Hindawi
International Journal of Agronomy
Volume 2018, Article ID 3439090, 12 pages
https://doi.org/10.1155/2018/3439090

Research Article

Estimates of Combining Ability and Heterosis for Yield and Its Related Traits in Pearl Millet Inbred Lines under Downy Mildew Prevalent Areas of Senegal

Ghislain Kanfany [1,2,3] Amadou Fofana,[3] Pangirayi Tongoona,[1] Agyemang Danquah,[1] Samuel Offei,[1] Eric Danquah,[1] and Ndiaga Cisse[2]

[1] *West Africa Centre for Crop Improvement, University of Ghana, PMB LG 30, Legon, Ghana*
[2] *Centre d'Etudes Régional pour l'Amélioration de l'Adaptation à la Sècheresse, BP 3320, Thies, Senegal*
[3] *Centre National de Recherches Agronomiques de Bambey, BP 211, Bambey, Senegal*

Correspondence should be addressed to Ghislain Kanfany; gkanfany@wacci.edu.gh

Received 11 December 2017; Accepted 22 March 2018; Published 2 May 2018

Academic Editor: Iskender Tiryaki

Pearl millet is an important cereal crop for smallholder farmers' food security in West and Central Africa. However, its production has stagnated due to several factors such as the continuous use of local populations. A set of 17 inbred lines was crossed with Sosat C 88 and Souna 3 following a line × tester mating design. The F_1 hybrids, their parents, and a check were evaluated in Bambey and Nioro research stations during the rainy season of 2017. Data on downy mildew incidence, plant height, flowering time, panicle length and diameter, productive tillers, thousand-grain weight, panicle, and grain yield were recorded. GCA and SCA mean squares were significant for most of the traits indicating that both additive and nonadditive gene effects were involved in the control of the inheritance of these traits. However, the contribution of GCA to total mean squares was higher than that of SCA for all the traits, providing that additive gene action was more important in their inheritance. The top-cross hybrid IBL155-2-1 × Sosat C 88 exhibited negative and significant SCA effects for downy mildew incidence, flowering time, and plant height. Lines IBL003-B-1, IBL091-1-1, IBL095-4-1, IBL110-B-1, and IBL 206-1-1 had positive GCA effects for grain yield and negative GCA effects for downy mildew, flowering time, and plant height. These lines can be used as parents to create synthetic varieties or hybrids.

1. Introduction

Pearl millet (*Pennisetum glaucum* (L.) R. Brown) is the 4th most important tropical cereal after rice, maize, and sorghum [1]. In 2014, global grain pearl millet production was estimated at 28 million tons, harvested from 32 million ha in Asia, Africa, and the Americas. The average yield is about 900 kg ha^{-1}. India and Africa are the most important producers with more than 85% of the total production in 2016 [1]. It is an important dual purpose cereal crop in Africa and Asia where it is considered as a staple food and source of fodder and feed for livestock for smallholders farmers [2]. The grain of pearl millet is a very rich source of protein, vitamins, and minerals in comparison with other cereals and is used for human consumption in diverse ways [3]. The pearl millet stover is used as fuel, material for building and fencing, and also a soil additive to enhance soil fertility [4]. It is also being experimented as a grain and forage crop in the USA, Canada, Mexico, India, and West and North Africa [5].

As the world population is continuously increasing and is projected to reach nine billion by 2050, pearl millet is expected to play an important role for achieving food security in West and Central African countries, which have the highest population growth rates in the world [6]. However, in this part of the world, yields of pearl millet are very low compared to yields in India and yet African farmers, particularly in Senegal, have not adopted improved varieties in a large scale. In pearl millet growing areas in Africa, adoption rate of improved OPVs varied from 5 to 37% [7]. In contrast, most Indian farmers are using improved varieties, particularly hybrids since the 1960s. Indeed, in India hybrids had 25–30% grain yield advantage over OPVs, leading to the rapid adoption of the hybrids whose yield increased from 305 kg ha^{-1} during 1951–1955 to 998 kg ha^{-1} during 2008–2012 [5]. Thus, enhancement of pearl millet production and productivity in Africa, which is a high priority, can be achieved through the identification of elite parent materials which can be used as parents to develop hybrid varieties.

ICRISAT has developed pearl millet inbred lines derived from landraces originating from West and Central Africa which can be useful in developing high yielding pearl millet hybrids and synthetic varieties with considerable adaptation to this pearl millet growing environment. These lines were screened for pearl millet downy mildew resistance in Senegal and some of them showed good agronomic traits and resistance to the pearl millet downy mildew. However, the per se performance of these pearl millet inbred lines does not predict the performance of hybrids for disease resistance and agronomic traits [8]. Therefore, to make effective use of these pearl millet inbred lines, their combining abilities need to be elucidated [9]. This genetic information can be obtained by different mating design including line × tester [10]. GCA and SCA estimates of pearl millet inbred parents or landraces for different traits such as micronutrients [11], grain quality [12], and fodder yield [13] were reported to be important. Additive genetic action was also reported to be important in controlling traits such as grain yield, flowering time, and panicle length [14]. There is scanty published information on the combining ability of the pearl millet inbred lines derived from landraces collected in West and Central Africa, known as the origin of the crop, for disease resistance and agronomic traits. The objectives of this study were to estimate combining ability and heterosis of pearl millet inbred lines for downy mildew, yield, and other agronomic traits under downy mildew infested fields and identify superior pearl millet hybrids for yield, yield components, and resistance to downy mildew.

2. Materials and Methods

2.1. Plant Material and Mating Design. Seventeen inbred lines were used as females and crossed each to two OPVs used as males according to the line × tester mating design [10] to generate 34 F_1 hybrids. The OPVs varieties were considered as testers and the inbred lines as lines. The two testers named Souna 3 and Sosat C 88 are popular varieties adapted to the groundnut agroecological zone. The pearl millet inbred lines used for the study were selected from a pool of pearl millet landraces from West and Central Africa converted to inbred lines through successive selfing up to S6 [15]. These inbred lines were selected through a downy mildew phenotypic evaluation conducted at Bambey and Nioro research stations during the rainy season 2016. They showed less than 10% DMI and were classified as resistant varieties. The seeds of the male parents were planted in 4 different dates in order to synchronise the flowering time of these male parents with the ones of the female parents. Thus, from January 2017, the sowing of the male parents was done every week and seeds of each of the male parents were sown in 5 rows of 15 hills per row. All the female parents were sown in one time during the second sowing date of the male parents in a one row-plot of 15 hills. At the booting stage, at least plant heads of 4 panicles per plant of the male and female parents were covered in order to avoid undesirable pollination. At flowering, each covered panicle of female plant was pollinated with bulk pollen collected from at least 20 different plants of the male parent.

At maturity stage, F_1 panicles of the female parents were harvested and the lower and upper parts of each panicle were cut before threshing to minimize outcrossing from unknown plants or selfing. Indeed, because of the protogynous nature of the crop the stigmata of a plant are receptive before the shedding of pollen and the flowering starts from the upper to the lower part. Then, the upper part of the panicle may be pollinated by unknown plants if not covered on the right time and the lower part of the panicle may be pollinated by the pollen from the same plant.

After threshing, F_1 seeds from the same female parent were bulked and used as F_1 hybrids. The 34 F_1 hybrids along with the 17 inbred lines, the two testers, and an OPV named Thialack II as check, providing 54 genotypes, were used for the evaluation (Table 1).

2.2. Study Sites, Experimental Design, and Field Management. The 34 hybrids, together with their parents and the OPV check, were evaluated under rainfed conditions during the rainy season of 2017 at two locations in Senegal. The study sites were Bambey (13°49′12″ North, 13°55′12″ West) and Nioro (13°45′0″ North, 15°48′0″ West) research stations. Both locations are in the groundnut agroecological zone, the main pearl millet growing area in Senegal, and were characterized as hotspots for downy mildew in the previous study. The genotypes were arranged in 9 × 6 alpha lattice design with three replications at each site. Each block was surrounded by a downy mildew infector row consisting of a downy mildew susceptible line, 7042 S, sown 3 weeks before the tested materials. Each plot consisted of one row of 8.1 m length with a spacing of 0.9 m between rows and between plants within a row. At least 10 seeds were planted per hole and later thinned to two plants two weeks after sowing. The fields were weeded two times after sowing. The trials received the recommended 15N-15P-15K basal fertilizer at a rate of 150 kg ha^{-1} just before sowing. During the crop development a top dressing using area at a rate of 100 kg ha^{-1} was done in two fractions: 50 kg ha^{-1} after thinning and 50 kg ha^{-1} after the second weeding.

2.3. Data Collection. The recorded data were collected according to the method described by Drabo [14]. Flowering (FWT) was recorded by counting the total number of days from sowing to the time when 50% of plants in a plot flowered. Downy mildew incidence (DMI) was obtained by dividing the total number of infected plants, 30 DAS from a plot, by the total number of plants. Panicles harvested in a plot were weighed to determine panicle yield (PY) and then threshed. Grains obtained in each plot were weighed and used

Table 1: List of parental lines and check used in the study.

Number	Genotype	Source	Role in crosses	Status	Response to downy mildew
1	IBL 001-4-1	ICRISAT	Line	Inbred line	Resistant
2	IBL 003-B-1	ICRISAT	Line	Inbred line	Resistant
3	IBL 011-4-1	ICRISAT	Line	Inbred line	Resistant
4	IBL 021-3-1	ICRISAT	Line	Inbred line	Resistant
5	IBL 055-4-1	ICRISAT	Line	Inbred line	Resistant
6	IBL 091-1-1	ICRISAT	Line	Inbred line	Resistant
7	IBL 095-4-1	ICRISAT	Line	Inbred line	Resistant
8	IBL 098-3-1	ICRISAT	Line	Inbred line	Resistant
9	IBL 106-B-1	ICRISAT	Line	Inbred line	Resistant
10	IBL 110-B-1	ICRISAT	Line	Inbred line	Resistant
11	IBL 114-6-1	ICRISAT	Line	Inbred line	Resistant
12	IBL 119-B-1	ICRISAT	Line	Inbred line	Resistant
13	IBL 155-2-1	ICRISAT	Line	Inbred line	Resistant
14	IBL 165-1-1	ICRISAT	Line	Inbred line	Resistant
15	IBL 179-2-1	ICRISAT	Line	Inbred line	Resistant
16	IBL 179-3-1	ICRISAT	Line	Inbred line	Resistant
17	IBL 206-1-1	ICRISAT	Line	Inbred line	Resistant
18	Souna 3	Senegal	Tester	OPV (improved)	Susceptible
19	Sosat C 88	Senegal	Tester	OPV (improved)	Resistant
20	Thialack II	Senegal	Check	OPV (improved)	Susceptible

to calculate grain yield (GY) in kg ha^{-1} using the following formula:

$$\text{GY}\ \left(\text{kg ha}^{-1}\right) = \left[\frac{\text{grain weight}\ \left(\text{kg plot}^{-1}\right) \times 10{,}000}{\text{plot size m}^2}\right]. \quad (1)$$

Five random plants were selected in each plot to measure the plant height (PH) from the base of the plant to the upper part of the panicle, number of productive tillers (PT) by counting the number of tillers per plant which produce productive panicles, panicle length (PL), and panicle diameter (PDIA). Five random samples of 1000 grains for each plot were weighed using a sensitive balance to determine the 1000-grain weight (TGW).

2.4. Data Analysis. Analysis of variance for each experimental site as well as for combined data after the homogeneity test of variance across the two experimental sites was performed using the general linear model (GLM) procedure in SAS version 9.4 (SAS Institute, Cary, NC). The following mathematical linear model was used:

$$Y_{ijk} = \mu + G_i + L_j + \text{GL}_{ij} + r_{jk} + b_{jk} + e_{ijk}, \quad (2)$$

where

Y_{ijk} is the observed value of the variable for the ith entry in the jth location within kth replication;

μ is the overall general mean;

G_i is the effect of the ith genotype;

L_j is the effect of the jth location;

GL_{ij} is the interaction effect of the ith entry and the jth location;

r_{jk} is the effect of the kth replication within the jth location;

b_{jk} is the effect of the lth block of the kth replication in the jth location;

e_{ijkr} is the experimental pooled error.

For the combining ability, analysis of variance was performed for traits that showed significant differences among hybrids using SAS software version 9.4 (SAS Institute, Cary, NC). Thus, the sum of squares of hybrids was partitioned into various variations due to lines, testers, and their interactions based on the following statistical model described by Singh and Chaudhary (1977):

$$Y_{ijk} = \mu + M_i + F_j + \text{MF}_{ij} + e_{ijk}, \quad (3)$$

where

Y_{ijk} is kth observation on the ith and jth progeny;

μ is the overall general mean;

M_i is the effect of the ith male;

F_j is the effect of the jth female;

MF_{ij} is interaction effect;

e_{ijk} is error associated with each observation.

Table 2: Mean squares for studied traits across locations.

Source of variation	d.f.	DMI	FWT	PH	PL	PDIA	PT	TGW	PY	GY
Rep (site)	4	232.4^{**}	28.4^{**}	746.4	28.5	0.4	2.2	4.9^{*}	2499694^{*}	1258762^{**}
Block (Rep × site)	48	85.5	8.2	359.9	32.9	0.14	1.5	2.3	817310	324630
Site	1	84.6	248.9^{***}	0.1	444.1^{**}	1.6^{**}	29.4^{**}	36.2^{***}	5279671^{*}	3168503^{**}
Genotype	53	156.4^{***}	82.3^{***}	3193.5^{***}	278.6^{***}	0.46^{***}	5.1^{***}	10.4^{***}	3975982^{***}	1157443^{***}
Genotype × site	53	72.7	13.62^{**}	488.1	45.1	0.19	2.0	2.4^{*}	1418904^{*}	603031^{**}
Error	164	60.04	7.9	474.7	31.6	0.17	1.9	1.6	997156	297217

DMI: downy mildew incidence; FWT: flowering time; PH: plant height; PL: panicle length; PDIA: panicle diameter; PT: productive tillers; TGW: 1000-grain weight; PY: panicle yield; GY: grain yield; d.f.: degree of freedom; Rep: replication. *,**,***Significant at 0.05 and 0.01 and 0.001 probability levels, respectively.

The values of the general combining ability for both male and female and the specific combining ability effects for all the studied traits were estimated as follows:

$$\begin{aligned} \text{GCA}_{\text{Line}} &= \text{Line mean } (X_i) - \text{Overall mean } (X\ldots) \\ \text{GCA}_{\text{tester}} &= \text{Tester mean } (X_j) - \text{Overall mean } (X\ldots) \\ \text{SCA}_{\text{line}\times\text{tester}} &= \text{Cross mean } (X_{ij}) - \text{Line mean } (X_i) - \text{Tester mean } (X_j) + \text{Overall mean } (X\ldots), \end{aligned} \tag{4}$$

where

$X\ldots$ is overall mean;

X_i is mean of all the hybrids containing an ith line average over all replications, sites, and males;

X_j is mean of all the hybrids containing a jth tester average over all replications, sites, and females;

X_{ij} is mean of the cross between ith line and jth tester across all replications and sites.

The significance of the GCA effects was tested using the formula described by Cox and Frey (1984):

$$\begin{aligned} t_{\text{cal}} &= \frac{\text{GCA}}{\text{SE}_{\text{gca (male)}}}, \quad \text{where, S.E}_{(\text{gca male})} = \sqrt{\frac{\text{Me}}{rts}} \\ t_{\text{cal}} &= \frac{\text{GCA}}{\text{SE}_{\text{gca (female)}}}, \quad \text{where, S.E}_{(\text{gca female})} = \sqrt{\frac{\text{Me}}{rts}} \\ t_{\text{cal}} &= \frac{\text{SCA}}{\text{SE}_{\text{SCA (line}\times\text{tester)}}}, \quad \text{where, S.E (sca)} = \sqrt{\frac{\text{Me}}{rs}}, \end{aligned} \tag{5}$$

where

Me is the error mean sum of squares;

r, t, l, s are numbers of replications, testers lines, and sites, respectively;

SE is standard error.

Standard, mid-parent, and better parent heterosis for grain yield were also calculated for each cross across locations following Hallauer et al. (2010):

$$\begin{aligned} \text{Standard heterosis (SH)} &= \frac{(F_1 - \text{Check})}{\text{Check}} \times 100 \\ \text{Mid-parent heterosis (MPH)} &= \frac{(F_1 - \text{MP})}{\text{MP}} \times 100 \\ \text{Better parent heterosis (BPH)} &= \frac{(F_1 - \text{HP})}{\text{HP}} \times 100, \end{aligned} \tag{6}$$

where F_1 denotes the mean performance of the hybrid averaged over the two locations. The mean value of the OPV check was used to calculate the standard heterosis. The parent with the highest mean value was used as better parent in the calculation of high-parent heterosis while the average between the two parents was used for the mid-parent heterosis.

3. Results

3.1. Performance of Hybrids and Parents across Locations. Combined analysis of variance across locations showed highly significant ($P < 0.01$) genotype effect for all measured traits (Table 2). Site effect was also significant for all the traits, except for DMI and PH. However, interaction genotype × site effect was only significant for FWT, TGW, PY, and GY.

All genotypes were resistant to downy mildew with a mean DMI of 4%, except for IBL 155-2-1 and its progeny with Souna 3 which displayed both 22% DMI (Table 3). Days from sowing to 50% flowering (DAS) of genotypes across the two sites ranged from 50 to 69 DAS with an average of 56 DAS. The genotypes were tall with plant height ranging from 2 to 3.2 m. Panicle length of the pearl millet genotypes varied from 27 to 58 cm with an average of 44 cm while their diameter ranged from 1.2 to 2.7 cm with a mean diameter of 2.1 cm. The number of productive tillers ranged from 2 to 6 tillers per plant with a mean value of 4 productive tillers per plant. The 1000 seeds weight varied from 5 to 12 g with a mean of 9 g. The panicle yield of genotypes across the two sites varied from 376 kg ha^{-1} for IBL 119-B-1 to 4190 kg ha^{-1} for IBL 110-B-1 × Souna 3 and their grain yield varied from 92 kg ha^{-1} for IBL 119-B-1 to 2024 kg ha^{-1} for IBL 206-1-1 × Souna 3.

As expected, the F_1 hybrids were generally more productive compared to the inbred lines and OPVs. The top five

Table 3: Performance of tested genotypes for studied traits across sites.

Genotype	DMI	FWT	PHIG	PLEN	PDIA	PT	TGW	PY	GY
IBL 001-4-1	2	60	255	34	2.1	2	10	1104	585
IBL 003-B-1	4	51	231	31	2.5	5	11	1872	1340
IBL 011-4-1	14	59	237	44	1.9	3	7	1164	428
IBL 021-3-1	0	63	223	32	2.1	2	8	1178	419
IBL 055-4-1	6	65	210	37	1.6	2	6	517	286
IBL 091-1-1	0	60	246	47	2.2	4	8	2328	1136
IBL 095-4-1	0	50	243	37	1.9	5	10	2015	947
IBL 098-3-1	11	51	239	31	1.8	4	10	1946	1188
IBL 106-B-1	6	54	278	39	1.8	3	10	1340	710
IBL 110-B-1	0	62	240	45	1.6	2	6	997	404
IBL 114-6-1	0	62	199	27	1.8	2	8	750	324
IBL 119-B-1	0	69	260	41	1.2	2	5	376	92
IBL 155-2-1	22	57	200	35	1.3	3	7	1099	466
IBL 165-1-1	2	64	238	39	1.6	4	7	1349	489
IBL 179-2-1	0	60	272	43	1.9	2	8	850	394
IBL 179-3-1	8	54	233	35	2.0	5	8	1497	886
IBL 206-1-1	0	56	228	38	1.8	4	8	2102	1126
IBL 001-4-1 × Souna 3	17	53	273	43	2.0	5	11	3475	1923
IBL 003-B-1 × Souna 3	8	52	259	44	2.1	4	9	3218	1646
IBL 011-4-1 × Souna 3	5	52	255	50	1.8	4	8	2368	942
IBL 021-3-1 × Souna 3	4	57	210	44	1.9	3	7	1772	852
IBL 055-4-1 × Souna 3	0	58	241	38	2.7	3	8	2232	1397
IBL 091-1-1 × Souna 3	0	54	250	54	2.0	4	8	2369	1211
IBL 095-4-1 × Souna 3	0	52	262	58	2.0	4	9	2975	1641
IBL 098-3-1 × Souna 3	19	54	277	46	1.9	4	9	2326	1289
IBL 106-B-1 × Souna 3	6	56	256	52	1.6	3	9	2462	1351
IBL 110-B-1 × Souna 3	0	56	274	52	2.6	5	7	4190	1493
IBL 114-6-1 × Souna 3	4	57	270	47	2.0	3	8	2991	1181
IBL 119-B-1 × Souna 3	0	56	321	49	2.0	5	9	3586	1530
IBL 155-2-1 × Souna 3	22	56	287	46	1.9	5	9	2562	1101
IBL 165-1-1 × Souna 3	0	59	289	45	2.1	4	8	3420	1612
IBL 179-2-1 × Souna 3	0	59	298	44	2.0	3	9	1906	735
IBL 179-3-1 × Souna 3	2	55	275	46	2.2	4	8	2943	1402
IBL 206-1-1 × Souna 3	2	54	245	44	2.1	5	9	3671	2024
IBL 001-4-1 × Sosat C 88	9	56	284	36	2.4	4	9	2997	1579
IBL 003-B-1 × Sosat C 88	2	50	234	28	2.6	4	12	3182	1883
IBL 011-4-1 × Sosat C 88	0	50	257	39	2.1	5	10	2468	1331
IBL 021-3-1 × Sosat C 88	0	54	284	37	2.3	4	10	3053	1654
IBL 055-4-1 × Sosat C 88	0	57	298	40	2.0	3	9	1824	1131
IBL 091-1-1 × Sosat C 88	0	50	260	41	2.3	4	10	2912	2019
IBL 095-4-1 × Sosat C 88	2	55	281	39	2.3	4	10	2426	1368
IBL 098-3-1 × Sosat C 88	6	57	285	43	2.2	3	9	2722	1381
IBL 106-B-1 × Sosat C 88	0	57	255	37	2.2	3	9	1933	949
IBL 110-B-1 × Sosat C 88	2	55	256	38	2.6	4	9	2827	1433
IBL 114-6-1 × Sosat C 88	0	52	264	31	2.4	5	9	2944	1416
IBL 119-B-1 × Sosat C 88	2	60	298	41	2.0	4	8	1993	871
IBL 155-2-1 × Sosat C 88	0	51	260	35	1.9	6	10	2414	1215
IBL 165-1-1 × Sosat C 88	0	60	287	39	2.5	4	10	2785	1114
IBL 179-2-1 × Sosat C 88	0	54	277	32	2.4	6	9	2920	1586
IBL 179-3-1 × Sosat C 88	0	56	260	29	2.4	4	9	2375	1247
IBL 206-1-1 × Sosat C 8	0	53	242	34	2.4	5	9	3325	1988
Souna 3	5	56	273	55	2.0	4	8	2918	1268

Table 3: Continued.

Genotype	DMI	FWT	PHIG	PLEN	PDIA	PT	TGW	PY	GY
Sosat C 88	2	51	251	33	2.3	4	10	2568	1548
Thialack II	7	53	292	54	1.9	4	8	3380	1694
Mean	4	56	259	41	2.1	4	9	2313	1171
Range	0–22	50–69	200–321	27–58	1.2–2.7	2–6	5–12	376–4190	92–2024
Standard deviation	5.6	4.1	25.8	7.3	0.3	0.9	1.4	868.8	483.1

DMI: downy mildew incidence; FWT: flowering, PH: plant height; PL: panicle length; PDIA: panicle diameter; PT: productive tillers; TGW: 1000-grain weight; PY: panicle yield; GY: grain yield.

genotypes across sites were hybrids IBL 206-1-1 × Souna 3 (2024 kg ha^{-1}); IBL 091-1-1 × Sosat C 88 (2019 kg ha^{-1}); IBL 206-1-1 × Sosat C 88 (1988 kg ha^{-1}); IBL 001-4-1 × Souna 3 (1923 kg ha^{-1}); and IBL 003-B-1 × Sosat C 88 (1883 kg ha^{-1}). Among these top hybrids, two involved the inbred line IBL 206-1-1 as parent. The hybrid IBL 179-2-1 × Souna 3 (735 kg ha^{-1}) was the lowest yielding among the tested hybrids. The check, Thialack II, was the most productive OPV with an average grain yield of 1694 kg ha^{-1} and ranked among the ten best genotypes. The best inbred line was IBL 003-B-1 (1340 kg ha^{-1}).

Genotypes flowered 2 days earlier in Nioro (55 DAS) compared to Bambey (57 DAS) (Table 4). The average TWG in Nioro was 8 g while in Bambey it was 9 g. The panicle yield of genotypes under Nioro conditions ranged from 461 kg ha^{-1} for the inbred line IBL 110-B-1 to 4647 kg ha^{-1} for hybrid IBL 110-B-1 × Souna 3 while under Bambey conditions it varied from 251 kg ha^{-1} for the inbred IBL 119-B-1 to 4660 kg ha^{-1} for the hybrid IBL 165-1-1 × Souna 3. Grain yield of genotypes under Bambey environment ranged from 61 kg ha^{-1} for inbred IBL 119-B-1 to 2162 kg ha^{-1} for hybrid IBL 165-1-1 × Souna 3. In Nioro, the grain yield varied from 87 kg ha^{-1} for inbred line IBL 110-B-1 to 2966 kg ha^{-1} for the hybrid IBL 206-1-1 × Sosat C 88.

Based on grain yield, the ten best genotypes in Nioro were only hybrids while in Bambey the three OPVs were among the top ten genotypes. The hybrids IBL 091-1-1 × Sosat C 88 and IBL 206-1-1 × Souna 3 performed well under both locations and were among the best ten genotypes across the two environments.

3.2. Combining Ability Analysis across Locations. The total variation due to crosses was partitioned into line, tester, and line × tester interaction (Table 5). The mean squares due to hybrids were significant for all the traits except for PY and GY. Line mean squares across the two locations were also significant for all the traits except for PDIA while tester mean squares were not significant for PT, PY, and GY. Line × tester mean squares were significant for most traits except PDIA, PY, and GY. The mean squares due to line × site were significant for TGW, PY, and GY whereas the mean squares due to tester × site interaction were significant for FWT and DMI. However, the mean squares due to site × line × tester interaction were not significant for all the traits across the two locations.

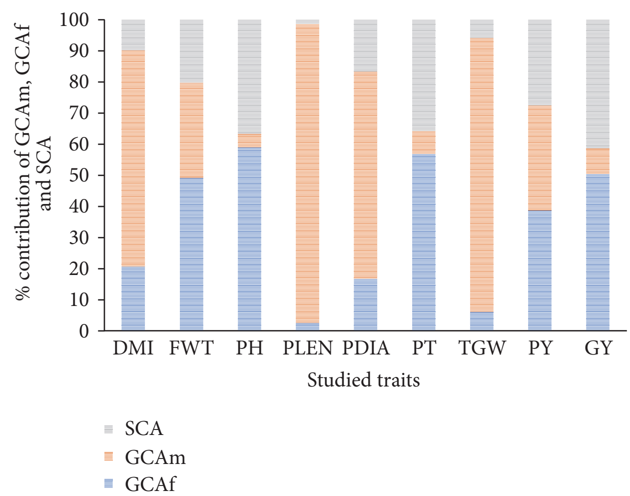


Figure 1: Proportion of total mean squares of studied traits attributable to GCA_m, GCA_f, and SCA across locations. DMI: downy mildew incidence; FWT: flowering time; PH: plant height; PL: panicle length; PDIA: panicle diameter; PT: productive tillers; TGW: 1000-grain weight; PY: panicle yield; GY: grain yield; GCA_m: general combining ability for male parent; GCA_f: general combining ability for female parent; SCA: specific combining ability.

3.3. Relative Contributions of Mean Squares to Additive and Nonadditive Effects. Across the two locations, the relative importance of mean squares, for additive effect (GCA_m + GCA_f), was higher for all the traits compared to the dominance effect (SCA) (Figure 1). GCA effects accounted for most of the variation observed for most of the traits with more than 80% of the total genotypic variation among hybrids except for PH, PT, PY, and GY. The overall contribution of GCA sums of squares to the total mean squares across the two locations varied from 58% for GY to 99% for PLEN while SCA varied from 1% for PLEN to 42% for grain yield. The contribution of GCA_m was higher than GCA_f and SCA for DMI, PLEN, PDIA, and TGW while GCA_f was larger than GCAm and SCA mean square for FWT, PH, PT, PY, and GY. The contribution of GCA_f (50%) was slightly higher than SCA (42%) to grain yield.

3.4. Estimation of General Combining Ability Effects. The contribution of lines and testers to crosses for traits studied across the two locations is presented in Table 6. For female lines, significant GCA effects were observed for most of

Table 4: Mean flowering time, yield, and related traits of genotypes per site.

Genotype	FWT (das)		TGW (g)		PY ($kg\,ha^{-1}$)		GY ($kg\,ha^{-1}$)	
	Bambey	Nioro	Bambey	Nioro	Bambey	Nioro	Bambey	Nioro
IBL 001-4-1	60	61	9	10	1284	924	768	402
IBL 003-B-1	51	52	11	12	1856	1888	1512	1168
IBL 011-4-1	63	55	7	7	1195	1132	437	419
IBL 021-3-1	62	63	9	7	1423	933	718	119
IBL 055-4-1	68	63	5	7	321	712	139	432
IBL 091-1-1	63	56	8	8	2557	2099	1140	1132
IBL 095-4-1	49	50	10	11	1658	2372	924	969
IBL 098-3-1	49	53	9	11	1687	2206	1057	1318
IBL 106-B-1	55	54	10	10	780	1900	428	992
IBL 110-B-1	61	62	7	5	1533	461	721	87
IBL 114-6-1	65	58	6	9	628	873	267	382
IBL 119-B-1	73	64	3	6	251	500	61	122
IBL 155-2-1	55	58	7	6	1235	962	649	284
IBL 165-1-1	64	63	7	8	1970	727	792	186
IBL 179-2-1	59	60	8	7	1078	622	559	228
IBL 179-3-1	54	53	8	8	1330	1664	746	1025
IBL 206-1-1	60	52	8	8	920	3283	564	1687
IBL 001-4-1 × Souna 3	54	51	10	12	2625	4325	1223	2624
IBL 003-B-1 × Souna 3	52	51	9	10	2758	3677	1011	2281
IBL 011-4-1 × Souna 3	54	50	9	8	2151	2585	923	961
IBL 021-3-1 × Souna 3	58	56	7	7	1672	1872	1113	591
IBL 055-4-1 × Souna 3	59	57	9	8	2140	2324	1609	1185
IBL 091-1-1 × Souna 3	55	53	8	7	2375	2363	1295	1127
IBL 095-4-1 × Souna 3	53	50	9	8	2847	3102	1513	1768
IBL 098-3-1 × Souna 3	56	53	7	10	1983	2669	1018	1559
IBL 106-B-1 × Souna 3	57	55	8	9	1908	3015	1005	1697
IBL 110-B-1 × Souna 3	59	53	7	7	3733	4647	934	2051
IBL 114-6-1 × Souna 3	57	56	7	10	3154	2828	1436	926
IBL 119-B-1 × Souna 3	59	53	10	8	4175	2996	1829	1231
IBL 155-2-1 × Souna 3	59	54	8	9	1913	3211	907	1294
IBL 165-1-1 × Souna 3	60	57	8	8	4660	2180	2162	1061
IBL 179-2-1 × Souna 3	60	58	9	8	1728	2084	617	854
IBL 179-3-1 × Souna 3	56	54	7	9	2031	3855	822	1982
IBL 206-1-1 × Souna 3	56	53	8	11	3285	4058	1609	2438
IBL 001-4-1 × Sosat C 88	57	54	9	10	2503	3490	1298	1860
IBL 003-B-1 × Sosat C 88	48	51	12	12	3562	2802	1959	1806
IBL 011-4-1 × Sosat C 88	49	51	10	10	2380	2555	1259	1403
IBL 021-3-1 × Sosat C 88	53	55	9	10	2526	3580	1304	2005
IBL 055-4-1 × Sosat C 88	58	56	9	9	1630	2017	1007	1255
IBL 091-1-1 × Sosat C 88	48	51	11	10	2563	3262	1976	2061
IBL 095-4-1 × Sosat C 88	56	53	9	10	1963	2889	1080	1657
IBL 098-3-1 × Sosat C 88	59	55	8	11	1260	4184	404	2357
IBL 106-B-1 × Sosat C 88	59	54	8	11	2133	1733	944	953
IBL 110-B-1 × Sosat C 88	56	53	9	10	2367	3288	1032	1835
IBL 114-6-1 × Sosat C 88	53	51	9	10	2917	2971	1662	1171
IBL 119-B-1 × Sosat C 88	59	60	9	7	2992	994	1261	482
IBL 155-2-1 × Sosat C 88	51	51	9	11	1939	2889	801	1630
IBL 165-1-1 × Sosat C 88	60	59	11	9	3801	1770	1450	778
IBL 179-2-1 × Sosat C 88	53	55	9	10	2449	3390	1103	2070
IBL 179-3-1 × Sosat C 88	58	54	9	10	1644	3107	727	1767

Table 4: Continued.

Genotype	FWT (das)		TGW (g)		PY (kg ha^{-1})		GY (kg ha^{-1})	
	Bambey	Nioro	Bambey	Nioro	Bambey	Nioro	Bambey	Nioro
IBL 206-1-1 × Sosat C 88	54	52	8	9	2411	4240	1010	2966
Souna 3	55	56	8	8	3465	2372	1731	805
Sosat C 88	50	52	9	10	2956	2180	1707	1389
Thialack II	54	52	7	8	3716	3044	1659	1729
Mean	57	55	8	9	2186	2441	1072	1270
SD	5	4	2	2	955	1089	476	703

FWT: flowering time; TGW: 1000-grain weight; PY: panicle yield; GY: grain yield.

Table 5: Mean squares for combining ability for studied traits across locations.

Source of variation	d.f.	DMI	FWT	PH	PLEN	PDIA	PT	TGW	PY	GY
Rep (site)	2	55.5	12.7	300.9	1.2	0.7	3.1	5.0	316965	25012
Site	1	158.8*	178.8***	711.6	280.0**	0.2	12.2*	26.1**	9629606**	6762757***
Hybrid	33	188.1***	45.7***	2852.4***	309.4***	0.5*	4.3**	6.2***	1962646	688597
Line (GCA)	16	229.6***	64.9***	3607.8***	160.6***	0.4	5.4**	4.4**	2290926*	775061*
Tester (GCA)	1	776.5***	40.5**	270.7	6226.1***	1.6*	0.7	64.8***	1998612	123285
Line × tester (SCA)	16	110.0**	26.8***	2258.6***	88.5***	0.4	3.4*	4.4***	1632117	637466
Site × line	16	52.4	7.5	311.4	18.0	0.3	2.3	3.9**	3292948**	1351732***
Site × tester	1	184.4*	54.0**	79.1	26.1	1.6	0.9	0.04	95074	444360
Site × line × tester	16	64.1	6.0	173.9	28.2	0.3	1.2	1.2	703213	424419
Error	134	39.7	5.3	281.7	25.4	0.3	1.9	1.8	1244846	414329

DMI: downy mildew incidence; FWT: flowering time; PH: plant height; PL: panicle length; PDIA: panicle diameter; PT: productive tillers; TGW: 1000-grain weight; PY: panicle yield; GY: grain yield; GCA: general combining ability; SCA: specific combining ability; d.f.: degree of freedom; Rep: replication. *,**,***Significant at 0.05 and 0.01 and 0.001 probability levels, respectively.

Table 6: Estimates of GCA effects of lines and testers evaluated across the two sites.

Lines	DMI (%)	FWT (das)	PH (cm)	PLEN (cm)	PDIA (cm)	PT	TGW (g)	PY (kg ha^{-1})	GY (kg ha^{-1})
IBL 001-4-1	9.7***	−0.8	10.1	−2.5	0.1	0.6	1.1	483.9	354.4
IBL 003-B-1	1.6	−4.2***	−21.7***	−5.7***	0.3	0.2	1.7*	447.9	367.4
IBL 011-4-1	−0.4	−3.8***	−12.0*	3.0*	−0.3	0.3	0.0	−334.1	−260.4
IBL 021-3-1	−1.1	0.8	−21.3***	−1.2	−0.2	−0.8	−0.5	−339.1	−143.8
IBL 055-4-1	−3.2	2.6**	0.9	−2.9*	0.3	−1.2**	−0.4	−724.2	−132.9
IBL 091-1-1	−3.2	−3.0**	−13.2*	5.5***	−0.1	−0.2	0.0	−111.2	217.9
IBL 095-4-1	−2.4	−1.7*	3.0	6.7***	−0.2	−0.2	0.0	−51.7	107.5
IBL 098-3-1	9.0***	0.8	12.5*	2.8*	0.0	−0.6	−0.1	−227.9	−62.2
IBL 106-B-1	−0.4	1.4	−12.5*	2.3	−0.2	−1.1*	0.1	−554.6	−247.0
IBL 110-B-1	−2.3	0.6	−3.4	3.0*	0.4	0.4	−0.9	756.7	66.2
IBL 114-6-1	−1.4	−0.5	−1.7	−2.7*	0.0	−0.2	−0.3	215.7	−98.2
IBL 119-B-1	−2.4	2.9**	41.2***	3.3*	−0.2	0.3	−0.4	37.4	−196.4
IBL 155-2-1	7.6**	−1.0	5.3	−1.2	−0.2	1.3**	0.2	−263.9	−239.0
IBL 165-1-1	−3.2	4.2***	19.8***	0.3	0.2	0.0	−0.1	350.7	−34.2
IBL 179-2-1	−3.2	1.6	19.4***	−3.7**	0.0	0.3	−0.1	−339.1	−236.0
IBL 179-3-1	−2.4	0.9	−1.1	−4.3**	0.1	−0.2	−0.3	−92.9	−72.4
IBL 206-1-1	−2.3	−0.9	−25.2***	−2.7*	0.0	0.9*	0.0	746.5	609.0
SE	*2.0*	*0.8*	*4.9*	*1.2*	*0.2*	*0.4*	*0.6*	*508.2*	*325.6*
Testers									
Souna 3	2.0	0.4	−1.2	5.5	−0.1	−0.1	−0.6*	99.0	−24.6
Sosat C 88	−2.0	−0.4	1.2	−5.5	0.1	0.1	0.6*	−99.0	24.6
SE	*1.0*	*0.5*	*0.6*	*0.4*	*0.1*	*0.1*	*0.0*	*21.6*	*46.7*

DMI: downy mildew incidence; FWT: flowering time; PH: plant height; PL: panicle length; PDIA: panicle diameter; PT: productive tillers; TGW: 1000-grain weight; PY: panicle yield; GY: grain yield. *,**,***Significant at 0.05 and 0.01 and 0.001 probability levels, respectively.

the traits while for male lines significant GCA effects were recorded only for TGW. For DMI, the GCA effects varied from −3.2 for IBL 091-1-1 to 9.7 for IBL 001-4-1. Positive and significant GCA effects for DMI were observed on parental lines IBL 001-4-1, IBL 098-3-1, and IBL 155-2-1. For FWT, GCA effects ranged from −4.2 for IBL 003-B-1 to 4.2 for IBL 165-1-1 and both positive and negative significant GCA effects were observed. Estimates of GCA effects for PH ranged from −25.2 for IBL 206-1-1 to 19.4 for IBL 179-2-1. Out of the 19 parental lines, six showed negative and significant effects whereas four lines exhibited positive and significant effects for PH. GCA effects for PLEN varied from −5.7 for IBL 003-B-1 to 6.7 for IBL 095-4-1 with both positive and negative significant effects whereas GCA effects for PDIA ranged from −0.3 for IBL 011-4-1 to 0.4 for IBL 110-B-1 with no significant effects. The GCA effects due to parental lines for PT across locations varied from −1.2 to 1.3 for IBL 055-4-1 and IBL 155-2-1, respectively. Significant positive GCA effects for PT were observed in lines IBL 155-2-1 and IBL 206-1-1 while significant negative GCA effects were observed in lines IBL 055-4-1 and IBL 106-B-1. Across research stations, the GCA for TGW ranged from −0.9 for IBL 110-B-1 to 1.7 for IBL 003-B-1. The tester Sosat C 88 and the inbred line IBL 003-B-1 had significant positive GCA effects while the tester Souna 3 showed significant negative GCA effects for TGW. For PY and GY traits, no significant GCA effects were showed. However, among parental lines, inbred lines IBL 206-1-1, IBL 003-B-1, IBL 001-4-1, IBL 091-1-1, IBL 095-4-1, and IBL 110-B-1 manifested desirable positive GCA effects for GY and most other studied traits for the two research stations. In contrast, inbred lines IBL 011-4-1, IBL 106-B-1, IBL 155-2-1, and IBL 179-2-1 ranked among the worst lines for GY with negative GCA effects.

3.5. Estimation of Specific Combining Ability Effects. Significant positive and negative SCA effects were recorded for all the observed traits (Table 7). The top-cross hybrid IBL 155-2-1 × Sosat C 88 was the only one which exhibited negative and significant SCA effects for DMI. In addition, its SCA effects for FWT and PH were negative and significant while its SCA effects for PT were significant and positive. Among 34 top-cross hybrids, six top-cross hybrids had significant SCA effects, of which three were positive. All the significant and positive SCA effects for PY and GY were recorded in the crosses among Sosat C 88 with the inbred lines IBL 179-2-1, IBL 091-1-1, and IBL 021-3-1.

3.6. Estimation of Standard, Best, and Mid-Parent Heterosis for Grain Yield across Locations. The estimates of best parent, mid-parent, and standard heterosis for grain yield are summarized in Table 8. The best parent heterosis for grain yield across the two locations varied from −44 to 60% and 17 hybrids displayed positive best parent heterosis. IBL 206-1-1 × Souna 3, followed by IBL 001-4-1 × Souna 3, had the largest best parent heterosis for grain yield and was among the best five hybrids while IBL 119-B-1 × Sosat C 88 had the least best parent heterosis value. The mid-parent heterosis varied from −16% for IBL 106-B-1 × Sosat C 88 to 125% for IBL 119-B-1 × Souna 3 which was not among the ten best hybrids. All the crosses displayed positive mid-parent heterosis for grain yield except IBL 106-B-1 × Sosat C 88 (−16%) and IBL 179-2-1 × Souna 3 (−12%). The standard heterosis values for grain yield across the experimental sites varied from −57% for IBL 179-2-1 × Souna 3 to 20% for IBL 206-1-1 × Souna 3. The crosses IBL 206-1-1 × Souna 3, IBL 091-1-1 × Sosat C 88, IBL 206-1-1 × Sosat C 88, IBL 001-4-1 × Souna 3, and IBL 003-B-1 × Sosat C 88 exhibited positive standard heterosis for grain yield. These hybrids were the top best five and displayed also both positive better and mid-parent heterosis values for grain yield.

4. Discussion

The significant differences observed among the genotypes for all the characters studied indicated the presence of large amount of genetic variability among the inbred lines, the OPVs, and their crosses, which is a prerequisite in the establishment of a successful breeding programme. Genetic variability for downy mildew disease and several agronomic traits has been also reported in many studies conducted in West and Central Africa [14, 16–19]. The results indicated also the influence of the environment on the performance of the genotypes for FWT, TGW, PY, and GY traits as their genotype × location interaction effect was significant. The environment effect in the performance of genotypes for flowering time was also reported in Burkina Faso [14]. The mean grain yield at Nioro research station was higher compared to Bambey research station. This could be explained by rainfall pattern and soil texture variability existing between the two locations where the experiments were established. Bambey research station is located in the northern part of the groundnut basin in the Sudano-Sahelian area and the soil texture is sandy while Nioro research station, located in the southern part of the groundnut basin in the Sudanese zone, has sandy-clay soil texture. However, despite the site effect on grain yield and yield related traits, some of the genotypes such as IBL 091-1-1, IBL 091-1-1 × Sosat C 88, and Thialack II have performed well under the two environments.

Besides the existence of useful variability, the establishment of a successful breeding programme depends on a deep understanding of the underlying gene action of the traits of interest. Indeed, this genetic information will guide breeders on which breeding methods and lines to use for the development of improved varieties [9]. In this study, GCA and SCA mean squares were significant for all the traits studied except for the SCA of PDIA, PY, and GY traits indicating that both additive and nonadditive gene actions were important for the inheritance of these traits across the two locations. This result is contrary to the findings of [16, 17] that reported only significant GCA effects for agronomic traits such as flowering time, downy mildew incidence, plant height, and panicle length. However, in the present study, the larger proportion of GCA over SCA mean squares for most of the traits such as DMI, FWT, PL, PDIA, and TGW indicated the preponderance of additive gene action over nonadditive gene action. This would imply that recurrent selection could be effectively used for improvement of these traits. The result of this study is consistent with that of [14] that reported additive gene action to be more important that

Table 7: Estimates of SCA effects for hybrids evaluated across the two sites.

Hybrid	DMI (%)	FWT (das)	PH (cm)	PLEN (cm)	PDIA (cm)	PT	TGW (g)	PY (kg ha^{-1})	GY (kg ha^{-1})
IBL 001-4-1 × Souna 3	2.5	−1.9*	−4.7	−1.8	0	0.6	1.2***	140.3	196.8
IBL 003-B-1 × Souna 3	1.1	0.5	13.8***	2.6	−0.3**	0.2	−0.9**	−81.1	−93.6
IBL 011-4-1 × Souna 3	0.8	0.7	0.2	0.2	−0.1	−0.1	−0.1	−148.8	−170.1
IBL 021-3-1 × Souna 3	0.1	1	−35.4***	−2.3	−0.1	−0.4	−0.8*	−739.7**	−376.5*
IBL 055-4-1 × Souna 3	−2	0.2	−27.2***	−6***	0.5***	0.4	0.1	105.2	157.6
IBL 091-1-1 × Souna 3	−2	1.8*	−3.7	0.9	0	−0.4	−0.9**	−370.6*	−379.3*
IBL 095-4-1 × Souna 3	−2.8	−2**	−8.3*	4.2**	0.1	0.4	0.1	175.4	160.8
IBL 098-3-1 × Souna 3	4.4	−1.7*	−2.9	−4*	−0.1	0.5	0.3	−296.6	−21.5
IBL 106-B-1 × Souna 3	0.9	−0.8	1.4	2.1	−0.1	−0.2	0.1	165.6	226
IBL 110-B-1 × Souna 3	−2.9	0.3	10.3**	1.9	0.2	0.6	−0.5	582.3*	54.2
IBL 114-6-1 × Souna 3	−0.2	1.8*	4.2	2.2	−0.1	−0.6	0	−75.6	−92.9
IBL 119-B-1 × Souna 3	−2.8	−2.3**	12.4**	−1	0.1	0.4	0.9**	697.4**	354.1
IBL 155-2-1 × Souna 3	8.8***	2.1**	14.5***	0.3	0.1	−0.8*	0	−25	−32.8
IBL 165-1-1 × Souna 3	−2	−0.9	2.3	−2.6	−0.2	0.4	−0.5	218.4	273.5
IBL 179-2-1 × Souna 3	−2	2.1**	11.8**	0.5	0.1	−1.2***	0.3	−605.7*	−400.8*
IBL 179-3-1 × Souna 3	−1.1	−0.9	8.5*	3.2*	−0.2	0.3	0	184.9	102.3
IBL 206-1-1 × Souna 3	−1	0.1	2.7	−0.4	0.1	−0.2	0.7*	73.9	42.3
IBL 001-4-1 × Sosat C 88	−2.5	1.9*	4.7	1.8	0	−0.6	−1.2***	−140.3	−196.8
IBL 003-B-1 × Sosat C 88	−1.1	−0.5	−13.8***	−2.6	0.3**	−0.2	0.9***	81.1	93.6
IBL 011-4-1 × Sosat C 88	−0.8	−0.7	−0.2	−0.2	0.1	0.1	0.1	148.8	170.1
IBL 021-3-1 × Sosat C 88	−0.1	−1	35.4***	2.3	0.1	0.4	0.8*	739.7**	376.5*
IBL 055-4-1 × Sosat C 88	2	−0.2	27.2***	6***	−0.5***	−0.4	−0.1	−105.2	−157.6
IBL 091-1-1 × Sosat C 88	2	−1.8*	3.7	−0.9	0	0.4	0.9**	370.6*	379.3*
IBL 095-4-1 × Sosat C 88	2.8	2**	8.3*	−4.2**	−0.1	−0.4	−0.1	−175.4	−160.8
IBL 098-3-1 × Sosat C 88	−4.4	1.7*	2.9	4*	0.1	−0.5	−0.3	296.6	21.5
IBL 106-B-1 × Sosat C 88	−0.9	0.8	−1.4	−2.1	0.1	0.2	−0.1	−165.6	−226
IBL 110-B-1 × Sosat C 88	2.9	−0.3	−10.3**	−1.9	−0.2	−0.6	0.5	−582.3*	−54.2
IBL 114-6-1 × Sosat C 88	0.2	−1.8*	−4.2	−2.2	0.1	0.6	0	75.6	92.9
IBL 119-B-1 × Sosat C 88	2.8	2.3**	−12.4**	1	−0.1	−0.4	−0.9**	−697.4**	−354.1
IBL 155-2-1 × Sosat C 88	−8.8***	−2.1**	−14.5***	−0.3	−0.1	0.8*	0	25	32.8
IBL 165-1-1 × Sosat C 88	2	0.9	−2.3	2.6	0.2	−0.4	0.5	−218.4	−273.5
IBL 179-2-1 × Sosat C 88	2	−2.1**	−11.8**	−0.5	−0.1	1.2***	−0.3	605.7*	400.8*
IBL 179-3-1 × Sosat C 88	1.1	0.9	−8.5*	−3.2*	0.2	−0.3	0	−184.9	−102.3
IBL 206-1-1 × Sosat C 8	1	−0.1	−2.7	0.4	−0.1	0.2	−0.7*	−73.9	−42.3
SE	*2.2*	*0.7*	*3.7*	*1.5*	*0.1*	*0.3*	*0.3*	*234.8*	*182.5*

DMI: downy mildew incidence; FWT: flowering time; PH: plant height; PL: panicle length; PDIA: panicle diameter; PT: productive tillers; TGW: 1000-grain weight; PY: panicle yield; GY: grain yield. *,**,***Significant at 0.05 and 0.01 and 0.001 probability levels, respectively.

nonadditive gene action in controlling agronomic traits such as grain yield, flowering time, and panicle length. Similarly, [20] reported the importance of additive gene action over nonadditive gene action in the expression of panicle length and diameter. The additive gene action was also reported for other traits in pearl millet such as Fe and Zn densities [11]. For grain yield, the significance of GCA_f and the lack of significance for SCA suggest that grain yield is controlled by additive gene effects as reported by several authors [14, 16]. However, the slight difference of their mean squares suggests that nonadditive gene action is also important in the inheritance of grain yield trait. This study has also provided information on parental effects in controlling the traits studied. The larger GCA_m mean squares over GCA_f mean squares for DMI, PL, PDIA, and TGW display the role of paternal effects in the control of these traits while the larger GCA_f mean squares over GCAm mean squares for FWT, PH, PT, and GY suggest the role of maternal effects in the control of these traits across the two locations. Similarly, [14] found a paternal effect in controlling PDIA and a maternal effect for FWT and PH under different locations in Burkina Faso. The best performing cross for high grain yield and resistance to downy mildew disease may be produced by crossing the male parents resistant to the disease with female parents having good yield potential.

Inbred lines IBL 001-4-1, IBL 003-B-1, IBL 091-1-1, IBL 095-4-1, IBL 110-B-1, and IBL 206-1-1 had positive GCA effects for grain yield indicating that these lines contributed

Table 8: Mean grain yield and best and mid-parent heterosis of pearl millet hybrid across locations.

Cross	GY (kg ha^{-1})	BPH	MPH	SH
IBL 001-4-1 × Souna 3	1923	52	108	14
IBL 003-B-1 × Souna 3	1646	23	26	−3
IBL 011-4-1 × Souna 3	942	−26	11	−44
IBL 021-3-1 × Souna 3	852	−33	1	−50
IBL 055-4-1 × Souna 3	1397	10	80	−18
IBL 091-1-1 × Souna 3	1211	−4	1	−29
IBL 095-4-1 × Souna 3	1641	29	48	−3
IBL 098-3-1 × Souna 3	1289	2	5	−24
IBL 106-B-1 × Souna 3	1351	7	37	−20
IBL 110-B-1 × Souna 3	1493	18	79	−12
IBL 114-6-1 × Souna 3	1181	−7	48	−30
IBL 119-B-1 × Souna 3	1530	21	125	−10
IBL 155-2-1 × Souna 3	1101	−13	27	−35
IBL 165-1-1 × Souna 3	1612	27	83	−5
IBL 179-2-1 × Souna 3	735	−42	−12	−57
IBL 179-3-1 × Souna 3	1402	11	30	−17
IBL 206-1-1 × Souna 3	2024	60	69	20
IBL 001-4-1 × Sosat C 88	1579	2	48	−7
IBL 003-B-1 × Sosat C 88	1883	22	30	11
IBL 011-4-1 × Sosat C 88	1331	−14	35	−21
IBL 021-3-1 × Sosat C 88	1654	7	68	−2
IBL 055-4-1 × Sosat C 88	1131	−27	23	−33
IBL 091-1-1 × Sosat C 88	2019	30	50	19
IBL 095-4-1 × Sosat C 88	1368	−12	10	−19
IBL 098-3-1 × Sosat C 88	1381	−11	1	−18
IBL 106-B-1 × Sosat C 88	949	−39	−16	−44
IBL 110-B-1 × Sosat C 88	1433	−7	47	−15
IBL 114-6-1 × Sosat C 88	1416	−9	51	−16
IBL 119-B-1 × Sosat C 88	871	−44	6	−49
IBL 155-2-1 × Sosat C 88	1215	−22	21	−28
IBL 165-1-1 × Sosat C 88	1114	−28	9	−34
IBL 179-2-1 × Sosat C 88	1586	2	63	−6
IBL 179-3-1 × Sosat C 88	1247	−19	2	−26
IBL 206-1-1 × Sosat C 8	1988	28	49	17

GY: grain yield; BPH: best parent heterosis; MPH: mid-parent heterosis; SH: standard heterosis.

favorable alleles for grain yield. They produced hybrids that were among the best 15 across the two locations. Thus, such lines could be used as parents to create high yielding synthetic or F_1 hybrid varieties. However, IBL 001-4-1 unlike the other five inbred lines had positive and significant GCA effect for downy mildew and produced hybrids with a certain level of disease incidence. The other lines showed negative GCA effects and would be good sources of resistance for downy mildew under Senegalese growing conditions. In addition, they had negative GCA effects for flowering time and plant height. Thus, their cross is expected to produce a medium plant height and early maturing synthetic pearl millet varieties, tolerant to the downy mildew disease with improved grain yield.

In this study, the top-cross hybrids performed better than the inbred lines and OPVs. The top five genotypes across the two locations were hybrids, showing evidence of heterosis for grain yield in pearl millet which has been also reported previously [5, 14, 16]. Grain yield showed a mid-parent heterosis ranging from −16% to 125% and most of the hybrids except IBL 106-B-1 × Sosat C 88 and IBL 179-2-1 × Souna 3 exceeded the parental lines. This finding is consistent with [18] that reported mid-parent heterosis ranging from 1.9 to 98% for top-crosses evaluated under low P conditions. Information about the performance of hybrids compared to the standard check is needed for the farmer to determine the benefit of growing hybrid. In this study, a maximum standard heterosis of 20% for grain yield was observed providing advantage of growing hybrids compared to the local cultivars. Similar standard heterosis for grain yield was also reported in Burkina Faso [14]. The higher mean performance of the crosses compared to their parents and the control check indicate great potential for hybrid pearl millet breeding. Therefore, this technology can be a good strategy to increase pearl millet production like in India where more than 70% of the pearl millet cultivated area is sown with F_1 hybrids [5]. However, a strong hybrid pearl millet breeding programme needs to be established.

5. Conclusion

The present study revealed that the crosses IBL 206-1-1 × Souna 3, IBL 091-1-1 × Sosat C 88, IBL 206-1-1 × Sosat C 88, IBL 001-4-1 × Souna 3, and IBL 003-B-1 × Sosat C 88 were the top five hybrids and exhibited positive best parent, mid-parent, and standard heterosis for grain yield. Furthermore, both additive and nonadditive gene action were involved in the inheritance of almost all the traits studied. However, the contribution of the additive gene action was higher than that of nonadditive gene action for all the traits. Inbred lines IBL 003-B-1, IBL 091-1-1, IBL 095-4-1, IBL 110-B-1, and IBL 206-1-1 exhibited positive GCA effects for grain yield and negative GCA effects for flowering time, downy mildew disease, and plant height. These lines can be used as parents for breeding high yielding synthetic varieties or hybrids F_1 adapted to West and Central African countries.

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

Acknowledgments

The authors are thankful to the West Africa Agricultural Productivity Program (WAAPP). This work could not have been done without the funding received from the WAAPP.

References

[1] FAO, *FAO Database for agriculture statistics*, 2015, http://faostat.fao.org.

[2] V. Rajaram, T. Nepolean, S. Senthilvel et al., "Pearl millet [Pennisetum glaucum (L.) R. Br.] consensus linkage map constructed using four RIL mapping populations and newly developed EST-SSRs," *BMC Genomics*, vol. 14, no. 1, pp. 1–15, 2013.

[3] V. S. Nambiar, J. J. Dhaduk, N. Sareen, T. Shahu, and R. Desai, "Potential functional implications of pearl millet (Pennisetum glaucum) in health and disease," *Journal of Applied Pharmaceutical Science*, vol. 1, no. 10, pp. 62–67, 2011.

[4] Y. Camara, M. C. S. Bantilan, and J. Ndjeunga, *Impacts of Sorghum and Millet Research in West And Central Africa (WCA): A Synthesis and Lessons Learnt*, International Crops Research Institute for the Semi-Arid Tropics, 2006.

[5] O. P. Yadav and K. N. Rai, "Genetic Improvement of Pearl Millet in India," *Agricultural Research*, vol. 2, no. 4, pp. 275–292, 2013.

[6] S. L. Tan, "Cassava silently, the tuber fills: the lowly cassava, regarded as a poor mans crop, may help save the Euphytica world from the curse of plastic pollution," *Utar Agriculture Science Journal*, vol. 1, pp. 12–24, 2015.

[7] B. A. Christinck, M. Diarra, and G. Horneber, *Innovations in Seed Systems, Lessons from the CCRP Funded Project Sustaining farmer-managed Seed Initiatives in Mali, Niger and Burkina Faso*, International Crops Research Institute for the Semi-Arid Tropics, 2014.

[8] A. R. Hallauer, M. J. Carena, and J. B. Miranda-Filho, *Quantitative Genetics in Maize Breeding*, Springer, New York, NY, USA, 2010.

[9] D. S. Falconer and T. F. C. Mackay, *Introduction to Quantitative Genetics*, Longman, New York, NY, USA, 1996.

[10] O. Kempthorne, *An introduction to genetic statistics*, John Wiley and Sons, Inc., New York, NY, USA and London, UK, 1957.

[11] M. Govindaraj, K. N. Rai, P. Shanmugasundaram et al., "Combining ability and heterosis for grain iron and zinc densities in pearl millet," *Crop Science*, vol. 53, no. 2, pp. 507–517, 2013.

[12] R. S. Parmar, G. S. Vala, V. N. Gohil, and A. S. Dudhat, "Studies on combining ability for development of new hybrids in pearl millet [Pennisetum gaucum (L.) R. BR.]," *International Journal of Plant Science*, vol. 8, no. 2, pp. 405–409, 2013.

[13] V. P. Chaudhary, K. K. Dhedhi, H. J. Joshi, and D. R. Mehta, "Combining ability studies in line x tester crosses of pearl millet [Pennisetum glaucum (L.) R. Br.]," *Research on Crops*, vol. 13, no. 3, pp. 1094–1097, 2012.

[14] I. Drabo, *Breeding pearl millet (Pennisetum glaucum (L) R. BR.) for downy mildew resistance and improved yield in Burkina Faso [Ph.D. thesis]*, University of Ghana, 2016.

[15] D. C. Gemenet, W. L. Leiser, R. G. Zangre et al., "Association analysis of low-phosphorus tolerance in West African pearl millet using DArT markers," *Molecular Breeding*, vol. 35, no. 8, pp. 1–20, 2015.

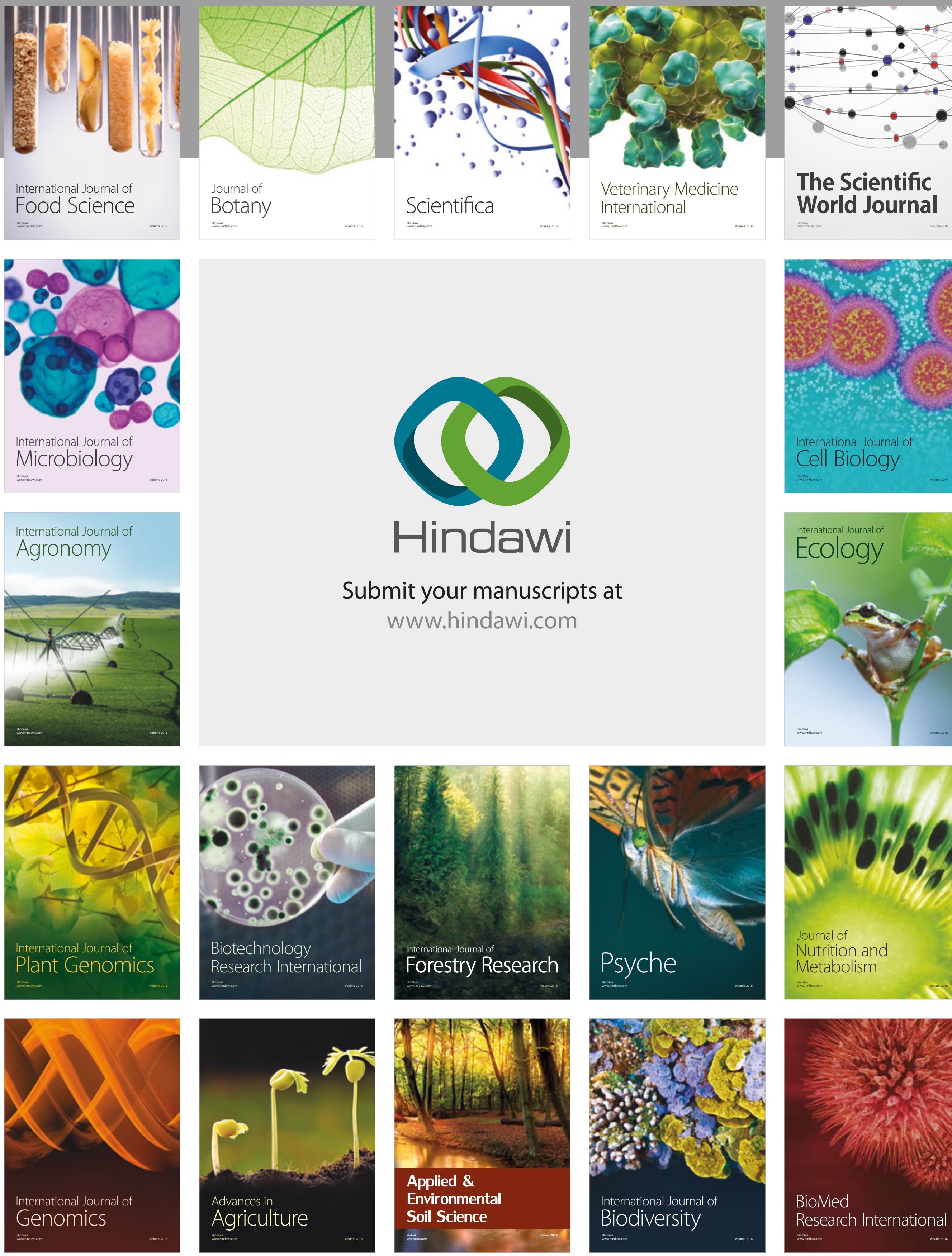
[16] B. Ouendeba, G. Ejeta, W. E. Nyquist, W. W. Hanna, and A. Kumar, "Heterosis and Combining Ability among African Pearl Millet Landraces," *Crop Science*, vol. 33, no. 4, pp. 735–739, 1993.

[17] A. Issaka, *Development of Downy Mildew Resistant F1 pearl millet Hybrids in Niger [Ph.D. thesis]*, University of Ghana, 2012.

[18] D. C. Gemenet, C. T. Tom, O. Sy et al., "Pearl millet inbred and testcross performance under low phosphorus in West Africa," *Crop Science*, vol. 54, no. 6, pp. 2574–2585, 2014.

[19] A. Pucher, O. Sy, M. D. Sanogo et al., "Combining ability patterns among West African pearl millet landraces and prospects for pearl millet hybrid breeding," *Field Crops Research*, vol. 195, pp. 9–20, 2016.

[20] A. S. Jethva, L. Raval, R. B. Madriya, D. R. Mehta, and C. Mandavia, "Combing ability over environments for grain yield and its related traits in pearl millet," *Crop Improvement*, vol. 38, no. 1, pp. 92–96, 2011.


International Journal of Food Science
Journal of Botany
Scientifica
Veterinary Medicine International
The Scientific World Journal
International Journal of Microbiology
Hindawi
Submit your manuscripts at
www.hindawi.com
International Journal of Cell Biology
International Journal of Agronomy
International Journal of Ecology
International Journal of Plant Genomics
Biotechnology Research International
International Journal of Forestry Research
Psyche
Journal of Nutrition and Metabolism
International Journal of Genomics
Advances in Agriculture
Applied & Environmental Soil Science
International Journal of Biodiversity
BioMed Research International