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Combining ability patterns among West African pearl millet landraces and prospects for pearl millet hybrid breeding

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ABSTRACT

Pearl millet (*Pennisetum glaucum* (L.) R. Br.) is an important hybrid crop in India. However, to date limited pearl millet hybrid development has been undertaken in West Africa (WA), which is the center of pearl millet origin and diversity and where this crop is most important outside India. Using a diverse set of WA pearl millet germplasm, objectives of this study were to determine the superiority of population hybrids over open-pollinated varieties for agro-morphological and agronomic traits in WA pearl millet germplasm; and (ii) to derive strategies for pearl millet hybrid breeding in WA, based on quantitative-genetic parameters, combining ability and heterotic patterns among geographically close *versus* distant pearl millet populations. A 10 × 10 factorial mating design was performed with four parental OPVs from each of five WA countries. The 100 population hybrids and their parents were tested for 14 traits at six locations in one year, thereby using contrasting locations to indirectly sample the rainfall variability inherent to WA pearl millet production environments. Grain yield showed an average panmictic midparent heterosis (PMpH) of 16.7%, ranging from −26 to 73%. The mean grain yield of hybrids based on inter-country crosses did not differ significantly from intra-country crosses. Geographic distance between parents was positively correlated with hybrid grain yield ($r = 0.31$), but not with PMpH . Some crosses between accessions from Niger/Nigeria and Senegal were outstanding. Predictability of population hybrid performance for grain yield was moderate based on midparent values ($r = 0.43$) and slightly better based on general combining ability (GCA) ($r = 0.56$). Overall, pearl millet hybrid breeding in WA seems very promising, but there do not seem to be clear “natural” heterotic groups among WA pearl millet landraces. Such heterotic groups as the basis of sustainable hybrid breeding need rather to be created systematically, by building on existing combining ability patterns and aiming to maximize combining ability between the groups.

1. Introduction

Pearl millet (*Pennisetum glaucum* (L.) R. Br.), the most heat tolerant and one of the most drought and salinity tolerant cultivated cereals, is a major food crop for smallholder subsistence farmers living on marginal agricultural lands in the semi-arid tropics of Africa and Asia. It is a highly cross-pollinated diploid, with 2n = 2x = 14 (Burton, 1974; Jauhar and Hanna, 1998), thus pearl mil-

Abbreviations: AMMI, Additive Main Effects and Multiplicative Interaction Model; CMS, cytoplasmatic male sterility; CP, compactness of panicles; DM, percentage of downy mildew infested hills; DSY, dry stover yield; FT, days to 50% flowering; G × E, genotype by environment; GCA, general combining ability; GY, grain yield; HI, harvest index; HP, hybrid performance; MP, midparent value; NKP, number of kernels per panicle; NPT, number of productive tillers per hill; OPV, open-pollinated variety; PC, panicle circumference; PBpH, panmictic better parent heterosis; pH, plant height; PL, panicle length; P_{max}, better performing parent; PMpH, panmictic midparent heterosis; SCA, specific combining ability; SV, seedling vigor; TKM, thousand kernel mass; VW, volumetric mass; WA, West Africa.

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let landraces represent heterozygous, genetically heterogeneous open-pollinating populations.

In India, pearl millet breeding programs have been developing hybrid cultivars since the 1960s; and these hybrids have been widely adopted by Indian farmers, especially in higher yielding environments. Together with improved crop management and agricultural input use, the introduction of hybrids contributed to a grain productivity increase from 305 kg ha^{-1} during 1951–1955 to 998 kg ha^{-1} during 2008–2012, registering an improvement of about 200% for pearl millet in India (Dave 1986; Yadav and Rai 2013). In contrast, West African (WA) pearl millet production is still predominantly based on landraces and did not increase substantially over the last decades. Estimated adoption rates for improved open-pollinated varieties (OPVs) range from 5% to 37% depending on the study and region (Christinck et al., 2014). Although limited pearl millet hybrid breeding has been undertaken by WA breeding programs for some time, there is no viable hybrid cultivar on the seed market yet. The initial success of pearl millet hybrids in India was due to commercially-viable single cross hybrids that yielded on average 20–30% more than adapted open-pollinated varieties of similar maturity (Andrews and Kumar 1992). Grain yields of hybrids have subsequently increased at >2% per year whereas those of OPVs stagnated (Yadav and Rai 2013) resulting in widespread adoption of hybrids in agro-ecologies where private-sector and/or public-sector breeding has focused on hybrids. Previous studies on African material reported about population hybrid performance. To describe the difference between a population hybrid and the mean of its two parental populations, the term panmictic midparent heterosis (PMpH) was introduced by Lamkey and Edwards (1999). This term will be used in the following to reflect the difference to the "conventional" midparent heterosis based on single crosses derived from homozygous inbred lines. Ouendeba et al. (1993) reported for African pearl millet a mean yield PMpH of 55% for a set of 10 WA population hybrids, while a mean heterosis of 8% was found by Bidinger et al. (2005) for Eastern African topcross hybrids.

Identification of heterotic patterns is the fundamental step for effective hybrid breeding seeking to exploit heterosis. In theory, heterotic groups are genetically distant to each other, are defined by their high combining ability when crossed, and should not be intercrossed for hybrid parent improvement (Melchinger and Gumber 1998). In some Indian pearl millet hybrid breeding programs, genotypes were not always explicitly allocated to either the female or male heterotic group, thus genetic intermixture has decreased the genetic distance between groups (Gupta et al., 2015). To avoid such inconsistencies in hybrid development, it is important to identify heterotic groups, where genotypes designated to one group will never be crossed to the other group for line development.

In WA, there have been only very limited systematic studies on population hybrids including diverse pearl millet populations or OPVs as parents. Previous pearl millet studies using genotypic and phenotypic data generally showed that genetically clearly distinct groups do not exist for WA pearl millet germplasm, rather a high degree of admixture was found (Bashir et al., 2014; Hu et al., 2015; Pucher et al., 2015). Similarly, Stich et al. (2010) did not observe clearly distinct clusters although they identified five subgroups using the software STRUCTURE (Pritchard et al., 2000) within a collection of 145 WA inbred lines genotyped with SSR markers. Gemenet et al. (2015) observed three subgroups in a diverse set of 155 WA pearl millet inbred lines based on DArT markers. The generally high degree of admixture found in the WA pearl millet germplasm is explained by the high outcrossing rate, variable planting dates, robust pollen, and long duration of the flowering growth stage within landraces and improved OPVs (Haussmann et al., 2007; Lakis et al., 2012), which results in overlapping flowering periods and gene flow even between early and late germplasm. Thus identification of initial putative heterotic groups does not seem straightforward by means of genetic diversity analysis. Although pearl millet is highly outcrossing, natural pollen flow should be localized within a certain geographic radius, thus a relation between genetic and geographic distance of landraces might be suspected. However, only a low association between geographic distance and dissimilarity measures has been detected. For example significant but low correlations were found by Pucher et al. (2015) using phenotypic data (r = 0.18), and by Mariac et al. (2006) using 25 microsatellite markers (r = 0.11). Similarly, based on whole-genome surveys with GBS markers, Hu et al. (2015) observed low but significant degrees of genetic similarity (as indicated by low F_{ST} values for accessions from two different countries) among pearl millet accessions originally collected from parts of Southern and Eastern Africa, and from Southwestern and South Asia, whereas higher F_{ST} values were observed between accessions from Senegal and those from surveyed countries in Southern and Eastern Africa and South Asia. The lowest observed F_{ST} values were observed when comparing accessions from Zimbabwe and South Africa. However, verification of the relationship between geographic distance of parental materials and heterotic response of the corresponding crosses is missing for pearl millet. None-theless, such relationships have supported heterotic grouping in other crops *e.g.* maize and ryegrass (Zheng et al., 2008; Posselt 2010).

Efficient breeding programs require an optimum allocation of resources, which is strongly dependent on the ratio of the genetic variance components, their environmental interactions, and the residual variance (Gordillo and Geiger 2008; Tomerius et al., 2008). Thus these quantitative-genetic parameters should be investigated at the beginning of a hybrid breeding program. Also the relationships between grain yield and other agro-morphological and phenological traits need to be investigated to enable analyses of trade-offs, a better understanding of mechanisms of adaptation and also to understand farmer preferences better.

So the main objectives of the present study were (i) to determine the superiority of population hybrids over open-pollinated varieties for agro-morphological and agronomic traits in WA pearl millet germplasm; and (ii) to derive strategies for pearl millet hybrid breeding in WA, based on quantitative-genetic parameters, combining ability and heterotic patterns among geographically close *versus* distant pearl millet populations.

2. Materials and methods

2.1. Plant materials

Four pearl millet populations (landraces or improved OPVs) each from five WA countries (Senegal, Mali, Burkina Faso, Niger and Nigeria) with early to medium maturity were randomly selected to develop 100 population hybrids using a ten × ten factorial mating design. The populations were part of a collection that was created jointly by the Institut de la Recherche pour le Developpement (IRD) and the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) during collection missions in 1976 and 2003. One earlier and one later flowering population/OPV from each country were used as female parents, and similarly for the male parents. Flowering time information was based on passport data from the accessions, and did not always hold true in our test and seed production environments. The 100 population crosses therefore represented intra-country and inter-country population crosses with variable geographic distance and partially variable flowering times among the parental populations. The population crosses were created in the irrigated offseason nursery of 2005/2006 at the ICRISAT Sahelian Center research station at Sadoré (Niger) using three sowing dates and profiting from the strong protogyny of pearl millet. At least 25 panicles from each female parent were pollinated