season planting) was to study the short photoperiod effect. A drip irrigation system was used to ensure lines development without water deficit.

Figure 8

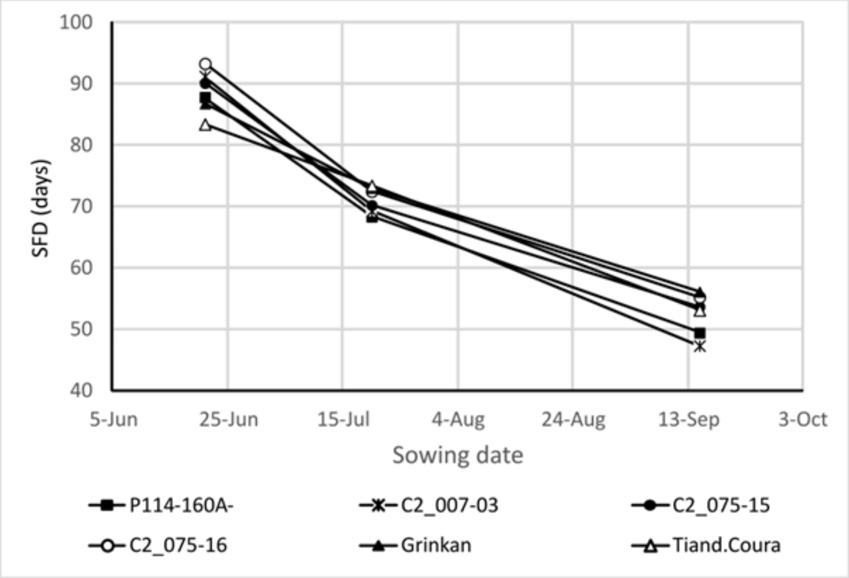

Figure 8 – Flag Leaf Ligulation from Planting (SFD in days) According to the Sowing Date of Six Varieties Studied in Sotuba, Mali in 2015

2.2 CERES Model Coefficient Calculation

Varietal responses to photoperiod were modeled using the sorghum linear CERES model (Alagarswamy & Ritchie, 1991; White et al., 2015). This model was based on a linear adjustment between photoperiod and vegetative phase length (Chantereau et al., 2001; Sanon et al., 2014). After emergence, the shortest thermal time required to reach panicle initiation was known as the Basic Vegetative Phase (BVP). During this phase, floral induction could not occur, no matter the photoperiod conditions. The CERES model considered that below a critical photoperiod (P2O), the vegetative stage duration was constant and equal to the BVP. Above the P2O, the vegetative stage duration increased as a linear function of a photoperiod, whose slope, P2R, defined the photoperiod-sensitivity in degree days per hour of the photoperiod increase (°Cd/h). A modified CERES model version was used (Folliard et al., 2004) whereby photothermal time accumulation was replaced by a critical photoperiod threshold (i.e., varying on plant age) below which sorghum panicle initiation occurred. The three model parameters (P2O, P2R, and BVP) were calculated using a simple method presented by Guitton et al. (2018).

2.3 Delineating Optimal Cultivation Areas

The method used comprised of identifying areas where a variety could be sown during a normal planting period to minimize biotic and abiotic risks. The optimum cultivation area of a variety was determined by combining information on photoperiod sensitivity, climatic variability, and a farmer's practices (e.g., early and staggering sowing dates; Soumaré, 2004). For each rainfall station in Mali, the onset and end of the rainy season was established using a simplified water balance model (Traoré et al., 2011). The flowering date was predicted using the CERES model. The difference (in days) between the predicted flowering date and the end of the rainy season gave an adaptation index, which was calculated for each variety based on the normal 1981–2010 Malian weather stations' data. A geographical information system (Surfer® 14, Golden Software, LLC) was used to delineate areas for which the adaptation index was between -20 and 0 because an adapted variety, which flowered in 20 days preceding the end of the rainy season, was considered (Kouressy et al., 2008a).

Spatial distribution of the adaptation index used a model of linear interpolation by kriging. This action was repeated for each variety, considering two sowing dates. A first sowing date was simulated immediately after the rainy season installation and a second sowing date was delayed by one month. This duration, period of sowing, corresponded to the general practice observed in farmers' fields.

Adaptation zones of the four studied varieties are presented in Figure 9. The delay in sowing caused a shift of the adaptation zone to the south.

An overlap of the two zones (in purple), due to photoperiod-sensitivity, corresponded to the optimum growing zone in which variety cultivation is possible within farmers' sowing periods.

This plant modeling approach revealed merging genetic information, environmental conditions, and sowing practices for predicting crop resilience to climate change scenarios. All optimal growing areas included the Bamako region, for which they were developed. Variety C2_007-03 was slightly more sensitive to photoperiod than the other three varieties. Therefore, its flowering dates were less affected by sowing date and the overlap of the two zones was more important.

Figure 9

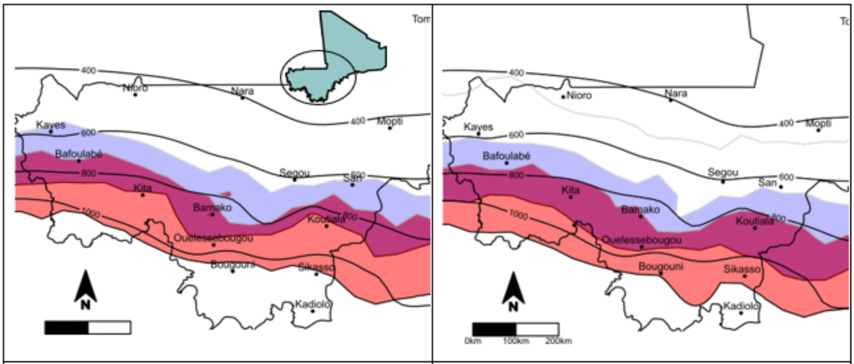

Fig.9a - Optimal growth area for P114-160

Fig.9b - Optimal growth area for C2_075-15

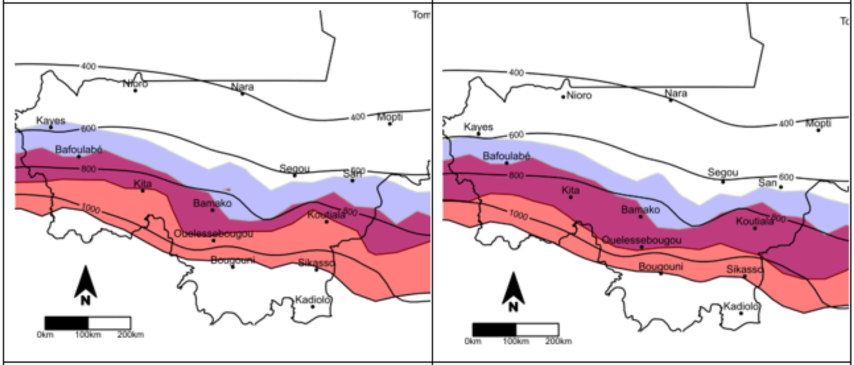

Fig.9c - Optimal growth area for C2_075-16

Fig.9d - Optimal growth area for C2_007-03

Figure 9 – Delineation of Optimal Growing Areas of Four MARS Varieties

Conclusion

Marker-assisted recurrent selection (MARS) has provided a way to sustainably raise sorghum productivity in future cropping intensification systems. The MARS project is an example of a successful integration of methodology, tools (quality control, genetic analyses, and decision support), services (genotyping), and capacity building into the Malian national sorghum breeding program. The implementation of this approach represented a significant change in conceiving and conducting sorghum breeding, which required qualified support staff and laborers. MARS application improved breeding efficiency because it allowed the rapid and simultaneous accumulation of many traits. Molecular approach alone is not sufficient to produce the end results. Close coordination between field teams and geneticists is necessary. To be successful, the approach must necessarily be trans-disciplinary, including crop physiology and modeling, quantitative genetics, genomic prediction, and breeding. Moreover, after QTL pyramiding, breeding continuation through classical genealogical selection allowed integration of traits not previously considered by genetic analysis. This work is a step towards creating varieties that are resilient to climate change and suitable for sustainable intensification. These two concepts are closely related, as improved climate risk management will provide the foundation for sustainable intensification. The end product of the MARS project was the registration of four elites in national and regional catalogs (Figure 10).

Figure 10

	
Fig.10a - C2_007-03 named Wilibalis	Fig.10b - C2_075-15 named Wassalen
	
Fig.10c - C2_075-16 named Falenba	Fig.10d - P114-160 named Tinsan Yerekelen

Figure 10 – Registered Varieties and Equivalent Names

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ENDNOTES

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18. Genetic Improvement of Pearl Millet in Senegal: Past, Present and Future Prospects

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Abstract

Pearl millet is an important cereal crop for smallholder farmers' food security in Senegal and is grown on approximately 800,000 ha of land with a total national production of 600,000 tons annually. However, its production has been affected by increasing biotic and abiotic stresses such as downy mildew disease, drought and heat, and use of unimproved varieties in farmers' fields. Genetic improvement of pearl millet started in Senegal nearly a century ago and experienced three major phases that were defined by different improvement targets. Over time, Progressive national yield improvements have been made. This chapter summarizes the breeding progress of the Senegal national breeding program in the past century. It also formulates future directions for further improvement of the productivity of pearl millet to meet the increasing national demand for food and nutrition security in the midst of climate change. This chapter posits that an ambitious pearl millet improvement strategy that integrates the modern genetic and genomic tools

and novel genetic resources for resistance to biotic and abiotic stresses with variety development work is urgently needed to revolutionize pearl millet production in Senegal.

Keywords: pearl millet, drought adaptation, genetic improvement, Senegal

Introduction

Pearl millet [*Pennisetum glaucum* (L.) R. Br. syn. *Cenchrus americanus* (L.)] is a diploid (2x = 2n = 14) C4 and allogamous crop that belongs to the family of Poaceae (Bono & Leclercq, 1963). Archaeological and genetic findings have inferred PM was domesticated about 4,900 years ago in the western Sahara belt, more precisely in Northern Mali (Burgarella et al., 2018; Manning et al., 2011; Oumar et al., 2008).

Pearl millet is currently the sixth most important cereal crop in the world following maize (*Zea mays*), rice (*Oryza sativa*), wheat (*Triticum aestivum*), barley (*Hordium vulgare*), and sorghum (*Sorghum bicolor*) based on harvested area (FAOSTAT, 2019). It accounts for more than half of global millet production and is mainly cultivated in West Africa and India for household food security and income generation, whereas it is cultivated mostly as forage in Brazil, the United States, Mexico, and Australia. West Africa and India cover more than 95% of its global production (FAOSTAT, 2019). India is the largest pearl millet producer, followed by West African countries including Nigeria, Niger, Burkina Faso, Chad, Mali, and Senegal.

In Sub-Saharan Africa, pearl millet was historically grown by farmers for their basic subsistence. Now, it has also become a commercial crop and the main source of income and nutrients in the most drought and heat-stressed production areas. It is one of the rare cereals of traditional farming systems that is able to withstand frequent and prolonged periods of drought and high temperature in saline soils, at both the vegetative and reproductive phases, which would cause crop failure or greater yield reduction in other cereals (Dussert et al., 2015; Serba et al., 2017). Compared to some other domesticated cereals, pearl millet shows a large genetic diversity and an exceptional potential of adaptation to a wide range of ecological conditions, especially drought, across the semiarid areas (Sehgal et al., 2015; Serba et al. 2019).

Another major asset of pearl millet is its potential to relieve malnutrition in developing countries. Food insecurity remains the major issue to be solved in Sub-Saharan Africa, where 22% of the population is severely food insecure (ANSD, 2018). Despite improvements over the last decade, the current food insecurity situation in Senegal remains critical, and 16.5% of the population was undernourished in 2018 (ANSD, 2018). The food demand will increase dramatically in the coming years following continued population growth, with the projected West African population (920 million in mid-2014) doubling by 2050. The Senegalese population is expected to reach 40 million by 2050 (FAOSTAT, 2019). Pearl millet significantly helps mitigate malnutrition, as it is more nutritious than maize, rice, wheat, and sorghum because its grain contains higher levels of protein, vitamins, amino acids, antioxidants, fibers, and essential micronutrients (Saleh et al., 2013; Serba et al., 2017). Additionally, this crop has a high potential for transformation into value-added products. Pearl millet grain is used to prepare many traditional foods and is consumed in both rural and urban areas in many forms, such as porridges, gruels, doughs, couscous, and breads. It is also used for forage purposes.

All actors in the Senegalese pearl millet value chain recognized the need to develop strategies to substantially enhance grain yield. Therefore, the breeding program is under time pressure to act as a bridge between the market demand and the crop productivity and should rapidly adopt an efficient breeding strategy to accelerate the improvement of new varieties with better resilience to climate variability in particular drought stress. This chapter highlights the progress in pearl millet breeding in the last several decades, identifies research gaps, and formulates actionable future strategies for improvement of this nationally important cereal crop, particularly in the context of climate change.

Status and Constraints for Pearl Millet Cultivation in Senegal

Pearl millet is the main staple cereal crop in Senegal, with approximately 800,000 ha of growing area, occupying about 60% of the crop area harvested (FAOSTAT, 2019). It is mainly cultivated in the central, southern, and south-eastern parts of the country, more specifically in the Fatick, Kaffrine, Kaolack, Diourbel, Thies, Tambacounda, and Kolda regions (Figure 1). In 2019, its production in these regions represented more than 80% of total national production (ANSD, 2020). As the populations living in these regions depend particularly on pearl millet production for their livelihoods, improved production technologies are highly sought.

Figure 1

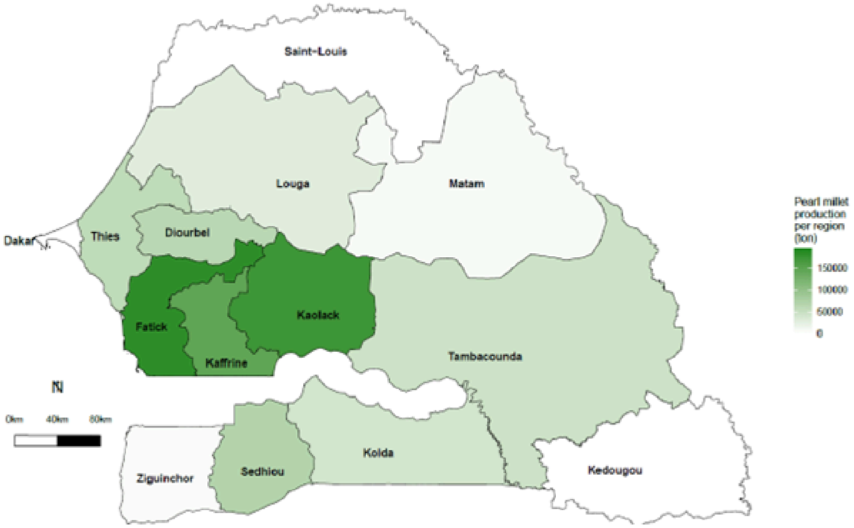

Figure 1 – Distribution of Pearl Millet Production Areas in Senegal During the Rainy Season of 2020

The total national production of pearl millet was 574,000 tons, which accounted for at least 33% of the total cereal production, behind only rice (44%) in 2018 (FAOSTAT, 2019). These ratios among different crops change over years depending on the financial support received for different grain crops (Figure 2A). Pearl millet has occupied the largest area harvested among the cereal crops, followed by rice, sorghum, and maize over the years (Figure 2B). However, the average grain yield remains very low and unstable, never reaching the threshold of 1000 kg ha-1 (Figure 2C). By comparison, pearl millet yields in India are 1,243 kg ha-1 for the same year (FAOSTAT, 2019). The adoption of hybrids has led to a significant improvement in productivity in India. The first public system for robust hybrid selection of pearl millet was established in the 1960s. This system has also been supported by the private sector and has facilitated significant improvement of productivity in the country with an average increase in grain yield of 24 kg/ha/year between 1996 and 2012 (Yadav & Rai, 2013). In 2006, over 70 hybrid varieties covered 60% of the cultivated area of pearl millet in India and these hybrid varieties were mainly developed by the private sector and consisted of more than 80% of varieties used at that time (Karandikar et al., 2018). In contrast, no hybrid variety was cultivated in Senegal.

Figure 2a

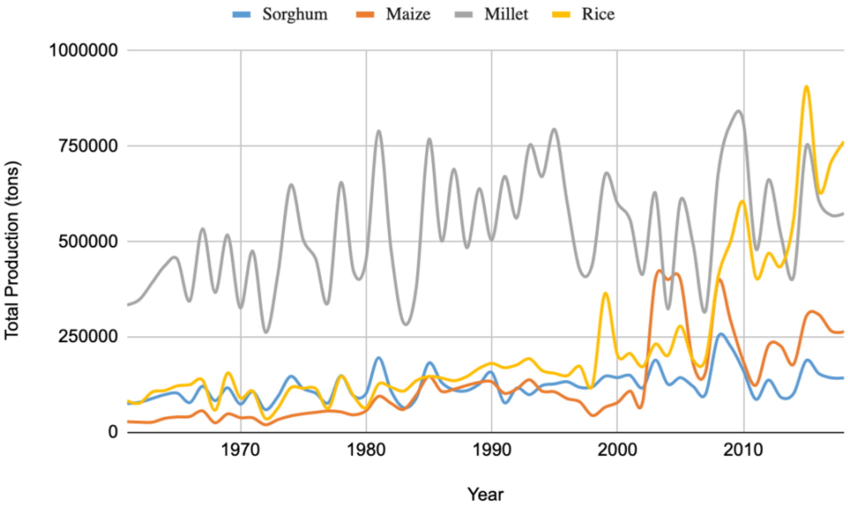

Figure 2a – Dynamics of Cereal Production by Crop in Senegal from 1961 to 2018- (A) Total Production of Cereals (tons)

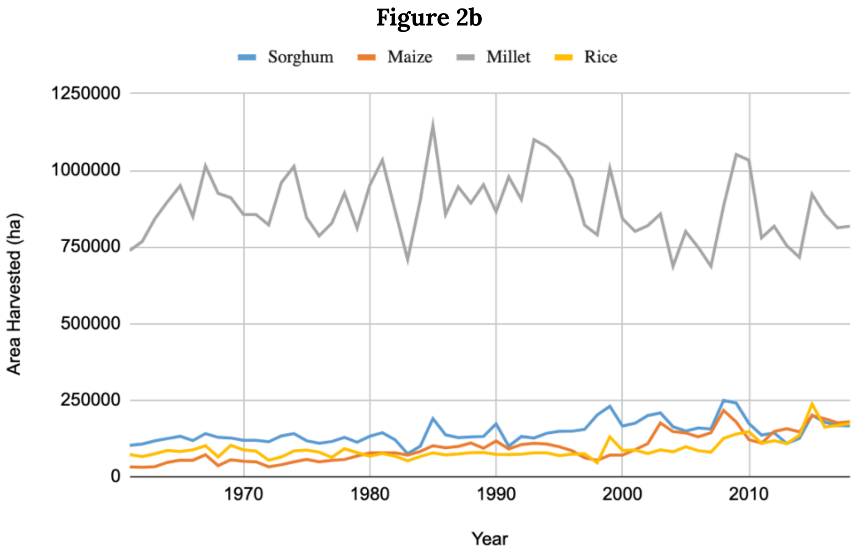

Figure 2b – Dynamics of Cereal Production by Crop in Senegal from 1961 to 2018- (B) Area Harvested (ha)

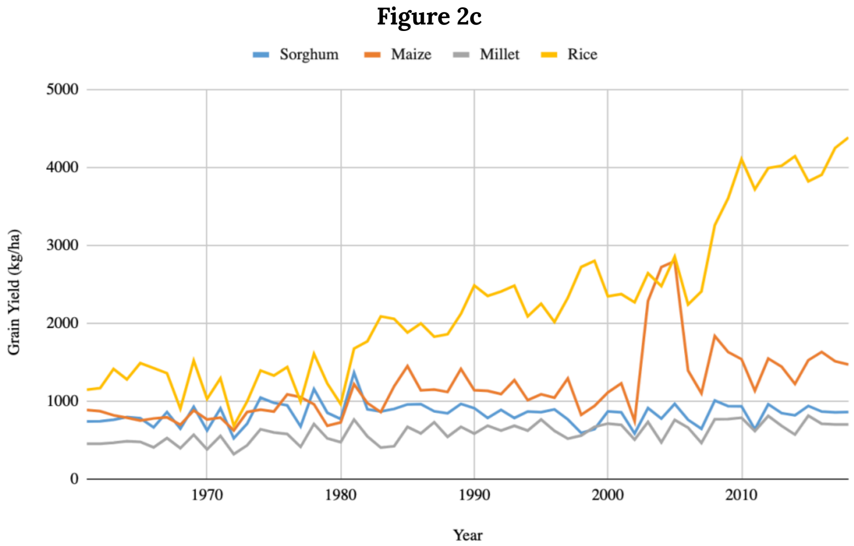

Figure 2c – Dynamics of Cereal Production by Crop in Senegal from 1961 to 2018)- (C) Grain Yield (kg ha-1)

In addition to the absence of hybrid varieties in cultivated areas, growing unimproved varieties has been the major constraint of pearl millet grain productivity (Kanfany et al., 2020). In 2009, only a few improved varieties were cultivated in 34.5% of the national production area. The varieties Thialack 2, Souna 3, and IBMV 8402 covered only 16.5%, 14%, and 4% of the area, respectively (Walker, 2015). In addition, various biotic and abiotic stress conditions, including *Striga* weed (*Striga hermonthica*), low soil fertility, drought, and insect pests are limiting factors for yield. Moreover, lack of machinery for sowing, disease and bird damage, limited access to certified seeds of high-yielding varieties, and cultivable land all affect production of pearl millet in Senegal (Kanfany et al., 2020). Meanwhile, significant improvement has been made for rice and maize, with an increased productivity of 66% and 282%, respectively, mainly due to the use of higher-yielding varieties and pertinent crop management practices to alleviate biotic and abiotic stresses.

In recent years, the reduction in rainfall volume and the short period of rainfall during the growing seasons have negatively impacted the performance of pearl millet in Senegal (ANSD, 2020). As farmers usually plant pearl millet while waiting for or in response to the first rain of the year, the crop can face severe drought stress in early stages. It is proven that drought stress at an early stage significantly reduces the plant height, biomass, and total grain number and weight in pearl millet inbred lines (Debieu et al., 2018). Early ending of the rainy season can also lead to terminal drought episodes at the grain filling stage, especially for late- maturing varieties.

According to the current climate models used in Saharan Africa, including Senegal, more inter- and intra-annual variability in the rainfall amount and distribution is expected (Brown & Lall, 2006), increasingly threatening pearl millet productivity in the country. Several studies have predicted that changed climatic conditions in Sub-Saharan Africa will lead to significant and increasing yield losses for major crops by the 2050s if cropping systems do not adapt. The associated yield losses are forecast at 17% for millet (Schlenker & Lobell, 2010). The Groundnut Basin agro-ecological zone is the most important part of the national pearl millet production area, but it is characterized by a Sudano-Sahelian climate and will be particularly affected by this climate variability.

Past Attempts of Genetic Improvement and Achievements

1. Phase 1: Exploitation of the Local Germplasm for Grain Yield Improvement

The pearl millet improvement program started in Senegal in 1931 at the National Center for Agronomic Research (CNRA) in Bambey. There are two ecotypes of pearl millet traditionally grown in Senegal based on life cycle length: the short cycle ecotype (65–90 days) called ‘Souna’ and the longer cycle (120–150 days) called ‘Sanio’. Souna morphotypes flower from 50 to 60 days after planting and are adapted to ecosystems with low and irregular water supplies (350–600 mm annually rainfall). They represent 85% of total millet production and cover the most important part of the nationwide production area in the north and central regions (Diack et al., 2017). Sanio morphotypes flower from 80 to 110 days after planting and are mainly cultivated in the southern region, receiving more important rainfall (900–1200 mm).

During the first phase of the breeding program, the selection was mainly focused on producing inbred lines using pedigree selection from the two ecotypes that were collected locally across the country (Fofana, 1987). This approach led to the development of 113 inbred lines by 1949. However, due to the cross-pollinated nature of pearl millet, these lines lost vigor (Jones & Mangelsdorf, 1925). For instance, one of the local populations gave 20% more grain yield when compared to the performance of the inbred lines selected from this population (Fofana, 1987). Bono & Leclercq, 1963 realized that this breeding method could not be directly used since it only allowed the development of interesting, inbred lines. However, when the inbred lines were crossed with local populations, the top-cross hybrids produced up to 147% yield compared to the local population. By 1959, 28 inbred lines were selected and evaluated for overall performance in three consecutive years based on uniformity, yield performance, and yield component traits. The results showed that even if the homogeneity was significantly improved, the grain yield of these lines was not better than farmers’ cultivars (Fofana, 1987).

Thus, pedigree selection breeding was judged as an unsuitable tool for pearl millet yield improvement.

In 1961, the national breeding program shifted from pedigree selection to recurrent selection using five local populations: three early (Souna) and two late (Sanio) pearl millet ecotypes (Etasse, 1965). The varieties, derived from the late populations, showed low performance in the first generation of recombination and selection was focused on the early maturing populations. The best progeny was selected from the three early populations and combined to create a synthetic variety named Souna 2. This variety showed high grain yield potential with a 107% and 121% yield increase compared to landraces in the first and second generation of recombination, respectively. However, the performance in farmer's fields was still variable, mostly lower than local varieties in farmers' fields (less than 2 t/ha). This variety was further improved by top-crossing with a local population (PC28)s using Souna 2 as the tester, resulting in the selection of eight elite lines from this population. The eight lines were combined in 1969 to form Souna 3, the first variety released by the breeding program (MAER, 2012). This synthetic variety was proposed for cultivation in the central and southeastern part of the Groundnut Basin agro-ecological zone (Table 1). This variety has a compact and cylindrical panicle, a resistance to smut and downy mildew, and a grain yield potential of 2.5 to 3.5 t ha^{-1} It has since been one of the most cultivated varieties in Senegal.

Table 1
Varieties Released for Pearl Millet Cultivation in Senegal

Variety Name	Type	Year of Creation	Year of Release	Maturity Cycle (days)	Potential Grain Yield (t ha^{-1})
Souna 3	Synthetic	1969	1972	90	3.5
IBV 8001	Synthetic	1980	1987	80	3.4
IBV 8004	Synthetic	1980	1987	75	2.6
IBMV 8402	Synthetic	1984	1987	80	2.5
ISMI 9507	Synthetic	1995	2010	85	2.5
Gawane	Composite	2006	2010	85	2.5
Thialack	Composite	2008	2010	95	3

Variety Name	**Type**	**Year of Creation**	**Year of Release**	**Maturity Cycle (days)**	**Potential Grain Yield (t ha^{-1})**
2					
Souna Sine	Composite	2018	2021	90	3
Souna Saloum	Composite	2018	2021	90	3
Souna Baol	Composite	2018	2021	90	2.5
Taaw	Hybrid	2017	2021	75	3.5

Note. Data compiled from ISRA's variety fact sheets

2. Phase 2: Genetic Improvement of Harvest Index and Resistance to Drought

To achieve self-sufficiency through the improvement of harvest index in local populations, a multi-disciplinary pearl millet program involving several scientists was launched in 1970 (Fofana, 1987). This was one of the first initiatives to strengthen the breeding program after independence in 1960. Thus, 29 populations that were collected from the five main West African countries growing pearl millet were crossed with three dwarf parents sourced from the USA [23 D25 and 239 D2B and India (I 472)] (Fofana, 1987). This program developed two dwarf synthetic varieties, GAM 73 and GAM 75 (Table 1) from I 472 x HK 1133 and Tift 23 D2 x Aniata, respectively (Bilquez, 1975). These varieties performed well under irrigated and highly fertilized conditions but could not express their potential under regular farmers' field conditions.

From the 1970s, Senegal experienced a period of severe drought that occurred throughout the entire Sahelian region, affecting crop production considerably (Nouaceur et al., 2017). In addition, the improved varieties in Senegal, as in most West African countries, were not widely diffused throughout the production area due to large environmental variations (Spillane & Gepts, 2001). The multidisciplinary team also developed early maturing (60 and 75 days) synthetic varieties, which were evaluated for overall performance from 1977 to 1979. However, these early varieties produced lower grain yield than Souna 3, even in the environments for which they were developed.

In 1974, the Senegalese Institute of Agricultural Research (ISRA) was established and started a new millet breeding program with the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) in 1977. This millet improvement program was funded by the United Nations Development Program (UNDP) with the main goal of diversifying the genetic bases to develop new varieties that combine stress tolerance and high grain yield potential. This effort made it possible to introduce several millet accessions from India. However, these accessions were not adapted to Senegalese growing conditions because they were matured too early,susceptible to diseases and insects, had small panicle size, and produced a similar grain yield as Souna 3. Besides the fact that the size of the panicle has been correlated with the grain yield, the length of the panicle is an important trait for the farmers related to the local practice during harvest. Indeed, the panicles are grouped and tied in heaps after harvest to facilitate transport.

Therefore, these accessions were crossed with local populations to generate new breeding materials, leading to the release of three varieties in 1987 (IBV 8001, IBV 8004, and IBMV 8402) to the central and northern part of the Groundnut Basin agro-ecological zone (Table 1). These varieties were early-maturing and tolerant to downy mildew (Gupta, 1986; Gupta & Ndoye, 1991). In order to boost the national pearl millet production, a small hybrid breeding program was initiated in 1982. Thus, several crosses were made between the selected inbred lines and the landraces with CMS lines introduced from ICRISAT in India. The best performing hybrid (ICMH 8413 from a cross of 81A x IBMI 8207) produced up to 50% more grain yield than Souna 3 (Ndoye & Gupta, 1987). However, these hybrids were not widely grown due to their downy mildew susceptibility, short panicle size, and dwarf stature as farmers preferred tall cultivars for complementary forage yield.

In the early 2000s, the West African National Agricultural Research Systems (NARS), ICRISAT, coordinated with Réseau Ouest et Centre Africain de Recherche sur le Mil (ROCAFREMI) and International Sorghum and Millet Collaborative Research Support Program (INTSORMIL) regional networks to characterize millet accessions collected from West and Central Africa

(Haussmann et al., 2006). Selected accessions were evaluated in regional trials to identify specific varieties that performed well within a country and/or across different agro-ecological zones in West Africa (Wilson et al., 2008). In Senegal, ICTP-8203 and GB-8735 were identified for the Sahelian zone, ISMI-9301 and ISMI-9305 for Sudano-Sahelian zone, and SOSAT-C88 and ICMV-IS-88305 for the Sudanian zone. These varieties increased grain yield up to 22%, on average, compared to the previously released varieties.

3. Phase 3: Current Genetic Improvement of Pearl Millet in Senegal: A Decade of Rapid Progress

Since 2007, millet genetic improvement in the National Pearl Millet Program has been financially supported by the West Africa Agricultural Productivity Program (WAAPP), a 10-year program funded by the World Bank and several other international funding programs. These funds offered new opportunities to the national program. Significant efforts have been made by the millet program to assemble and define a national core collection, improve local populations, train young scientists. Progress has also been made on strengthening collaboration with National Agricultural Research Institutes and Advanced Research Centers for Germplasm Exchange and Evaluation, integrating new tools, such as molecular markers and high-throughput phenotyping with conventional breeding, and defining breeding product profile.

Genetic diversity of the germplasm used in a breeding program determines the potential genetic gain achievable through selection (Ambati & Singh, 2017). The national breeding program has made a particular effort to understand, conserve, exploit, and manage the available genetic resources across the country. The national pearl millet collection was updated in 2014 for better representation of the different varieties covering the entire national territory, especially the late flowering varieties (Diack et al., 2017). This new collection contained 477 accessions, including 353 early flowering (Souna), 112 late flowering (Sanio) and 12 improved varieties. These accessions showed high genetic diversity (He = 0.55). This consistently resulted in a greater genetic diversity in Senegalese landraces compared to other regions of Africa and Asia and was surely linked to the proximity of the center of domestication of the crop (Hu et al., 2015).

To facilitate the exploitation of all this diversity in the breeding program, a core collection was established based on phenotypic and genotypic data (SSR markers), using an advanced maximization strategy with a heuristic approach (Kim et al., 2007). This core collection consisted of 91 accessions (22% of total accessions), including 31 Sanio and 60 Souna, that captured as much genetic diversity as possible from the collected genetic material. The assessment of this core collection's structure revealed two genetic pools (genetic differentiation between Sanio and Souna). Each pool was further divided into three phenotypic subgroups based on the targeted phenotypic traits, such as yield and flowering time. Phenotyping of this core collection revealed five traits, including two phenological traits (heading and flowering) and three morphological traits (biomass, plant height, and tillering) that could clearly differentiate the Souna ecotype from the Sanio ecotype (Diack et al., 2020).

These identified groups and subgroups constituted potential heterotic groups that could be exploited in the millet breeding program to improve the phenotypic traits associated with these differentiations. Heterotic groups are very important for hybrid breeding because they guide the choice of parental lines, optimize the use of genetic material, and maximize the performance of derived hybrids (Meena et al., 2017). The Senegalese breeding program recently initiated studies to identify and validate heterotic groups in the core collection for hybrid breeding as part of a USAID-funded project (Genetic Enhancement of Pearl Millet). This study identified the most representative genotypes of the core collection and produced F1s from crosses between these individuals. Evaluation of these F1s and their parents for general and specific combining ability is currently in progress.

As performance of hybrid lines can be predicted based on general combining ability, trait introgressions in recurrent selection schemes are more efficient using divergent heterotic groups than genetically similar heterotic groups (Reif et al., 2007). Evaluation of hybrids, generated by crossing 17 open-pollinated varieties (OPVs) in a diallel mating design in nine environments over two years in Niger and Senegal resulted in the identification of 5 potential parental lines (Nigerien CIVT, H80-10Gr, Taram and Senegalese Thialack 2, and Souna 3). These five parental lines have a high combining ability that can be used to initiate reciprocal recurrent selection (Sattler et al., 2019).

The combining ability and heterosis for grain yield and its associated traits (i.e., plant height, flowering time, panicle length and diameter, productive tillers, thousand grains weight, and panicle and downy mildew) were assessed by crossing 17 inbred lines with Sosat C88 and Souna 3. The results indicated that the inheritance of these traits was controlled by both additive and nonadditive gene effects although the contribution of the additive genes was greater (Kanfany et al., 2018a). Some inbred lines (IBL003-B-1, IBL091-1-1, IBL095-4-1, IBL110-B-1, and IBL206-1-1) showed positive General Combining Ability (GCA) effects on grain yield and negative GCA effects on downy mildew, flowering time, and plant height; therefore, they are good parents for breeding high-yielding open-pollinated varieties and hybrids (Kanfany et al., 2018b).

Crop breeding is now undergoing a paradigm shift with the development of modern approaches. These methods, such as marker assisted selection or genomic selection, are more accurate and less costly in time and effort and are a byproduct of next-generation sequencing (NGS). In an effort to understand the genomic diversity and population structure of Senegalese germplasm, all accessions in the core collection were characterized using Genotype By Sequencing (GBS). This yielded 21,663 polymorphic (biallelic) and high-quality Single Nucleotide Polymorphism (SNP) markers. Marker-trait association identified markers linked to the adaptive genes *PgPHYC* and *PgMADS11* that were involved in the variation of flowering time in millet (Diack et al., 2017). Eighteen SNPs and genes have been associated with flowering time, plant height, number of tillers, and biomass, with some of these genes acting as candidate genes for abiotic stress adaptation. These identified markers, after validation, will be useful for marker-assisted selection in the program.

Cost and time efficiency in breeding programs depend on the ability to identify parental lines at an early stage of the breeding scheme (Ambati & Singh, 2017). To this end, studies were carried out to identify donor parents for the traits of farmers' interest. Firstly, genotypes with desirable agronomic traits and stable resistance to downy mildew (DM) were identified in hotspot areas (Zoclanclounon et al., 2019). Then, inbred lines, derived from a collection of landraces originating from West and Central African countries, were evaluated in the Bambey and Nioro Research Stations under field conditions with spreader rows of DM, using SOSAT-C88 and 7042S as resistant and susceptible controls, respectively (Kanfany et al., 2018b). Highly significant differences were observed among 101 lines tested for DM incidence and severity as well as agro-morphological traits, including plant height, flowering time, panicle length, and productive tillers. Based on DM incidence and severity of control varieties used, the testing lines were grouped into three categories: resistant (55, including SOSAT-C88), moderately resistant (16), and susceptible (30, including 7042S). Also, using DM resistance and plant height as the most discriminant factors, hierarchical ascendant cluster analysis grouped these entries into three clusters, confirming the previous categorization.

Conversely, the released Senegalese varieties (Gawane, ISMI9507, Thialack2 varieties, IBV8004, and Souna 3) were evaluated for resistance to stem borers and maize head miner (MHM) under natural infestation in the 2014 and 2015 cropping seasons (Goudiaby et al., 2018). Gawane was identified to be tolerant to stem borers and Thialack2 and ISMI9507 were identified to be resistant to MHM (Goudiaby et al., 2018). This effort to identify new sources of resistance to several diseases under Senegalese agro-ecological conditions provides new genetic resources for improvement of pearl millet for agronomic traits and resistance to DM, MHM, and stem borer. These new resources will be used in the national breeding program to combine into new varieties resistant to biotic stresses and with desirable adaptation traits.

All these efforts allowed the breeding program to select and propose four new pearl millet varieties for release in 2021, including three OPV (SL28, SL169, and SL423) and one top-cross hybrid. The OPVs were derived from local populations, which were improved through recurrent selection using the S1 method. The top-cross hybrid named TAAW was created by crossing a local population (SL175) to a male sterile parent sourced from ICRISAT (ICMA-177090).

4. Productivity Improvement Over the Different Phases

The average rates of yield gains from each of the three phases of pearl millet improvement in Senegal are listed in Figure 3. In the first phase (1961–1973), low average grain yield was observed throughout the country, mainly due to drought stress in early stages and lack of adapted varieties (ANSD, 2020). Thus, the breeding efforts at that period were focused on the development of varieties adapted to specific agroclimatic zones. The breeding effort in the second phase (1974–2007) led to the release of several new varieties, with an increased yield of 2.06 kg/ha. The highest rate of productivity was achieved in the third phase (2008–2019), with a yield gain of 2.7 kg/ha/yr. However, the genetic gain through these three phases remains unknown.

Figure 3

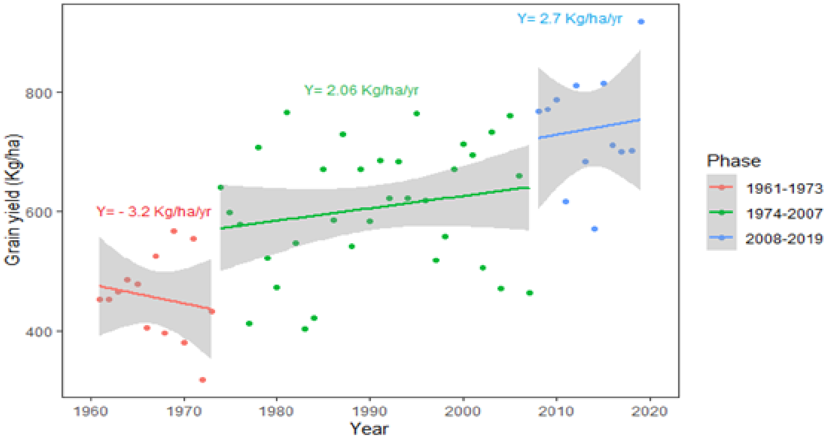

Figure 3 – Productivity Improvement Rates for Pearl Millet Productivity During the Three Phases of Pearl Millet Breeding in Senegal

Assuming that this continued increase in average grain yield has been achieved through genetic gain, it promises great potential for further improvement in millet yield, especially with the help of newly developed genomic tools. However, it should be considered that this rapid increase in grain yield may be caused by the combination and fixation of favorable alleles at major effect loci that underlie traits positively correlated with grain yield. Indeed, selection has been shown to generally fix favorable alleles at major effect loci faster than those at minor effect loci (Mayo & Hancock, 1981). In this case, it would be expected that the yield improvement be less significant in the coming years since it would be mainly driven by the fixation of favorable alleles at loci with minor effects and would depend more heavily on better management practices (Mayo & Hancock, 1981; Xu et al., 2017; Yeaman, 2022). Nevertheless, the breeding history described above and the current breeding pipeline which regularly brings genetic material from the associated programs suggest that the large effect variants have not yet segregated into the breeding germplasm (Mayo & Hancock, 1981; Muleta et al., 2019). Therefore, more significant yield improvement through genetic improvement should reasonably be targeted.

Future Genetic Improvement Strategies

Grain yield is unanimously considered the most important trait by farmers (Kanfany et al., 2020). Drought tolerance, adaptation to low soil fertility, grain color, disease and insect resistance, and early maturity are also important traits to be considered when farmers select a pearl millet variety to grow in their fields (Kanfany et al., 2020). Therefore, these should be the target traits for developing a variety that grows in Senegalese conditions. However, the order of priority for these traits varies from location to location. Incorporating farmers' preferred basic and value-added traits into the breeding product profile would certainly increase farmer acceptance of released varieties.

The breeding goal in Senegal is to release pearl millet varieties with high yields (15% increase in grain yield over Souna 3 and Thialack II), high iron contents (with > 40 ppm Fe), and better adaptation in the two agro-ecological zones (Table 2). The combined strategies described below should enable the National Pearl Millet Improvement Program to diversify its sources of germplasm and accelerate varietal development with better selection accuracy.

Table 2

Breeding Targets for the Two Agro-climatic Zones in Senegal Where Pearl Millet is Mostly Produced

Breeding Targets	Target Agro-ecologies	Maturity (days) & Rainfall	Resistance/ tolerance Required	Basic Traits	Value Added Traits	Breeding Goals
High yielding, early maturing pearl millet **OPVs** for adaptation to Sahelian zone of Senegal	Target: Central and northern part of the peanut basin agro-ecological zone	Early maturity 70–90 days (350–600 mm/ annul)	**Biotic stresses:** Downy mildew, millet head-miner Striga hermonthica**Abiotic stresses:** Drought, Low soil fertility	2 tons/ha, \n Downy mildew resistance\n \n Head length > 40 cm"}">Grain Yield of >2 tons/ha, Downy mildew resistanceHead length > 40 cm	High grain iron and zinc content. Striga tolerance Drought tolerance Head miner tolerance	40 ppm Fe"}"> 10% increase in grain yield over improved check (Souna 3) with >40 ppm Fe
Medium maturity, high yielding pearl millet **OPV** Soudanian zone of Senegal	Target: Southern part of the peanut basin agro-ecological zone	90 days\n \n (500–900 mm/ annum)"}">Medium maturity/ >90 days(500–900 mm/annum)	**Biotic stresses:** Downy mildew, head miner, striga hermonthica**Abiotic stresses:** Drought, low soil fertility	2 tons/ha, \n downy mildew resistance\n \n Head length > 50 cm"}">Grain Yield of >2 tons/ha, downy mildew resistanceHead length > 50 cm	High grain iron and zinc content. Striga tolerance	40 ppm Fe"}"> 10% increase in grain yield over improved check (Thialack II) with >40 ppm Fe
Early maturity, high yielding hybrids for adaptation to better endowed environments	Target: central and northern part of the peanut basin	Early 70–90 days / (350–800 mm/ annum)	**Biotic stresses:** Downy mildew resistance, head miner**Abiotic**	2.0 tons/ha\n Downy mildew resistance\n \n Head	High grain iron and zinc content.	40 ppm Fe"}"> 15% increase in grain yield over improved check

Breeding Targets	Target Agro-ecologies	Maturity (days) & Rainfall	Resistance/ tolerance Required	Basic Traits	Value Added Traits	Breeding Goals
of West Africa	agro-ecological zone		**stresses:** Drought, low soil fertility	length > 50 cm"}">Grain yield of > 2.0 tons/ha Downy mildew resistanceHead length > 50 cm	Striga tolerance Drought tolerance	(Souna 3) with >40 ppm Fe

I. Towards Implementing Gonomics-enabled Breeding

In the current breeding scheme, phenotypic selection remains the major method used in Senegal. However, this approach may not be able to properly examine the hidden genetic variation available for complex agronomic traits, such as grain yield and drought resistance, as these traits typically have low heritability and are heavily influenced by environments (Wu et al., 2012). Moreover, phenotypic selection involves many selection cycles in multi-trials in different environments to accurately evaluate progeny performance, which not only needs large amounts of seed for replicated trials, but is also laborious, time-consuming, and costly. However, such tests may not be realized due to insufficient seed amount and financial support for resource-limited breeding programs of developing countries like Senegal. Furthermore, the current and predicted variation in rainfall amount and distribution in the Sahel zone has emphasized the difficulty to control genotype x environment (GxE) interactions.

In light of the challenge of increasing genetic gain with limited resources, the National Pearl Millet Improvement Program has considered making greater use of currently available genomic resources to help breeders make more informed decisions about crosses at early breeding stages. The availability of the pearl millet reference genome sequence (~1.79 Gb) and the reduction in the cost of high-throughput data acquisition offers the opportunity to strengthen the breeding pipeline (Varshney et al., 2017). Nevertheless, the choice of modern breeding tools and methods to integrate must be evaluated with the utmost caution, considering several factors, including the genetic architecture of the targeted traits. For instance, the results of simulations performed by Muleta et al. (2019) showed that there are specific conditions under which genomics-assisted recurrent selection (GARS) should be considered by small breeding programs, according to the genetic architecture of the trait. In fact, this study showed a lower cost per unit gain using phenotypic recurrent selection (PRS) compared to GARS for oligogenic traits in small new breeding programs, while GARS gave lower cost per unit gain than PRS with larger populations and polygenic traits. Thus, understanding the genetic architecture of target traits will guide the breeding program in adopting the most effective breeding pipeline to maximize genetic gain given available resources.

Genomics-assisted breeding that integrates advanced genomic tools with conventional breeding has been one of the main strategies for developing high-yielding crop varieties that are resistant to biotic and abiotic stresses. Over the past decade, the National Pearl Millet Improvement Program has focused on understanding the genomic diversity of available germplasm, identifying genetic variants of targeted traits, and uncovering the molecular and physiological mechanisms underlying the expression of these traits. Phenotypic variants identified for downy mildew, MHM, and drought tolerance and allelic variants (SNPs) identified for flowering time provide new genetic resources for the development of molecular markers linked to favorable alleles. Therefore, more accurate selection for these traits could be achieved using marker-assisted backcrossing to shorten breeding cycles (Bernardo, 2016). In the years to come, the National Pearl Millet Improvement Program will take advantage of new financial resources from the Sorghum and Millet Innovation Lab (SMIL), Innovation Lab for Crop Improvement (ILCI), and Desira-ABEE to set up a strong marker-assisted breeding program to accelerate the introgression of these genetic variants into elite lines to improve the genetic gain.

2. Breeding for Drought Adaptive Traits in the Senegalese Agro-ecosystem

Drought tolerance is a polygenic trait significantly influenced by the environment (Serba & Yadav, 2016). The development of drought-tolerant varieties is a challenging task that can be achieved through the introgression of adaptive traits that allow plants to grow and produce satisfactory yields under water-limited conditions. In some cases, complex traits, such as drought, can be more efficiently improved by targeting simpler and more strongly correlated traits with them (Breseghello & Coelho, 2013). Drought adaptive traits can be categorized into three main strategies: drought escape, dehydration avoidance, and dehydration tolerance (Basu et al., 2016). Drought escape allows plants to accelerate their life cycle and reproduce before drought occurs (Turner, 1896). This strategy is commonly used by annual plants although the yield is generally decreased (Lisar et al., 2016). Dehydration avoidance is a strategy for preserving the high-water potential of plants mainly by reducing water loss through transpiration and optimizing water uptake from the soil by the root system (Basu et al., 2016). Because the mechanisms involved in this strategy consume additional energy, plant yield is generally decreased and the plants are small (Lisar et al., 2016). Avoidance is mainly achieved through traits related to root architecture, stomatal control, and transpiration efficiency (Basu et al., 2016). Dehydration tolerance involves mechanisms to maintain functionality in a water stressed environment (Turner, 1896). Dehydration tolerance involves traits such as cell remobilization of stem water-soluble carbohydrates, membrane stability and osmotic adjustment (Lisar et al., 2016). A drought tolerance cultivar can be defined as a genotype that detects water deficiency and effectively adopts combined strategies to grow and produce a satisfactory yield. Understanding the traditional cropping systems' response to water deficiency and identifying the valuable traits to be targeted are critical steps in breeding a drought tolerant cultivar.

Through evolution, traditional pearl millet landraces showed evidence of different mechanisms of adaptation to climate change, resulting from natural selection as well as from farmers' selection. On the one hand, the development of the root system of pearl millet is distinguished by a fast-growing primary root that rapidly colonizes the deeper horizons of the soil at an early stage (Passot et al., 2016). This trait allows access to the water available in a deeper soil horizon. Comparison of root development parameters in 16 inbred lines originating from Indian, West African, and Central African landraces showed significant variation in primary root length and lateral root density that could be exploited in subsequent breeding efforts (Passot et al., 2016). On the other hand, West African pearl millet farmers preferably cultivate high tillering landraces with small grains (Serba & Yadav, 2016). These landraces can produce secondary tillers and fill the grain very quickly. Since yield potential is related to the number of tillers and grains, among other morphological traits, this strategy allows them to efficiently improve yield under drought conditions. Finally, evidence is beginning to accumulate that flowering time is under selection in West Africa in response to rainfall variability. Flowering time directly correlates with annual rainfall (Saïdou et al., 2009).

Comparison analysis of pearl millet accessions collected in 1976 and 2003 in Niger showed a significant shift: varieties collected in 2003 flowered slightly earlier and had a shorter spike than in 1976 (Saïdou et al, 2009). This response to selection for flowering time was significantly associated with polymorphisms in two genes PHYC and PgMADS11 (Mariac et al., 2011; Saïdou et al., 2009). These polymorphisms for early and late flowering alleles in these two genes were found in the landraces in Niger and were also more recently revealed in the Senegalese germplasm (Diack et al., 2020; Vigouroux et al., 2011). These findings suggest that drought escape is a main mechanism of adaptation to drought in West Africa. Understanding the genetic basis of these morpho-physiological traits associated with drought tolerance, in particular the flowering period, and then identifying the favorable alleles to introgress into the elite background are promising steps for the rapid selection of a drought-tolerant cultivar.

3. Reinforcement of Hybrid Breeding Strategies

In view of the urgent need for a rapid increase in productivity, it is crucial to establish a strong hybrid breeding program to focus on breeding high-yielding hybrid cultivars. Combining ability studies have clearly highlighted the prevalence of high levels of heterosis and potential to breed for hybrids with high and stable yield, as well as multiple disease resistance and abiotic stress tolerance in Senegalese environments. Previous studies showed the superiority of hybrid varieties over the best landraces for agro-morphological and agronomic traits in West African pearl millet germplasm (Pucher et al., 2016).

Inspired by the success of hybrids in India, a collaboration has been initiated by millet breeding programs in several West African countries (Senegal, Niger, Burkina Faso, and Mali) as part of the SMIL project for the development of dual-purpose pearl millet hybrid lines with enhanced grain nutritional quality and stover digestibility. The aim of the SMIL project was to characterize genetic diversity, validate superior germplasm accessions, and identify genetic variants for traits related to stover quality and digestibility (i.e., grain mineral content, grain and stover yields) using 100 germplasm accessions collected from the related countries (Serba et al., 2020). Adoption of dual-purpose pearl millet hybrid varieties are expected to improve nutritional security of smallholder farming families, crop-livestock integration, and income generation.

Conclusion

Pearl millet is the main cereal grown in Senegal. The traditional farming system has played a crucial role in creating and maintaining a high diversity among landraces. The Senegalese breeding program has invested a great deal of effort for nearly a century in collecting, maintaining, and more recently understanding this genetic diversity. In parallel, several varieties were derived from the local population using the conventional breeding approach. The regional and international partnerships developed have made it possible to enrich the genetic material and support all these selection efforts, resulting in a significant improvement in yield performance, especially in the last phase ranging from 2008–2019. This last decade was particularly marked by progress towards the implementation of genomics-based breeding and the strengthening of hybrid breeding strategies. Despite their yield performance, the varieties released so far do not seem to hold all the agro-morphological characteristics that lead to their high adoption by farmers. The high genetic variation found in Senegalese landraces that possess adaptive traits to the local environment, as well as traits preferred by farmers, is a promising resource for developing high-yielding crop varieties that are resistant to specific biotic and abiotic stresses. In addition, the future breeding strategies outlined in this chapter, and the more participatory breeding approach should enable the breeding program to improve genetic gain more effectively for farmers' priority traits. Further, they will contribute to addressing the challenge of sustainably improving pearl millet productivity for food security and income generation in Senegal.

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19. Breeding for Drought Adaptation and Fresh Seed Dormancy of Groundnut in Senegal: Advances, Challenges, and Prospects

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Abstract

Groundnut (*Arachis hypogaea* L.) is a multi-purpose legume widely cultivated in the semiarid tropics. In Senegal, groundnut is historically an important crop, and it remains one of the commodities with a huge potential for exports. However, due to the country's location in the Sahelian zone in West Africa, crop production is subject to low and erratic rainfall patterns and unpredictable end of the rainy season. Therefore, groundnut breeding programs were initiated early in the 20th century to develop and release drought-tolerant cultivars with fresh seed dormancy (to avoid rapid sprouting). This review highlights the significant advances made in these research areas to reduce yield losses and groundnut quality deterioration. Challenges concerning the effects of climate change on agricultural production, which will keep increasing over the coming decades, are also addressed herein. Finally, we provided some insights on integrating the new breeding tools and methods such as high-throughput phenotyping, marker-assisted and genomic selection to breed groundnut varieties that are more adapted to the agro-ecologies in Senegal.

Keywords: groundnut, drought, stress, seed dormancy, cultivars, Senegal

Background

In Senegal, the agricultural sector accounts for more than 9.8% of the gross domestic product (ANSD, 2022), with groundnut being the most important cash crop. Groundnut crop also plays a central role in the development of the rural economy. It employs nearly 87% of the working population, positioning Senegal among the 10 largest world producers. However, groundnut productivity in Senegal (1.46 kg ha^{-1}) is still less than the world average yield, estimated at 1.69 kg ha^{-1} (FAOSTAT, 2020).

Drought stress is the foremost limiting constraint of sub-Saharan African countries' agriculture (Burke et al., 2010; World Bank, 2015). If one were to estimate the influence of different types of deficiency on the balance of world agricultural production, lack of water would appear to be one of the most important limiting factors. This statement is particularly true in countries located in Sub-Saharan Africa. In addition, there is still a dynamic increase in these countries' populations (Guengant & May 2013) posing an additional challenge for local agriculture, which remains the main source of income for 90% of workers and provides more than 50% of export earnings. Thus, it becomes imperative to enhance crop productivity by increasing yield to provide sufficient food to that increasing population. Although investigations in water resources management to deal with water scarcity have been extensively conducted, drought stress remains the most important limiting factor for agricultural productivity.

Lack of fresh seed dormancy can lead to heavy crop sprouting and yield loss, particularly when terminal drought spells occur. In addition, it may be associated with heavy aflatoxin contamination as the causal fungus, *Aspergillus flavus*, can invade sprouting pods easily during germination compared to intact seeds (Martin et al., 1999). Therefore, as an important agronomic trait, fresh seed dormancy contributes to groundnut-based food safety I it may prevent kernels from being contaminated by aflatoxin. In general, cultivars belonging to the subspecies *Arachis hypogaea subsp. hypogaea* (Virginia and Runner types) have inherent dormancy, while those of the *Arachis hypogaea subsp. fastigiata* (Spanish and Valencia types) are extremely prone to sprouting because they usually lack fresh seed dormancy. From a breeding perspective, a few Spanish-type varieties with fresh seed dormancy have been developed from intersubspecific (i.e., Spanish x Virginia) crosses. In Sub-Saharan African countries, where most groundnut cultivars are of the Spanish type, fresh seed dormancy is a desirable trait to offset in situ germination that may occur due to late rains after groundnut maturity. However, until now, only a few Spanish varieties with fresh seed dormancy have been released. Taaru was a recent Spanish-type variety with deep fresh seed dormancy released by the ISRA groundnut breeding program in Senegal (CORAF, 2018).

In this chapter, we highlighted the main achievements in developing and releasing varieties adapted to drought-prone environments, including the potential use of high-throughput phenotyping methods and recently available groundnut genomic and genotyping resources in modern breeding approaches for improving groundnut varieties' tolerance to drought stress. We also discussed state of the art practices in fresh seed dormancy phenotyping and genetics and pointed out the main achievements of ICRISAT and ISRA breeding programs.

An Overview of the History of Groundnut Breeding at ISRA

In Senegal, research in groundnut improvement started in 1898 when the Bambey research station was a pilot site to serve as a research platform for the French colonies in the Sudanian zone in Africa. Since then, groundnut has remained an important cash crop in Senegal. Over decades, the variety development was conditioned by the scenario of prevailing climatic conditions.

Before 1970: There was no water deficit constraint. The cv. 55-437 and 47-16 were released and widely cultivated in the northern region of Senegal (Louga). These cultivars are both 90-day maturing varieties, but the cv.

55-437 is an erect type, while cv. 47-16 is a spreading type. In the central region (Diourbel, Thiès, and Kaolack), the 120-day maturing varieties 57-422 and 48-15 were the largest cultivated varieties.

1971–1983: This period corresponded to the beginning of the drought periods in all the Sahel zone. During the 1970s, the drastic reduction of the rainfall and its erratic pattern, particularly in the Northern region of Senegal, resulted in the replacement of the cv 47-16 by the cv. 55-437 and was the only variety recommended in the Northern region (Louga). Breeding programs established during this period created a new cultivar: cv. 73-30 was released for its drought tolerance and fresh seed dormancy (Bockelee-Morvan, 1983). The late-maturing cv. 57-422 (120 days) was replaced in this large production area by the newly released cv. 73-33 that matures in 110 days. The cv. 57-422 was cornered to a small area around Diourbel.

1984–1996: This period was characterized by the release of the cv. Fleur 11, a variety with high yield potential and drought tolerance. Because of its big seed size, it has been recommended for confectionery, particularly when produced under irrigated conditions, to prevent pre-harvest aflatoxin contamination. Meanwhile, a breeding program that focuses on short duration varieties was established and resulted in the release of cv. GC-8-35 (80 days) for the replacement of cv. 55-437 in the Northern region of Senegal, where the rainy season was shortening considerably in comparison to the rest of the country. The cv. 55-422 was almost replaced by the medium duration cv. 73-33 in the Central and Southern region of the groundnut basin.

1997–2010: During this period, the breeding program on earliness also resulted in the release of four cultivars, 78-936, 73-9-11, 55-33, and SRV1-19 in 2009. Now, the cv. GC-8-35 is replaced by cv. 55-33 because the latter produces a higher haulm while maturing in 80 days. Its geographical area is expanding to the Central region of the groundnut basin.

2011–Present: In 2004, we started a new breeding program using wild species as a donor of favorable alleles. With this breeding program, chromosome segment substitution lines (CSSLs) were developed, and six were released in 2017/2018. These lines have a high yield associated with bigger seed sizes (Tossim et al., 2020), particularly those named “Tosset” and “Rafet Kaar.” These cultivars have a 100-kernel weight (60 to 65g), much higher than the recurrent parent, cv. Fleur 11. The remaining cultivars (Raw Gadu, Yaakar, Jambar, and Kom Kom) are high-yielding and show better yield stability in the Senegalese groundnut basin than Fleur 11.

Regarding fresh seed dormancy, a specific breeding program for this trait was initiated in 1997. It resulted in developing seven lines with deep fresh seed dormancy (Ndoye, 2001). However, it was only in 2018 that the line named “Taaru” was released for cultivation in Senegal for its good yield, deep fresh seed dormancy, and high oil content.

Groundnut Improvement for Drought Adaptation

1. Description of the Different Drought Scenarios and Implications in Breeding

Senegal has a decreasing rainfall gradient, ranging from less than 474 mm in the Northern groundnut basin to more than 1034 mm in the Southern region (Table 1). The upper northern groundnut basin region is drier (less than 400 mm/year), and only extra-early maturing varieties with drought tolerance traits are recommended for cultivation there. Overall, the rainfall trend shows a neat decrease since the 70s, and more frequent and severe dry spells are noted, even in Southern Senegal. Severe dry spells occurring at an early stage of the groundnut cultivation, particularly in the Northern region, might have a significant effect on productivity. There are also dry spells at later stages of the growing season, which somewhat contribute to the gap between potential crop yield and on-farm production. Therefore, both intermittent and terminal drought stress need to be considered when selecting drought tolerant varieties in Senegal.

Table 1a

Average Rainfall, Rainy Season Duration, Dry Spells Frequency and Duration at Early and Late Stages in Selected Sites Across Agroecological Zones in Senegal Over the Period 1981–2010

Agroecological Zone/Site	Average Rainfall (mm)	Growing Season Duration (days)	Occurrence of Dry Spells (lasting at least 10 days) at Early Stage
North Groundnut Bassin- Bambey	487.4	74	18/40
North Groundnut Bassin-Diourbel	474.4	77	21/40
South Groundnut Bassin- Kaolack	610	99	13/40
Eastern region-Sinthiou Maleme	713	96	13/40
Southern region- Kolda	1034.3	105	14/40

Table 1b

Agroecological Zone/Site	Duration of Drought Spells at Early Stage and Mean Standard Error	Occurrence of Dry Spells (lasting at least 10 days) at Late Stage	Duration of Drought Spells at Late Stage and Mean Standard Error
North Groundnut Bassin- Bambey	10±1 (24)	13/40	9±1 (26)
North Groundnut Bassin-Diourbel	10±1 (22)	15/40	9±1 (21)
South Groundnut Bassin- Kaolack	9±1 (23)	30/40	12±1 (20)
Eastern region-Sinthiou Maleme	8±1 (16)	Dec-40	8±1 (14)
Southern region- Kolda	8±1 (15)	16/40	9±1 (17)

Note. Values between brackets are the maximum duration of dry spells observed (Source: Service d'Agroclimatologie, ISRA/CNRA, Bambey, 2010)

To overcome the severe drought episodes in the 1970s, groundnut breeding programs in Senegal focused on developing and releasing early and drought-tolerant varieties. Three major occurrences of drought were identified and characterized: early-stage drought (after emergence or early vegetative phase), intermittent drought (at flowering and pod development stage), and terminal drought (at pod filling stage), with all types being detrimental to yield and/or its components (Clavel et al., 2007; Rao et al., 1985). Three different strategies that are related to drought tolerance have been identified in plants, including legumes (Turner et al., 2001):

Drought escapers: genotypes belonging to this class are extra-early (75–80 days) or early (90 days) maturing varieties. This drought adaptation strategy is particularly important in dry regions with frequent end-season droughts. In the northern part of Senegal, where the rainy season lasts less than 90 days, extra-early maturing varieties have been recommended for cultivation. For instance, the variety GC-8-35 was released in 1996 to replace the variety 55-437, which was previously largely cultivated in this region. Cultivar 55-437 is a 90-days maturing cultivar that was no longer getting enough rain to mature in Northern Senegal at the end of the 1990s. The breeding programs released four other extra-early maturing lines (78-936, 55-33, 73-9-11, and SRV1-19). Except for line 78-936 (an introduction), all the other ones have been developed from crosses between Chico and Senegalese elite varieties (55-437 and 73-30). The varieties 55-33 and SRV1-19 were developed from crosses between 55-437 and Chico, using a backcross and a recurrent selection scheme, respectively. These extra-early maturing varieties have higher yield performances under drought stress because they avoid drought better than CG-8-35, thanks to their physiological and membrane resistance. A breeding program is ongoing to improve these extra-early maturing lines for higher (pod and haulm) yields associated with drought tolerance traits.

Drought avoiders: genotypes that can cope with drought stress using mechanisms limiting water loss. They have different physiological mechanisms to avoid drought stress: i) a deep root system for better water uptake). This trait is critical to avoiding drought, but its limitation is a weak correlation between measurements in controlled environments and the field.

With the availability of large-capacity lysimetric tubes that were recently developed at ISRA, one could investigate better the correlation of root growth parameters with physiological traits and yield under drought stress for many entries; ii) stomatal conductance (Gs) and transpiration rate (E) – in groundnut, intervarietal differences are difficult to observe even under severe drought stress. Likely, there is not much genetic variability in groundnut.

Drought tolerant: These plants would use osmotic adjustment – this mechanism has been extensively investigated in Senegal. Still, little or low genetic variability was observed between genotypes of the same phenology. Clavel et al. (2007) found that genotypic differences are greatest two weeks after drought onset.

Integrating drought adaptation traits (especially for avoidance and tolerance) in breeding programs requires high throughput phenotyping methods to screen large numbers of lines quickly.

2. Boundaries to Improve Genotypes for Drought Tolerance

Breeding for drought escape by reducing the growth duration of the varieties has been an important strategy adopted by breeding programs to tackle late water deficit stress and ensure good yields under end-season drought stress. However, breeding programs have to deal also with dry periods occurring during the plant's developmental stage since drought spells are frequent in the Sahelian zone. The most widely used approach to evaluate genotypes' adaptation to drought is an empirical approach that measures yield under water-limiting conditions after withholding irrigation for a given period during the developmental and reproductive stages to mimic drought spells (Clavel et al., 2007; Nigam et al., 2005). However, inconsistent climatic conditions across studies have led to contradictory statements. Besides, drought tolerance is a complex and polygenic trait.

Attempts to integrate physiological traits and yield in variety development for drought tolerance have resulted in limited success. For instance, low-cost, rapid, and easily measurable indicators for three significant physiological features of drought tolerance – the amount of water transpired (T), water-use efficiency (W), and harvest index (HI) – were developed to assess drought tolerance in crops (Devi et al., 2010; Devi et al., 2019; Tuberosa, 2012). However, application in groundnut breeding programs has been limited because of practical difficulties associated with measuring these traits under field conditions in large breeding populations. Songsri et al. (2008) found high correlations between drought tolerance index (DTI), pod yield, root length density (RLD), and harvest index (HI), indicating that RLD contributed greatly to pod yield and HI under drought conditions. This association is relevant to groundnut because pods develop underground and adequate moisture in the root zone is critical for peg and pod development. However, phenotyping for root traits in field conditions and in a large population is quite challenging.

Drought tolerance can be enhanced by improving soil water extraction and/or water use efficiency. Therefore, we recently developed a good capacity for phenotyping using a lysimetric system and high-throughput phenotyping platforms to optimize the measurements of physiological and root traits under drought stress conditions. Besides, the high throughput phenotyping methods are paving the way to solving the issue of accurate drought phenotyping in breeding programs as they usually evaluate large populations in a short period of time. Our preliminary results in this research area are quite promising as significant correlations were found between measurements of leaf temperature and leaf area index using handheld devices and with cameras embarked on drones.

3. Genetic and Genomic Resources to Breed Drought-Tolerant Genotypes

3.1 Collections

The key to success for any breeding program is the availability of a large genetic diversity for economically important traits. Characterizing and identifying the sources of variability are important steps in the pre-breeding activities of any species. In groundnut, thousands of accessions are maintained in different countries, including India (15445 accessions), the

USA (9310 accessions), and China (7837 accessions) (Barkley et al., 2016). To dispose of an easily manageable and cost-effective germplasm set, it is recommended to establish a core collection (representing 10% of the overall collection) or even a mini core collection (10% of the core collection and therefore 1% of the overall collection). Thus, from the various collections kept in different countries, core collections of 1704, 831, and 576 accessions were developed and maintained respectively in India, the USA, and China (Pandey et al., 2012). From these core collections, mini core collections of 184, 112, and 298 accessions have been developed in India, the USA, and China, respectively (Jiang et al., 2010; Upadhyaya et al., 2002). Based on phenotypic data, geographic origin, and taxonomy, ICRISAT developed, as part of the Generation Challenge Program (GCP) initiative, a composite reference set of 300 genotypes (Pandey et al., 2012). Recently, in the framework of the Peanut Innovation Lab (PIL), a USAID Feed the Future initiative, ISRA has assembled a collection of 1049 accessions from nine countries in West, East, and Southern Africa, in partnership with breeders from national research programs of these countries. These accessions were genotyped at the University of Georgia (UGA) using the Affymetrix chip (45K SNP markers). The genotypic data have been made publicly available at https://www.peanutbase.org. From that germplasm, a subset of 300 accessions representing the whole genetic diversity in the entire collection was established using both the genotypic data and breeders' knowledge. That subset is characterized in all the nine germplasm-contributing countries for various traits, including yield, drought tolerance, and fresh seed dormancy. The phenotypic data generated will be used for association mapping studies to better understand the genetics and mechanisms involved in drought tolerance in groundnut.

Because of the narrow genetic base of groundnut, compared to other crop species, wild species related to cultivated groundnut represent valuable sources of useful alleles essential for groundnut improvement. Major centers holding wild *Arachis* species collections include Texas A&M University (1200 accessions), U.S. Department of Agriculture (USDA, 607 accessions), North Carolina State University, (NCSU, 406 accessions), Brazil EMBRAPA-CENARGEN (1220 accessions), ICRISAT in India (477 accessions) and the Instituto de Botánica del Nordeste (IBONE, 472 accessions) in Argentina (Pandey et al., 2012). In addition, breeding programs worldwide have developed different types of biparental populations, including recombinant inbred lines, advanced backcross QTL lines, and chromosome segment substitution lines (Foncéka et al., 2012; Table 2). These genetic materials could be useful sources for identifying QTLs involved in drought tolerance using high-throughput genotyping and accurate and rapid phenotyping approaches.

Table 2
List of Main Interspecific Populations Derived from Cultivated and Wild Species of Groundnut

Population	Lines/ Types	Segregating Traits	Research Institute /University
A. duranensis × A. stenosperma	87 RILs	Late leaf spot resistance, transpiration, response to drought stress, various aspects of plant morphology	EMBRAPA
A. hypogaea cv. Fleur11 × (A. ipäensis × A. duranensis)	81 BC4F7	Seed size and pod and haulm yield, disease resistance	ISRA (CERAAS), CIRAD
A. hypogaea cv. Fleur11 × (A. batizocoi×A. duranensis)	133 BC2F7	Seed size and pod and haulm yield, disease resistance	ISRA (CERAAS)
A. hypogaea cv. Fleur11 × (A. valida×A. duranensis)	300 BC2F7	Seed size and pod and haulm yield, disease resistance	ISRA (CERAAS)
Tifrunner × C76-16, Florida-07 × C76-16	400 RILs	Drought tolerance and reduced PAC	USDA-ARS, UGA, NCSU
TAG 24 × ICGV 86031	318 RILs	Drought related traits	ICRISAT
ICGS 44 × ICGS 76	188 RILs	Drought related traits	ICRISAT
ICGS 76 × CSMG 84-1	176 RILs	Drought related traits	ICRISAT

3.2 Genomics Resources

Genomic resources are powerful tools to harness the genetic variation in germplasm collections for the faster generation of improved varieties. The groundnut scientific community has made a considerable leap from insufficient to abundant genomic resources in this area. Multiple publications provide details on the available resources (Ozias-Akins et al., 2017; Pandey et al., 2012; Pandey et al., 2014; Varshney et al., 2014; Vishwakarma et al., 2017). All these tools and technologies are useful for basic and applied groundnut improvement research. In addition to the various molecular markers and genetic maps, the genome sequences of the wild diploid parents of cultivated groundnut (*Arachis ipaensis* and *Arachis duranensis*) and the tetraploid variety Tifrunner (Bertioli et al., 2016; Chen et al., 2016) are valuable resources. Sequencing the reference genome is one of the most important milestones for any crop species to accelerate the process of understanding genome architecture, gene discovery and molecular breeding for complex traits such as drought. Available groundnut genome sequences paved the way for the development and deployment of highly informative Affymetrix technology Single Nucleotide Polymorphism (SNP) chips "Axiom_Arachis" containing 58k and 48k markers (Clevenger et al., 2017; Pandey et al., 2017). Genome sequencing has also enabled the development of more simple sequence repeats (SSR) and insertions/deletion (INDELs) markers (Vishwakarma et al., 2017; Zhao et al., 2017). After completing the reference genome sequences, a great challenge for researchers is understanding the functions of the entire sets of genes. The gene expression atlas of groundnut provides detailed information on gene expression in different genotypes, organs, tissues, cells, and developmental stages (Pandey & Varshney, 2018). Such resources were developed by the University of Georgia using RNA sequencing data generated from 22 tissues (Clevenger et al., 2017). ICRISAT also reported the development of another gene expression atlas (AhGEA) using RNA-Seq data of 19 tissues from five stages of an early maturing, high-yielding, drought-tolerant groundnut variety, ICGV 91114 (Pandey & Varshney, 2018). These resources could be useful for conducting high-resolution trait mapping, marker development, candidate gene discovery, and molecular breeding for drought tolerance in groundnut.

Moreover, several QTLs are identified for drought tolerance traits, but their validation and application in marker-assisted selection (MAS) are challenging (Foncéka et al., 2012; Faye et al., 2015; Gautami et al., 2012; Ravi et al., 2011). These authors suggested that marker-assisted recurrent selection or genomic selection (GS) would be more appropriate in order to combine favorable alleles from so many regions. GS-assisted breeding has been tested in groundnut using a training population (TP) of 340 advanced breeding lines followed by multi-seasons and multi-locations phenotyping for important agronomic traits (Janila et al., 2016a). Currently, few successful examples of molecular breeding products are available in groundnut (Chu et al., 2011; Janila et al., 2016b; Varshney et al., 2014). With the greater development of genetic resources and advanced genomic tools, the potential to develop drought-tolerant cultivars is greater than ever. New emerging breeding technologies and methods such as genomic selection and genome editing are promising tools. Genetic engineering and genome editing have great potential in improving groundnut for drought tolerance as such technologies are not limited by ploidy and cross ability barriers. Several research groups, particularly in the United States, China, and India, have developed transgenic groundnut lines to resist viruses, insects, fungi, as well as for drought tolerance, and grain quality. Brasileiro et al. (2014) reviewed the progress achieved in *Arachis* genetic transformation. Tolerance was reported in drought-susceptible groundnut variety JL24 by over-expressing the gene DREB1A (Bhatnagar-Mathur et al., 2008). This transgenic event improved groundnut yield through a complex molecular mechanism involving a cascade of stress signaling and growth-regulating genes. However, in most West African countries, particularly Senegal, limited by the availability of research funds, suitable infrastructures, and regulatory approval, the use of genetic engineering tools remains uncertain. In such conditions, crop modeling is more applicable, especially for traits that are difficult to phenotype, such as physiological traits.

Groundnut Improvement for Seed Dormancy

In the Sahelian zone, late rains after groundnut's physiological maturity can cause important yield losses (20 and 50%) in varieties lacking fresh seed dormancy (Gautreau, 1984; Khalfaoui, 1991; Ndoye, 2001). In addition, the sprouting of non-dormant varieties can increase aflatoxin contamination of kernels (Martin et al., 1999). Thus, there is a need to develop Spanish–type varieties with fresh seed dormancy to improve groundnut productivity and seed quality for areas prone to late rains.

1. Development and Release of Dormant Varieties

ICGV 86155, ICGV 86156, ICGV 86158, ICGV 87378, and ICGV 87921 Spanish groundnut (*Arachis hypogaea* L. subsp. *fastigiata Waldron* var. *vulgaris* Harz) improved germplasm lines (Reg. no. GP-79 to GP-83, P1 594969 to P1 594973), bred by ICRISAT, India, were released in 1995 for their fresh seed dormancy in the Spanish background (Upadhyaya et al., 1997). Another improved Spanish peanut (*Arachis hypogaea* L. subsp. *fastigiata* var. *vulgaris*) germplasm bred by ICRISAT, ICGV 93470 (Reg. no. GP-102, PI 614087) was released in 1999 for its early-maturity and fresh seed dormancy (Upadhyaya et al., 2001).

In Senegal, the first Spanish dormant variety released is the variety 73-30 (Bockelee-Morvan, 1983). It has deep dormancy and could be used as a donor parent in breeding programs for early maturing and dormant groundnut varieties. A second dormant Spanish variety derived from a cross between the variety Fleur 11 and 73-30 was recently released. That new variety named "Taaru" has a bigger seed size than variety 73-30, while its oil content is higher (53%) than most of the Senegalese groundnut varieties.

Screening of various groundnut germplasm, including core collections, should allow the identification of new sources of fresh seed dormancy for further varietal improvement. In our breeding program, we recently evaluated the above-mentioned collection of 289 accessions for fresh seed dormancy. Among the 189 short-duration cycle accessions, 16 were classified as having deep dormancy (percentage of germinated seeds < 10%), 23 were classified as having light dormancy (< 30%), and the remaining 150 accessions were classified as non-dormant (percentage of germinated seeds > 30%). Out of the 100 long-duration cycle accessions, 40 accessions were classified with deep dormancy, 26 accessions with light dormancy, and 34 accessions as non-dormant (Unpublished data). Some accessions with fresh seed dormancy are listed below (Table 3). This germplasm is an important source of accessions with fresh seed dormancy.

Table 3

List of Selected Accessions with Deep Fresh Seed Dormancy Maintained in Breeding Programs in Africa

Duration Cycle Length	Origin /Country /Maintainer	Accessions	Other Characteristics
Short	Senegal/ISRA	73-30	Drought tolerance
Short	Senegal/ISRA	Taaru	High oleic content (53%)
Long	Senegal/ISRA	69-101	Leaf spot & Rosette resistance
Long	Senegal/ISRA	Turquie 2	Confectionery type and mid-oleic content
Short	Ghana/CSIR-SARI	ICGV 13110	ND
Short	Ghana/CSIR-SARI	ICGV 15017	ND
Long	Ghana/CSIR-SARI	NUMEX 05	High yield
Short	Uganda/NARO	SVG-GB-10010	ND
Short	Uganda/NARO	ICGV SM 08577	ND
Short	Malawi/DAR	ICGV SM 5738	ND
Short	Malawi/DAR	ICGV 6057	ND
Short	Malawi/DAR	ICGV SM07544	ND
Short	Mozambique/IIAM	Pan 13005	ND
Short	Mozambique/IIAM	ICGV-SM 03530	ND

Note. ND: not determined

2. Phenotyping for Fresh Seed Dormancy

Assigning a phenotypic value to every individual of the population is critical to achieving a genetic gain in any breeding program; in other words, assuming the same selection intensity and population variance, the higher the heritability, the more important the genetic gain. However, because heritability is somewhat a matter of accuracy of the phenotyping approach, biases can sometimes be misleading. Phenotyping for seed dormancy can be done either by evaluating the *in situ* number of sprouts or weight and expressing it as a percentage of the total number or mass of harvested seeds or by performing an *in vitro* seed germination test (Faye et al., 2010;

Gautreau, 1984; Khalfaoui, 1991; Ndoye, 2001; Upadhyaya & Nigam, 1999) using fresh or cured seeds. Considering the above statements related to dormancy phenotyping, it seems necessary to highlight tips that can improve phenotyping and, subsequently, the selection of dormant cultivars. Firstly, one needs to make sure the seeds are fully mature. Due to its indeterminate nature of flowering, seed maturity level may vary from one pod to another for the same individual plant. A simple method for selecting mature seeds is the observation of the black coloration of the hull's internal parenchyma (Miller & Burns, 1971). This parenchyma turns brown to black when the pod is fully mature and white to yellow if the pod is immature. Secondly, as the seed coat and cotyledons and embryos have a role in imparting dormancy in groundnut (Nautiyal et al., 1994), care should be taken when shelling pods for the *in vitro* seed germination tests. Thirdly, two-seeded pods have deeper dormancy at their basal seed than at their apical seed (Ketring & Morgan, 1971). Therefore, it seems more relevant to use only apical seeds when phenotyping for fresh seed dormancy to harmonize sampling.

3. Genetic Improvement for Seed Dormancy

Various genetic studies were carried out to understand the inheritance of fresh seed dormancy in peanuts (Asibuo et al., 2008; Faye et al., 2010; Gautreau, 1984; Khalfaoui, 1991; Lin & Lin, 1971; Ndoye, 2001; Upadhyaya & Nigam, 1999). Some studies revealed that fresh seed dormancy is controlled by a dominant allele of a single gene (Asibuo et al., 2008; Faye et al., 2010; Upadhyaya & Nigam, 1999). In contrary, other studies (Khalfaoui, 1991; Ndoye, 2001) reported polygenic inheritance with epistasic effects. More recently, Vishwakarma et al. (2016) found that the trait is controlled by two recessive genes. These converses may be due to the different phenotyping methods and the nature of the crosses used by authors. Some crosses were intra-subspecific (Spanish × Spanish), while others were inter-subspecific (Spanish × Virginia). In most of the studies of seed dormancy genetics in groundnut, authors concluded that broad sense heritability was moderate to high (<0.50), indicating the involvement of both significant genetic and environmental factors (Faye et al., 2010; Khalfaoui, 1991; Ndoye, 2001). In addition, significant genotype × year effects were reported (Ndoye, 2001).

4. Toward the Identification of Molecular Markers Linked to Seed Dormancy in Groundnut

Vishwakarma et al. (2016) identified two major QTLs (qfsd-1 and qfsd-2) for fresh seed dormancy in the linkage groups A05 and B06, respectively. Using a recombinant inbred line (RIL) mapping population derived from a cross between Tifrunner (a dormant Runner type) and GT-C20 (a non-dormant Spanish type), Wang et al. (2022) identified two major seed dormancy QTLs on chromosome A04 and A05 with 43.2% and 51.6% of the phenotype variation explained, respectively. Besides, a candidate gene (Arahy.KB746A) coding and ethylene-responsive transcription factor was found very close to the QTL mapped on chromosome A05. Deploying the QTL-seq approach, Kumar et al. (2020) identified other key genomic regions and candidate genes for fresh seed dormancy on the B05 and A09 pseudomolecules. They developed a validated marker (GMFSD1) that can be used in MAS programs to improve seed dormancy in groundnut.

In our breeding program in Senegal, we developed two RILs populations for fresh seed dormancy. One of the RILs populations is derived from a cross between cv. Fleur 11 and cv. 73-30, while the other is derived from a cross between ICGV 96894 and cv. 73-30. We identified eight lines with deep dormancy, 3 RILs (C1P15-18-4, C1P24-1-1, C1P18-6-5, and C1P30-9-8) of the population Fleur 11 × 73-30, and 4 RILs (C3P11-8-2; C3PNI-1-3, C3P7-1-1, and C3P6-2-5) from the cross ICGV 96894 × 73-30 (Figure 1). Further analyses are ongoing for the mapping of seed dormancy QTLs in these two populations.

Figure 1

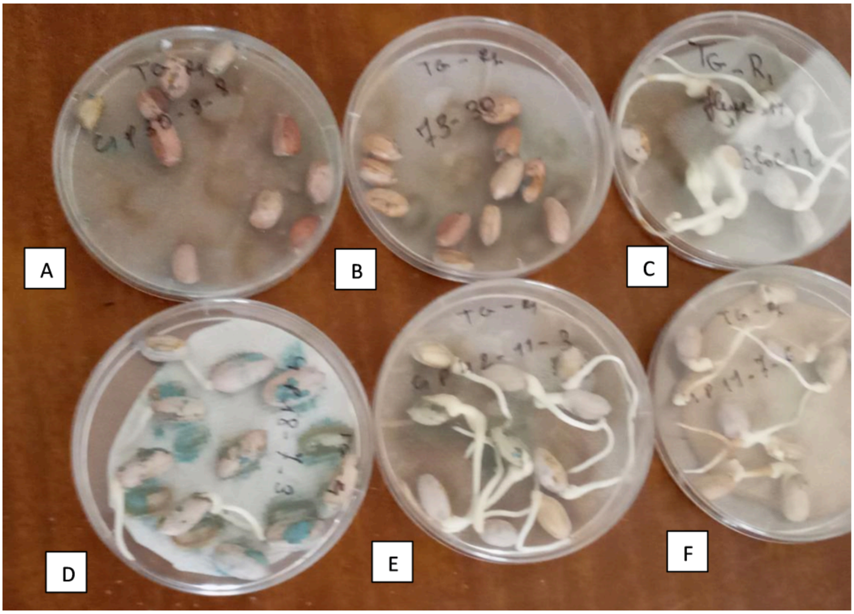

Figure 1 – Germination Test of Fresh Seeds of Recombinant Inbred Lines Along with the Parental Lines

Note. (A): C1P30-9-8, a line with deep fresh seed dormancy; (B): cv 73-30, the dormant parental line; (C): cv Fleur 11, the non-dormant parental line; (D), (E) and (F) are non-dormant recombinant inbred lines.

Conclusion

In Senegal, the groundnut breeding program was established in the early 20th century. Among its great achievements is the development and registration of very early-maturing varieties (75–80 days), among which cv. 55-33 and GC-8-35 are widely cultivated in the Northern region of Senegal where the rainfall is particularly low and the rainy season is very short (less than three months). Similarly, a clear shortening of the rainy season in the southern region of the Groundnut Basin has led to the release of Spanish varieties maturing 90-days after planting, among which is «Taaru», a variety with 2-3 weeks post maturity fresh seed dormancy. Other short-duration varieties with bigger grain sizes than previous varieties were developed

(Raw Gadu, Rafet Kaar, Yaakar, Tosset, Jaambar, and Kom Kom) using wild introgressions from the synthetic (*Arachis duranensis* × *Arachis ipaënsis*). As wild-related species have been proven effective in improving groundnut productivity under harsh conditions such as drought and diseases, new crosses, including other wild-related species, have been initiated to develop advanced backcross populations. Beyond the long-term objective of releasing new varieties, those populations could be useful in deciphering physiological and genetic traits related to drought tolerance in groundnut. On another hand, breeding for short-duration varieties with fresh seed dormancy is necessary to facilitate farmers' wide adoption of these varieties. Therefore, it is critical to consider fresh seed dormancy as a key selection trait, particularly when breeding groundnut for Sahelian and Sudano-Sahelian zones. With the fast development of high throughput phenotyping platforms and the availability of groundnut genomic resources, significant progress could be achieved toward higher genetic gains for all the traits contributing to yield and seed quality in groundnut under marginal environments.

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Book Abstract

This book focuses on three important elements in the development of cereal and legume crops in semi-arid West Africa. The first section illustrates the socioeconomic factors that affect the food system for these crops and contains an overview of crop production and consumption in the region. Then, important inputs that affect system productivity are presented: preferences for new seed varieties, yield response to fertilizer, counterfeit herbicides, climate information, and the way farmers develop expectations about the weather events that shape cropping outcomes. The final chapter of section one is dedicated to understanding urban consumer preferences for processed food products derived from pearl millet.

The second section addresses the state of the art of phenotyping and the modeling of crop adaptation to dryland farming systems. Chapters in section two focus on the regional network for phenotyping, high throughput phenotyping in field situations, root architectures, and crop ideotypes. In addition, empirical evidence is presented on root and soil interactions and the effectiveness of unmanned aerial vehicles (UAVs to assess sorghum physiology.

Finally, the third section investigates the genetic diversity and improvement of dryland crops. Chapters in this section focus on biodiversity and agricultural system sustainability, orphan crops such as fonio, and the utilization of a regional germplasm collection in the improvement of cowpea, groundnut, pearl millet, and sorghum.