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Strategies for sustainable pearl millet hybrid breeding in West Africa

Dissertation

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2) Sattler, F.T., Pucher, A., Kassari Ango, I., Sy, O., Isaaka, A., Hash, C.T., Haussmann, B.I.G., 2019. Identification of combining ability patterns for pearl millet hybrid breeding in West Africa. Crop Sci. 59, 1590–1603. https://doi.org/10.2135/cropsci2018.12.0727

3) Sattler, F.T., Haussmann, B.I.G., 2020. A unified strategy for West African pearl millet hybrid and heterotic group development. Crop Sci. 60, 1–13. https://doi.org/10.1002/csc2.20033

List of Abbreviations

AICPMIP	All India Coordinated Pearl Millet Improvement Program
AOCC	African Orphan Crops Consortium
AR1	Autoregressive models of the first order
CMS	Cytoplasmic male sterility
E	Environment
G	Genotype
GCA	General combining ability
ICRISAT	International Crops Research Institute for the Semi-Arid Tropics
IER	Institut d'Economie Rurale
INERA	Institut de l'Environnement et Recherches Agricoles
INRAN	Institut National de la Recherche Agronomique du Niger
ISRA	Institut Sénégalais de Recherches Agricoles
KASP	Competitive allele specific PCR
LCRI	Lake Chad Research Institute
MPH	Mid-parent heterosis
OPV	Open-pollinated variety
PBPH	Panmictic better-parent heterosis
QTL	Quantitative trait loci
RRS	Reciprocal recurrent full-sib selection
SCA	Specific combining ability
SCLB	Southern corn leaf blight
Tcms	Texas CMS
WA	West Africa(n)
WCA	West and Central Africa(n)

General Introduction

Today, we share this planet with more than 7.5 billion people and the world population is constantly growing. In developed countries, the number of people is expected to be almost constant for the next 50 years, while the population in less developed countries will continue to increase. An immense population growth can be observed and is expected for West Africa (WA). In 1970, a little more than 100 million people were living in this region and today there are more than 400 million. With population growth rates of currently 2.6% p.a., WA is expected to be inhabited by more than 1.1 billion people in 2070 (UN DESA/population division, 2017). The entire agricultural sector (including forestry and fishing) contributed 29% to the total GDP in WA (excluding Saint Helena, Ascension and Tristan da Cunha), ranging from 6% in Cape Verde to 60% in Sierra Leone in 2017 contrasting the world wide average of only 3.5% (World Bank, 2019). However, these numbers underestimate the importance of agriculture in WA since most of subsistence farmers' products do not enter markets and it is difficult to quantify the amount of people that rely on subsistence farming (Breman, 2003). In this context, the development and cultivation of higher-yielding and stable cultivars of the major staple crops grown by the subsistence farmers can contribute to enhancing food production and thereby food security of the growing population.

Pearl millet

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is a staple crop for more than 90 million subsistence farmers, mostly in the drylands of Sub-Saharan Africa and India (Varshney et al., 2017). It is primarily grown for human consumption and possesses good nutritional properties, like high iron and zinc grain content (Pucher et al., 2014; Sawaya et al., 1984), and provides additionally fodder and building material. In drought prone regions where maize (*Zea mays* L.) and even sorghum (*Sorghum bicolor* L. Moench) would fail, pearl millet is still capable of producing grain (Vadez et al., 2012). It is commonly grown in regions with 300 – 500 mm of precipitation on sandy soils with low plant-available phosphorus levels, and survives temperatures of more than 42°C (Gemenet et al., 2016; Vadez et al., 2012; Yadav et al., 2015). Pearl millet is a highly heterozygous diploid (2n = 2x = 14) C4 plant species. Its predominantly allogamous nature caused by protogynous flowering in combination with windborne pollen that survives Sahelian conditions easily results in outcrossing rates of more than 70% (Burton, 1974;

Hoekstra et al., 2006). Manning et al. (2011) dated residues of domesticated pearl millet in the lower Tilmesi Valley in Northern Mali to 2500 BCE, using accelerator mass spectrometry radiocarbon dating. These findings and more recent whole genome data lead to the conclusion that pearl millet originated in WA, before spreading over Sahelian Africa and already in ~2000 BCE to India (Burgarella et al., 2018; Fuller and Boivin, 2009; Oumar et al., 2008). Therefore, WA also represents a center of diversity for pearl millet – and herewith “a gold mine” for plant breeders.

Yield-limiting constraints in WA environments

While pearl millet is able to survive under the most adverse conditions, its yield potential is highly limited due to a large spectrum of abiotic and biotic stresses. The most limiting factor is the total scarcity of precipitation and its highly variable distribution over the growing period, resulting in flooding and/or dry spells in WA (Haussmann et al., 2012). While pearl millet is able to compensate mild early drought to a certain extent, it is susceptible to terminal drought stress during the grain filling stage (Mahalakshmi et al., 1987). Climate change effects (drought, flooding, etc.) are expected to occur more often resulting in yield losses of 10% in pearl millet and aggravating cereal deficits (Cooper et al., 2008; Knox et al., 2012). Additionally, drought stress can reduce the up-take of phosphorus (Gemenet et al., 2016; Hash et al., 2002; Sinclair and Vadez, 2002), which is already deficient in WA soils (Bationo et al., 1992; Bekunda et al., 1997). Poor, sandy, highly weathered soils with low pH levels are common in Sahelian Africa (Kochian, 2012) leading to fixation of phosphorus (Holford, 1997), nitrate leeching (Bagayoko et al., 2000) and aluminum toxicity (Kochian, 1995).

Besides these abiotic stresses, pearl millet faces several biotic threats. Humid conditions at the peak of the rainy season promote the propagation of *Scelerospora graminicola* (Sacc.) J. Schroet. It can inflict severe damage causing the downy mildew disease after infecting the host plant (Singh, 1995). Striga (*Striga hermonthica* (Del.) Benth.), a parasitic weed, is a major thread infesting pearl millet and stealing nutrients and water from it. It has the potential to overgrow entire fields causing a total crop loss (Wilson et al., 2000; Haussmann et al., 2001; Kountche et al. 2013). Furthermore, several insect pests are feeding on the stover like the stem borer (*Coniesta ignefusalis*) or the flowers and floral peduncles like the head miner (*Heliocheilus albipunctella*) (Rai et al., 1999; Payne, 2006).

WA subsistence farmers do not have the means to counterweight these production constraints. Fertilizer and pesticides are mostly too expensive, not accessible in remote regions and farmers might harm themselves or the environment due to a lack of training in correct application practice (Cordell et al., 2009; Payne et al., 2011; Valluru et al., 2010). Unfortunately, it is impossible to tackle the multitude of constraints with a single and simple solution. Several agronomic aspects have to be improved. For example, replenishing nutrient depleted WA soils would be a corner stone for enhancing WA pearl millet production (Sanchez and Leakey, 1997). Finding antagonists to the most important insect pests like the parasitoid *Habrobracon hebetor*, which feeds on head miner larvae, could be an effective and affordable alternative to pesticides (Payne et al., 2011). If possible, catch crops should be planted to “protect” pearl millet from Striga inflicted crop losses (Lagoke et al., 1991).

Improving pearl millet yields can be supported in several ways. It is crucial to support farmers in acquiring suitable methods like intercropping, crop rotations, micro-dosing fertilizer application and understanding advantages and risks of pesticide application (Abdoulaye and Sanders, 2005; Henry et al., 2009; Horst et al., 2001; Williamson et al., 2008). Harvesting water could help to gather water from non-arable land and/or save it for dry spells during the growing period (Tabor, 1995; Cowden et al., 2008). Creating a suitable policy environment considering improving infrastructure and education, the access to credit and inputs, and expansion of markets, involving private and public sector has the potential to improve farmers’ livelihood (Sanchez and Leakey, 1997; Hollinger and Staatz, 2015).

Breeding efforts

WA pearl millet breeding is almost exclusively done by national (e.g. Institut d'Economie Rurale, IER in Mali; Institut de l'Environnement et Recherches Agricoles, INERA in Burkina Faso; Institut National de la Recherche Agronomique du Niger, INRAN; Institut Sénégalais de Recherches Agricoles, ISRA; Lake Chad Research Institute, LCRI in Nigeria) and international (International Crops Research Institute for the Semi-Arid Tropics, ICRISAT) public institutions. WA breeders have to handle large environmental variability (Haussmann et al., 2012) and have to define specific traits to counter low-input conditions. WA farmers rely on landraces and partly on improved open-pollinated varieties (OPVs) (Christinck et al., 2014), and yields remain low (648 kg ha^{-1}; FAO, 2017). In contrast, single-cross hybrids are widely adopted in large parts of India, except for Rajasthan with its difficult environmental and agronomic conditions, similarly to WA. They contributed largely to a yield increase across all millets from 305 kg ha^{-1} (1951 – 1955) to 1157 kg ha^{-1} (2010 – 2014) (Dave, 1986; Yadav and Rai, 2013; FAO, 2017). Single-cross hybrid production and cultivation is common in most pearl millet growing regions in India, because the required expertise, resources, a well-established seed industry, a cytoplasmic male sterility (CMS) system in adapted germplasm, and elite lines are available (Kumara Charyulu et al., 2014; Serba et al., 2017). Developed pearl millet growing countries have largely different breeding targets compared to India or Sahelian Africa. In Australia, Brazil, Canada and the US, pearl millet is primarily grown as a forage crop and increasingly as grain feed under high input conditions in relatively stable environments (De Assis et al., 2017; Gulia et al., 2007; Senthilvel et al., 2008). In Brazil it serves additionally as an important cover crop in no-till soy bean cropping system (De Assis et al., 2017).

Pivotal pearl millet characteristics for WA

Identifying and introgressing specific traits is a key aspect to increase pearl millet yields in WA. Two different plant characteristics, photoperiodic sensitivity and intra-varietal flowering variability, are playing an important role in adaption to variable environments by increasing the chance to escape drought stress (Haussmann et al., 2012, 2007). Several attempts to understand drought tolerance and the underlying mechanisms in pearl millet have been conducted (Beggi et al., 2015; Bidinger et al., 1987a, 1987b; Gupta et al., 2015). Indirect mechanisms, like a general or a photoperiodic sensitivity induced early flowering to escape terminal drought (Clerget et al., 2007), and directly related traits, like reduced transpiration rates (Kholová et al., 2010) have been identified. Furthermore, several studies described drought-related quantitative trait loci (QTLs) that can support breeding efforts (Bidinger et al., 2007; Tharanya et al., 2018; Yadav et al., 2004, 2002).

Other studies found genetic variation for multiple nutrient uptake and utilization related traits. Brück et al. (2003) reported substantial varietal differences in root length density, root dry matter and total root length. Increasing the tolerance to low-phosphorus soils is crucial when developing new varieties (Hash et al., 2002). Gemenet et al. (2016b, 2016a, 2015a, 2015b, 2014) investigated the large genetic variation for phosphorus uptake and utilization efficiency and were able to associate several markers with phosphorus efficiency related traits.

Downy mildew resistance is another fundamental trait, widely considered in pearl millet breeding programs (Rai et al., 1999) and numerous QTLs have been found (Jones et al., 1995, 2002; Hash and Witcombe, 2001; Taunk et al., 2018). Striga resistance has been investigated considerably less compared to downy mildew, although recurrent selection for developing resistant varieties has been quite successful in field experiments conducted in Niger and Mali (Kountche et al., 2013).

Besides these agronomical relevant aspects, it is important to consider nutritional content and local preferences regarding specific characteristics of the crop (Christinck and Weltzien, 2013; Christinck, et al., 2005; Omanya et al., 2007). Micronutrients are often deficient in WA diets (Birner et al., 2007). So far, iron and zinc biofortified pearl millet varieties have been released in India and Niger (HarvestPlus, 2019; Saltzman et al., 2013). WA farmers prefer a dual-purpose crop (grain and stover) and particularly Nigerien and Senegalese farmers prefer long panicles. Dark colored grains are less targeted by birds and have additional health benefits due to anthocyanin, which causes the dark coloring. However, Nigerien farmers prefer light colored millet, because they often consume it as a porridge, which looks terribly unappetizing when made from dark grains (personal communication, CT Hash, 2017).

Hybrid breeding

Introduction of commercial pearl millet hybrid breeding

Pearl millet hybrid breeding in WA is still in its infancy, while single-cross hybrids are widely adopted in most developing and developed countries. The start of commercial hybrid breeding was enabled with the discovery of the CMS system A_1 and the development of the first CMS inbred line Tift 23A in the US (Burton, 1958). This led to the search and identification of several maintainer and fertility restorer lines and a subsequent release of many commercial CMS based hybrids (Appadurai et al. 1982; Burton, 1977, 1958; Burton and Athwap, 1967; Christensen et al., 1984; Rai et al., 2009, 2001). In India, the first grain hybrid was released in 1965 (Athwal, 1965; Pray and Nagarajan, 2009) and today single-cross hybrids are sown on more than 70% of the total pearl millet production area (Yadav and Rai, 2013).

Vulnerability of uniform single-cross hybrids

Single-cross hybrids are usually superior over OPVs in terms of yield level under stable and predictable environmental conditions, at least when considering out-crossing species. Additionally, their uniformity facilitates mechanical harvesting practices. On the downside, this homogeneity makes single-cross hybrids vulnerable to unpredictably variable biotic and abiotic stresses. The first pearl millet hybrids in India were based on the Tift 23A line. These hybrids contributed largely to an immense production increase. However, these hybrids suffered tremendously under annually reoccurring downy mildew epidemics since Tift 23A lines were bred in Georgia, USA, a downy mildew free environment. The first epidemic in India in 1971 reduced total yield production from ~8 to 3 million tonnes causing a famine in the pearl millet growing regions even leading to a depletion of convertible currency because of indispensable food imports. After rapidly releasing one new Tift 23A based variety after the other, it became clear that a long-term solution is required. The All India Coordinated Pearl Millet Improvement Program (AICPMIP) quickly focused on diversifying the germplasm and finding downy mildew resistance genes to introgress them into elite material (Safeeulla, 1977; Serba et al., 2017). A similar reason provoked the southern corn leaf blight (SCLB) epidemics in the US in 1970s. The Texas cms (Tcms) was discovered and transferred into several elite lines. In 1970, 85% of the US maize hybrids had a Tcms background, which turned out to be highly susceptible to SCLB (Ullstrup, 1972). These examples are very drastic, but quite rare. Nevertheless, with increasing levels of biotic and abiotic stresses and risk-averse farmers like in WA, resistances, local adaption and yield stability in general become more important (Oosterom et al., 1996; Weltzien-R et al., 1998). Especially in WA environments, both dynamic ("individual buffering") and static ("population buffering") stability, are very important (Haussmann et al., 2012).

The first concept refers to the ability of individual plants to respond or adapt to occurring stresses - or improving environmental conditions. Example traits include photoperiod sensitivity, resistances, plastic tillering, and the ability to dynamically compensate among yield components. The second concept refers to the heterogeneity within one population for specific adaptation traits. (Allard and Bradshaw, 1964; Annicchiarico, 2002; Becker and Leon, 1988). For example, static stability based on heterogeneity for flowering time would allow a fraction of the plants within one population to escape or avoid periodical drought stress. Intra-varietal heterogeneity for susceptibility to a certain pathogen can slow down epidemics. Specific stress responses and therefore yield stability via individual buffering can be considered in single-cross hybrid breeding programs. In contrast, static stability can only be found in genetically heterogeneous variety types like populations, population-derived hybrids and synthetics. WA farmers are aware of the importance of static stability and prefer one or rather several varieties with a large heterogeneity. Distributing the risk of crop failure lowers the chances to fully exploit the yield potential, but increases the chance to guarantee livelihood (Cooper et al., 2008; Yesuf and Bluffstone, 2007).

The uniformity of single-cross hybrids is an advantage in industrialized countries with high fertilizer and pesticide application and fully mechanized harvesting, but the same characteristic is a disadvantage for WA subsistence farmers. Lack of population buffering capacity and the lack of resources, training, markets and a CMS system in locally adapted material make single-cross hybrids risky and inappropriate for WA conditions (Kumara Charyulu et al., 2014; Serba et al., 2017). However, WA farmers could largely benefit from alternatives that exploit heterosis to a larger extend than OPVs, but are more stable that single-cross hybrids. Population hybrids, derived from crossing two OPVs, or top-cross hybrids derived from one OPV and one inbred line have proven their value in on-station trials (Bidinger et al., 1994; Gemenet et al., 2014; Ouendeba et al., 1993; Pucher et al., 2016; Yadav, 2006).

Heterosis and heterotic groups

An increased vigor in hybrids caused by heterozygosity was already known when Shull (1914) expanded the theory and coined the term heterosis. The total heterosis effect is the difference between the mean of the absolute homozygous parents and the absolute heterozygous offspring. However, the term heterosis is often used to describe this difference without considering the inbreeding coefficient of the parents. Heterosis plays a major role in population, clonal and especially in hybrid breeding. The amount of heterosis depends on the levels of homozygosity and inbreeding depression in the parents, type of reproduction (allogamous, autogamous), and the genetic distance between the parents (Melchinger, 1999).

Regardless of the preferred hybrid type, it is crucial for the success of a long-term hybrid breeding program to identify and maintain heterotic groups. A heterotic group is a set of genotypes showing similar combining ability and heterotic response when crossed with a genetically distant group of genotypes (Melchinger and Gumber, 1998). Historically, heterotic groups were often created by geographic separation (naturally or anthropogenic). A larger heterosis was observed in genetically distant varieties (rice, *Oryza sativa* L., Xiao et al., (1995); rapeseed, *Brassica napus* L., Grant and Beversdorf (1985); rye, *Secale cereale* L., Hepting (1978); maize, *Zea mays* L., Reif et al., (2010)), since the chance of relatedness and therefore homozygosity and inbreeding depression are reduced is reduced (Shull, 1952).

Additionally, a larger genetic distance facilitates hybrid prediction. The additive variance increases with genetic distance between two varieties, increasing the additive to dominance variance ratio and therefore the general combining ability (GCA) variance to specific combining ability (SCA) variance ratio (Melchinger, 1999; Melchinger and Gumber, 1998; Reif et al., 2007; Schrag et al., 2006). A large σ^2_{GCA} to σ^2_{SCA} ratio enables early-testing, while small ratios require late-testing to cover these dominance effects (Melchinger et al., 1987).

Evaluation of diversity patterns

Characterization studies are meant to address two important objectives. First, creating passport data for undescribed cultivars, for example from genebank collections. These accessions are potential plant genetic resources that can be useful for breeders. They might contain untapped alleles that can be harnessed to enrich a breeding program by increasing the genetic variance or with specific traits (e.g. disease resistance).

Second, characterizing the existing diversity is especially important, if heterotic patterns are unknown. Melchinger and Gumber (1998) recommend grouping varieties based on phenotype, genotype, pedigree and geographic origin as a starting point to facilitate heterotic grouping substantially. Based on this information it is possible to design diallel crosses to study combining ability patterns among genotypes and to identify initial combining ability groups.

Despite significant endeavors in pearl millet considering diversity and heterotic grouping, research is still in a comparably early stage. Phenotypic and genotypic diversity of any crop is usually the largest in its center of origin, which also applies to the highly out-crossing crop pearl millet. Numerous studies confirmed a great diversity for various agro-morphological traits like flowering time, panicle and grain characteristics including nutritional value, tolerance or resistance to drought, pests and diseases using morphological or molecular markers (Bashir et al., 2014b; Bhattacharjee et al., 2007; Pucher et al., 2014, 2015; Stich et al., 2010; Upadhyaya et al., 2011). Some of these studies were able to group cultivars by pheno- or genotype, often related to geographic origin, but it was not possible to draw conclusions regarding heterotic grouping (Stich et al., 2010; Pucher et al., 2015).

Several studies evaluated relatedness among Indian CMS-based hybrid parents in which maintainer (B) and restorer (R) lines were mostly grouped in separate clusters (Gupta et al., 2017; Ponnaiah et al., 2019). Gupta et al. (2015) detected additional subgroups within each cluster. They also observed decreasing genetic distance between B- and R-lines over time, suspecting the involvement of common parents. Despite these findings, none of these studies was successful in identifying distinct heterotic groups. Varshney et al. (2017) found 170 promising candidates from 580 lines with a genomic hybrid prediction approach and proposed to use the respective lines as initial heterotic pools.

Systematical heterotic group development

In maize, the basis for the European Flint pool, being genetically distinct from the US Dent pool, was initially created, when Christopher Columbus brought maize from the Americas to Europe (Rebourg et al., 2003). In rice, existing subspecies (*O. sativa* ssp. *indica*, ssp. *javanica* and ssp. *japonica*) serve as heterotic groups (Melchinger and Gumber, 1998; Xiao et al., 1995). However, without already existing groups, heterotic patterns have to be developed systematically. The two large subgroups within the US Dent pool, Stiff Stalk and Non Stiff Stalk, were created based on pedigree information and combining ability studies over several decades (Duvick et al., 2004). Based on the work of Shull (1908, 1909, 1910) and Jones (1918), homogeneous lines and subsequently hybrids were developed. The severe inbreeding depression in maize at the beginning of line development increased seed costs tremendously. This led to the development of double-cross hybrids to increase seed multiplication (Jones, 1922), before a reduction of the genetic load allowed single-cross production. Hayes (1939) and Eckhardt and Bryan (1940) realized that the best hybrids originated from divergent lines. Stringfield (1947) emphasized the importance of developing lines within one group to maintain genetic variance between the groups. The groups were expanded by assigning inbreds to the initial groups (Hallauer, 1999) and recurrent selection methods (Hallauer et al., 1988). Similar methodologies were and are still used to detect and/or develop heterotic groups in rye (Hepting, 1978), rapeseed (Grant and Beversdorf, 1985), faba bean (*Vicia faba* L., Link et al., 1996) and wheat (*Triticum aestivum* L., Boeven et al., 2016).

As highlighted before, conditions in Sahelian Africa are very different. Heterotic groups are non-existent so far and many diversity studies failed to detect reasonable starting points due to the strong admixture among Sahelian pearl millets (Bashir et al., 2014c; Lewis, 2010; Pucher et al., 2015; Stich et al., 2010). To solve this issue, several combining ability studies have been conducted based on factorial or diallel mating designs. Ouendeba et al. (1993) evaluated five African pearl millet populations (Iniari from Togo, Mansori from Sudan, Ex-Bornu from Nigeria, Ugandi from Uganda and P_3Kollo from Niger) in a diallel design and found large heterosis and GCA effects for grain yield. Pucher et al. (2016) designed a ten × ten factorial with WA cultivars and observed a superiority of Nigerian × Senegalese or Nigerien × Senegalese cultivars regarding grain yield. These combining ability patterns have to be validated and investigated in detail in order to derive a unified strategy for pearl millet hybrid breeding in WA.

Objectives of this study

The overall goal of this thesis was to guide heterotic group development for sustainable WA pearl millet breeding. In particular, the specific objectives were to:

(i) facilitate efficient use of pearl millet gene bank accessions,

(ii) identify diversity patterns based on phenotypic and genetic relationships,

(iii) validate the yield superiority and stability of pearl millet population hybrids over OPVs,

(iv) derive a more comprehensive picture about combining ability patterns, and

(v) develop a unified strategy for heterotic grouping and sustainable hybrid breeding based on quantitative-genetic parameters and combining ability patterns.

Characterization of West and Central African accessions from a pearl millet reference collection for agro-morphological traits and Striga resistance

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Abstract

To promote the utilization of West and Central African (WCA) genetic resources of pearl millet [*Pennisetum glaucum* (L.) R. Br.], this study aimed at agro-morphological characterization of selected accessions from the pearl millet reference collection, established by the Generation Challenge Program and the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT). A total of 81 accessions were included, comprising 78 landraces originating from 13, pre- dominantly WCA countries and three improved cultivars. All 81 accessions were evaluated together with 18 checks for resistance to the parasitic weed *Striga hermonthica* (Del.) Benth. in an artificially infested field at one location in Niger. Determined by available seed quantity, 74 accessions were characterized together with seven checks in the rainy season 2009 in field trials under low-input and fertilized conditions in Nigeria, Niger and Mali, respectively. Wide ranges were observed for various traits. Several accessions were identified as sources for specific traits of interest, i.e. long panicles, high-grain density, earliness, Striga resistance and stable yielding across environments. The observed yield inferiority of all Genebank accessions compared with checks may indicate lost adaptation or inbreeding depression due to an insufficient effective population size during multiplication. A principal component analysis revealed an immense diversity but also strong admixture among the tested accessions, i.e. there were no clearly distinct groups. The seed of all genotypes is available from ICRISAT. The online availability of the characterization data is expected to facilitate efficient use of these pearl millet accessions by breeding programmes in WCA and worldwide.

Sattler, F.T., Sanogo, M.D., Kassari, I.A., Angarawai, I.I., Gwadi, K.W., Dodo, H., Haussmann, B.I.G., 2018. Characterization of West and Central African accessions from a pearl millet reference collection for agro-morphological traits and Striga resistance. Plant Genet. Resour. 16, 260–272. https://doi.org/10.1017/S1479262117000272

Identification of combining ability patterns for pearl millet hybrid breeding in West Africa

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Abstract

Diets of West African (WA) smallholder farmers are built on pearl millet [*Pennisetum glaucum* (L.) R. Br.]. Sustainable pearl millet hybrid breeding is challenging in WA, mostly due to an extensive genetic diversity combined with a high degree of admixture. In the absence of natural heterotic groups, understanding combining ability patterns can enable systematic development of heterotic groups and make sustainable hybrid breeding feasible. The objectives of this study were to evaluate heterosis and combining ability patterns and their relationship with genetic distance among WA pearl millets based on population hybrids, and to derive conclusions for future breeding programs. Therefore, 17 open-pollinated varieties (OPVs) were crossed in a diallel mating design and tested together with their offspring in nine environments over 2 yr in Niger and Senegal. Genetic distances between the OPVs were evaluated with twenty microsatellite markers. Average panmictic better-parent heterosis (PBPH) was 18% (1–47%) for panicle yield. A principal coordinate analysis based on genotyping results separated parental OPVs clearly by geographic origin. Although there was no relationship between genetic distance among OPVs and PBPH, we confirmed good combining ability among selected OPVs from Niger vs. Senegal. The identified cultivars (Nigerien CIVT, H80-10Gr, and Taram and Senegalese Thialack 2 and Souna 3) with high combining ability are recommended for founding divergent heterotic pools targeting long-panicle pearl millet hybrids. Our study shows the benefits of population hybrids and represents an important step to identify combining ability patterns and initial heterotic groups for WA pearl millet hybrid breeding.

Sattler, F.T., Pucher, A., Kassari Ango, I., Sy, O., Isaaka, A., Hash, C.T., Haussmann, B.I.G., 2019. Identification of combining ability patterns for pearl millet hybrid breeding in West Africa. Crop Sci. 59, 1590–1603. https://doi.org/10.2135/cropsci2018.12.0727

A unified strategy for West African pearl millet hybrid and heterotic group development

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Abstract

Smallholder farmers in Sahelian West Africa (WA) grow pearl millet (*Pennisetum glaucum* (L.) R. Br.) as staple cereal in harsh and highly variable environments, predominantly relying on landraces or open-pollinated varieties (OPV) with an average grain yield of 648 kg ha-1 (2017). Encouraging initial results with experimental pearl millet population or topcross hybrids and the available diversity in its WA center of origin offers a great opportunity for a regionally coordinated hybrid breeding approach. This review is therefore meant to summarize information on pearl millet hybrid breeding with emphasis on WA and to suggest a unified strategy as way forward. Observed average better-parent heterosis ranged from 4 to 18% and 0 to 88% in population and topcross hybrids, respectively, across several studies, and the yield stability was comparable or better relative to the parental OPVs. Diversity and combining ability studies pointed at eastern and western WA as promising starting points for systematic development of heterotic groups. Building on respective groups, reciprocal recurrent selection (RRS) in combination with integration of further adapted genetic resources is recommended to systematically diversify and build up the heterotic parental pools, increase combining ability to the opposite group, and create a continuous output of OPV and hybrid varieties. Molecular markers supporting cytoplasmic male sterility (CMS) introgression are available, and genomic tools can improve hybrid prediction. Regarding the unpredictability and intensity of biotic and abiotic stresses, heterogeneous population and topcross hybrids appear most suitable to sustainably increase pearl millet yields and give maximal benefits to WA farmers.

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General Discussion

Despite being the sixth most widely cultivated cereal in the world in terms of acreage (Khairwal et al., 2007), pearl millet was neglected over decades and is still considered as an orphan crop by some researchers (Debieu et al., 2017). The African Orphan Crops Consortium (AOCC, 2019) does not list pearl millet and the term orphaned crop should be abandoned considering the advances in pearl millet breeding, comprehensively reviewed by Serba et al. (2017). However, these advances contributed to a large yield increase in India and the US, while yield levels almost stagnated in WA (FAO, 2017). Environmental challenges, a weak public and an almost non-existent private seed sector are largely contributing to this difference between developing and developed countries, and least developed countries (Poku et al., 2018; Tripp and Rohrbach, 2001; World Bank, 2016).

Handling WA environments – large- and small-scale variability

A high inter-annual variability, as already highlighted in the introduction, largely affects the genotype (G) × environment (E) interaction. Our studies confirmed the tremendous importance of G × E interactions for variety testing and development in the WA target environment (Sattler et al., 2018, 2019). A better understanding of this large-scale variability requires a better understanding of the G × E variance. In Sattler et al. (2018) we dissected the G × E variance further into G × location, G × fertilizer and the threefold interaction variance, with G × location being the largest. Gemenet et al. (2016) separated the total G × E into G × (location × year), G × phosphorus (P) and G × (location × year) × P, where P represents two soil phosphorus levels. The soil P hardly influenced the total G × E interaction variance, although direct selection for P efficiency under low P conditions was more efficient than indirect selection under high P conditions. In Sattler et al. (2019) we observed the largest differences between years at the same locations. Likewise, Bashir et al. (2014a) observed a large G × year and G × location × year interaction variance, while G × location interaction variance played a minor role across the rainfed test locations. In all studies, the amount and distribution of precipitation highly influenced the determination of the G × E interaction variance. However, it was impossible to estimate all interactions of the genotypes with the multitude of possible environmental influences, and precipitation cannot explain the total interaction variance on its own. Breeding for specific stress environments requires a particular genotype/variety with the optimum stress response (Mittler, 2006). However, large inter-annual year effects and the non-repeatable mega environments across years (Bashir et al., 2014a; Pucher et al., 2016; Sattler et al., 2019, 2018) render this goal impossible for pearl millet breeders in WA. Instead, it is necessary to develop varieties with a broad yield stability across environments.

In addition to genotypic interactions with locations, soil treatments and years (Sattler et al., 2019, 2018), it is interesting to address micro-variability within single environments. Beside the diallel trials (Sattler et al., 2019), we evaluated a set of single-cross, top-cross and population crosses in similar environments (same years, same locations, different fields). These trials were meant to illuminate the capability of different hybrid types to cope with the high G × E interaction in WA and to compare their yield stability. These trials were even more affected by environmental hazards such as flooding and drought stress than the diallel trials. This led to a large field variability and subsequently to a substantial residual error variance, so that the data set had to be discarded entirely. High variability within a single field is common in WA and an enormous challenge for breeders, since it ultimately reduces repeatability estimates and complicates the interpretation of the field data (Voortman et al., 2004).

We evaluated the two trials (diallel and stability) each in nine similar environments over two years in the same locations (Sattler et al., 2019; Sattler, unpublished data, 2019). The Senegalese environments received a high precipitation and the field variability was relatively low. Unfortunately, this was usually not the case in the Nigerien environments. We observed flooding due to a proximity to the river Niger with a strong gradient of the negative effect from the one side, facing the river, to the other side of the field. Another field experienced erratic rainfalls leading to a stream of water flowing through the field, even shifting entire plots. In one field, data from one entire replication was lost, due to a combination of strong rainfalls and a supposedly water-impermeable soil horizon. Finally, in several occasions we observed several large termite mounds that destroyed multiple adjacent plots at once. Generally, a high small-scale variability regarding available soil nutrient content and overall plant growth in WA was described in several studies (Brouwer et al., 1993; Lamers and Feil, 1995; Leiser et al., 2012; Voortman et al., 2004).

Controlling this micro-variability is crucial and requires knowledge about specific local conditions. We tried to achieve this by optimizing an alpha lattice design with small blocks for spatial adjustment. Field gradients were supposed to be controlled with the two-dimensional blocking along rows and columns across all replications, while small blocks covered the micro-variance. The R package DiGGer (NSW DPI, Wagga, Australia) was used to design the two-dimensional blocked alpha lattice. Due to the unavailability of a coherent area in five out of nine locations, we had to separate the single replications, which deterred us from applying the spatial design. Nevertheless, we applied one- and two-dimensional autoregressive models of the first order (AR1 × AR1) (Gilmour et al., 1997) with row and column factors in the single environment analysis. Including these effects was only beneficial in three environments, where replications were planted side-by-side and a strong gradient was observable. Analyzing the data in a one-step approach across all environments finally nullified the small effects of the spatial adjustment, when regarding the heritability estimates. Where possible and reasonable, we organized four plots in a two by two pattern, leading to an unusual block shape of 9.6 m × 3 m, while the short width was oriented in the direction of the gradient within the field. Although it was not possible to compare our block size and shape with another design, it became obvious that we managed to cover the field variability quite well in almost all environments, where the diallel trials were evaluated. While spatial models have proven their advantages in controlling field variability, it is more important to put time and effort into a suitable blocking. Likewise, Leiser et al. (2012) recommended the AR1 × AR1 model for sorghum breeding under WA conditions. However, at the same time, they also emphasized the relevance of a suitable field design and blocking.

This detailed description is meant to depict the difficulties a breeder has to face in reality, while scientific articles often explain difficult environmental conditions only briefly. Under such conditions, it is important to be aware of different field designs, statistical approaches, supporting data (e.g. soil conditions) and the necessity of having more than one replication or at least repeated check cultivars within one field.

Essential traits and where to find them

We evaluated the relevance of several agro-morphological traits for yield performance in our studies (Sattler et al., 2018, 2019). Early seedling establishment was always beneficial and early flowering was associated with an increased yield level in environments with limited precipitation, especially terminal drought (Gemenet et al., 2016, 2015a; Pucher et al., 2015; Sattler et al., 2019, 2018; Sattler, unpublished data, 2019). However, a longer period between sowing and flowering allows pearl millet to accumulate more biomass (Pucher et al., 2015), increasing the potentially attainable grain yield. This higher potential grain yield can be realized if sufficient precipitation is available (Sattler et al., 2018). Varieties with a longer time to flowering can be found in the Sudanian zone of WA, while early-flowering varieties are more prominent in the Sahelian zone (Padilla, 2007; Pucher et al., 2015; Upadhyaya et al., 2016). Interestingly, extra-early varieties are also common in Sudanian Togo and Ghana (Pucher et al., 2015; Sattler et al., 2018; Upadhyaya et al., 2016). On the other hand, more humid environments require more downy mildew resistant pearl millet varieties (Sattler et al., 2018). This trait is more difficult to assess, due to a large G × E interaction and high pathogen variability (Kountche et al., 2013), and results are sometimes contradictory (Pucher et al., 2015; Upadhyaya et al., 2016). Nevertheless, both studies found high frequencies of promising downy mildew resistance sources. Especially Mali, the center of origin of pearl millet (Burgarella et al., 2018; Manning et al., 2011), seems to be promising to find downy mildew resistance sources (Padilla, 2007; Sattler, unpublished data, 2018; Upadhyaya et al., 2016). Likewise, a Striga resistance trial found the most resistant variety originating from Mali (Sattler et al., 2018). However, this has to be verified in multi-environment trials. The highly variable precipitation can also lead to sudden drought stress and a subsequent reduction of P-uptake (Hash et al., 2002; Sinclair and Vadez, 2002) making P-uptake and use efficiency even more important. A large variation for P-uptake and use efficiency is present in WA (Gemenet et al., 2014, 2015b, 2015a, 2016), but the geographical distribution has not been evaluated, yet. These characterization studies are crucial to facilitate selecting adequate cultivars for region-specific variety development.

Pearl millet hybrids as a chance for WA subsistence farmers

Potential of pearl millet hybrids for WA

Ouendeba et al. (1993) were the first to describe population hybrids in WA pearl millet. These hybrids showed an impressive potential with a panmictic better-parent heterosis (PBPH) of 44% on average, ranging from 25 to 81%. Several population hybrid studies followed, observing positive average PBPH ranging from 4 to 18%, while some hybrids yielded an impressive 62% more than their superior parent (Dutta, 2019; Pucher et al., 2016; Sattler et al., 2019; Sattler, unpublished data, 2019). The parental per se performance played a major role for creating high yielding population hybrids (Dutta, 2019; Ouendeba et al., 1993; Presterl and Weltzien, 2003; Pucher et al., 2016; Sattler et al., 2019; Sattler, unpublished data, 2019).

A second option for harsh drylands across India and Sahelian Africa are topcross hybrids (Bidinger et al., 1994, 2005; Kanfany et al., 2018; Mahalakshmi et al., 1992; Yadav et al., 2000).

These studies are reporting an average heterosis relative to the population pollinator parent from 0 to 80% across test environments.

High-yielding single-cross hybrids are common in large parts of India, since the required expertise, resources, a well-established seed industry, a cytoplasmic male sterility (CMS) system in adapted germplasm, and elite lines are available (Dave, 1986; Kumara Charyulu et al., 2014; Serba et al., 2017; Yadav and Rai, 2013). A recent study including two large sets of inbred testcrosses showed average mid-parent heterosis (MPH) of 77% and 86% per set, respectively (Gupta et al., 2017). A rare example of single-cross evaluation in WA observed an average MPH of 39% (Gemenet et al., 2014). However, these heterosis levels are difficult to compare with the topcross and population hybrid studies, since the heterosis is estimated relative to an inbred and not an OPV parent.

Different hybrid types for different conditions

Cultivation of single-cross hybrids would be very risky for WA subsistence farmers, due to highly variable environments (Haussmann et al., 2012; Oosterom et al., 1996; Weltzien-R et al., 1998). The uniformity of single-cross hybrids makes them vulnerable to all kinds of environmental stresses and pests (Bidinger et al., 2008). Large G × E interaction variance estimates are common in WA and it has proven difficult/impossible to define repeatable mega-environments (Pucher et al., 2016; Sattler et al., 2018, 2019). Finding the appropriate hybrid type with sufficient heterosis and stability for WA conditions is crucial. Heterosis effects are sufficiently large in OPV-derived population and topcross hybrids and the heterogeneity improves yield stability in contrast to homogeneous single-cross hybrids (Mahalakshmi et al., 1992; Ouendeba et al., 1993; Bidinger et al., 1994, 2005; Presterl and Weltzien, 2003; Pucher et al., 2016; Sattler et al., 2019). Readily available, locally adapted improved OPVs can be used to develop population hybrids or topcross hybrids when combined with publicly available male-sterile seed parents (Bidinger et al., 2005; Sattler et al., 2019; Talukdar et al., 1999).

Understanding diversity patterns

Multiple studies are pointing at WA as the center of origin for pearl millet, indicating a large phenotypic and genotypic diversity, and on-going gene flow to wild relatives (Bashir et al., 2014b; Brunken et al., 1977; Burgarella et al., 2018; Diack et al., 2017; Gemenet et al., 2015b, 2015a; Manning et al., 2011; Mariac et al., 2006; Pucher et al., 2015; Sattler et al., 2018; Tostain and Marchais, 1993; Upadhyaya et al., 2011). ICRISAT puts great efforts in conserving this diversity with a collection of 23,092 pearl millet germplasm accessions including 809 wild relatives from 52 countries (Upadhyaya et al., 2016).

Several phenotypic and genotypic studies described the high degree of admixture in pearl millets in Sahelian Africa and especially WA (Bashir et al., 2014b, 2014c; Padilla, 2007; Sattler et al., 2018; Tako et al., 2015). Several subgroups could be identified either clustered by origin or associated with specific traits (Diack et al., 2017; Gemenet et al., 2015b; Sattler et al., 2019; Stich et al., 2010). Indian seed and pollinator parents hybrid parents were mostly clustered into separate groups (Gupta et al., 2017, 2015; Ponnaiah et al., 2019). However, none of these studies was able to define putative heterotic groups.

Understanding combining ability patterns

Without naturally existing genetically distinct groups, combining ability studies were necessary to identify starting points for heterotic groups. Ouendeba et al. (1993) made first conclusions about combining ability in WA pearl millet by intercrossing five improved landraces in a diallel mating scheme. They covered a large genetic variation with one variety each from Togo, Sudan, Nigeria, Uganda and Niger and observed large GCA and heterosis effects.

This work was pursued in the mid-2000s with a diallel with six WA and one Sudanese cultivar (Dutta, 2019), a factorial with 10 Sub-Saharan cultivars (Sattler, unpublished data, 2019), a factorial with 20 WA cultivars (Pucher et al., 2016) and finally a diallel with 17 OPVs originating primarily from Niger and Senegal (Sattler et al., 2019).

As expected from the diversity studies, it was not possible to find clear heterotic groups, but the highest yielding hybrids were mostly derived from Niger/Nigeria x Senegal/Mauritania crosses, while Malian varieties seem to combine well with both of these groups. Specific varieties with a high *per se* performance and GCA produced high-yielding offspring. Senegalese Thialack 2 and Souna 3, and Nigerien CIVT, H80-10Gr and Taram, are a promising start to diverge the WA germplasm into distinct pools.

Predicting hybrid performance

Increasing the genetic distance will also improve hybrid prediction accuracy by increasing the σ^2_{GCA} to σ^2_{SCA} ratio, which translates into a more prominent additive variance (Jumbo and Carena, 2008; Melchinger, 1999; Melchinger and Gumber, 1998; Reif et al., 2007; Schrag et al., 2018, 2006; Technow et al., 2014).

Reducing the range of geographic distance and therefore, potentially the genetic distance of evaluated cultivars from Sahelian Africa to WA and finally to Niger and Senegal made initial heterotic group recommendations possible (Dutta, 2019; Ouendeba et al., 1993; Pucher et al., 2016; Sattler et al., 2019). However, it also reduced the σ^2_{GCA} to σ^2_{SCA} ratio, impeding GCA based hybrid prediction (Melchinger et al., 1987). Building groups based on selected cultivars from eastern WA and western WA with a high GCA and *per se* performance and continuously diverging these groups to initiate heterotic grouping in WA pearl millets seems promising.

Modern breeding tools to accelerate hybrid breeding

Phenotyping large number of test-crosses is a major limitation for hybrid prediction (Bernardo, 1994), especially in WA, where highly variable environments require large MET to asses GCA and SCA (Dutta, 2019; Ouendeba et al., 1993; Pucher et al., 2018, 2016; Sattler et al., 2019). Molecular markers and especially genomic selection can support phenotypic evaluation and accelerate hybrid prediction considerably (Bernardo, 1998; Crossa et al., 2017; Meuwissen et al., 2001).

Zhao et al. (2015a) found heterotic patterns in rice using a three-step genomic selection based approach to identify groups. Varshney et al. (2017) adopted this step-wise approach to predict pearl millet single-cross hybrid performance and identified two sets of lines whose offspring are having an 8% above average yield. Genomic selection research still requires large funds, limiting the application to mostly private companies and well-funded public research institutes (Zhao et al., 2015a). However, genomic selection is a valuable option to support heterotic grouping (Varshney et al., 2017)

Utilizing CMS in WA pearl millet hybrid production

CMS is a central aspect of commercial hybrid seed production by inhibiting pollen production to prevent self-pollination (Duvick, 1959; Schnable and Wise, 1988; Wise and Pring, 2002). The discovery of the Tift A1 CMS source marked the start of pearl millet single-cross hybrid breeding (Burton, 1958; Christensen et al., 1984). Many of these Tift23A lines went into the Indian pearl millet hybrid breeding programs (Andrews et al., 1993). Soon it became necessary to find alternative CMS sources, since they are highly susceptible to downy mildew (Safeeulla, 1977; Serba et al., 2017). The A_2, A_3 and $A_{\text{ß}}$ CMS sources were discovered soon (Appadurai et al. 1982; Burton and Athwap, 1967), but the first reliable alternatives were the A_4 and A_5 CMS systems (Rai et al., 2009, 2001).

CMS maintainer alleles are common in WA germplasm (Bachir Bounou, 2011; Rai et al., 2009) and maintainer versions of existing populations can be developed via recurrent selection methods (Rai et al., 2000). Fertility restoration genes are far less common and screening of OPVs for fertility restoration ability is challenging and still on-going (Rai et al., 2006).

Recently, Pucher et al. (2018) suggested screening WA germplasm for A_4 male-fertility restoration genes or transferring them via backcrossing into WA adapted material with marker assisted selection. Inheritance of the A_4 male-fertility restoration genes is most likely dominant and monogenic (Gupta et al., 2012). Phenotypic data from Pucher et al. (2018) supported a dominant inheritance, but their QTL analysis for pollen production and selfed seed set explained only 14.5% and 9.9% of the phenotypic variance, respectively. This led to the conclusion that, additionally to this major QTL, minor or modifying genes are present.

Nevertheless, their developed competitive allele specific PCR (KASP) markers for male fertility restoration in the A_4 CMS system have the potential to facilitate the development of distinct male and female heterotic groups. They still need to be validated, but will allow breeders to focus on other relevant restorer and maintainer characteristics like pollen shedding and seed set or seed size.

A unified framework for sustainable pearl millet hybrid breeding and heterotic grouping in WA

The third thesis manuscript describes a comprehensive strategy for systematic WA pearl millet heterotic pool and variety development (Sattler & Haussmann, 2020). The first two tasks have already been completed and starting points for initial combining ability groups were identified:

1. Evaluation of diversity found initial patterns (Bashir et al., 2014c; Lewis, 2010; Pucher et al., 2015; Sattler et al., 2018, 2019; Stich et al., 2010).
2. Combining ability studies revealed that eastern WA and western WA cultivars form loose groups that combine well with each other (Dutta, 2019; Pucher et al., 2016; Sattler et al., 2019; Sattler, unpublished data, 2019).

The following steps (three and four) are necessary to diverge the two groups and create distinct heterotic groups, and to develop superior pearl millet hybrids.

3. Initiating a inter-population reciprocal recurrent full-sib selection (RRS) (Comstock et al., 1949; Jones et al., 1971) program, possibly supported by modern breeding tools (e.g. genomic selection, Zhao et al., 2015b), to diverge the two groups further, while

improving the intra-pool *per se* performance. This continuous diversification of both pools by RRS and introgression of new material into each pool separately based on genetic distance and combining ability allows distinct female and male pool development, line development and introgression of a CMS system.

4. Creating OPVs and population hybrids early (Pucher et al., 2016; Sattler et al., 2019) and aiming for long-term development of topcross hybrids from improved OPVs and newly derived lines (Bidinger et al., 2005) is possible alongside to the heterotic pool development. Additionally, the RRS lays the foundation for possible future single-cross hybrid breeding programs.

Pursuing this framework requires long-term commitment and is highly ambitious, but it will advance WA hybrid breeding substantially. However, it will only impact the livelihood of WA subsistence farmers if integration into the agricultural production systems is successful. Establishing or strengthening seed sectors and improving the poor infrastructure, especially in rural areas are a great challenge (Ceccarelli et al., 2009). National and international research institutes have to involve farmer cooperatives from the beginning to overcome this issue and increase the low adoption rates (Christinck et al., 2014; Weltzien et al., 2006).

A common concern, when recommending hybrid varieties to subsistence farmers is their dependency on large seed companies and the necessity to buy expensive seeds annually. This fear can be rebutted, at least when regarding the current situation. First, WA pearl millet breeding is almost exclusively done by national and international public institutes. They are striving to support subsistence farmers instead of maximizing their profits. Second, topcross and especially population hybrids can be regrown without having to accept potentially large yield losses due to a drop of heterozygosity from the F1 to the F2 generation. Third, heterosis in all hybrid types is large enough to compensate the increased seed production costs easily (Sattler et al., 2019). Sorghum hybrid production in Mali, organized by farmer cooperatives, was very successful, and helped to double hybrid seed production annually over the last years (Kante et al., 2017). Strengthening farmer cooperatives according to the Malian example seems to be a promising approach for WA pearl millet.

Conclusions and implications for pearl millet hybrid breeding and heterotic pool development

This research is meant to guide WA pearl millet breeders in developing heterotic groups to increase yield levels substantially. The main findings of the three studies (Sattler et al., 2019, 2018; Sattler & Haussmann, 2020) were:

- Germplasm collections, like the ICRISAT genebank are fundamental to maintain the rich genetic diversity in pearl millet and to allow breeders its employment.
- There is significant genetic variation for specific traits of interest, i.e. long panicles, high-grain density, earliness, Striga resistance, high yield potential and high yield stability across environments in West and Central African (WCA) pearl millet.
- Local adaption is crucial for yield stability and has to be preserved. Local adaption can be lost, possibly during the *ex situ* conservation and regeneration.
- Phenotypic diversity studies are unable to identify clearly distinct germplasm groups among WCA pearl millets.
- Genotypic diversity studies are suitable to separate genotypes by origin without making conclusions about heterotic grouping.
- Population hybrids are generally superior to their parents regarding yield and yield stability.
- Heterosis in population hybrids is potentially large enough to justify increased seed costs and to start production on a commercial scale.
- Hybrid performance is largely dependent on parental *per se* performance.
- Combining ability among selected OPVs from Niger vs. Senegal is superior to combining ability compared to other inter-country crosses.
- Selected genotypes with high GCA and *per se* performance from eastern and western WA, respectively, are promising founder populations for heterotic groups (e.g. Nigerien CIVT, H80-10Gr, and Taram and Senegalese Thialack 2 and Souna 3).
- Initiating a RRS program will diverge the two groups further, while improving the inter-pool *per se* performance at the same time.
- Distinct female and male pools, a CMS system and line development have to be established.
- Modern breeding tools (e.g. genomic selection and marker-assisted selection) can be applied to support hybrid prediction and CMS introgression and to accelerate heterotic grouping.
- Population hybrids can be developed almost instantly and topcross hybrids within a few years to benefit WA subsistence farmers.

Summary

We share this planet with more than 7.5 billion people and the world population is constantly growing. The number of people is expected to remain almost constant in developed countries, while an immense population growth can be observed for West Africa (WA). Today there are more than 400 million people living in WA and the population is expected to reach more than 1.1 billion people in 2070. The entire agricultural sector contributed 29% to the total GDP in WA, ranging from 6% in Cape Verde to 60% in Sierra Leone in 2017. However, these numbers underestimate the importance of agriculture in WA since most of subsistence farmers' products do not enter markets and it is difficult to quantify the amount of people that rely on subsistence farming. Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is a staple crop for more than 90 million subsistence farmers, mostly in the drylands of Sub-Saharan Africa and India. It is primarily grown for human consumption and possesses good nutritional properties, and provides additionally fodder and building material. In drought prone regions where maize (*Zea mays* L.) and even sorghum (*Sorghum bicolor* L. Moench) would fail, pearl millet is still capable of producing grain. It is commonly grown in regions with 300 – 500 mm of precipitation and low soil phosphorus levels, and survives temperatures of more than 42°C. Pearl millet is a highly heterozygous diploid ($2n = 2x = 14$) C4 plant species. Its predominantly allogamous nature caused by protogynous flowering in combination with windborne pollen that survives Sahelian conditions easily results in outcrossing rates of more than 70%. Radiocarbon dating of grain residues found in the lower Tilmesi Valley in northern Mali and whole genome data of present-day cultivars lead to the conclusion that pearl millet originated in WA ~2500 BCE, before spreading over Sahelian Africa and already in ~2000 BCE to India.

Despite being the sixth most widely cultivated cereal in the world in terms of acreage, pearl millet was neglected over decades and is still considered as an orphan crop by some researchers. However, great advances were made in pearl millet breeding that contributed to a large yield increase in India and the US, while yield levels almost stagnated in WA. Challenging, highly variable environments, especially regarding inter-annual rainfall distribution, requires heterogeneous cultivar types with a reliable yield stability. Additionally, a weak public and an almost non-existent private seed sector are largely contributing to this difference between developing and developed countries, and least developed countries. The overall goal of this thesis was to guide heterotic group development for sustainable WA pearl millet breeding. In particular, the specific objectives were to (I) facilitate efficient use of pearl millet gene bank accessions, (II) identify diversity patterns based on phenotypic and genetic relationships, (III) validate the yield superiority and stability of pearl millet population hybrids over OPVs, (IV) derive a more comprehensive picture about combining ability patterns, and (V) develop a unified strategy for heterotic grouping and sustainable hybrid breeding based on quantitative-genetic parameters and combining ability patterns.

A total of 81 accessions acquired from the pearl millet reference collection and originating from 13, predominantly West and Central African countries, was evaluated for resistance to *Striga hermonthica* (Del.) Benth. in one artificially infested field in Niger. A subset of 74 accessions was characterized in the rainy season 2009 in multi-environment trials (MET) under low-input and fertilized conditions in Nigeria, Niger and Mali, respectively. The general superiority of local check varieties compared to the genebank accessions highlighted the importance of local adaptation, possibly lost during the *ex situ* conservation and regeneration. Nevertheless, the development and preservation of germplasm collections *ex situ* are important to maintain the rich genetic diversity in pearl millet. The MET identified several accessions as sources for specific traits of interest, i.e. long panicles, earliness, Striga resistance, high yield potential and yield stability across environments. The trials revealed an immense diversity but also strong admixture among the tested accessions and it was not possible to determine distinct groups.

This extensive genetic diversity combined with a high degree of admixture makes sustainable pearl millet hybrid breeding challenging in WA, and underlines the need to study combining ability patterns in order to develop heterotic groups. Therefore, 17 WA open-pollinated varieties (OPVs) were crossed in a diallel mating design and tested together with their offspring in nine environments over two years in Niger and Senegal. Results from these MET justified population hybrid development by verifying large heterosis effects with an average panmictic better-parent heterosis (PBPH) of 18% (1–47%) for panicle yield. Distinct interactions of the trial environments with the tested genotypes and a large G × E interaction variance were confirmed. It was not possible to define a repeatable mega-environment on a biannual level. Importantly, yield stability was more pronounced in the population hybrids compared to their parental OPVs. Furthermore, combining ability patterns revealed a superior combining ability among selected OPVs from Niger *vs.* Senegal. The evaluated OPVs were clearly grouped by origin based on modified Roger's distance determined by microsatellite markers. Nevertheless, there was no significant relationship between genetic distance among OPVs and PBPH.

These findings together with initial results from experimental pearl millet population or topcross hybrid varieties have been promising. Heterosis effects are sufficiently large, while the heterogeneity is expected to assure a reliable yield stability. Together with the available pearl millet diversity in its WA center of origin, this offers a great opportunity for a regionally coordinated hybrid breeding approach. To suggest a way forward for pearl millet breeders in WA, a unified strategy was developed with a continuous output of different hybrid types, specifically tailored to this region. First, existing information about diversity and combining ability patterns should be used, building on observations that western WA and eastern WA cultivars form loose groups that combine well with each other. Selected genotypes with high general combining ability (GCA) and *per se* performance from eastern and western WA, respectively, are promising founder populations. Initiating a reciprocal recurrent selection (RRS) program, possibly supported by modern breeding tools (e.g. genomic selection), will diverge the two groups further, while improving the inter-pool *per se* performance at the same time. RRS in combination with continuous diversification of both pools allows distinct female and male pool development, line development and introgression of a cytoplasmic male sterility system. Creating OPVs and population hybrids early and aiming for long-term development of topcross hybrids from improved OPVs and newly derived lines is possible alongside to the heterotic pool development. Additionally, the RRS lays the foundation for possible future single-cross hybrid breeding programs. The suggested framework is highly ambitious and requires long-term commitment, vision and financial resources. Considering the flexibility regarding single steps and the possibility to develop different types of varieties at every stage of the pool diversification, it has the potential to enhance gains from selection and, with the continuous output of new high-yielding and stable cultivars, to improve the livelihood of WA subsistence farmers substantially.

Zusammenfassung

Wir teilen diesen Planeten mit mehr als 7,5 Milliarden Menschen und die Weltbevölkerung wächst ständig. In den entwickelten Ländern wird die Zahl der Menschen voraussichtlich nahezu konstant bleiben, während für Westafrika (WA) ein immenses Bevölkerungswachstum zu beobachten ist. Heute leben mehr als 400 Millionen Menschen in WA und die Bevölkerung wird im Jahr 2070 voraussichtlich mehr als 1,1 Milliarden Menschen erreichen. Der gesamte Agrarsektor trug 29% zum BIP in WA in 2017 bei, wobei der Anteil von 6% in Kap Verde bis 60% in Sierra Leone schwankte. Diese Zahlen unterschätzen jedoch die Bedeutung der Landwirtschaft in WA, da die meisten Produkte von Subsistenzbauern nicht gehandelt werden und es schwierig ist, die Anzahl der Menschen, die auf Subsistenzwirtschaft angewiesen sind, zu quantifizieren. Perlhirse [*Pennisetum glaucum* (L.) R. Br.] ist ein Grundnahrungsmittel für mehr als 90 Millionen Subsistenzbauern, hauptsächlich in den Trockengebieten Subsahara-Afrikas und Indiens.

Sie wird in erster Linie für den menschlichen Verzehr angebaut, besitzt gute ernährungsphysiologische Eigenschaften und dient zusätzlich als Tierfutter und Baumaterial. In dürregefährdeten Regionen, in denen der Anbau von Mais (*Zea mays* L.) und sogar Sorghum (*Sorghum bicolor* L. Moench) fehlschlagen würde, ist Perlhirse noch in der Lage, Körner auszubilden. Sie wird häufig in Regionen mit 300 - 500 mm Niederschlag und niedrigem Phosphorgehalt im Boden angebaut und übersteht Temperaturen von mehr als 42°C. Perlhirse ist eine hoch heterozygote, diploide (2n = 2x = 14) C4 Pflanzenart. Ihre überwiegend allogame Natur, die durch protogynes Blühen in Kombination mit flugfähigem Pollen, der sahelische Bedingungen leicht übersteht, verursacht wird, führt zu Auskreuzungsraten von mehr als 70%. Radiocarbondatierungen von Getreideresten im unteren Tilmesi-Tal im Norden Malis und Gesamtgenomdaten heutiger Kulturarten lassen den Schluss zu, dass Perlhirse ihren Ursprung ~2500 v. Chr. in WA hatte, bevor sie sich über Sahelzone Afrikas und bereits ~2000 v. Chr. nach Indien ausbreitete.

Obwohl Perlhirse, gemessen an der Anbaufläche, das sechstwichtigste Getreide der Welt ist, wurde sie über Jahrzehnte hinweg vernachlässigt und wird von einigen Forschern immer noch als wenig beachtete Kulturpflanze betrachtet. Es wurden jedoch große Fortschritte bei der Perlhirsezüchtung erzielt, die zu einem starken Ertragsanstieg in Indien und den USA beitrugen, während das Ertragsniveau in WA fast stagnierte. Anspruchsvolle, sehr variable Umwelten, insbesondere bezüglich der jährlichen Niederschlagsverteilung, erfordern heterogene Sorten mit einer zuverlässigen Ertragsstabilität. Darüber hinaus tragen eine schwache öffentliche und eine fast nichtexistierende private Saatgutwirtschaft weitgehend zu diesem Unterschied zwischen Entwicklungs- und Industrieländern auf der einen Seite, sowie den am wenigsten entwickelten Ländern auf der anderen bei. Das Hauptziel dieser Arbeit war es, die heterotische Gruppenentwicklung für eine nachhaltige WA Perlhirsezüchtung zu lenken. Die spezifischen Ziele waren insbesondere (I) die effiziente Nutzung von Perlhirsesorten aus Genbanken zu erleichtern, (II) Diversitätsmuster auf der Grundlage phänotypischer und genetischer Beziehungen zu identifizieren, (III) die Ertragsüberlegenheit und Stabilität von Perlhirsepopulationshybriden gegenüber OPVs zu validieren, (IV) die Erstellung eines umfassenderen Bildes über die Kombinationsfähigkeitsmuster und (V) die Entwicklung einer

einheitlichen Strategie für heterotische Gruppierung und nachhaltige Hybridzüchtung auf der Grundlage quantitativ-genetischer Parameter und Kombinationsfähigkeitsmustern.

Insgesamt 81 Genotypen aus der Perlhirse Referenzsammlung aus 13, überwiegend west- und zentralafrikanischen Ländern stammend, wurden auf Resistenz gegen *Striga hermonthica* (Del.) Benth. in einem künstlich infizierten Feld im Niger untersucht. Davon wurden 74 Genotypen in mehrortigen Versuchen (MET) unter gering und regulär gedüngten Bedingungen in der Regenzeit 2009 in Nigeria, Niger und Mali charakterisiert. Die allgemeine Überlegenheit der lokalen Standards gegenüber den der Genbank entnommenen Genotypen unterstrich die Bedeutung der lokalen Anpassung, die möglicherweise durch die *ex situ* Erhaltung und Regeneration verloren ging. Dennoch ist die Entwicklung und Erhaltung von Keimplasma-Sammlungen *ex situ* wichtig, um die reiche genetische Vielfalt der Perlhirse zu erhalten. Die MET identifizierten mehrere Genotypen als Quellen für spezifische relevante Merkmale, d.h. lange Rispen, Frühzeitigkeit, Striga-Resistenz, hohes Ertragspotenzial und Ertragsstabilität über allen Umwelten. Die Studien zeigten eine immense Vielfalt, aber auch eine starke Vermischung der getesteten Genotypen und es war nicht möglich, eindeutige Gruppen zu bestimmen.

Diese große genetische Vielfalt in Kombination mit einem hohen Grad an Vermischung macht eine nachhaltige Perlhirse Hybridzüchtung in WA schwierig und unterstreicht die Notwendigkeit, Kombinationsfähigkeitsmuster zu untersuchen, um heterotische Gruppen zu entwickeln. Daher wurden 17 WA offen bestäubte Sorten (OPVs) in einem Diallel-Paarungsschema gekreuzt und zusammen mit ihren Nachkommen in neun Umwelten über zwei Jahre im Niger und Senegal getestet. Die Ergebnisse dieser MET rechtfertigen die Entwicklung von Populationshybriden durch den Nachweis großer Heterosiseffekte mit einer durchschnittlichen panmiktischen Heterosis relativ zum besseren Elter (PBPH) von 18% (1-47%) für den Rispenertrag. Deutliche Interaktionen der Versuchsumwelten mit den getesteten Genotypen und eine große G × E Interaktionsvarianz wurden bestätigt. Es war nicht möglich, eine wiederholbare Mega-Umwelt über zwei Jahre zu definieren. Wichtig ist, dass die Ertragsstabilität bei den Populationshybriden stärker ausgeprägt war als bei den elterlichen OPVs. Darüber hinaus ergaben die Kombinationsfähigkeitsmuster eine überlegene Kombinationsfähigkeit bestimmter OPVs aus Niger *vs.* Senegal. Die evaluierten OPVs wurden, basierend auf der modifizierten Rogers Distanz, die durch Mikrosatellitenmarker bestimmt wurde klar nach Herkunft gruppiert. Dennoch gab es keinen signifikanten Zusammenhang zwischen dem genetischen Abstand zwischen OPVs und PBPH.

Diese Erkenntnisse sowie erste Ergebnisse aus experimentellen Perlhirse Populations- oder Topcross-Hybridsorten waren vielversprechend. Heterosiseffekte sind ausreichend groß, während die Heterogenität eine zuverlässige Ertragsstabilität gewährleisten kann. Zusammen mit der verfügbaren Perlhirsediversität in ihrer WA Ursprungsregion bietet dies eine große Chance für einen regional koordinierten Hybridzüchtungsansatz. Um den Perlhirsezüchtern in WA einen Weg nach vorne aufzuzeigen, wurde eine einheitliche Strategie mit kontinuierlicher Produktion verschiedener Hybridtypen entwickelt, die speziell auf diese Region zugeschnitten ist. Zunächst sollten bestehende Informationen über Diversität und Kombinationsfähigkeitsmuster genutzt werden, basierend auf Beobachtungen, dass Sorten aus westlichem WA und östlichem WA lose Gruppen bilden, die sich gut miteinander kombinieren lassen. Ausgewählte Genotypen mit hoher genereller Kombinationsfähigkeit (GCA) und

Eigenleistungen aus Ost- und West-WA sind vielversprechende Gründerpopulationen. Die Initiierung eines reziproken rekurrenten Selektionsprogramms (RRS), eventuell durch moderne Züchtungsmethoden (z.B. genomische Selektion) unterstützt, wird die beiden Gruppen weiter divergieren und gleichzeitig die Eigenleistung je Formenkreis verbessern. RRS in Kombination mit kontinuierlicher Diversifizierung beider Formenkreise ermöglicht die Entwicklung eines jeweils eindeutig weiblichen und männlichen Formenkreises, Linienentwicklung und Introgression eines zytoplasmatischen männlichen Sterilitätssystems. Neben der Entwicklung heterotischer Formenkreise ist es möglich, OPVs und Populationshybride frühzeitig zu erzeugen und auf eine langfristige Entwicklung von Topcross-Hybriden aus verbesserten OPVs und neu entwickelten Linien hinzuarbeiten. Darüber hinaus legt die RRS den Grundstein für mögliche zukünftige Zweiweghybridzüchtungsprogramme. Das vorgeschlagene Grundgerüst ist sehr ambitioniert und erfordert langfristiges Engagement, Voraussicht und finanzielle Ressourcen. In Anbetracht der Flexibilität der einzelnen Schritte und der Möglichkeit, verschiedene Sortentypen in jeder Phase der Formenkreisdiversifizierung zu entwickeln, hat es das Potenzial, die Selektionserfolge zu steigern und mit der kontinuierlichen Produktion neuer ertragreicher und stabiler Sorten die Lebensgrundlage der Subsistenzlandwirte in WA erheblich zu verbessern.

Resumé

Nous partageons cette planète avec plus de 7,5 milliards de personnes et la population mondiale ne cesse de croître. Le nombre de personnes devrait rester presque constant dans les pays développés, tandis qu'une croissance démographique très forte peut être observée en Afrique de l'Ouest (AO). Aujourd'hui, plus de 400 millions de personnes vivent en AO, et la population devrait atteindre plus de 1,1 milliard en 2070. L'ensemble du secteur agricole contribue à hauteur 29% au produit intérieur brut (PIB) total en AO, allant de 6% au Cap-Vert à 60% en Sierra Leone, en 2017. Cependant, ces chiffres sous-estiment l'importance de l'agriculture en AO, car la plupart ce qui est produit par les agriculteurs de subsistance n'entre pas sur les marchés, et il est difficile de quantifier le nombre de personnes qui dépendent de cette agriculture. Le mil [*Pennisetum glaucum* (L.) R. Br.] est une culture de base pour plus de 90 millions d'agriculteurs de subsistance, principalement dans les zones arides de l'Afrique subsaharienne et de l'Inde. Il est principalement cultivé pour la consommation humaine, possède de bonnes propriétés nutritionnelles et fournit en outre du fourrage et des matériaux de construction. Dans les régions sujettes à la sécheresse, où le maïs (*Zea mays* L.) et même du sorgho (*Sorghum bicolor* L. Moench) ne seraient pas productifs, le mil est capable de produire des grains. Il est couramment cultivé dans les régions avec entre 300 et 500 mm de précipitations et de faibles niveaux de phosphore dans le sol, et survit à des températures de plus de 42° C. Le mil est une plante C4 diploïde ($2n = 2x = 14$) et hautement hétérozygote. Sa nature principalement allogame conférée par sa protogynie, combinée avec un pollen éolien qui survit aux conditions sahéliennes, entraîne facilement des taux de croisement supérieurs à 70%. La datation au le carbone 14 de résidus de grains trouvés dans la basse vallée de Tilmesi, dans le nord du Mali, et les données génomiques des cultivars actuels ont révélé que le mil est originaire d'AO, environs 2500 avant notre ère, avant de s'étendre à l'Afrique sahélienne, et, déjà en environs 2000 avant notre ère, à l'Inde.

Bien qu'il soit la sixième céréale la plus cultivée au monde en termes de superficie, le mil a été négligé pendant des décennies, et est toujours considéré par certains chercheurs comme une culture orpheline. Cependant, de grands progrès ont été réalisés dans la sélection du mil. Ces progrès ont contribué à une forte augmentation des rendements en Inde et aux États-Unis, tandis que les niveaux de rendement ont presque stagné en AO. Avec des conditions environnementales difficiles et très variables, en particulier la distribution pluviométrique interannuelle, les producteurs ont besoin de cultivars hétérogènes, avec une stabilité de rendement fiable. En outre, un secteur public semencier faible et un secteur semencier privé presque inexistant contribuent largement à cette différence entre les pays en développement, les pays développés et les pays les moins avancés. L'objectif global de ce thèse était de guider le développement de groupes hétérotiques pour une sélection durable de mil en AO. Les objectifs spécifiques étaient de (I) faciliter une utilisation efficace des accessions de la banque de gènes du mil, (II) identifier les structures de diversité basées sur des relations phénotypiques et génétiques, (III) valider la supériorité de rendement et la stabilité des hybrides population de mil par rapport aux variétés à pollinisation libre (OPV), (IV) obtenir une tableau plus complet des modèles d'aptitude à la combinaison, et (V) développer une stratégie unifiée pour un groupement hétérotique et une sélection hybride durable, basés sur des paramètres génétiques quantitatifs et les modèles d'aptitude à la combinaison.

Quatre-vingt-un accessions acquises à partir de la collection de référence de mil, et provenant de 13 pays principalement d'Afrique de l'Ouest et du Centre, ont été évaluées pour leur résistance à *Striga hermonthica* (Del.) Benth. dans un champ infesté artificiellement au Niger. Un sous-ensemble de 74 accessions a été caractérisé au cours de l’hivernage 2009 dans des essais multi-locaux (MET), dans des conditions à faible teneur en intrant, et des essais fertilisés au Nigeria, au Niger et au Mali, respectivement. La supériorité générale des variétés « témoin » locales par rapport aux accessions issues de la banque de gènes a montré l'importance de l'adaptation locale, éventuellement perdue lors de la conservation et de la régénération ex-situ. Néanmoins, le développement et la préservation des collections de matériel génétique ex-situ sont importants pour maintenir la riche diversité génétique du mil. Le MET a identifié plusieurs accessions comme sources de caractères spécifiques d’intérêt, à savoir de longues panicules, la précocité, la résistance au Striga, un rendement potentiel élevé et une stabilité de rendement dans tous les environnements. Les essais ont révélé une immense diversité mais également un fort mélange parmi les accessions testées, et il n'a donc pas été possible de déterminer des groupes hétérotiques distincts.

Cette large diversité génétique, combinée à un haut degré de mélange, rend difficile la sélection durable d’hybrides de mil en AO, et souligne la nécessité d'étudier les modèles d’aptitude à la combinaison afin de développer des groupes hétérotiques. Par conséquent, 17 OPV d’AO ont été croisées selon un diallèle et testées avec leur descendance dans neuf environnements sur deux ans au Niger et au Sénégal. Les résultats de ces MET ont justifié le développement d'hybrides population en vérifiant les larges effets d'hétérosis, avec une meilleure hétérosis panmictique du meilleur parent (PBPH) de 18% (1–47%) pour le rendement en panicule. Des interactions distinctes des environnements où les essais étaient conduits avec les génotypes testés, et une grande variance de l'interaction G×E ont été confirmées. Il n'a pas été possible de définir un méga-environnement reproductible au niveau semestriel. Il est important de noter que le rendement des hybrides population était plus stable que celui de leurs parents OPV. En outre, les modèles d’aptitude à la combinaison ont révélé une capacité à la combinaison supérieure parmi les OPV du Niger par rapport à ceux du Sénégal. Les OPV évaluées ont été clairement regroupées par origine sur la base de la distance de Roger modifiée, déterminée par des marqueurs microsatellites. Néanmoins, il n'y avait pas de relation significative entre la distance génétique entre les OPV et les PBPH.

Ces résultats, ainsi que les premiers résultats d'une population expérimentale de mil ou d’hybrides topcross, sont prometteurs. Les effets d'hétérosis sont suffisamment importants, tandis que l'hétérogénéité devrait assurer une stabilité du rendement. Ceci, associé à la diversité du mil disponible dans son centre d'origine ouest africain, offre une excellente opportunité pour une approche de sélection hybride coordonnée au niveau régional. Pour suggérer une voie à suivre pour les sélectionneurs de mil en AO, une stratégie unifiée a été développée avec une production continue de différents types d'hybrides, spécifiquement adaptés à cette région. Premièrement, les informations existantes sur la diversité et les modèles d’aptitude à la combinaison devraient être utilisées, en s'appuyant sur les observations selon lesquelles les cultivars de l'ouest et de l'est de l’AO forment des groupes distincts qui se combinent bien. Des génotypes sélectionnés avec une aptitude générale à la combinaison générale (GCA) élevée et une performance per se de l'est et de l'ouest de l'AO, respectivement, sont des populations fondatrices prometteuses. Le lancement d'un programme de sélection récurrente (RRS),

éventuellement soutenu par des outils de sélection modernes (par exemple, la sélection génomique), séparerait davantage les deux groupes, tout en améliorant simultanément les performances per se inter-groupe. La RRS, en combinaison avec une diversification continue des deux groupes, permet le développement distinct du groupe femelle et mâle, le développement de lignées et l'introgression de la stérilité mâle cytoplasmique. La création précoce d'OPV et d'hybrides de population, visant le développement à long terme d'hybrides topcross à partir d'OPV améliorées et de lignées nouvellement dérivées, est possible parallèlement au développement d'un groupe hétérotique. De plus, la RRS pose les bases de futurs programmes de sélection hybrides simples. Le cadre proposé est très ambitieux et nécessite un engagement à long terme, une vision et des ressources financières. Compte tenu de la flexibilité concernant les étapes uniques et de la possibilité de développer différents types de variétés à chaque étape de la diversification du groupe hétérotique, il a le potentiel d'améliorer les gains à la sélection et, avec la production continue de nouveaux cultivars à haut rendement et stables, d'améliorer les moyens de subsistance des agriculteurs en AO.

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Curriculum Vitae

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Education

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2012 – 2014	MSc in Crop Sciences. Majors ‘Plant Breeding and Seed Science’. Thesis: ‘*Phenotypic and genotypic diversity of Abaca (Musa textilis Née) on Biliran Island, Philippines’*
2007 – 2012	BSc in Agricultural Sciences. Thesis: ‘*Calcium peroxide as oxygen source for the germination of hermetically sealed rapeseed*’
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