Stirring up sorghum hybrid breeding targeting West African smallholder farmers' low input environments

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General introduction

West African (WA) population is rapidly increasing, with an improvement of health care practices and health research, policies and technologies (Aidam and Sombié, 2016; Defor et al., 2017), having a huge positive impact on child survival and life expectancy. Despite the relatively low gross domestic product (GDP) of WA countries (The World Bank Group, 2018), WA population, estimated to 306 million in 2010, is expected to reach 550 to 700 million in 2050 (Courtin and Guengant, 2011). Paradoxically, much of the population growth occurs in the less suitable zones for rapid economic development (Bloom and Sachs, 1998). Those regions are the rural, landlocked, and arid areas, where people rely on the primary sector. Food supply and income in these rural areas depend strongly on the local production, and mostly on farmers' field production. Root and tuber crops and cereals constitute the main agricultural production (FAOSTAT, 2018) and play an essential role in the diet of WA population. The hunger indices are moderate to serious in WA (Lobell et al., 2008; Roser and Ritchie, 2018) and six out of fourteen WA countries have experienced slight to dramatic increases in hunger between 1990 and the early 2000 (International Food Policy Research Institute, 2004). Further, in the scenario in which 68% of the population will be living in cities in 2050 (Courtin and Guengant, 2011), they would still need a sustained food supply from rural areas (ECOWAS, 2008). In low- and middle-income countries, WA included, more land are being cultivated (The World Bank Group, 2018) with generally no or little improvement of the cropping system. Yields on farmers' fields are low due to basic cultural systems, combined with low structural soil fertility in some areas and fluctuating climatic conditions. Drought episodes are foreseen to last longer, to be more frequent and more severe than experienced over the past century (Shanahan et al., 2009). Such drought will likely affect national revenues and restrain the already modest capability of low GDP countries to acquire grain on the global market (Brown and Funk, 2008). Median temperatures in WA are expected to increase (with a maximum prediction of about 1.5°C) in 2030, and probabilistic projections of production impacts show that sorghum and pearl millet yields will be less affected by climate change, as compared to rice and maize (Lobell et al., 2008). Thus, climate change resilient crops, along with efficient cropping systems, will have a key role to play in ensuring smallholder farmers food security and cash income for a sustainable rural development. Effort must therefore be put into providing resource-limited farmers with such resilient cultivars that can sustainably perform well in their erratic cultivation conditions, while possessing desired food properties.

Sorghum in West Africa

Sorghum bicolor (L.) Moench is a self-pollinated diploid (2n=2x=20) drought-tolerant grass. It is the fifth most important cereal worldwide, in terms of production, and the third most important in WA as in 2016 (FAOSTAT, 2018). Sorghum is a multi-purpose cereal, mainly used for human consumption, feeding livestock, production of alcoholic and other malted beverages, sugar, biofuels, fencing, roofing, and cash income in some areas. It is a major staple cereal crop in the Sahelian and savannah zones of WA where it constitutes the main cereal in the diet of millions, mostly living in rural areas (National Academy of Sciences, 1996). This C_4 grass is typically grown with minimal manufactured inputs, generally in environments where water availability and soil conditions do not allow the cultivation of rice or maize (Fusiller, 1994; National Academy of Sciences, 1996; Blum, 2004; Reynolds et al., 2015), or in certain sandy soils where pests or diseases preclude pearl millet cultivation (Weltzien et al., 2018). From 1960 to the early 2000s, sorghum production in WA varied from 13 to 20% as related to the global sorghum production (from 5.37 of 40.93 million tons to 11.15 of 53.44 million tons), and the harvested area varied similarly from 15 to 31% (from 7.15 of 46.00 million ha to 12.65 of 41.33 million ha) (FAOSTAT, 2018). Low production progress relative to harvested area reflects to some extent the stagnation of sorghum yields on farmers' fields, averaging only one t ha^{-1} since decades. Nigeria, Niger, Burkina Faso and Mali are the top WA sorghum producers, averaging over 90% of total WA production as in 2016 (FAOSTAT, 2018).

Based on their panicle and spikelet morphology, cultivated sorghums are classified into five botanical (i.e. Bicolor, Caudatum, Durra, Guinea and Kafir) and ten stable intermediate races (Harlan and de Wet, 1972). The Guinea race was domesticated in West and Central Africa (WCA) (Dahlberg, 2000) and is predominantly cultivated across WA (de Wet and Huckabay, 1967; Barro-Kondombo et al., 2008), from Senegal to the western border of Nigeria. It has the broadest geographical distribution (Harlan and de Wet, 1972; de Wet et al., 1972) and the greatest genetic diversity of the major sorghum races (Menkir et al., 1997; Folkertsma et al., 2005; Bhosale et al., 2011; Kitavi et al., 2014; Cuevas et al., 2018).

Sorghum local value chains in West Africa

WA agricultural sector possesses an important potential, and is a source of economic growth accounting for around 35% of the regional GDP (Blein et al., 2008; FAO et al., 2015). Regional cereal product flows (not considering transits of imported products) in WA mainly concern pearl millet and sorghum, and Mali and Nigeria remain the largest suppliers (Soulé, 2011; Gourichon, 2013; FAO et al., 2015). Sorghum local or primary transformation mainly consists of fermentation, preparation of pre-cooked and enriched couscous, ready-to-use flour, and industrial production of livestock feed and nutritious fortified foods (David-Benz et al., 2005; Alabi, 2008; Gourichon, 2013; Feed the Future Innovation Lab for Collaborative Research on Sorghum and Millet, 2018). Different projects and Non-governmental organizations (NGO) are providing support to local processing companies (David-Benz et al., 2005; Havard and Side, 2016; Feed the Future Innovation Lab for Collaborative Research on Sorghum and Millet, 2018). Yet, this potential is still largely untapped and well-structured value chains are in an establishment stage. Moreover, sorghum low yields, its position as a staple crop, presence of counterfeit products (Staatz et al., 2011; Macauley and Tabo, 2015; Theriault et al., 2018), and the lack of adequate infrastructure and transportation system (Porter, 2002; Dorosh et al., 2010; FAO et al., 2015) make challenging a sustainable value chain development through exploitable and marketable surpluses. There is a difference between WA countries in terms of value chain creation. In Nigeria, Ghana and Sierra Leonne to some extent, sorghum value chains are relatively more developed than in other countries. There was an improvement in local policies (Macauley and Tabo, 2015) and a development of an industrial- or transformation- sector that, in some cases, provides farmers with seeds (Weltzien et al., 2018) and buys all or part of small-scale farmers' and outgrowers' production for beer processing (EUCORD, 2008; Gourichon, 2013). In Mali, farmer associations (e.g. Union Locale des Producteurs de Céréales, ULPC) play a key role by buying the surplus of production from farmer members and reselling it on the market in areas where the production is not sufficient. A local seed value chain is sustained by those farmer associations trained in multiplying variety seeds or in producing hybrid seeds from the parental material (Weltzien et al., 2006, 2018). This system ensures farmers the possibility to purchase reliable seeds (Siart et al., 2008; Smale et al., 2014) of familiar cultivars and to market their surplus of production in a trustworthy environment. They are therefore not directly involved in the large-scale trade that can be disadvantageous with the presence of many intermediaries or operators (FAO, 2013), and the unstable market prices (Brown et al., 2009).

Sorghum in WA smallholder farmers' fields

In the Sahelian and Savannah zones of WA, sorghum is mainly cultivated during the rainy season, between the 500 and 1300 mm rainfall isohyets. Sorghum production areas are primarily characterized by low precipitations (Le Barbé et al., 2002; Weltzien et al., 2018), with temporary shortages or surpluses of rainfall throughout the cultivation period (Le Barbé and Lebel, 1997; Tarhule and Woo, 1998; Shinoda et al., 1999; Sanogo et al., 2015). Mechanization level is still low (Soule, 2013; Macauley and Tabo, 2015) due to the reluctant efforts- followed lately by a disengagement- of local governments, and despite the involvement of the private sector in locally assembling tractors and agricultural equipment (Fonteh, 2010). Apart from few regions where efforts were put in developing mechanization at farmer level (Blein et al., 2008; Kansanga, 2017), farmers essentially use animal traction and human force to achieve most of their field work (Havard et al., 2004; Vall et al., 2004; Havard and Side, 2016). This consists mainly in the soil preparation before sowing, removal of weed, mounding and the transportation of field production (Havard et al., 2004). Mechanization is not used for harvesting sorghum and generally in none of the post-harvest processes at the smallholder farmer's field level.

Sorghum is sowed after the first effective precipitation, which usually occurs between June and July. Photoperiod sensitive varieties are widely used (Grenier et al., 2001), as flowering time occurs at a rather fixed date regardless of the high variability in sowing dates due to the unpredictable onset of rainfalls. Farmers typically use seeds from their own production of the previous season and, occasionally, seeds from other trusted farmers of their own village or other villages, projects, and markets (Yapi et al., 2000; Blein et al., 2008; Siart et al., 2008; Weltzien et al., 2018). Traditional variety seeds and varieties improved from local material are extensively preferred over introduced ones, essentially because of their good grain quality characteristics, their adaptation to farmers' diverse cultural conditions, with low or inexistent fertilizer application (Curtis, 1968; Yapi et al., 2000). There is consequently a broad range of landrace (Zeven, 1998) varieties, which allow farmers in different areas to attain a minimum yield for subsistence periods despite the several biotic and abiotic constraints to sorghum cultivation.

Sorghum cultivation in WA faces many biotic (pests, diseases and weeds) stresses leading to reduced yields or to the complete failure of the crop (ICRISAT, 1980; Forbes et al., 1992; Ajayi and Ratnadass, 1998; Ratnadass et al., 2003; Guo et al., 2011; Reynolds et al., 2015). Sorghum midge (*Stenodiplosis sorghicola*) is one the most important sorghum pests in WA causing over 30% of yield losses (Harris, 1961; Bowden, 1965; Nwanze, 1988; Thiam et al., 2018). Leaf anthracnose (*Colletotrichum graminicola*) and grain mold are of the most important WA sorghum diseases. Anthracnose causes up to 67% of grain yield loss (Thomas et al., 1995), while grain mold reduces yields from 30 to 100%, depending on the cultivar under consideration, flowering time and weather conditions (Forbes et al., 1992; Néya and Le Normand, 1998; Singh and Bandyopadhyay, 2000; Ratnadass et al., 2003). *Striga hermonthica* is the most widespread parasitic weed, causing severe yield reduction and great economic losses in African cereal fields (Ramaiah, 1983; Musselman et al., 1991; Sauerborn, 1991). Depending on the species, the variety infected and the degree of infection, Striga damage can vary from a small drop to severe losses in yields (Doggett, 1965; Kim et al., 1994). The presence of Striga is usually associated with high cultural intensity, precarious environments and low soil fertility.

Soils fertility levels are low in most WA sorghum growing areas where continuous cropping on arable soils and poor soil management are combined to the already low structural soil-fertility (Jones, 1973; Kang, 1986). There is a negative soil nutrient balance in Africa (Stoorvogel and Smaling, 1990; Reynolds et al., 2015) and losses in nitrogen (N), phosphorus (P) and potassium

(K) are (6, 2 and 15% respectively) larger than annual fertilizer input (Sanchez et al., 1997). This, along with low manure (Cleaver and Schreiber, 1994; Williams, 1999) and mineral fertilizer (Theriault et al., 2015, 2018) application, and inadequate management of residues after harvesting (Bationo and Mokwunye, 1991), contributes to the ever-decreasing soil fertility levels. N and P deficiency and aluminum (Al) toxicity are the main soil constraints in the arable soils of semi-arid to arid savannah zones of WA (Penning de Vries and Djitèye, 1982; Mokwunye and Vlek, 1986; Doumbia et al., 1993, 1998; Leiser, 2014). P deficiency is the most serious sorghum growth limiting factors in WA (Pichot and Roche, 1972; Doumbia et al., 1993). In Malian sorghum farmers' fields for instance, Leiser et al. (2012) reported a mean and a median plant-extractable P level of 7.4 and 5.5 mg[P]/kg soil Bray 1-P, respectively (n= 207). These low-P (LP) levels are far below the 11.6 mg [P]/kg soil threshold for sorghum cultivation (Doumbia et al., 1993), reflecting the significance of P limitation for WA sorghum farmers. Sorghum in P deficient soils experiences mostly reduced plant height, delayed flowering, and reduced stover and grain yields as compared to high-P (HP) soils (Doumbia et al., 1993, 1998; Sahrawat, 1999; Bayu et al., 2002; Camacho et al., 2002; Leiser et al., 2012b).

Options for management of biotic and abiotic constraints to sorghum production have been documented (Bandyopadhyay et al., 2000; Haussmann et al., 2000a, 2012; Marley et al., 2005; Joel et al., 2007; Erpelding, 2008, 2012; Farooq et al., 2009; Prom et al., 2014; Thompson et al., 2017; Feed the Future Innovation Lab for Collaborative Research on Sorghum and Millet, 2018). Options for overcoming P deficiency, a major sorghum growth-limiting factor in WA, had been exhaustively documented (Leiser, 2014; Gemenet et al., 2016; Weltzien et al., 2018). From the plant breeding standpoint, genetic enhancement for better-adapted genotypes to LP soils, using the tremendous genetic diversity present in WA sorghum germplasm, can be a sustainable option for boosting grain yield on farmers' fields (Leiser et al., 2014b; Macauley and Tabo, 2015; Gemenet et al., 2016; Weltzien et al., 2018). Taking advantage of the benefits of heterosis (Gowen, 1952; CIMMYT, 1997; Lippman and Zamir, 2007), hybrids bear the potential of being a suitable option for a sustainable improvement of sorghum yields under farmers' cultivation conditions (Haussmann et al., 2012). Sorghum hybrids have shown potential to outyield their parents and local varieties in diverse limiting conditions in Eastern Africa (Blum et al., 1992; Haussmann et al., 1997, 1998, 1999, 2000b), and were explored in WA in the early 1970s (Andrews, 1975). Heterosis levels of Guinea-race based hybrids was reported in the early 1990s (Touré et al., 1996). Hybrid crosses of Malian landraces with introduced Caudatum-race seed parents showed good heterosis for grain yield (Toure and Scheuring, 1982). However, no hybrids were released or commercialized, a major challenge with these initial hybrids being their poor and unacceptable grain quality, despite their relatively high grain yield.

Sorghum improvement and research at ICRISAT

Initial work

An overview of the initial sorghum and pearl millet breeding by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT)-Mali was reported by Yapi et al. (2000). Sorghum breeding in ICRISAT was, in an initial phase, focused on grain yield improvement using the local germplasm. This process consisted mainly in purifying local varieties, and resulted thus in a series of locally adapted varieties (*generation 1*) possessing acceptable grain quality and yield, with a wide adaptation to harsh farming conditions. Further, exotic material was introduced and used in breeding programs for crossing and introgression, leading to the *generation 2* material. This material was selected based on diverse traits considered important for an intensification in stress prone areas, e.g. short duration, drought tolerance, emergence in high soil temperature, high yield, disease and pest resistance, wide adaptation, and also improved quality (Yapi et al., 2000; Atokple, 2003). Population improvement targeting such traits was undertaken through on-station mass, recurrent or family-based selection (Rattunde et al., 1997; Atokple, 2003). Guinea, Caudatum and Guinea × Caudatum populations were developed in Mali, resulting in improvement of yields. At the farmer level, adoption rates of *generation 1* Guinea-race material were higher than those of *generation 2*. Choice for adoption was not essentially based on grain yield advantage, but rather on the grain quality and the early maturity (ability to cope with short rainy seasons) of varieties improved from local material (Yapi et al., 2000; Weltzien et al., 2006). The photoperiod sensitive tall cultivar Tieble (CSM335), developed from the Malian collection, is widely cultivated by farmers for its yield stability and good grain quality. It is also used as a local check variety in various ICRISAT field studies.

Participatory breeding and variety selection

A lesson learnt with these first released cultivars was the negative effects of not including farmers in the breeding and selection process. Although, farmers are the growers and in most cases the end users, they were only consulted for final adoption purposes. Their criteria for adopting new material in their unpredictable environments are not only based on grain yield but are rather complex. It was therefore important to ICRISAT sorghum breeders to include farmers' appreciation in all steps of the breeding program and to consider farmers' diverse and low-input cultural conditions while drawing their breeding strategies (Weltzien et al., 2006, 2008a). Farmers reinforce research by providing key information based on their knowledge and experiences, contributing with genetic materials, conducting trials, and selecting and evaluating new germplasm (Weltzien et al., 2001). Zone-specific sorghum populations with a broad genetic base were created and selection was made based on panicle and grain traits that are important to farmers, e.g. photoperiod sensitivity, large grain size, high number of grains and midge resistance. From on-farm trials conducted between 2003 and 2004, new varieties showed superior grain yields as compared to the farmers' control varieties, and acceptable farmer preference scoring (Weltzien et al., 2006). Lata, a variety with farmers preferred traits (development cycle, appropriate height, and grain yield and quality) was developed from random-mating Guinea populations, and identified with farmers from the participatory approach. Further, Lata is the male parent of most popular hybrids in WA. Participatory breeding and variety selection was therefore a good option for overcoming low yields and low adoption rates of purely breeder-selected cultivars in Mali while maintaining diversity and grain quality.

Simultaneously, ICRISAT insisted in strengthening the relations with small-scale farmers and their associations for a better characterization of their different environments. There is an opportunity for breeding and testing new material with farmers (Rattunde et al., 2016). Research has established fruitful relations with them, and has a better understanding of farmer preferences and their diverse socio economic environments (Diallo et al., 2018). Spatial adjustment methods provide the possibility to exploit most information from on-farm trials that are known to be highly heterogeneous (Leiser et al., 2012a). Further, farmer associations work closely with the ICRISAT breeding program and they have been trained in seed multiplication and hybrid seed production. Fertilizer supply chain (Theriault et al., 2015), seed system (Weltzien et al., 2018; Smale et al., 2018) and the first impacts of participatory breeding and farmer's adoption criteria (Smale et al., 2014, 2018; Theriault et al., 2015; Diallo et al., 2018), were documented and options for their improvement, if applicable, were suggested. Further, research focused in resistance or tolerance to- and management of- biotic stresses such as Striga and abiotic stresses with a focus on drought and P deficiency (Haussmann et al., 2012; Leiser, 2014; Gemenet et al., 2016; Weltzien et al., 2018). To diversify the existing breeding populations, backcross nested association mapping (BCNAM) populations were developed using Lata as the recurrent parent and 13 donors selected for various traits (e.g. Striga or midge resistance) and originating from several WA countries. This resulted in the development of 1083 BC_1F_4 male lines that provided a large basis for hybrid breeding and testing in WA. Efforts made by ICRISAT and its partners with farmers and farmer associations through participatory selection, seed system development and better characterization of social realities (Weltzien et al., 2006, 2018; Diallo et al., 2018) indicated the possibility of producing hybrids to exploit heterosis in the WA context.

Hybrids for WA agro ecologies

Experimental hybrids in on-farm famer-managed yield trials

Efforts by ICRISAT and the Institut d'Economie Rurale (IER-Mali) to create cytoplasmic male sterile seed parents based on WA Guinea-race germplasm enabled production of the first guinea-race based hybrids, with both parents having Guinea-race background. Based on grain yield and plant height data from trials in 2007 and 2008, eight short and seven tall statured sorghum hybrids, out of a set of 55 hybrids, were identified for on-farm farmer-managed participatory testing between 2009 and 2011. The shorter hybrids have shown satisfactory grain quality, and up to 37% yield advantages over Tieble, under contrasting productivity conditions (Rattunde et al., 2013). Further, farmers are adopting these newly developed hybrids (Smale et al., 2014, 2018) and the adoption rates increase yearly. These positive advances attained by ICRISAT and its partners justified establishing a long-term hybrid-breeding pipeline to produce hybrids that meet farmers' demands in this major sorghum-producing zone. New hybrids should hence be selected based on their adaptation to farmers' LP soils and their grain quality properties.

Challenges and steps forward

Tall hybrids in on-farm yield trials

Hybrids are expected to have, in addition to higher yields, farmer-preferred characteristics, such as taller height, lax panicles, and high grain quality. As already documented, low input conditions, specifically P deficiency, can reduce plant height by a meter as compared to plant height in HP conditions (Leiser et al., 2015). Although short hybrids attained acceptable grain yield and quality, their plant height in LP may expose them to transhumant animal grazing at maturity. Information from high statured experimental hybrid data (see above section) would give an insight in how advantageous such hybrids are to smallholder farmers, in comparison with the short hybrid set and the local check Tieble. Further, essential to any long-term breeding program, selection strategies for hybrid breeding targeting low input conditions of WA have not been yet documented. To achieve such strategies, expected to improve sorghum performance in WA farmers' low input environments, there is need for a better understanding of the quantitative genetics underlying the inheritance of important traits, and parental and hybrid value in a specific environment.

Heterosis and combining ability of new material

Efforts are underway to create new seed parents and identify other restorer lines to diversify the female and the male parental pools beyond the limited initial A/B pairs and restorer lines, and thereby sustain hybrid breeding and exploit heterosis with more distinct and better combining parents. However to date, no combining ability analysis or estimates of heterosis are available with these Guinea-race materials to help guide the breeding efforts. Both additive and non-additive gene actions control the inheritance of grain yield in WA sorghum studies (Kenga et al., 2004; Akata et al., 2017) with larger general combining ability (GCA) variance for male parents. Nevertheless, differences between traits and the experienced stress level during the cropping cycle influence the relationship between *per se* and hybrid performance (Chaubey et al., 1994; Betrán et al., 2003). Combining ability patterns and heterosis estimates obtained under LP conditions would ease the identification of superior parents and hybrids under such conditions, and the description of gene effect patterns involved in different traits of interest in different P levels, providing overall information on how to select parental lines to obtain the most promising hybrids. Breeding programs could also be strengthened by deeper insights on how accurately we can predict hybrid performance based only on parental per se performance in LP and in HP, and how effective a hybrid indirect selection in HP- vs direct selection in LP-conditions would be.

Molecular markers and fertility restoration in WA

Many quantitative trait loci (QTL) and diversity studies have been conducted by ICRISAT and several research institutions and projects working in WA (Haussmann et al., 2004; Deu et al., 2005; Bhosale et al., 2012; Leiser et al., 2014a; Bouchet et al., 2017; Feed the Future Innovation Lab for Collaborative Research on Sorghum and Millet, 2018; Olatoye et al., 2018). Most studies targeted important traits such as Striga resistance, insect and disease resistance, adaptive traits, photoperiod sensitivity and drought tolerance or genetic diversity, germplasm characterization, etc. Nevertheless, there is no wide, routine and effective use of such QTL or derived markers in marker-assisted breeding programs.

Intensive hybrid breeding and seed production in many crop species became possible with the identification and characterization of a stable and heritable cytoplasmic male sterility (CMS) mechanism. CMS is a maternally inherited defect where, as the result of specific nuclear and mitochondrial interactions, plants fail to produce functional pollen, or to ensure normal anther dehiscence, without affecting the female fertility (Duvick, 1959; Laughnan and Gabay-Laughnan, 1983; Hanson and Conde, 1985; Levings and Brown, 1989). A CMS system depends on a set of male-sterility-causing cytoplasms and dominant or recessive alleles in the nuclear genome, which either restore the fertility or maintain the sterility (Maunder and Pickett, 1959; Rooney and Wayne Smith, 2000). Fertility is restored in the progenies when a cytoplasmic male-sterile female is crossed with a male carrying the corresponding nuclear-encoded genes (restorer of fertility, *Rf*) that partially or completely restore the fertility. To date, a detailed genetic study of fertility restoration in West African Guinea-race germplasm has not been accomplished, with prior studies focusing on Australian, Indian and US breeding materials (Klein et al., 2001, 2005, Jordan et al., 2010, 2011, Praveen et al., 2015, 2018). A good understanding of the restoration and maintenance capacity of WA germplasm is essential for a long-term WA hybrid-breeding program. Use of cost-effective molecular markers for fertility restoration based on WA germplasm will fasten the identification of potential maintainer and restorer lines in WA breeding material.

Objectives of the study

The overall goal of this study is to set the basis of a long-term hybrid-breeding program targeting small-scale farmers' low input environments of WA. Specific objectives are to:

- Determine the yield advantage, if any, of tall photoperiod sensitive sorghum hybrids relative to farmers' adapted landrace varieties under a range of Malian farmers' production conditions;
- Understand genetics underlying the pollen fertility restoration in key WA hybrid parents;

- Develop diagnostic and cost-efficient molecular markers for fertility restoration that can be used in WA hybrid breeding programs and
- Estimate sorghum quantitative-genetic parameters to guide hybrid breeding targeting farmers' low input environments.

Chapter 1

Can tall Guinea-race sorghum hybrids deliver yield advantage to smallholder farmers in West and Central Africa?

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Abstract

Many farmers in West and Central Africa (WCA) prefer tall (>3 m) grain sorghum [Sorghum bicolor (L.) Moench] for various reasons. This study seeks to determine (i) what yield superiority newly bred, tall, photoperiod-sensitive Guinea race sorghum hybrids can provide relative to an adapted landrace variety across a wide range of productivity conditions, and (ii) the risk of these hybrids failing to provide yield superiority for individual farmers. Seven hybrids, one local check, and eight pure-line progenies were evaluated in 37 farmer-managed, on-farm yield trials across three Malian zones and 3 yr. Environments were classified into four productivity groups (low [78–110 g m^{-2}], mid-low [110–150 g m^{-2}], mid-high [150–200 g m^{-2}] and high [200–265 g m^{-2}]) based on their trial mean grain yield. Mean yields of the seven tall hybrids were 3 to 17% (ranging from 6 to 28 g m^{-2}) higher than that of the local check across all environments and were highest (14–47%) averaged across the seven trials with the lowest mean yields. The individual overall highest-yielding hybrid showed superiorities over the local check in the low, mid-low, mid-high, and high productivity levels of 43 (47%), 14 (10%), 47 (27%),and 34 (14%) g m^{-2}, respectively. The tall hybrids rarely had yields significantly inferior to the local check. Farmers' preference for, and the possible benefits of, taller plant types may lead farmers to grow tall hybrids, particularly under the typical low-productivity production conditions of WCA.

Abbreviations

AMMI, additive main effect and multiplicative interaction; EM, expectation maximization; GEI, genotype-by environment interaction; ICRISAT, International Crops Research Institute for the Semi-Arid Tropics; IER, Institut d'Economie Rurale; IPC, interaction principal component; Kp, photoperiod sensitivity index; PLEC, pure-line experimental cultivars; WCA, West and Central Africa.

Chapter 2

QTL mapping and validation of fertility restoration in West African sorghum A_1 cytoplasm and identification of a potential causative mutation for Rf_2

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Abstract

Key message

Major A_1 cytoplasm fertility-restoration loci, *Rf_2* and *Rf_5*, were found in the West African sorghum. A potential causative mutation for *Rf_2* was identified. KASP markers were validated on independent material.

Abstract

To accelerate the identification and development of hybrid parental lines in West African (WA) sorghum, this study aimed to understand the genetics underlying the fertility restoration (Rf) in WA A_1 cytoplasmic male sterility system and to develop markers for a routine use in WA breeding programs. We genotyped by sequencing three F_2 populations to map the Rf quantitative trait loci (QTL), validated the molecular KASP markers developed from those QTL in two $F_{2:3}$ populations, and assessed the most promising markers on a set of 95 R- and B-lines from WA breeding programs. Seven QTL were found across the three F_2 populations. On chromosome SBI-05, we found a major fertility restorer locus (*Rf_5*) for two populations with the same male parent, explaining 19 and 14% of the phenotypic variation in either population. Minor QTL were detected in these two populations on chromosomes SBI-02, SBI-03, SBI-04 and SBI-10. In the third population, we identified one major fertility restorer locus on chromosome SBI-02, *Rf_2*, explaining 31% of the phenotypic variation. Pentatricopeptide repeat genes in the *Rf_2* QTL region were sequenced, and we detected in Sobic.002G057050 a missense mutation in the first exon, explaining 81% of the phenotypic variation in a $F_{2:3}$ population and clearly separating B- from R-lines. The KASP marker developed from this mutation stands as a promising tool for routine use in WA breeding programs.

Abbreviations

GBS, Genotyping by sequencing; ICRISAT, International Crops Research Institute for the Semi-Arid Tropics; IER, Institut d'Economie Rurale; KASP, Kompetitive allele-specific polymerase chain reaction; ORF, Open reading frame; PCR, Polymerase chain reaction; PPR, Pentatricopeptide repeat; QTL, Quantitative trait loci; Rf, Fertility restoration locus/gene; SNP, Single nucleotide polymorphism; WA, West Africa.

Chapter 3

Sorghum hybrids for low-input farming systems in West Africa: quantitative-genetic parameters to guide hybrid breeding

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Abstract

The development of sorghum [*Sorghum bicolor* (L.) Moench] hybrids with Guinea-race parents is a promising approach to increase yields in West Africa (WA). There is heretofore no quantitative genetic information about the genetic value of new hybrids and their parents, or about the efficiency of alternative selection methods for targeting yield performance under the predominantly low-input, P-deficient production conditions. This study aims to estimate the heterosis levels attainable by new Guinea-race hybrids and the combining abilities of the current suite of parents with partial- to full-Guinea-race backgrounds of contrasting geographic origins, and to determine the effectiveness of direct selection under low-P (LP) relative to indirect selection under high-P (HP) conditions. Single-cross hybrids were evaluated in 2015 and 2016 for yield under both LP and HP conditions at two locations in Mali. The hybrid yields were substantially superior to farmers' local Guinea-race varieties, with 20 to 80% higher means in both LP and HP environments. Average midparent and better-parent heterosis estimates were, respectively, 78 and 48% under HP, and 75 and 42% under LP. Direct selection for yield under LP was predicted to be 20 to 60% more effective than indirect selection under HP conditions. The combining ability estimates provided initial insights into the potential benefit of germplasm from more eastern and humid regions of WA for developing a restorer pool distinct and complementary to the female pool from Mali and surrounding countries. Substantial yield superiorities of hybrids over local varieties suggested that a hybrid breeding strategy based on Guinea germplasm could help improve WA smallholder farmers' livelihood.

Abbreviations

BCG, backcross group; BLUP, Best linear unbiased predictor; GCA, general combining ability; GCV, genetic coefficient of variation; HP, high phosphorus; ICRISAT, International Crops Research Institute for the Semi-Arid Tropics; IER, Institut d'Economie Rurale; Kda, Kolombada; LP, low phosphorus; SCA, specific combining ability; WA, West Africa; WCA, West and Central Africa.

General discussion

Improvement of yields on small-scale farmers' fields is a necessity for improving rural livelihood, and providing food supply to an increasing population. Improved cultivars that possess farmers' preferred traits must be attained by research for a sustainable rural development. Sorghum hybrids present a huge potential for attaining such yield advantages in a climate change context, and breeding strategies for a long-term hybrid breeding are needed in WA. My thesis contributes to stir up the basis of such breeding pipeline targeting WA agro-ecologies, using a large set of breeding lines and hybrids in diverse cultural conditions.

Hybrids as an option for improving smallholder farmers' livelihood

Advances from experimental hybrids

From the progresses in Malian sorghum-hybrid development, Guinea-race based sorghum hybrid breeding stands a very promising strategy to contribute to the improvement of the livelihood of many smallholder farmers. Evaluation of short and tall experimental hybrids in on-farm farmer-managed trials confirmed the potential of experimental hybrids to attain significant yield superiorities over the locally adapted variety check (Tieble) under contrasting cultivation conditions in WA (Rattunde et al., 2013; Kante et al., 2017). Developed from the same Guinea-race male parent (Lata), Fadda and Pablo were the overall best yielding hybrids from the short and tall hybrid sets, respectively. Fadda showed a relatively constant superiority (~32%) over Tieble across productivity levels, as compared to Pablo (24, 27 and 14% of superiority in increasing productivity levels). These two hybrids, further identified by farmers during the on-farm evaluations due to their satisfactory yield and quality properties, are widely cultivated and the seed demand is increasing every year. Research no longer considers them as experimental hybrids, but rather as full part of the sorghum farming environment in Mali. This confirms the fact that Guinea race hybrids are a very suitable option for overcoming low yields in WA savannah agro-ecologies.

Furthermore, hybrids developed from new female and male lines from different racial and geographic background yielded more than Tieble, Pablo and Fadda under HP and LP conditions (Table 1; Kante et al., 2019), indicating the potential for a higher heterosis from the WA germplasm in low and improved cultural input conditions. Such heterosis levels over the better parents and over the local checks attained by these new experimental hybrids point to the effectiveness of introgressing Guinea landraces from different WA agro ecologies into the well-adapted Lata. On-farm trials were conducted in 2017, with hybrids from new parental sets in several Malian environments, and the preliminary results are very encouraging (Nébié et al., 2018). These hybrids exhibited 30 to 86% and 47 to 110% of gain over Fadda and Tieble, respectively in on-farm trials. Most hybrids had better preference score for combined plant architecture, grain aspect and panicle yield potential than Fadda and Tieble. Their adoption rates are expected to exceed those of already registered hybrids (Fadda and Pablo). These new hybrids bred from a wider WA Guinea race germplasm and already demonstrated to increase yields on farmers' field stand as game-changers for WA small-scale farmers. Such increase would contribute to food security and be a source of income with the commercialization of possible surpluses with relatively low additional input, relative to landrace cultivation. Theoretically, only the seed cost would be a required additional cost for farmers, and hybrids showed sufficient yield superiority to recover hybrid seed cost (Kante et al., 2017). Although there is confidence in the yield potential of developed hybrids, research will need to rely on a long-term strategy for hybrid production in order to avoid a chaotic hybrid development that would not be optimum for continuous genetic gain (Pfeiffer et al., 2018) and would jeopardize recent achievements.

Table 1: Number and percent of experimental hybrids (used in Kante et al. (2019)) with significant (α=0.05) yield superiority, and the % yield superiority of the best yielding hybrid per environment over the local check Tieble and two commercial hybrids, Pablo and Fadda, used in Malian sorghum production.

	Checks	Sko_HP	Sko_LP	Kda_HP	Kda_LP
Number (%) of hybrids significantly superior to	Pablo	33 (21)	24 (15)	0 (0)	66 (42)
	Fadda	51 (32)	66 (42)	11 (7)	10 (6)
	Tieble	43 (28)	142 (94)	85 (55)	83 (53)
% yield superiority best hybrid over	Pablo	43	55	4	82
	Fadda	49	81	41	46
	Tieble	48	169	69	96

Plant height and photoperiod sensitivity of new experimental hybrids

New experimental hybrids' plant height, which attained 2.5 m or more in LP environments, was comparable to local landrace plant height, thus offering the possibility to reach appropriate plant height for low production environments. Despite the yield advantage and the response of short- vs. tall-hybrids to different fertility levels (van Oosterom and Hammer, 2008; Rattunde et al., 2013; Kante et al., 2017), factors such as competitiveness with weeds (Traore et al., 2003) and the preference for- and possible benefit of- taller sorghum plant types may still lead farmers to grow tall Guinea-race sorghum hybrids. Tall Guinea-race sorghums, by attaining a minimal plant height under low input conditions, are supposedly less exposed to risks of transhumant cattle grazing and bird damage than short stature hybrids. However, their tall height and high yields make them more susceptible to stalk lodging as compared to pure lines (Haussmann et al., 1998), and therefore reduced yield and grain quality (Rajkumara, 1980). Thus, medium tall Guinea-race hybrids should be attained by breeders, as they would have required plant height, grain yield and quality, and most probably a higher harvest index, thus would still show a high adoption rate among farmers.

Photoperiod sensitivity, another important trait for sorghum adaptation to WA agro ecologies (Grenier et al., 2001; Clerget et al., 2008), enables flowering at a rather fixed calendar date for appropriate grain filling at the end of the rainy season despite highly variable sowing dates. Photoperiod-sensitive landraces of millet and sorghum showed seemingly stronger resilience to future climate conditions as compared to non-photoperiod sensitive ones (Sultan et al., 2013). Further, photoperiod sensitive hybrids are more likely to be adopted by farmers who mainly cultivate photoperiod sensitive landraces. A large portion of our experimental hybrids (Kante et al., 2019) are expected to be photoperiod sensitive since used parental materials (Lata or Fambe for instance) and first series of hybrids produced with these parents possess photoperiod sensitivity similar to that of Guinea-landrace varieties (Rattunde et al., 2013; Kante et al., 2017). Even though some new hybrids have shown photoperiod sensitivity in P-managed trials (Kante et al., 2019), assessing the photoperiod sensitivity level of future hybrids and/or hybrid parental lines is required.

Genotypes by environment interactions

Sorghum in WA is cultivated in a wide range of environments, with differences in rainfall, cultural intensity, soil fertility among other factors that make the cultivation conditions very heterogeneous among farmers in different areas. It is necessary, if not compulsory, for a plant-breeding program to understand the interactions between the genetic structure of promising material and the environments where this material will be cultivated. The significant GxE interaction (GEI) variances for grain yield and crossovers between different (both tall and short) hybrids were found in reaction norms across contrasting environments in Mali (Rattunde et al., 2013; Kante et al., 2017). These interactions, attributed to interactions at the individual farmer-field level, indicated different reactions (changes in genotype ranking) of hybrids in individual farmers' field and different productivity environments. Large GxE interactions were likewise generally found in on-farm trials in Malian agro ecologies (Rattunde et al., 2016) and in three way interaction from trials over several years and locations (Leiser et al., 2012b). Consequently, there is a priori no need to examine hybrid performances within specific mega-environments as, referring to grain yield, there is no one-fits-all hybrid. Further, the <1 GCA/SCA ratio found in Kante et al. (2019) in LP environments confirm the point that specific hybrid combinations will be needed in specific environments to attain substantial yield increase in farmers' fields. Evaluation of newly developed hybrids will have to be completed in environments where those hybrids are destined to be cultivated.

The term GEI was so far referred to as the interaction of genotypes with a unique field trial in a specific year. Productivity conditions are the sum of different predictable and unpredictable factors (Allard and Bradshaw, 1964) such as the physical environment (weather conditions, soil properties, biotic and abiotic pressures…), the crop management, and the socio-economic context. Additionally to the structural fertility differences in their sorghum fields, WA farmers use different levels of manure and mineral fertilizer, which contributes to the large differences in soils fertility in WA sorghum cropping environments and consequently differences in genotype reactions. Further, as already documented, sorghum is produced in a relatively wide range of rainfall and drought episodes that are neither occurring nor endured the same way in different production zones. Therefore, the cultivation conditions across years is very unpredictable. In these conditions, hybrids that can attain acceptable yields in low- as well as in high- productivity environments would be ideal. Characterization of cropping environments along with new and future hybrid-yield stability needs a special focus in all breeding programs. At the same grain quality level, farmers would need specific hybrids improved to attain a higher production in their very unpredictable environments (Allard and Bradshaw, 1964). These dynamically stable (Becker and Leon, 1988) hybrids will still need to be evaluated in target environments for farmers to select the best hybrids for their specific environments. It would be therefore interesting to examine hybrid performance for different management conditions for research to provide the best-adapted hybrids for a specific context.

No rainfall change was predicted to counterbalance the negative effects of temperature rise (above +2°C) on sorghum and pearl millet in WA (Sultan et al., 2013). More than providing hybrids adapted to the current cultivation conditions, and given the time needed to develop and release a noteworthy hybrid in a hybrid-breeding program, it would be valuable that research focuses specially on the future environmental and socio economic challenges, and include future changes in the cropping system. (Bänziger and Cooper, 2001; Sultan et al., 2013) in their breeding schemes. Prediction of the future cropping season conditions (onset of rain, drought episodes, biotic pressures…) can guide breeders and seed providers to select/predict the most suitable hybrid for a specific year x location x management combination.

CMS system in WA sorghum

Genetics of fertility restoration

Depending on the restorer line under consideration, one or multiple dominant loci plus partial restorer genes control the fertility restoration in WA sorghum (Kante et al., 2018). The detected major loci (Rf_2 and Rf_5) are neither limited to WA germplasm nor specific to any sorghum race (Jordan et al., 2010, 2011; Praveen et al., 2018; Kante et al., 2018). One single gene controls the fertility reaction in some restorer lines carrying the Rf_2 locus while in other lines this mechanism is highly quantitative with one major locus on chromosome SBI-05 (Rf_5) and multiple partial restoration loci.

Regardless to differences between environments, a stable male-sterile line should not produce pollen, thus no seed set when selfed. It would be worthwhile to characterize most WA restorer and lines for the monogenic or polygenic nature of their fertility reaction in CMS lines. Such information would help optimizing the breeding schemes and ease the identification of progenies carrying a specific *Rf* loci of the restorer line in R-line development. This is even more important for lines carrying several small effect restorer loci, which can stay unobserved for generations depending on the environmental conditions (Jordan et al., 2010, 2011). Until the genetics of the fertility restoration with these male lines is assessed by further studies, these lines should be identified and the environmental stability of their fertility reaction in seed production environments evaluated, to avoid fertility restoration in female lines, and/or only partial restoration in F_1 progenies. While small effect loci in A- and B-lines, if not selected against, lead to a partial restoration of fertility in A-lines and decrease hybrid seed quality, their inclusion into R-lines would be beneficial for a complete restoration of fertility in progenies. Use of large and repeatable populations (Meirmans, 2015) can allow a better understanding of the mechanism of fertility reaction in WA breeding material carrying Rf_5 and partial restorer loci in several environments. Until such studies are undertaken, and the genetics of fertility restoration, as well as the interaction of small effect QTL with the environment understood, breeders will have to rely on extensive field evaluations in environments where hybrid seeds will be produced.

Further CMS systems for WA breeding programs

Disease susceptibility, if cytoplasmically inherited, can be related to the type of CMS, as it was observed in maize (Levings, 1990). Even though this problem so far has not been reported in sorghum, risk of having such diseases that would lead to severe yield loss for WA farmers should be avoided with the introduction of other CMS types into WA breeding programs. The A_2 cytoplasm was demonstrated to yield comparably to the generally used A_1 cytoplasm, contrarily to the A_3 cytoplasm (Moran and Rooney, 2003). In ICRISAT-Mali, lines with the A_2 CMS were recently introduced from India and the field evaluation process is ongoing. As described in Jordan et al. (2011) fertility restoration QTL mapped on chromosome SBI-05 for the A_1 CMS could also restore fertility in the A_2 CMS system, however no information on small effect loci to this regard is available. A deeper understanding of Rf_5 locus (along with the supposed partial restorers) for the WA A_1 CMS (Kante et al., 2018), and informative marker creation based on such QTL can allow an assessment of the fertility restoration/sterility maintenance capacity of such loci on newly created A_2 CMS based WA sorghum. If Rf_5 is confirmed to restore fertility in introduced A_2 cytoplasm, breeding for "universal restorers" by introgessing both Rf_2 and Rf_5 (and partial restorers) in R-lines can allow the restoration of fertility in both A_1 and A_2 cytoplasm by the same parental lines, and ease the identification and the use of potential male parents. Stability A- and R-lines. Yield advantage and stability of A_2-cytoplasm hybrids in WA context must be assessed for the identification of stable restorer lines, and providing farmers with good quality seed and higher yields.

Markers for fertility restoration and their usefulness

PPR Sobic.02G057050 seems to control the fertility restoration in some Australian (Jordan et al., 2010), Indian (Praveen et al., 2018) and WA (Kante et al., 2018) breeding lines. If validated, the mutation found in Kante et al. (2018), potentially responsible of the restoration of the fertility, will serve sorghum-breeding programs in WA and worldwide. The KASP marker for fertility restoration/sterility maintenance (Sobic.02G057050_1090), developed from the reported mutation, stands already as a promising tool for routine use in sorghum hybrid breeding programs because it could differentiate a set of B- from R- lines in the validation study (Kante et al., 2018). Molecular marker can play an important role in a plant-breeding program by reducing field trial evaluations, time and costs of producing one final variety (Collard and Mackill, 2008). Despite the several bottlenecks for an efficient use of molecular markers in developing countries reported by Ribaut et al. (2010), Sobic.02G057050_1090 can allow a successful marker-assisted assessment of fertility restoration or sterility maintenance of some breeding lines, and can be more efficient, labor- and cost-effective than direct field evaluation. It will allow WA breeders to select in their breeding programs (and from introduced material) lines carrying- or not- Rf_2 for male parent identification and development of the parental pool- or for the A/B pair creation.

Awaiting further insights on other Rf genes controlling the fertility restoration in WA sorghum (Rf_5 and small effect genes), Sobic.02G057050_1090 is publically available for direct use by breeders in their respective breeding programs. The availability of lab facilities in local breeding programs should not be a constraint. For instance, breeders that want to screen their breeding material for potential restorer or maintainer lines can ship their (leaf or extracted DNA) samples to LGC genomics for genotyping with a relatively accessible price (https://www.lgcgroup.com/).

Conclusions and significances for sorghum- hybrid breeding- and farmers in West Africa

Sorghum hybrids breeding for low input environments stands as a very promising tool for attaining sustainable food security and rural development. Sorghum hybrid breeding at ICRISAT is enforced with conclusions from my thesis, with several tools and strategies for a long-term hybrid-breeding program targeting WA agro ecologies:

- ✓ Tall hybrids present meaningful yield advantage over the local check in on-farm farmer-managed environments, specially under low-yielding environments;
- ✓ There is a priori no need to examine hybrid performances within specific mega-environments;
- ✓ Hybrids attain the minimum advantages to recover the seed cost;
- ✓ Hybrids present dynamic stability with increasing yield in increasing fertility conditions;
- ✓ One or multiple dominant loci- plus modifier and/or partial restorer- genes control the fertility restoration in WA sorghum;
- ✓ Two major QTL for fertility restoration of the A_1 CMS, Rf_2 and Rf_5, have been identified in WA sorghum;
- ✓ Small effect QTL were found in the restorer lines carrying Rf_5;
- ✓ A potential mutation for Rf_2 was identified;
- ✓ A molecular (KASP) marker (from the above-mutation) is available for routine use in WA breeding programs;
- ✓ New experimental Guinea-race hybrids present significant yield advantage over parents and local checks under HP and LP conditions;
- ✓ There is a need for specific hybrids for LP environments;
- ✓ Adapted male parents to LP soils are needed for hybrid performance under LP;

- ✓ Direct selection under LP is more effective than indirect selection under HP for hybrid performance under LP conditions.

Perspectives and challenges

Breeding challenges

Heterotic grouping

Hybrid breeding in the US recorded 0.008 t ha^{-1} of annual increase in grain yield (Pfeiffer et al., 2018). One of the reasons listed for this relatively small progress was the nonexistence of well-established heterotic groups (Melchinger and Gumber, 1998) in sorghum (Rooney, 2004; Menz et al., 2010; Pfeiffer et al., 2018). Grouping existing germplasm in different heterotic groups is an essential step for a mid/long-term hybrid-breeding program to attain higher heterosis and genetic gain by exploiting the genetic diversity between distinct pools. Intercrosses between lines from two distinct heterotic groups were demonstrated to be superior to intra-group crosses in maize and in rice (see Melchinger and Gumber, 1998 for references). This occurs by attaining a superior mean heterosis and hybrid performance and an increased GCA/SCA ratio (Reif et al., 2007). Performance of superior hybrids can therefore be predicted based on the GCA estimates of the parental lines in early generations. Sorghum hybrids in WA showed already high gains in grain yield with the first set of parents developed from the local WA material (Rattunde et al., 2013; Kante et al., 2017, 2019). However, not defining heterotic pools may lower the proportion of genetic gain attained in long-term hybrid breeding programs, leading to an underuse of the available genetic potential. Until functional heterotic groups are established, breeding programs will still need testcross evaluations in the latest stages given the significant SCA variance of our tested material (specially under LP conditions) (Kante et al., 2019). So far, in WA sorghum, there is no defined heterotic grouping, on which sorghum breeders can rely to develop their proper hybrid breeding material. It is therefore essential for WA breeding programs to find heterotic patterns in their diverse breeding lines in order to establish the basis of hybrid breeding. Insights for possible creation of the male pool was proposed in Kante et al. (2019).

In a long-term breeding program, reciprocal recurrent selection (RRS) method can be applied between the male and the female pools to improve the genetic diversity of breeding materials "for the future" (Schnell, 1961). RSS provides the prospect of achieving further improvement, even if the breeding program starts with already high performing material (Comstock et al., 1949). The latter-cited authors established the superiority of RRS procedure as compared to recurrent selection for general combining ability for loci presenting overdominance, and for specific combining ability with respect to loci with partial dominance. Further, the RSS procedure can still be modified and paired with the available resources and the local conditions (Russell and Eberhart, 1975), with the use of the adequate tester in early generations, for efficiently and simultaneously improve breeding populations and develop elite single cross hybrids.

Selection of parental material

Ribdahu, IS15401 (Guinea lines introduced from Nigeria and Cameroon, respectively) and Ngolofing (a Malian Guinea landrace) were introduced and introgressed into Lata (resulting in backcross groups of lines, BCG_Lata//Ribdahu, BCG_Lata//IS15401 and BCG_Lata//Ngolofing, respectively) to diversify hybrid male parental pool in Mali. These lines were crossed onto female parents developed from Malian material. The generally positive GCA estimates of Ribdahu used as male parent, and those of BCG_Lata//Ribdahu and BCG_Lata//IS15401 groups, and the negative GCA of Ngolofing and BCG_Lata//Ngolofing, suggest the usefulness of introducing germplasm from further east WCA in producing high yielding Guinea hybrids under LP and HP conditions. This could be due to the conceivably larger genetic distance between lines from further east WA and the Malian female lines. To diversify the male parental lines, introduction of Guinea material from different geographical origins, further introgressed in locally adapted varieties, can be very valuable for hybrid performance under WA agro ecologies.

Breeding programs will benefit more from such introduced lines if the latest-mentioned are first assessed for their adaptation to LP soils, as hybrid performance under LP conditions was generally correlated to male parent's performance especially under LP conditions (Kante et al., 2019). Further, introgressing introduced lines into locally adapted material would allow a better adaptation (e.g. heading date, plant height, P-stress tolerance) of breeding material from further east WA.

For such breeding scheme, many questions remain unanswered. Patterns observed in Kante et al. (2019) have to be confirmed with a larger set of diversified male and female parents given the limited set or material used. Sampling of diversified female lines will give insights on how to select the best female line within the available germplasm for hybrid performance and hybrid-seed production. Given the importance of the choice of testers for a specific target environment (Lopez-Perez, 1979; Chaubey et al., 1994), information about the adaptation level of tester line(s) to LP- *vs* HP- conditions would be very valuable. Therefore, further studies are needed to determinate the best tester(s) from the A/B pool for early generation testing of male combining ability for hybrid performance under LP.

Socio-economic defies and general considerations

Hybrids present various benefits for smallholder farmers and their families in WA. However, advances attained with hybrids will be undermined in low-input farming conditions if the depletion of soil fertility is not reversed and climate change impacts are not anticipated. More than possessing higher yields than the local checks under low productivity environments, hybrids showed a good dynamic stability (Becker and Leon, 1988), with increasing grain yields in increasing productivity levels (Kante et al., 2017), or increasing soil-P contents (Kante et al., 2019). Assisting small-scale farmers for a sustainable and integrated improvement of the soil properties by different means (Whalen, 2012; Tonitto and Ricker-Gilbert, 2016) becomes critical in order to increase yield on farmers' fields and consequently their livelihood.

Research should also be focused, beyond the physical properties of grains, on hybrid grain quality to contribute to the reduction of the hidden hunger. Hidden hunger, and mostly iron, zinc and vitamin A deficiency has very dramatic consequences on rural population and endangers child health in many areas (Mangusho, 2013; Ruel-Bergeron et al., 2015; Uche and Familusi, 2018).

Despite yield superiorities over several checks attained by hybrids in on-farm and on-station trials, and the increasing adoption rate of hybrids (Smale et al., 2014, 2018), many farmers remain reluctant to the hybrid technology, mainly because of a lack of information. In some rural areas, hybrids are still considered as genetically modified organisms and therefore not trusted for cultivation (Christinck et al., 2018). A detailed diagnostic- and possible ways of improving- seed systems was reported by (Westengen et al., 2014; Falconnier et al., 2016; Christinck et al., 2018). More effort must be put in transferring the knowledge around hybrids to farmers, such as better and inclusive communication methods (social media, communitarian radios…).

In 2005, the ECOWAS stated a new agricultural policy (ECOWAP) aiming to contribute sustainably to meeting the population food needs, to attaining an economic and social development and to achieving the reduction of poverty in the member states (ECOWAS, 2008). Modern and sustainable agriculture based on the efficiency and effectiveness of family farms and the promotion of agricultural enterprises through the involvement of the private sector are the backbone of this politic. However, in practice, farmers' still lack assistance in accessing credit, obtaining required inputs, and transforming and marketing their surpluses. More efforts for the practical efficiency of those politics are needed. In addition, farmers who grow under low fertility conditions, and are highly dependent on rainfall, should be provided with adequate assistance in achieving a sustainable land and water management.

Summary

Food supply and income in rural areas of West Africa (WA) depend strongly on the local production, and mostly on farmers' field production of root and tuber crops, and cereals. To feed an ever-increasing population in a context of climate-change and low-input cultural conditions, breeding for resilient crops can guarantee smallholder farmers food security and cash income for a sustainable rural development.

Sorghum bicolor (L.) Moench is a C_4 cereal crop that is of vital importance for many smallholder farmers and their families in various regions of WA. Those farmers work almost entirely under low-input conditions, and low soil fertility (mostly P deficient) contributes largely to reducing sorghum production, and weakening their livelihood. Farmers preferentially cultivate their locally adapted, tall, photoperiod sensitive Guinea-race varieties that possess the desired grain quality, and satisfactory yields. Yet, yields are low, averaging 1 t ha^{-1} (100 g m^{-2}) since decades, despite the varieties developed by research.

Sorghum hybrids for WA were first explored in the early 1970s and hybrid crosses of Malian landraces with introduced Caudatum-race seed parents were evaluated in the early 80s. Although those hybrids exhibited good heterosis for grain yield, their lack of grain quality made them commercially unsustainable. Efforts by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) and its partners resulted in the first series of Guinea-race based hybrids. The short statured hybrids were evaluated in several on-farm farmer-managed yield trials, and showed satisfactory grain yield and quality under farmers' cultivation conditions. Although taller- relative to shorter- height sorghum can help reduce risks of panicle loss by grazing transhumant cattle, no indication on the yield potential of the tall statured hybrids is available.

The advances achieved by ICRISAT and its partners in hybrid development justified establishing a long-term hybrid breeding program to provide farmers with hybrids with sufficient grain yield and good grain quality under low input conditions. However, the lack of quantitative genetic information about the genetic value of new experimental hybrids and their parents (Guinea-Caudatum to complete Guinea background, from different WA origins), or about the efficiency of alternative selection methods for targeting yield performance in the predominantly low-input and phosphorous-deficient sorghum production conditions hinders sorghum hybrid development for this region.

Sorghum hybrid breeding was commercially feasible only after the identification of a heritable and stable cytoplasmic male sterility (CMS) mechanism. Hybrid breeding in WA can benefit from molecular marker, especially for the fertility restoration/sterility maintenance of the predominant A_1-type of CMS.

The major outcomes of this thesis are presented as follow:

Mean yields of tall hybrids were 3 to 17% (ranging from 6 to 28 g m^{-2}) higher than that of the local check across all 37 on-farm farmer-managed environments and were highest (14–47%) averaged across the seven trials with the lowest mean yields. The yields of the new set of experimental hybrids were substantially superior to farmers' local Guinea-race varieties, with 20 to 80% higher means over all hybrids in both low phosphorus (LP) and high phosphorus (HP) environments. Average mid-parent and better-parent heterosis estimates were respectively 78 and 48% under HP, and 75 and 42% under LP. Direct selection under LP was predicted to be 20 to 60% more effective than indirect selection under HP conditions, for hybrid performance under LP. The combining ability estimates provide initial insights into the potential benefit of germplasm from further east in West and Central Africa for developing a male parental pool that is distinct and complimentary to the Malian female pool.

On chromosome SBI-05, we found a major A_1 CMS fertility restorer locus (Rf_5) explaining 19 and 14% of the phenotypic variation in either population. Minor quantitative trait loci (QTL) were detected in these two populations on chromosomes SBI-02, SBI-03, SBI-04 and SBI-10. In the third population, we identified one major A1 CMS fertility restorer locus on chromosome SBI-02, Rf_2, explaining 31% of the phenotypic variation in the F_2 mapping population. Pentatricopeptide repeat genes in the Rf_2 QTL region were sequenced, and we detected in Sobic.002G057050 a missense mutation in the first exon, explaining 81% of the phenotypic variation in an $F_{2:3}$ validation population and clearly separating B- from R-lines.

The Guinea-race hybrids' substantial yield superiorities over well adapted local Guinea-race varieties suggests that a strategy of breeding hybrids based on Guinea-germplasm can contribute to improving the livelihood of many smallholder farmers in WA. Although the usefulness of direct selection under LP for hybrid performance in the predominantly P-limited target environments was proven, companion evaluations of hybrids under HP would be desirable to identify also new hybrids that can respond to improved fertility conditions for sustainable intensification. The developed KASP marker stands as a promising tool for routine use in WA breeding programs.

Zusammenfassung

Die Nahrungsmittelversorgung und das Einkommen in den ländlichen Gebieten Westafrikas (WA) hängen stark von der lokalen Produktion, vor allem von der Wurzel- und Knollenpflanzen sowie der Getreideproduktion der Landwirte ab. Um eine ständig wachsende Bevölkerung in Anbetracht des Klimawandels und unter Anbaubedingungen mit geringem Produktionsmitteleinsatz zu ernähren, kann die Züchtung widerstandsfähiger Nutzpflanzen den Kleinbauern Ernährungssicherheit und Einkommen für eine nachhaltige ländliche Entwicklung garantieren.

Sorghum bicolor (L.) Moench ist ein C4-Getreide, das für viele Kleinbauern und ihre Familien in verschiedenen Regionen von WA von entscheidender Bedeutung ist. Diese Landwirte arbeiten fast ausschließlich mit geringem Produktionsmitteleinsatz, und die geringe Bodenfruchtbarkeit (meist P-Mangel) trägt weitgehend dazu bei, die Sorghumproduktion zu reduzieren und ihre Lebensgrundlage zu schwächen. Die Landwirte bauen vorzugsweise ihre lokal angepassten, photoperiodisch sensitiven, hohe Guinea-Rasse Sorten an, die die gewünschte Kornqualität und zufriedenstellende Erträge aufweisen. Dennoch sind die Erträge niedrig und liegen trotz der von der Forschung entwickelten Sorten seit Jahrzehnten im Durchschnitt bei 1 t ha^{-1} (100 g m^{-2}).

Sorghum-Hybriden für WA wurden erstmals in den frühen 1970er Jahren erforscht und Hybridkreuzungen malischen Landrassen mit eingeführten Saat-Eltern der Caudatum Rasse wurden Anfang der 80er Jahre evaluiert. Obwohl diese Hybriden eine gute Heterosis für den Getreideertrag aufwiesen, machte sie ihre mangelnde Getreidequalität kommerziell nicht nachhaltig. Die Bemühungen des „International Crops Research Institute for the Semi-Arid Tropics“ (ICRISAT) und seiner Partner führten zur ersten Serie an, auf der Guinea Rasse basierenden, Hybriden.

Die kleinwüchsigen Hybriden wurden in mehreren, von Landwirten geführten Ertragsversuchen auf landwirtschaftlichen Betrieben evaluiert und zeigten unter den Anbaubedingungen der Landwirte zufriedenstellende Getreideerträge und -qualität. Obwohl größeres, im Vergleich zu kürzerem Sorghum - dazu beitragen kann, das Risiko eines Rispenverlustes durch die Beweidung in Wanderweidewirtschaft gehaltenem Vieh zu verringern, gibt es keine Hinweise auf das Ertragspotenzial der hochwüchsigen Hybriden.

Die Fortschritte, die ICRISAT und seine Partner bei der Hybridentwicklung erzielt haben, rechtfertigten den Aufbau eines langfristigen Hybridzuchtprogramms, um den Landwirten Hybriden mit ausreichenden Getreideerträgen und guter Getreidequalität bei geringem Produktionsmitteleinsatz zur Verfügung zu stellen. Der Mangel an quantitativen genetischen Informationen über den genetischen Wert neuer experimenteller Hybriden und ihrer Eltern (Guinea-Caudatum bis vollständiger Guinea Hintergrund, aus unterschiedlicher WA Herkunft) oder über die Effizienz alternativer Selektionsmethoden zur Ausrichtung der Ertragsleistung unter den überwiegend phosphorarmen Bedingungen mit geringem Produktionsmitteleinsatz behindert jedoch die Hybridentwicklung von Sorghum für diese Region.

Die Sorghum-Hybridzüchtung war erst nach der Identifizierung eines vererbbaren und stabilen zytoplasmatischen männlichen Sterilisationsmechanismus (CMS) kommerziell möglich. Die

Hybridzüchtung in WA kann von molekularen Markern, vor allem für die Fruchtbarkeitswiederherstellung/Sterilitätserhaltung des vorherrschenden A_1 CMS Typs, profitieren.

Die wichtigsten Ergebnisse dieser Arbeit werden wie folgt dargestellt:

Die mittleren Erträge hoher Hybriden waren 3 bis 17% (im Bereich von 6 bis 28 g m^{-2}) höher als die der lokalen Kontrollsorte in allen 37 von Landwirten verwalteten Umwelten und waren am höchsten (14-47%), gemittelt über die sieben Versuche mit den niedrigsten Durchschnittserträgen. Die Erträge der neuen, experimentellen Hybriden waren mit 20 bis 80% höheren Mittelwerten über alle Hybriden, wesentlich höher als die der lokalen Guinea-Rasse Sorten der Bauern. Sowohl in Umwelten mit niedrigem Phosphorgehalt (LP) als auch mit hohem Phosphorgehalt (HP). Die durchschnittlichen Schätzungen der Heterosis über das Elternmittel sowie über den besseren Elter lagen bei 78 bzw. 48% unter HP und 75 bzw. 42% unter LP. Es wurde berechnet, dass die direkte Selektion unter LP 20 bis 60% effektiver ist als die indirekte Selektion unter HP-Bedingungen für die Hybridleistung unter LP. Die Schätzung der Kombinationsfähigkeit liefern erste Erkenntnisse über den potenziellen Nutzen von Genmaterial aus weiter östlich gelegenen Gegenden West- und Zentralafrikas für die Entwicklung eines männlichen Elternpools, der sich vom malischen weiblichen Pool unterscheidet und ihn ergänzt.

Auf dem Chromosom SBI-05 fanden wir einen großen A_1 CMS Fertilitätswiederherstellungs-Locus (Rf_5), der 19 und 14% der phänotypischen Variation in beiden Populationen erklärt. Regionen eines quantitativen Merkmals (QTL) mit geringem Effekt wurden in diesen beiden Populationen auf den Chromosomen SBI-02, SBI-03, SBI-04 und SBI-10 nachgewiesen. In der dritten Population identifizierten wir einen großen A_1 CMS Fertilitätswiederherstellungs-Locus auf dem Chromosom SBI-02, Rf_2, der 31% der phänotypischen Variation in der F_2-Kartierungspopulation erklärt. „Pentatricopeptid repeat“ Gene in der Rf_2-QTL-Region wurden sequenziert, und wir entdeckten in Sobic.002G057050 eine sinnverändernde Punktmutation im ersten Exon, die 81% der phänotypischen Variation in einer $F_{2:3}$-Validierungspopulation erklärt und B- von R-Linien klar trennt.

Die erheblichen Ertragsüberlegenheiten der Guinea-Rasse Hybriden gegenüber gut angepassten lokalen Guinea-Rasse Arten deuten darauf hin, dass eine strategische Hybridzüchtung auf der Grundlage von Guinea-Keimmaterial zur Verbesserung der Lebensgrundlage vieler Kleinbauern in WA beitragen kann. Obwohl die Nützlichkeit der direkten Selektion unter LP für die Hybridleistung in den überwiegend P-begrenzten Zielumwelten etabliert wurde, wären Begleitbewertungen von Hybriden unter HP wünschenswert, um auch neue Hybride zu identifizieren, die auf verbesserte Fertilitätsbedingungen für eine nachhaltige Intensivierung reagieren können. Der entwickelte KASP-Marker steht als vielversprechendes Werkzeug für den routinemäßigen Einsatz in WA-Zuchtprogrammen bereit.

Résumé

L'approvisionnement en nourriture et les revenus dans les zones rurales d'Afrique de l'Ouest (AO) dépendent fortement de la production locale, et principalement de la production issue des champs des producteurs de racines, tubercules et céréales. Pour nourrir une population sans cesse croissante, dans un contexte de changement climatique et de conditions de culture utilisant peu d'intrants, la sélection pour des cultures résilientes peut garantir une sécurité alimentaire et des revenus en espèces aux petits exploitants agricoles, pour un développement rural durable.

Sorgho bicolor (L.) Moench est une culture céréalière C_4 d'une importance vitale pour de nombreux petits exploitants et leurs familles dans diverses régions d'AO. Ces agriculteurs travaillent presque entièrement dans des conditions de faibles intrants, et la faible fertilité des sols (principalement déficients en P) contribue largement à réduire la production de sorgho et à affaiblir les moyens de subsistance de ces agriculteurs. Ces derniers cultivent de préférence leurs variétés à taille haute de la race Guinea, photopériodiques, adaptées aux conditions locales, et qui possèdent les qualités de grain requises et des rendements satisfaisants. Toutefois, les rendements sur les champs de sorgho sont toujours faibles en AO, atteignant en moyenne 1 t ha^{-1} (100 g m^{-2}) depuis des décennies, malgré les variétés développées par la recherche.

Les hybrides de sorgho pour l'AO ont été explorés pour la première fois au début des années 1970 et des hybrides issus du croisement de variétés locales maliennes et des parents femelles introduites de la race Caudatum ont été évalués au début des années 80. Bien que ces hybrides aient présenté une bonne hétérosis quant au rendement en grain, leur manque de qualité les rendait commercialement inintéressants. Les efforts de l'Institut international de recherche sur les cultures dans les zones tropicales semi-arides (ICRISAT) et de ses partenaires ont abouti à la première série d'hybrides basée sur la race Guinea. Les hybrides à taille courte ont été évalués dans plusieurs essais de rendement gérés par des producteurs, et ont eu un rendement et une qualité de grain satisfaisants dans les conditions de culture des agriculteurs. Bien que le sorgho de taille haute puisse aider à réduire les risques de perte de grain due à la transhumance bovine, aucune indication sur le potentiel rendement des hybrides de grande taille n'est disponible.

Les progrès réalisés par l'ICRISAT et ses partenaires dans le développement des hybrides ont aussi justifié la mise en place d'un programme à long terme de sélection hybride visant à fournir aux agriculteurs des hybrides avec un rendement en grain suffisant et une bonne qualité de grain dans des conditions de faible apport en intrants. Cependant, le manque de données quantitatives sur la valeur génétique des nouveaux hybrides expérimentaux et de leurs parents (des races Guinea-Caudatum à complétement Guinea, et de différentes origines en AO), ou sur l'efficacité de méthodes alternatives de sélection pour cibler le rendement dans des conditions essentiellement faibles en intrants ou déficientes en P, entrave le développement d'hybrides de sorgho dans cette région.

La culture extensive d'hybrides de sorgho n'était commercialement faisable qu'après l'identification d'un mécanisme héréditaire et stable de stérilité mâle cytoplasmique (SMC). La sélection hybride en AO peut tirer parti des marqueurs moléculaires, en particulier pour la restauration de la fertilité/le maintien de la stérilité du SMC du prédominant type A_1.

Les principaux résultats de cette thèse sont présentés comme suit:

Les rendements moyens des hybrides de taille hautes étaient de 3 à 17% (allant de 6 à 28 g/m²) supérieurs à ceux du témoin local dans les 37 environnements gérés par les agriculteurs, et étaient les plus élevés (14 à 47%) en moyenne sur les sept essais avec les plus faibles rendements moyens. Les rendements du nouvel ensemble d'hybrides expérimentaux étaient nettement supérieurs à ceux des variétés paysannes locales appartenant à la race Guinea, avec des moyennes supérieures de 20 à 80% dans les environnements à faible teneur en phosphore (LP) et à teneur élevée en phosphore (HP). Les estimations moyennes de l'hétérosis « parent moyen » et l'hétérosis « meilleur parent » étaient respectivement de 78 et 48% sous HP, et de 75 et 42% sous LP. La sélection directe sous LP était 20 à 60% plus efficace que la sélection indirecte sous HP, pour la performance des hybrides sous LP. Les estimations des aptitudes à la combinaison fournissent un premier aperçu des avantages potentiels du matériel génétique provenant de régions plus à l'est de l'Afrique de l'Ouest et du Centre pour le développement d'un pool parental mâle distinct, complémentaire du pool femelle malien.

Sur le chromosome SBI-05, nous avons trouvé un locus majeur de restauration de la fertilité chez la SMC de type A_1 (Rf_5) expliquant 19 et 14% de la variation phénotypique dans deux populations F_2. Des loci à caractères quantitatifs (QTL) mineurs ont été détectés dans ces deux populations sur les chromosomes SBI-02, SBI-03, SBI-04 et SBI-10. Dans la troisième population, nous avons identifié un locus majeur de restauration de la fertilité chez la SMC de type A_1 sur le chromosome SBI-02, Rf_2, expliquant 31% de la variation phénotypique dans la population F_2. Les gènes à motifs PPR présents dans la région de Rf_2 ont été séquencés, et nous avons détecté dans Sobic.002G057050 une mutation non-sens dans le premier exon, expliquant 81% de la variation phénotypique dans une population de validation $F_{2:3}$, et séparant clairement les lignées B des lignées R.

Les rendements supérieurs des hybrides de la race Guinea par rapport aux variétés bien adaptées de race Guinea locale suggèrent qu'une stratégie de sélection d'hybrides basée sur du matériel génétique Guinea peut contribuer à améliorer les moyens de subsistance de nombreux petits exploitants agricoles en AO. Bien que l'utilité de la sélection directe sous LP pour la performance des hybrides dans les environnements cibles à faible P ait été prouvée, l'évaluation simultanée des hybrides sous HP serait souhaitable pour identifier également de nouveaux hybrides pouvant répondre à de meilleures conditions de fertilité pour une intensification durable. Le marqueur KASP développé constitue un outil prometteur pour une utilisation de routine dans les programmes de sélection.

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Resumen

El suministro de alimentos y los ingresos en las zonas rurales de África occidental (AO) dependen en gran medida de la producción local, y principalmente de la producción de los campos de productores de raíces, tubérculos y granos. Para alimentar a una población cada vez más grande, en un contexto de cambio climático y de condiciones de cultivo de bajos insumos, el desarrollo de cultivos resilientes puede garantizar la seguridad alimentaria e ingresos en efectivo para los pequeños agricultores, para un desarrollo rural sostenible.

El *Sorgho bicolor* (L.) Moench es un cereal C_4, vital para muchos pequeños productores y sus familias en varias regiones de AO. Estos agricultores trabajan casi por completo en condiciones de bajos insumos, y la baja fertilidad del suelo (principalmente deficiente en P) contribuye en gran medida a reducir la producción de sorgo y debilitar los medios de vida de estos agricultores. Estos últimos cultivan preferentemente sus variedades de la raza Guinea de gran altura, fotoperiódicas, adaptadas a las condiciones locales, y que poseen las cualidades de grano requeridas y rendimientos satisfactorios. Sin embargo, los rendimientos en los campos de sorgo todavía son bajos en AO, promediando 1 t ha^{-1} (100 g m^{-2}) durante décadas, a pesar de las variedades desarrolladas por la investigación.

Los híbridos de sorgo para AO se exploraron por primera vez a principios de la década de 1970, y los híbridos de variedades locales malienses y de progenitores hembras de la raza Caudatum fueron evaluados a principios de la década de 1980. Estos híbridos mostraron una buena heterosis en el rendimiento de grano, pero su falta de calidad de grano los hizo comercialmente poco interesantes. Los esfuerzos del Instituto Internacional de Investigación de Cultivos para los Trópicos Semiáridos (ICRISAT) y sus socios han dado como resultado la primera serie de híbridos basados en la raza Guinea. Los híbridos de baja postura se evaluaron en varios ensayos de rendimiento gestionados por los agricultores, y tuvieron un rendimiento y una calidad de grano satisfactorios en las condiciones de cultivo de los agricultores. Aunque el sorgo de alta postura pueda ayudar a reducir el riesgo de pérdida de grano debido a la trashumancia del ganado, no hay datos sobre su potencial rendimiento.

El progreso realizado por ICRISAT y sus socios en el desarrollo de híbridos ha justificado el establecimiento de un programa a largo plazo de mejoramiento de híbridos para proporcionar a los agricultores híbridos con suficiente rendimiento y una buena calidad de grano en condiciones de bajos insumos. Sin embargo, la falta de datos cuantitativos sobre el valor genético de los nuevos híbridos experimentales y sus progenitores (desde razas Guinea-Caudatum hasta la raza totalmente Guinea, y de diferentes orígenes en AO), o sobre la efectividad de métodos alternativos de selección para aumentar el rendimiento principalmente en condiciones de bajo en insumo o deficientes en P, dificulta el desarrollo de híbridos de sorgo en esta región.

El cultivo extenso de híbrido de sorgo ha sido comercialmente factible tan solo después de la identificación de un mecanismo heredable y estable de esterilidad masculina citoplasmática (CMS). La selección híbrida en AO puede beneficiarse de marcadores moleculares, particularmente para la restauración de la fertilidad/mantenimiento de la esterilidad del CMS del tipo predominante A_1.

Los principales resultados de esta tesis se presentan de la siguiente manera:

Los rendimientos medios de los híbridos "altos" fluctuaron entre el 3 y el 17% (rango de 6 a 28 g/m²) por encima de los del control local en los 37 ambientes gestionados por los agricultores, y fueron más altos (del 14 al 47%) promediado en los siete ensayos con los rendimientos promedio más bajos. Los rendimientos del nuevo conjunto de híbridos experimentales fueron significativamente mayores que los de las variedades campesinas locales de la raza Guinea, con promedios de 20-80% más altos en ambientes con bajo contenido de fósforo (LP) y alto contenido de fósforo. (HP). Las estimaciones medias de la heterosis "progenitor promedio" y la heterosis "mejor progenitor" fueron 78 y 48% en HP, y 75 y 42% en LP, respectivamente. La selección directa bajo LP fue de 20 a 60% más eficiente que la selección indirecta bajo HP, para el rendimiento de los híbridos bajo LP. Las estimaciones de la aptitud de combinación ofrecen una primera perspectiva sobre los beneficios potenciales del material genético de las partes más orientales de África occidental y central para el desarrollo de un grupo parental de machos separado de grupo hembra maliense.

En el cromosoma SBI-05, encontramos un locus principal de restauración de fertilidad en el CMS de tipo A1 (Rf5) que explica el 19 y el 14% de la variación fenotípica en dos poblaciones F2. Se detectaron loci a carácter cuantitativo (QTL) menores en estas dos poblaciones en los cromosomas SBI-02, SBI-03, SBI-04 y SBI-10. En la tercera población, identificamos un importante locus de restauración de la fertilidad en el CMS de tipo A1 en el cromosoma SBI-02, Rf2, que representa el 31% de la variación fenotípica en la población F2. Los genes con motivos PPR presentes en la región Rf2 fueron secuenciados, y detectamos en Sobic.002G057050 una mutación "sin sentido" en el primer exón, que representa el 81% de la variación fenotípica en una población de validación F2:3, y separando claramente las líneas B de las líneas R.

Los rendimientos altos de los híbridos de la raza Guinea en comparación con los de las variedades locales bien adaptadas sugieren que una estrategia de mejora genética basada en el material genético de la raza Guinea puede ayudar a mejorar los medios de vida de muchos pequeños agricultores en AO. Aunque se haya comprobado la utilidad de la selección directa bajo LP para el rendimiento híbrido en medios con bajo P, sería deseable hacer la evaluación simultánea de los híbridos HP para identificar también nuevos híbridos que puedan responder a mejores condiciones de fertilización para una intensificación sostenible. El marcador KASP desarrollado es una herramienta prometedora para un uso rutinario en programas de mejoramiento.

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Photo credit:
Front cover: Fred Rattunde.
Back cover: Moctar Kante.

Photo description:
Front cover: Bala Berthe in his field of the tall hybrid Pablo, nearby Bamako.
Back cover: Women farmers in on-farm participatory trials, Dioila zone.