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Heterosis and combining ability among West African pearl millet improved and landrace varieties

Issaka Ahmadou^{1,2*}, Ofori Kwadwo², Gracen Edward Vernon^{2,3}, Danquah Yirenkyi Eric²

¹West African Centre for Crop Improvement (WACCI), University of Ghana Legon, Accra, Ghana / Institut National de la Recherche Agronomique du Niger (INRAN), Niger

²West African Centre for Crop Improvement (WACCI), University of Ghana Legon, Accra, Ghana Kofori@wacci.ug.edu.gh (O.K), edanquah@wacci.ug.edu.gh (D.Y.E)

³West African Centre for Crop Improvement (WACCI), University of Ghana Legon – Accra, Ghana / Cornell University USA vg45@cornell.edu

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Abstract

Heterosis and CA of sixteen hybrids developed from eight varieties belonging to two putative heterotic groups were studied. Entries were tested in two locations during two years in RCBD. Data on yield and productivity related traits were recorded. Eight hybrids outyielded the check which in turn performed better than the best parent. Hybrids were more stable than all of the parents. Parents HKB, Ankoutess, and Gamoji had the best GCA for grain yield. Gamoji x HKB, involving two parents with high and positive GCA, showed the highest SCA and the best mid-parent heterosis for grain yield. Ex-Borno, H80-10Gr, Moro, and HKP-GMS had negative GCA for grain yield, but the hybrids Ex-Borno x H80-10Gr and Moro x HKP-GMS showed high and positive SCA for this trait. Increased grain yield was found to be positively and highly correlated with peduncle girth while hybrids showed more phenotypic uniformity than their parents. Mean squares for GCA were significant for most traits underlining the importance of additive gene effects. The ratio GCA/SCA for grain yield was less than one indicating the prevalence of non-additive gene effects in the yield control. There was G x E interactions suggesting the necessity of further testing of the germplasm.

Keywords: Pearl millet, Hybrid, Heterosis, GCA, SCA, G x E.

Abbreviations: RCBD: randomized complete block design, CA: combining ability, GCA: general combining ability, SCA: specific combining ability, G x E: genotype by environment, ANOVA: analysis of variance, DNA: deoxyribonucleic acid.

INTRODUCTION

Continued improvement for grain yield and quality traits of pearl millet, the major cereal in Niger, is a high priority in breeding programs to provide food security for an increasing population (De Rouw, 2004, République du Niger, 2020). Hybrid breeding is the most cost effective way to increase the yield per hectare of this cereal (Vettriventhan *et al.*, 2008) while improving other qualitative traits such as plant uniformity (Falconer and Mackay, 1996), preferred by pearl millet growers. Successful hybrids require high levels of heterosis (Springer and Stupar,

2007). Heterosis or hybrid vigor is a natural phenomenon whereby hybrid offspring of genetically diverse individuals exhibit improved physical and functional features relative to their parents (Srivastava *et al.*, 2020). Phenotypic selection of parents for hybridization based on their performance *per se* alone may not always be a viable procedure, since phenotypically superior genotypes may yield inferior hybrids and/or poor recombinants in the segregating generations. It is, therefore, essential that parents are selected on the basis of their combining ability (Banerjee and Kole, 2009; Pucher *et al.*, 2016). GCA effects are due to additive and additive x additive gene actions and progeny performance is predictable from generation to generation (Falconer and Mackay, 1996). SCA,

*Corresponding author Email: ahmad455@yahoo.fr Cell phone: +227 9676 6271

controlled by non-additive genetic effects produces progeny whose performance is not predictable from generation to generation (Wricke and Weber, 1986). It is very important to identify parents with high GCA value for the trait to be improved because GCA is economically important in hybrid seed production as it influences the *per se* yield of parents and the female should have good yielding potential. Male parents should have good GCA and high tillering capacity which contributes to abundant and continued pollen shed (Andrews *et al.*, 1997; Talukdar *et al.*, 1999). However, since heterosis relies primarily on over dominance and epistatic gene interactions which are non-additive, GCA plays a lesser role in determining heterosis than does SCA (Syed and Chen 2005; Lanzhi *et al.*, 2008). The genotypic value of a given variety depends not only on the environmental conditions but possibly also on the effect of interaction of the given genotype and the considered environment. Because of this reason multi-environment trials are necessary to identify superior cultivars for a target region (Dehghani *et al.*, 2006; Bos and Caligari, 2008). The objectives of this research were to determine the combining abilities of eight improved varieties and landraces belonging to two supposed heterotic groups and to identify parents that will be involved in developing early to medium maturity and high-yielding F_1 hybrids for release.

MATERIAL AND METHODS

Eight open pollinated varieties belonging to two putative heterotic groups were used in this study. HKB, HKP-GMS, H80-10Gr, and Souna-3 from western Niger heterotic group were used as males to cross to 4 varieties from eastern cluster consisting of Ankoutess, Ex-Borno, Gamoji, and Moro. The former cluster consists of genotypes with long and thin panicles while the corresponding group is characterized by ecotypes with short and large panicle's diameter. Souna-3 and Ex-Borno originating from Senegal and Nigeria, respectively are improved varieties. Almost all the remnant material was developed through mass selection from local cultivars. A North Carolina Design II was used to generate sixteen hybrids. Parents, hybrids and a check variety (Zatib), also a hybrid population; were tested during two rainy seasons (2010 and 2011) in INRAN stations of Bengou and Maradi in Niger. The two sites were chosen for their difference in soil type and annual rainfall. Soil in Bengou (11°15' N and 3°18' E) is characterized by a pH of 4.3 and 63% sand, 21% silt, 15% clay, and 0.5% organic matter. The rainfall was 815.27 mm in 2010 and 812.8 mm in 2011. Soil in Maradi (15°26' N and 8°33' E) has a pH of 6.5 and 90% sand, 8% clay, and 2% organic matter. The rainfall was 595.5 mm in 2010 and 495 mm in 2011. Seeds were treated with a systemic fungicide (Aprostar) before sowing. Accessions were planted in a randomized complete block design in three replications. Each plot was 4 rows of 9 m. Only the 2 middle rows were used for gathering data. The plot consisted of 16 m². Spacing between rows as between hills was 1m. Fertilizers were applied at the recommended INRAN rate (50 kg/ha of NPK 15-15-15, and 100 kg/ha of urea in two fractions). In addition, animal manure was applied in Maradi station before sowing. The trials were hand weeded, and thinned 16 to 18 days after sowing to leave one plant per hill.

Data were recorded on (i) days to flowering (DSF): number of days from sowing to the time at which 50% of plants within a plot flowered; (ii) plant height (PH): height of the plant from the ground level to the spike tip in centimeter; (iii) main shoot diameter (MSD): main stem girth at half height in millimeter; (iv) peduncle diameter (PD): diameter of the peduncle at its half length in millimeter; (v) spike length (SPL): interval between the tip of the spike and its bottom in centimeter; (vi) spike diameter (SPD): spike girth at its middle distance in centimeter; (vii) spike number (SPN): number of spikes per plot; (viii) grain yield (GY): grain weight per plot. Grain yield was measured as kg per plot, and then converted to kg per hectare. Data (ii), (iii), (iv), (v), and (vi) on varieties were collected on three plants taken at random within each plot. Mid-parent heterosis was calculated using the formula: MPH = 100 x (F - P)/P where F is the genotypic value of the hybrid, P = (P₁ + P₂)/2 is the average performance of the two hybrid parents (Melchinger *et al.*, 2007). The combining ability value was deduced from the equation: $Y_{ij} = \mu + G_i + G_j + S_{ij}$ where Y_{ij} is the genotypic value of the hybrid; μ is the overall mean performance of the population; G_i and G_j are the general combining effects or GCA of i^{th} and j^{th} parents, respectively; S_{ij} is the specific effect or SCA of the i^{th} parent with the j^{th} parent (Shattuck *et al.*, 1993). Analysis of variance was carried out using GenStat to sort out the difference between treatments and interactions. The analysis was performed first on plot-mean values for all characters across locations within each year. A combined analysis across years was implemented thereafter.

RESULTS

Significance among variables: Among the parental material, HKB and Moro were the earliest in terms of number of days to flowering as opposed to Gamoji and HKP-GMS, the latest ones (Table 1). HKB and H80-10Gr were the tallest entries and had the longest spikes; in contrast Ankoutess and Ex-Borno were the shortest plants with the shortest spikes. From what precedes one can easily imagine the positive correlation between plant height and spike length. Souna-3 showed the biggest main stem diameter and had together with H80-10Gr, HKB, and Gamoji the largest peduncle girth. Ankoutess and Gamoji had a spike diameter above the overall mean while Moro and HKP GMS showed the lowest value of this trait. Concerning the tillering ability HKP-GMS, Ankoutess, and Souna-3 were the best. The shortest entry among the Western Niger heterotic group, HKP-GMS, was the tallest compared to the entries composing the Eastern Niger cluster. Similarly, the former cluster developed the longest spikes compared to the latter one.

The check, Zatib yielded more than the best parent Souna-3. Among the hybrids, those which outyielded the check were: 17 Gamoji x HKB, 15 Ex-Borno x H80-10Gr, 22 Moro x HKP-GMS, 9 Ankoutess x HKB, 10 Ankoutess x HKP-GMS, 12 Ankoutess x Souna-3, 20 Gamoji x Souna-3, and 13 Ex-Borno x HKB. Apart from grain yield other traits such as earliness, spike length, and tillering ability also influence the choice of pearl millet growers particularly in the Sahelian Niger. The hybrid Ankoutess x Souna-3 was the earliest. Gamoji x HKB had the longest spikes while Ex-Borno x Souna-3, Ankoutess x HKP-GMS, and Ankoutess x Souna-3 showed the best tillering ability. All the three hybrids involving Ankoutess as a parent yielded more than this parent. Two of them, Ankoutess

Table 1: Mean performance of 25 pearl millet genotypes for 8 traits across 2 sites over 2 years

Entry	Germplasm	DSF	PH	MSD	PD	SPL	SPD	SPN	GY
1	Ankoutess	58	215	16	12	31	17.4	68	1527
2	Ex-Borno	59	229	16	11	32	12.5	63	1542
3	Gamoji	63	232	17	13	43	14.8	60	1461
4	Moro	57	248	16	11	43	10.7	66	1479
5	HKB	56	252	17	13	62	12.1	59	1797
6	HKP-GMS	60	249	17	12	54	11.8	70	1720
7	H80-10Gr	58	254	17	13	55	12.2	62	1824
8	Souna-3	58	251	18	13	47	12.8	67	1869
9	Ankoutess x HKB	58	240	17	12	46	14.9	64	1953
10	Ankoutess xHKP-GMS	60	232	17	12	39	14.8	75	1950
11	Ankoutess x H80-10Gr	61	223	16	11	41	12.4	66	1884
12	Ankoutess x Souna-3	57	228	16	12	39	15.2	75	1933
13	Ex-Borno x HKB	58	244	17	12	45	13.7	68	1917
14	Ex-Borno x HKP-GMS	58	242	17	12	42	13.5	67	1772
15	Ex-Borno x H80-10Gr	59	252	17	12	41	14.0	73	1996
16	Ex-Borno x Souna-3	59	243	17	12	39	14.7	76	1881
17	Gamoji x HKB	58	256	17	13	51	13.6	55	2132
18	Gamoji x HKP-GMS	62	250	17	13	53	13.3	67	1865
19	Gamoji x H80-10Gr	60	242	18	12	49	13.4	66	1803
20	Gamoji x Souna-3	58	241	18	13	48	14.0	68	1919
21	Moro x HKB	58	245	17	12	48	11.7	69	1732
22	Moro x HKP-GMS	59	246	17	12	43	12.5	74	1971
23	Moro x H80-10Gr	60	237	16	12	46	11.3	64	1870
24	Moro x Souna-3	56	239	17	12	46	11.9	69	1711
25	Zatib	57	243	17	12	50	11.5	62	1891
	Mean	59	241	17	12	45	13.0	67	1816
	Significance	ns	ns	ns	ns	*	*	ns	ns

*significant at <0.001; ns = none significant.

x HKP-GMS and Ankoutess x Souna-3 tillered more than Ankoutess. For peduncle girth which is significantly correlated with grain yield, Gamoji x HKB and Gamoji x Souna-3 showed the highest value. Gamoji x HKB and Ex-Borno x H80-10Gr were the tallest hybrids.

Except for the number of days to flowering, all characters showed positive correlation with the grain yield (Table 2). Nonetheless, the correlation was significant only with the peduncle girth. The correlation with tillering ability was significant for Maradi during the first year when and where that with plant height was high. There was a highly significant correlation ($P < 0.001$) between plant height and spike length on one side and between plant girth and peduncle diameter on another side.

To determine the difference between check, parents, and hybrids for the agronomic traits we calculated their combined means separately. Mean grain yield of hybrids (1972) was superior to that of the check (1891) and that of the parents (1653). For tillering ability, mean of hybrids (69) was also

greater than that of parents (64) and check (62). For earliness, the check (57) was earlier than hybrids (58), but hybrids were earlier than the parents (59). For the spike length, the check (50) was greater than parents (46) and hybrids (44).

Significance among variables and interactions: Except the DSF, the mean squares for localities and years were all highly significant for all the agronomic traits. There was significant interaction between grain yield and both year and location. Similarly, the GCA for DSF, SPL, and SPN were controlled by the environment while there was no significant SCA interaction (Table 3). All the mean squares for the different characters, except for the spike number, were higher among the parents than among the hybrids indicating the hybrids were more homogeneous than their parents.

Heterosis: For six agronomic traits assessed on the eight hybrids (Table 4), grain yield showed the highest heterosis followed by that on spike number. The heterosis for the grain yield was superior to the sum of the remaining traits' heterosis in agreement with Lanzhi *et al.* (2008). Among the 8 hybrids,

Table 2: Correlation of grain yield with 8 agronomic traits.

Site™	Year	DSF	PH	MSD	PL	PD	SPL	SPD	SPN
Bengou	2010	-0.1	0.1	0.5*	0.3	0.2	0.2	-0.1	0.01
Maradi	2010	-0.3	0.7**	0.4	0.3	0.3	0.3	-0.2	0.5*
Bengou	2011	0.1	0.4	0.1	0.003	0.2	0.3	-0.1	0.2
Maradi	2011	0.2	-0.3	-0.1	0.2	0.1	0.01	0.2	0.5
All		-0.1	0.38	0.34	0.38	0.48*	0.3	0.1	0.1

*significant at 0.01; **significant at <.001

Table 3: Mean squares from sources of variation in combined ANOVA across 2 sites in 2 years.

Source variation	of	df	DSF	PH	SPL	SPN	GY
Locations (L)	1		1663.7***	37393.7***	1552.9***	22976***	6942829***
Years (Y)	1		54.3	18486.6***	629.3**	22990.9***	14033686***
L x Y	1		142.9***	46719.2***	4.3	542.8	324375
Replications/L-Y	8		39.9***	1255.1**	56.39	520.6*	482914*
Entries	24		31.7***	1182.3***	549.3***	346.9	232062
Parents	7		16.7	818.4	477.7***	62.6	112261
Hybrids	15		8.8	287.5	75.9	114.8	44471
GCA	7		4.10*	116.5	37.2*	40*	6063
SCA	15		3.4	58.1	10.5	42.6	32554
L x Entries	24		7.4	910***	141.4**	119.7	124285
Y x Entries	24		21 **	349.8	79.8	286	294185
L x Y x Entries	24		16.9	508.3	72.1	185.3	179735
Error	295		19.7	871.6	119.9	383.4	271190
Mean			58.7	241.2	45.3	66.8	1820
$\sigma_{GCA}^2 : \sigma_{SCA}^2$			1.2	2	3.5	0.9	0.2

*significant at 0.01; **significant at 0.005; ***significant at <.001

Gamoji x HKB had the highest heterosis for grain yield and plant height. The heterosis for spike number per plot and main stem diameter were highest for Ex-Borno x H80-10Gr. Moro x HKB and Ankoutess x HKB had the best and similar heterosis for peduncle diameter. There is positive heterosis for spike length only in the case of cross between Gamoji and Souna-3.

Combining abilities: HKB, Ankoutess and Gamoji together had the best GCA for grain yield. Moreover, Gamoji had the best GCA for plant height, spike length, stem and peduncle girths (Table 5). Souna-3 had the highest GCA for tillering ability while H80-10Gr showed the best GCA for earliness. The hybrids Gamoji x HKB, Moro x HKB, and Ex-Borno x H80-10Gr gave the highest SCA for grain yield (Table 6). Ex-Borno x H80-10Gr had the highest SCA for plant height

and tillering ability. For earliness; 4 hybrids: Ankoutess x HKB, Ankoutess x HKB, Ex-Borno x HKB, and Gamoji x Souna-3 had the highest and the same SCA of 0.2. Ankoutess x HKB had the best SCA for spike length of 1.5.

Ex-Borno and H80-10Gr from one side and Moro and HKB from another side had negative GCA for grain yield, but their respective crosses showed high SCA for this trait. Whilst both HKB and Ankoutess had acceptable heterosis and positive GCA, their progeny showed negative SCA.

DISCUSSIONS

Eight hybrids outyielded the check Zatib which in turn improved on the best parent, Souna-3. Exploitation of hybrid vigor or heterosis is therefore a way to increase the productivity

Table 4: Hybrids' heterosis for grain yield and other traits.

Entry	Germplasm	GY	PD	PH	MSD	SPN	SPL
9	Ankoutess x HKB	17.2	2.2	3.2	1.5	5.5	-1.5
10	Ankoutess x HKP-GMS	22.7	6.7	0.0	-0.2	8.7	-7.5
12	Ankoutess x Souna 3	14.2	1.2	-2.0	-7.7	11.2	-1.2
13	Ex-Borno x HKB	17.0	6.0	2.0	2.5	6.2	-2.5
15	Ex-Borno x H80 -10Gr	19.2	1.7	5.0	4.2	17.7	-3.7
17	Gamoji x HKB	37.2	0.0	8.0	2.7	-3.2	-2.0
20	Gamoji x Souna 3	20.7	-3.0	0.7	1.0	9.0	6.0
22	Moro x HKP-GMS	23.0	6.5	-0.5	1.7	9.2	-11.0
	Mean	18.7	1.0	0.7	-0.7	7.6	-3.3

Table 5: Average parents' GCA for grain yield and other traits.

Entry	Germplasm	DSF	PH	MSD	PD	SPL	SPN	GY
1	Ankoutess	0.0	-10.2	-0.6	0.0	-3.5	2.0	37.0
2	Ex-Borno	0.0	3.8	0.1	-0.2	-2.7	2.5	-1.5
3	Gamoji	0.7	6.0	0.7	0.4	5.5	-4.0	37.0
4	Moro	-0.7	0.7	-0.2	-0.2	1.0	1.0	-72.1
5	HKB	-1.0	5.1	0.1	0.2	3.2	-4.5	40.4
6	HKP-GMS	0.7	1.1	0.0	0.1	-0.5	2.5	-3.5
7	H80-10Gr	1.5	-2.8	-0.1	-0.4	-0.5	-1.0	-4.9
8	Souna-3	-1.5	-3.4	0.0	0.0	-1.7	4.0	-32.0
		**	ns	ns	ns	*	**	ns

*significant at 0.01; ** significant at 0.005

Table 6: Average hybrids' SCA for grain yield and other traits.

Entry	Germplasm	DSF	PH	MSD	PD	SPL	SPN	GY
9	Ankoutess x HKB	0.2	3.2	0.4	0.0	1.5	-2.2	-15
10	Ankoutess xHKP GMS	0.2	-0.5	0.0	0.4	-1.5	1.7	26
12	Ankoutess x Souna-3	-0.2	-0.7	-0.4	0.2	-0.7	0.7	37
13	Ex-Borno x HKB	0.2	-4.2	-0.3	0.2	0.0	1.2	-13
15	Ex-Borno x H80 -10Gr	-0.7	9.0	0.4	0.5	0.0	2.7	111
17	Gamoji x HKB	-0.2	3.5	-0.3	0.1	-2.5	-5	163
20	Gamoji x Souna-3	0.2	-2.7	0.3	0.0	-1.0	0.0	23
22	Moro x HKP GMS	0.0	3.0	0.1	0.2	-1.5	0.2	155
		ns	ns	ns	ns	ns	ns	ns

ns = none significant

in pearl millet as indicated by the low ratio GCA/SCA for grain yield of 0.2. Similar results were reported by Vetriventhan *et al.* (2008) and by Dangarya *et al.* (2009), in contrast with the findings by Yagya *et al.* (2002). Assessed entries in the

current study were significantly different according their spike girth and length in agreement with Tostain (1994). These two traits would be fundamental in the expression of the highest SCA for grain yield obtained in the three crosses evolving

each parents from the two clusters. Nonetheless, some crosses between parents from such heterotic grouping did not work particularly when both parents have large spike diameter, in one hand. In another hand, Moro as well as Souna-3 will belong to one heterotic group according their spike girth and to the corresponding ones in view of their spike length. Thus, the heterotic grouping of pearl millet established by Tostain (1994) can be more defined through the use of DNA markers that are less sensitive than isozymes (Besançon, 2003). Ultimately, the use of the two categories of markers for genetic clustering may not be enough to predict the best crosses and should be completed by field evaluation of testcrosses (Fischer *et al.*, 2010). For instance, Sattler *et al.* (2019) demonstrated genetic distance among West African OPVs using microsatellite markers. Although there was no relationship between the genetic distance and better parent heterosis, field testing illustrated good combining ability among entries from Niger vs. Senegal. The identified OPVs (Nigerien CIVT, H80-10Gr, and Taram and Senegalese Thialack-2 and Souna-3) are a promising start to diverge the West African germplasm into distinct pools. The highest yielding hybrid, Gamoji x HKB showed also the best SCA for grain yield. It was developed from parents which had high and positive GCA for grain yield. In contrast Ex-Borno, H80-10Gr, Moro, and HKP-GMS had negative GCA for grain yield. But the hybrids Ex-Borno x H80-10Gr and Moro x HKP-GMS showed high and positive SCA for this trait. Grain yield is then primarily controlled by non-additive (SCA) effects. This showed that selection of variety populations based only on *per se* performance is not effective for providing for heterosis. Whilst non-additive effects primarily control heterosis; the additive gene actions contribute to other traits like number of days to flowering, spike length, and plant height (Dangarya *et al.*, 2009). In sum, there was a high significance between varieties according 2 traits: SPL, SPD for making parents choice. The 2 former traits, in agreement with the findings of Kumar *et al.* (2022), should be considered for exploiting heterosis while the latter would indicate possibility to develop cost effective hybrids with good nicking parents. HKB, Ankoutess, and Gamoji showed the largest spike diameter and had the best and positive GCA for grain yield. All of them were developed by simple mass selection. Yet, Ex-Borno and Souna-3 both developed from recombined lines, a more improved selection method, and even showing larger panicle girth had negative GCA for grain yield. The spikes of the former group were the loosest whilst the latter cluster was characterized by compact ones. For effective study on GCA, genetic material of early stage should be considered (Falconer and Mackay, 1996). Some hybrids like Ankoutess x HKP-GMS and Gamoji x Souna-3 showed very low statistical estimates of SCA for grain yield, while having a high heterosis for this trait signifying the limitations of the statistical design in estimating SCA.

The aim of the breeder of cross-pollinated crops is to increase the amount of heterosis over the level already found in random mating populations. This can be achieved by crossing two selected genetically different populations. As the exploitation of hybrid vigor is fundamentally based on the genetic difference expressed between the two parents of hybrid, inbreeding that can lead to complete differentiation

between lines followed by crossing would be the best method for yield improvement. Inbred lines provide maximum heterosis effects when they are fixed at loci involved in the hybrid reaction (Wricke and Weber, 1986; Falconer and Mackay, 1996; Patil *et al.*, 2021). Therefore, inbred lines could be derived from the 3 crosses: Gamoji x HKB, Ex-Borno x H80-10Gr, and Moro x HKP-GMS that showed high SCA for grain yield. Following an evaluation at regional level, Sattler *et al.* (2019) found that 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. For improved grain yield, reciprocal recurrent selection method could be followed concerning Gamoji x HKB to exploit both additive and non-additive gene actions. Selection should be deferred to later generations of segregation for dissipation of non-additive gene action with regard to the two latter hybrids (Banerjee and Kole, 2009; Hallauer, 2010). Breeding for high yield could possibly be enhanced by the selection for peduncle girth which had the highest coefficient of correlation with yield in agreement with Mahadevappa and Ponnaiya (1967). Grain yield was negatively and very slightly correlated with the number of days to blooming, that is, the earlier hybrids were higher yielding. Earliness is reported to be associated with higher yield under terminal drought (Jika, 1989; Maman *et al.*, 1999; Rai *et al.*, 1999). Ausiku *et al.* (2022) found pearl millet hybrid to have substantially higher water use efficiency characteristics compared to improved and landrace varieties for grain yield. Producing hybrid seeds by hand is laborious and cannot be sustainable except for research purposes. For large scale seed production, it is crucial to introgress a cytoplasmic male sterility system into the female component. This will make the hybrid development operational simpler and, therefore, commercially feasible, as underlined by Andrews and Bramel-Cox (1993).

The hybrids tillered more than both the check and the parents. Tillering ability was positively correlated with grain yield. Results in that order are in agreement with the findings by Sattler *et al.* (2019) and Rasitha *et al.* (2020), respectively. The best hybrid in matter of SCA was that one showing the best tillering ability. Otherwise, one of the specific characters that is usually sought in pollinators is tillering which contributes to abundant and continued pollen shed (Andrews *et al.*, 1997; Talukdar *et al.*, 1999). Souna-3, HKP-GMS, and Ex-Borno showing the best GCA for tillering ability could be used thus as or to develop pollinators. The best hybrid combinations comprise those involving one line with good tillering habit and the other with high grain mass per head (Niangado and Ouendeba, 1987; Andrews *et al.*, 1997; Talukdar *et al.*, 1999). For large scale production of hybrid seed an efficient pollination through the use of synchronous flowering parents - the pollinator should preferably flower before the female parent - will be necessary. So, the direction of some crosses should be changed. Indeed, for the hybrids Ankoutess x HKP-GMS and Moro x HKP-GMS, both female parents flowered before the male parent HKP-GMS. The change is further of worth value because both female parents also yielded less than HKP-GMS. In seed production it is economically important to use the higher yielding parent as the female to increase the production per unit area (Andrews *et al.*, 1997;

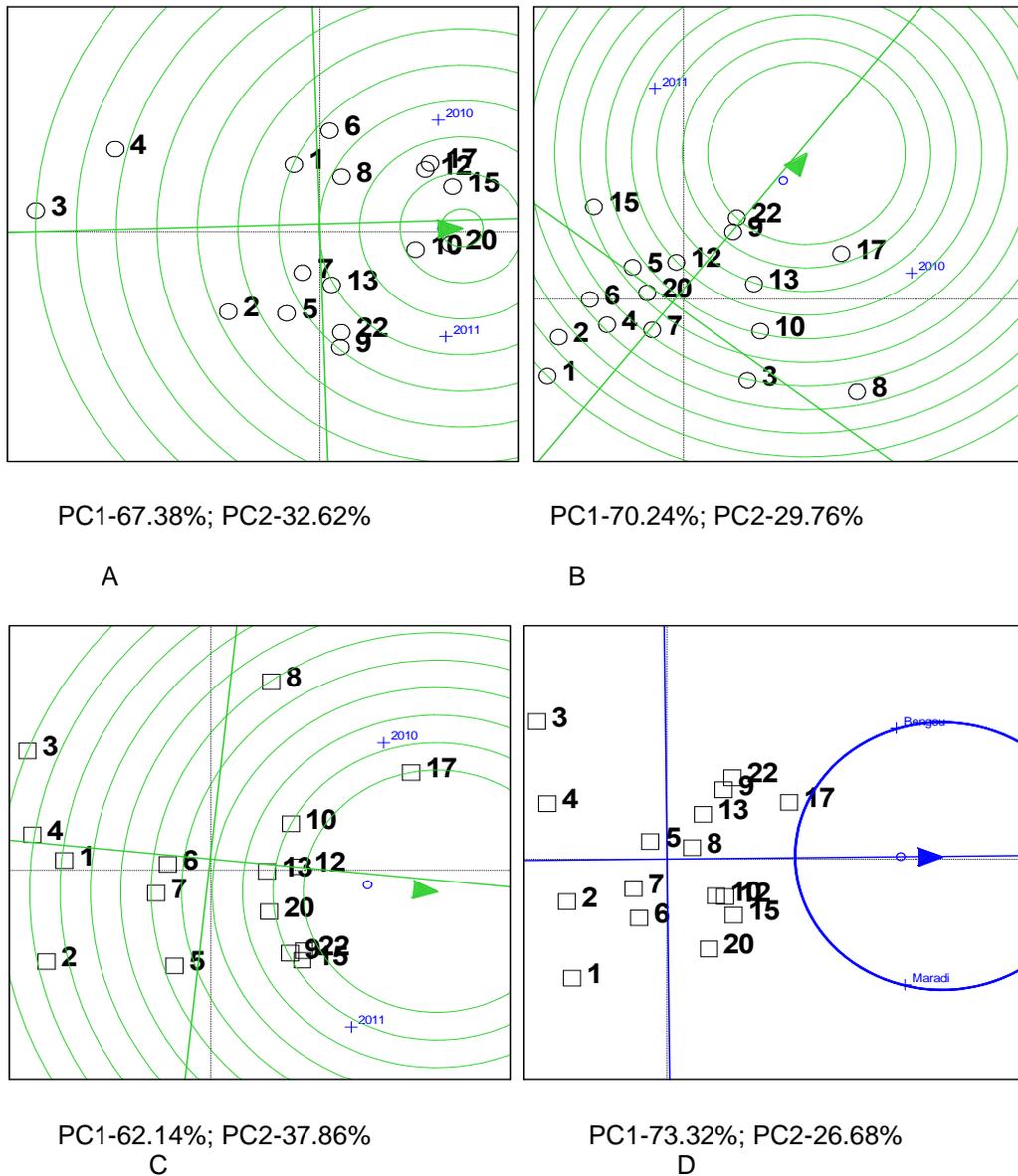


Figure 1: Biplots of the locations and their winning hybrids based on both average yield and stability (A = Maradi, B = Bengou), Biplot of overall adaptation of hybrids and their parents (C), Comparison of the sites based on their discriminating ability of genotypes (D).

Talukdar *et al.*, 1999). Otherwise, among the genetic material studied, HKB and Moro had being the earliest in terms of number of days to flower could be considered as pollinators in future breeding work. The use of HKB as pollinator is reinforced by the fact that it was the tallest entry and had high GCA for plant height. Besides synchronous flowering, plant height is another important factor in the choice of hybrid parents as the height of the male parent should be greater than that of the female. Taller male parent allows for free flow of pollen across the rows and thus cuts down the seed production cost by giving better seed set, and consequently higher hybrid seed yield per unit area. This allows as well planting greater female/male ratio, which also leads to higher hybrid seed yield (Prem *et al.*, 2006). In sum, pollinators

should be preferably selected among the Western cluster as the shortest entry in this group revealed taller than the tallest of the Eastern cluster. Conversely, Gamoji and HKB-GMS were the latest maturing entries indicating the interest of these varieties to be used as female parents in hybrid breeding based on current germplasm. The role of female parent for Gamoji is further supported by its highest GCA for PD, MSD, and SPL. All these 3 parameters were positively correlated with grain yield, PD showing the highest coefficient of determination and the most significant correlation. Gamoji like Ankoutess definitely showed good GCA for grain yield. Ankoutess, the shortest entry among the parents should be naturally exploited as female parent like mentioned earlier. There was a general reduction of the spike length in the hybrids.

Indeed, positive heterosis for spike length was recorded only in the case of cross between Gamoji and Souna-3, the latter genotype originating from Senegal. This would mean the possibility to develop varieties with long spike through crossing between Niger and Senegal germplasm. Moreover, the hybrid Gamoji x HKB developed longer spikes than the parental mean and the check. Long spikes are well appreciated by farmers in Senegal and in the central and south Niger where pearl millet is sold as bundle (Bezançon *et al.*, 2001; Buerkert *et al.*, 2001; Bassirou *et al.*, 2023). In this regard parental material of Western heterotic group would provide a germplasm source of high value. Even though the trait was positively correlated with the grain yield, the correlation was not significant. Thus, the reduction of spike length should be not considered as a limiting factor in breeding pearl millet for increased grain yield. Gamoji x HKB was also the tallest hybrid and the best in terms of grain yield. Such double purpose hybrid could play an important role in Sahel rural areas where pearl millet stover represents the principal source for animal feed during the long dry season. Yadav *et al.* (2009) found that increased grain and stover yields were achieved primarily due to the higher biomass productivity in drought-prone arid areas of India. However, the green revolution in Asia occurred with genotypes of intermediate height (1.4 – 2 m) in more favorable environments. For the reasons, it is interesting to provide Niger farmers with a phenotypic array of hybrids for them to choose that fit in their local environment. HKB and H80-10Gr the tallest varieties had the best spike length too. HKB showed the second best GCA value for spike length. As opposed, the shortest entries, that is, Ankoutess and Ex-Borno showed the smallest values of the trait. In brief the correlation between plant height and spike length was highly significant from our study. Therefore, the two former entries could be used in breeding program whenever the spike length constitutes a farmer-preferred trait (Omanyia *et al.*, 2007; Sattler *et al.* 2019; Bassirou *et al.*, 2023). HKB the earliest flowering entry was further among the tallest genotypes, that is, it has high plant growth rate. It could be involved in developing early flowering and high yielding hybrids which could escape terminal drought very frequent in the Sahel Africa, particularly with the now climate change.

Ankoutess and Gamoji had a spike diameter above the overall mean while Moro and HKP-GMS showed the lowest estimate of this trait. The spike girth is determined by the length of the peduncle of spikelet. More this peduncle is longer, more the spike girth is enlarged giving loose panicle. In contrast, thin spikes result from spikelet developed on short peduncles. This may lead to head compactness (Claude, 1983), a desirable trait for pearl millet producers leaving between 11° and 16° latitudes where head miner occurs. Head compactness may represent an avoidance mechanism to the attack of this insect pest as it hinders the movement of the larvae through the spike (Nwanze, 1991). Compactness is also equivalent to increased grain yield. The hybrid developed by crossing HKP-GMS to Moro was the third best for grain yield. Moro and HK-GMS could be exploited for developing new cultivars with improved spike compactness.

An ideal genotype is one that has both high mean yield and high stability. Analysis using GGE (Genotype + Genotype x

Environment) advocates that the center of the concentric circles (Fig. 1) represents the position of an ideal genotype. A genotype is more desirable if it is closer to the ideal genotype (Lubadde *et al.*, 2017). Therefore genotypes 20 Gamoji x Souna-3, 15 Ex-Borno x H80-10Gr, and 10 Ankoutess x HKP-GMS were the most desirable in Maradi (Fig. 1A); respectively. Similarly the hybrids 22 Moro x HKP-GMS, 9 Ankoutess x HKB, and 17 Gamoji x HKB performed better in Bengou (Fig. 1B). Globally, all of the hybrids were more desirable than all of the parents (Fig. 1C). The hybrid 17 Gamoji x HKB showed the best overall adaptation. Dabholkar (2006) reported that hybrids have been instrumental in scaling up not only the productivity of various crops but are often more stable as compared to varieties. Several studies have found evidence for novel mainly non additive expression patterns in hybrids such that the hybrid expression level is outside the range of the level of the parents (Springer and Stupar, 2007). Souna-3, though developed in Senegal showed a good adaptation in Niger environment and could be selected as parent for breeding purpose in African Sahel. Improved varieties like 5 HKB, 6 HKP-GMS, 7 H80-10Gr, and 8 Souna-3 were more desirable than the landraces 1 Ankoutess, 3 Gamoji, and 4 Moro. An important component in breeding new cultivars apart from high yielding potential is the stability of the performance. The stability of the production must be viewed as of primary concern when it is known that in Niger, like in most growing spiked millet areas, the crop constitutes the first staple food (Peace Corps/Niger, 2007; Haussmann *et al.*, 2012; Sattler and Haussmann, 2020). Multiplication testing should be extended to a large number of sites to confirm the performance of the different hybrids over their parents. Otherwise, an ideal environment should be highly differentiating of the genotypes. The ideal environment represented by the small circle with an arrow pointing to it (Fig. 1D) is the most discriminating of genotypes (Dehghani *et al.*, 2006). Therefore, Maradi and Bengou distributed on the same concentric circle were almost equal in terms of discriminating of candidates.

Results from current study showed breeding hybrid populations as a plausible way to increase pearl millet production. Besides being higher yielding, hybrids were more uniform for many agronomic traits and more stable than their parents OPVs. Deriving lines from parents involved in the best combinations followed by crossing would be the best way to exploit heterosis. Otherwise, the germplasm used in the current study provide evidence to develop an array of genotypes for kinds of adaptation and farmers desired traits. Nonetheless, for commercial exploitation of hybrids, introgression of cytoplasmic male sterility in the West African pearl millet genetic resources will be of great importance. Still the transfer of sterility system into a whole OPV taken as seed parent is difficult to handle. Top-cross hybrid – an inbred or F₁ seed parent pollinated by an OPV – may be the most practical of the genetically heterozygous hybrid cultivar type in pearl millet and has real advantage for Africa in terms of durability of disease resistance and stability of adaptation.

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