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Heterosis and Inheritance of Quantitative Characters in a Diallel Cross of Pearl Millet (*Pennisetum glaucum* L.)

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Abstract: A nursery experiment was conducted during the dry season of 2003 to March 2004, at the Lake Chad Research Institute Maiduguri, Nigeria under irrigation with 10 (ten) pearl millet inbred lines to form an F_1 population by crossing in all possible combinations excluding reciprocals through diallel (Griffing's Method 2 Model 1). The 45 hybrids and the 10 parental lines were evaluated during the cropping seasons of 2004 and 2005 at two locations, Maiduguri and Yola, Nigeria in a Randomized Complete Block Design (RCBD) with three replications. The Analysis of Variance (ANOVA) indicated that there were significant differences among the entries for most of the traits evaluated. Both additive and non-additive genetic effects were involved in the control of the traits, but non-additive genetic effect was the most important in that regard. This study identified ACC-1022-1-2SPT and SOSAT-C88 as the best parents in total grain yield considering there *per se* performance. The parents, BONKOK-SHORT, DMR 43, DMR22 and LCIC9702 were identified as the best general combiners in terms of GCA effects. The hybrids DMR22×LCIC9702, DMR43×LCIC9702, DMR22×LCIC9703-27, D2P29×EX-BORNO were observed to have recorded the highest SCA effects in various traits. Similarly, the hybrids D2P29×DMR43, DMR22×LCIC9702, DMR43×LCIC9702, BONKOK-SHORT×SOSAT-C88 and D2P29×EX-BORNO were the highest in terms of *per se* performance. It has been observed however, that some hybrids with high SCA effects were also high in *per se* performance. A fair general parallelism existed in most cases between GCA effects and the performance of the parental lines *per se*. Similar general parallelism also existed between SCA effects and *per se* performance of hybrids and between SCA effects of hybrids and levels of higher parent heterosis. Considerable higher parent heterosis was exhibited among the hybrids in almost all the traits. Higher parent heterosis of 85.13 and 114.05 for yield per plant and total grain yield per hectare, respectively were obtained in this study. There is therefore a great potential for the production of hybrid pearl millet varieties with increased total grain yield. The preponderance of non-additive genetic effect and the tremendous levels of higher parent heterosis observed among the traits in the parents and the hybrids studied would be great asset in choosing pearl millet cultivars for inter crossing and development of varieties and hybrids for commercial production.

Key words: *Per se* performance, additive genetic effect, non-additive genetic effect, high parent heterosis short running title: Genetic study in a diverse population of pearl millet

INTRODUCTION

Pearl millet (*Pennisetum glaucum* L.) is a staple food crop in arid and semi-arid areas of Africa and Asia (Khairwal *et al*., 1999). In addition as being the principal food cereal in arid and semi-arid regions and as forage, it also has a potential as an early-maturing summer grain crop in temperate regions (Anand Kumar and Andrews, 1993; Yoshida and Sumida, 1996). Pearl millet has high yield potential and responds well to water and soil fertility (Poelhman, 1994). However, several pearl millet cultivars existing in West Africa have low grain yields when grown under harsh conditions characterized by poor, eroded soils and low uneven rainfall (Ouendeba *et al*., 1993). This is because these cultivars have an inherent insignificant yield gains. Information on the combining abilities and heterosis of diverse breeding population are therefore needed for efficient choice of breeding parental materials and methods to use in developing productive base population for grain yield improvement. Therefore

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knowledge on the relative performance and magnitude of genetic variability of the desired agronomic traits within the population would be important.

At present little information on genetic variability in pearl millet are available in semi arid region of northern Nigeria (Izge *et al*., 2005). Information on the combining abilities and heterotic patterns among pearl millet cultivars that are grown in the Sahel and the Sudan savanna agricultural zones of Nigeria are also limited. This information if available would be helpful in the development of a successful breeding program, because mass selection within the pearl millet populations have not increased grain yield significantly. Jauhar (1981) reported that among the important breeding procedures of pearl millet is the exploitation of hybrid vigor for both grain and forage yields. Nwasike *et al*. (1992) and Ouendeba *et al*. (1993) reported significant level of heterosis in pearl millet diallel studies involving five parental lines. Gardener and Eberhart (1966) and Barker (1978) and Izge (2006) however, expressed reservation on such results and reported that any diallel involving less than ten parental lines may not give accurate results.

Previous research in pearl millet dwelt so much on downy mildew disease resistance without considering the other important yield traits. For this reason, further research should focus on the yielding ability in addition to other traits in the cultivars commonly produced. The objectives of this study were therefore to determine the General Combining Ability (GCA) and Specific Combining Ability (SCA) variances. The study was also aimed at estimating the GCA effect of parents and the SCA effects of hybrids and to identify the level of heterosis among the hybrids in all the traits evaluated.

MATERIALS AND METHODS

Ten (10) pearl millet inbred lines chosen based on their geographical and genetic diversity were randomly selected and crossed in all possible combinations (diallel) without reciprocals during the dry season of 2003 to March 2004 under irrigation applied to soil field capacity every three days to maturity, at the Lake Chad Research Institute (LCRI), Maiduguri, Nigeria. The genetic materials were procured from LCRI, Maiduguri and ICRISAT India viz, ACC-1022-1-2SPT, BONKOK-SHORT, DMR43, DMR22, LCIC9702, LCIC9703-27, D2P29, EX-BORNO, SOSAT-C88 and IMV11-3-3SPT.

All the 45 hybrids (F_1) and the ten parental lines were grown for evaluation at two locations, Yola (9^0 8^IN, 12^0 16^I E), in northern guinea savanna and Maiduguri (11^0 53^I 13^0 16^I E), in Sudan savanna agricultural zones of Nigeria. The two locations provide difference in soil type and rainfall representing the two main pearl millet growing areas in Nigeria and indeed West Africa and Asia. The Maiduguri soils are characteristically sandy with a low moisture holding capacity Rayar (1986), while Yola soils are sandy loams with relatively high moisture holding capacity. The weather during the research was characterized by low temperature and dry air that is typical of the harmttan period.

The materials were grown in a Randomized Complete Block Design (RCBD), with three replications both at Yola and Maiduguri locations during the 2004 and 2005 cropping seasons. The genetic seed materials were planted on 22nd and on 29th of June in 2004 and 2005 respectively at Maiduguri location, while it was planted on 04th and 11th July in 2004 and 2005, respectively at Yola location. The plot size was made up of four rows each 5 m long and spaced 75 cm between rows and 50 cm within stands. Seeds sun dried to 10 moisture content were sown by hand as a pinch after treatment with Apron-Star WS (Metalaxyl active ingredient) at the rate of 15 g kg^{-1} of pearl millet seeds. Seeds after germination were thinned to 2 plants per stand at 3 weeks after sowing. Compound fertilizer (N.P.K 27:10:10) at the rate of 600 kg ha^{-1} was applied in two split doses, one at planting and the other at 5 weeks after sowing. Weed control was done by hoe at three weeks and seven weeks after sowing, according to Onwueme and Sinha (1991). Harvesting was done manually using hoe and knife after the plants have matured.

Data collections were done on the following traits according to the procedure of Nwasike *et al*. (1992) and Izge *et al*. (2005). The traits were; Days to 50 flowering, number of tillers/plant, number of leaves/plant, downy mildew incidence, plant height, panicle length, number of seeds/panicle, 1000-grain weight, threshing , grain yield/plant and grain yield/ha.

The statistical Analysis of Variance (ANOVA) was performed based on plot mean values for all the parameters combined across locations and years. The combining ability analysis was done according to Griffing (1956) Method 2 Model 1 using SAS 2005 package from Zhang *et al*. (2005), based on the following linear additive model:

$$Y_{ijkl} = \mu + L_i + Y_j + (LY)_{ij} + R_{(ij)k} + E_l + (LE)_{il} + (YE)_{jl} + (LYE)_{ijl} + \in_{(ijkl).}$$

Where:

Y_{ijkl} = Observation of any variable in the i_{th} location, j_{th} year, k_{th} replication, of the l_{th} entry;
μ = Over all mean; L_i = effect of the i_{th} location,
I = 1, 2; $Y_{j =}$ effect of the j_{th} year, j = 1, 2;

$(LY)_{ij}$ = Location×year interaction;
$R_{(ij)k}$ = Random error effect of the k_{th} replication nested in locations and years;
E_l = Effect of the l_{th} entry, $l = 1 \ldots 55$;
$(LE)_{il}$ = Location×entry interaction;
$(YE)_{jl}$ = Year×entry interactions;
$\epsilon_{(ijkl)}$ = Random error effect of the $ijkl_{th}$ plot observations.

The estimation of heterosis as an increase in F_1 means over higher parent means were expressed as percentage and computed using the formula of Liang *et al.* (1972) as follows:

$$H = F_1\text{-}Hp/Hp\text{x}100,$$

where:
H = higher parent heterosis,
F_1 = mean performance of hybrids and
Hp = mean performance of the higher parent.

RESULTS

The results indicated that significant difference existed in most of the traits (Table 1). However, there was no significant difference among hybrids, parents and GCA variance in total grain yield/ha. There was also no significant difference among parents, hybrids and in GCA, SCA, GCA×location, SCA×location in grain yield/plant. Similarly, no significant difference were observed in SCA, GCA×location, GCA×year, SCA×year and GCA×year×location in downy mildew incidence. The GCA×location, year×location, year×location×entry and parents×hybrids variance interactions were highly significant for days to 50 flowering. However, SCA×location interaction was significant for downy mildew incidence and threshing . The ratio of GCA to SCA variance indicated that the major part of the total genetic variability was due in part by additive genetic effect, but mostly by non-additive genetic effect where ratios were less than unity.

None of he parental lines exhibited any significant GCA effect for total grain yields. None of the parental lines also exhibited significant difference in GCA effects in number of tillers per plant, number of leaves/plant, threshing and grain yield/plant (Table 2). The parental line BONKOK-SHORT, exhibited the highest and significant negative GCA effects in days to 50 flowering, plant height, panicle length and number of seeds/panicle. Similarly, DMR22 exhibited the highest significant positive GCA effects in days to 50 flowering and plant height. The results revealed that BONKOK-SHORT and LCIC9702 were the best general combiners for earliness, because both the parental lines exhibited highly significant and negative GCA effects for days to 50 flowering. The result also indicated that DMR43 and DMR22 together are good general combiners for plant height, while DMR43 is a good general combiner for panicle length and number of seeds/panicle. Similarly BONKOK-SHORT is a good general combiner for 1000-

Table 1: Mean squares of entries and analysis of variance for combining ability in a 10×10 diallel cross of pearl millet, combined across locations (Maiduguri and Yola) and years (2004 and 2005)

Sources of variation	df	Days to 50% flowering	No. of tillers/ grain plant	No. of leaves/ plant	Downy mildew incidence (%)	Plant height (cm)	Panicle length (cm)	No. of seeds /panicle	1000-grain wt. (g)	Threshing (%)	Grain yield/ plant (g)	Yield (kg ha^{-1})
Year	1	12023.46**	38.30**	593.75**	3401.91**	145726.07*	28.54	949319.64	5.44	3858.69**	1150.75*	3050913.91**
Location	1	1071.63**	4.58*	2397.82**	150.11	7845.06*	580.81**	85116754.98**	6.87	27001.22**	19806.58**	4662672.07**
Rep/Location	4	17.59	1.04	52.58*	295.59*	2957.70*	25.16	593193.80	6.89	403.131*	361.309	611726.71*
Hybrids	44	23.20**	0.43	21.16	118.89*	1111.80*	92.31**	603710.31	3.84	99.883	131.933	170527.34
Parents	9	18.06	0.68	17.22	107.36	2017.25*	236.5**	1398635.83*	0.89	91.721	77.551	50638.32
Entries	54	48.99**	0.54	30.17**	134.38*	2826.99**	258.3**	1178341.79**	6.663	133.476	165.736*	357260.96**
Year×location	1	765.94**	0.34	3.20	172.62	22256.95**	181.4*	7539570.98*	2.64	18850.53**	9820.69**	10047516.93**
Year×Parent	9	8.21	0.20	14.72	43.93	562.82	10.91	444656.85	1.93	73.092	140.796	159736.17
Year×Entries	54	9.79	0.36	8.41	72.74	521.65	16.71	516737.49	2.75	97.526	97.969	113649.56
Year×location × Entr.	54	20.30**	0.395	14.576	46.71	1122.89**	12.96	801148.59*	3.903	423.607	265.3**	259882.16**
Location×Parents	9	26.73	0.377	12.51	139.14	729.17	21.35	628349.37	1.341	82.144	192.58	295204.78
Location×Entries	54	11.02	0.36	14.55	73.15	714.25	14.55	577551.27	3.452	177.25	113.56	16210.06
Parents×Hybrids	1	548.01*	5.643**	177.23*	115.86	70.87**	87.05	947769.75	11.383	19.037	1209.99*	8348714.21**
GCA	9	112.53**	0.44	12.91	269.11**	4589.89**	849.19**	2391364.92**	13.56**	171.625	94.901	204495.29
SCA	45	30.15**	0.59	25.11*	83.79	1657.24**	80.20**	436522.43	3.835	125.272	117.377	292038.10**
GCA×location	9	28.25**	0.25	12.08	99.36	774.32	23.93	335857.54	1.23	70.773	153.908	259721.92
SCA×location	45	9.12	0.33	13.24	104.49*	724.26	16.05	409541.64	4.745	167.354*	98.133	103469.14
GCA×year	9	28.26	0.19	11.74	106.56	1076.32	89.55**	529963.41	3.919	126.07	80.767	54885.71
SCA×year	45	10.51	0.35	10.95	74.34	598.61	29.78	369998.23	3.104	74.282	92.274	96701.63
GCA×year × Location	9	18.44	0.75	11.79	74.11	497.92	17.02	369884.49	3.59	200.67	145.18	118156.73
Pooled error	409	9.02	0.35	14.69	58.54	606.73	20.36	550391.3	2.97	93.11	99.23	119185.40
GCA: SCA	-	0.408	0.35	0.00	0.69	0.316	1.15	1.34	1.02	0.20	0.19	0.29

*: Significant; **: Highly sig significant; Ns: Non-significant

Table 2: Estimates of general combining ability effects for yield and yield traits in ten pearl millet inbred lines, combined across locations (Maiduguri and Yola) and years (2004 and 2005)

S/No.	Parental lines	Days to 50% flowering	No. of tillers/plant	No. of leaves/plant	Downy mildew incidence (%)	Plant height (cm)	Panicle length (cm)	No. of seeds/panicle	1000-grain weight (g)	Threshing (%)	Grain yield/ plant (g)	Grain yield (kg ha^{-1})
1	ACC-1022-1-2SPT	-0.38	-0.028	-0.247	-1.518	1.612	1.9	219.625	-0.255	0.912	-3.353	-67.01
2	BONKOK SHORT	-4.110**	0.032	-1.065	-1.562	-23.088**	-14.605**	-810.733**	1.955**	4.495	-1.246	-59.441
3	D2P29	0.477	0.007	-0.675	-4.371*	9.98	2.835*	94.707	-0.437	-2.809	0.68	17.946
4	DMR43	2.008**	0.006	0.753	-1.145	10.499*	7.449**	306.602*	0.047	-2.666	3.155	88.091
5	DMR22	2.392**	-0.162	-0.122	1.92	10.810*	2.933**	236.178	-0.149	-0.591	-0.19	-4.366
6	E×-BORNO	1.259*	0.141	0.851	1.519	4.375	-0.927	101.813	0.039	-1.415	0.935	3.941
7	IMV 11-3-3SPT	0.144	-0.04	0.503	2.919	1.159	1.664	52.39	-.818*	-1.308	0.694	35.459
8	LCIC9702	-1.565**	0.03	0.227	0.189	-16.243**	-0.684	-77.85	-0.155	2.333	0.285	48.657
9	LCIC9703-27	-0.219	-0.004	-0.288	2.578*	1.196	-0.442	-128.58	-0.265	1.034	-0.954	-48.587
10	SOSAT-C88	-0.006	0.018	0.064	-0.528	-0.301	-0.125	5.848	0.038	0.015	-0.006	-14.69
	LSD (0.05)	4.806	NS	NS	12.245	39.419	7.221	118.726	2.759	NS	NS	NS
	LSD (0.01)	6.317	NS	NS	16.094	51.808	9.491	156.04	3.626	NS	NS	NS
	r (Mean and GCA)	0.629*	0.088	0.698*	0.55*	0.962**	0.919**	0.694*	0.865**	0.643*	0.136	0.4

Table 3: Estimates of specific combining ability effects for yield and yield traits among 45 hybrids of pearl millet, combined across locations (Maiduguri and Yola) and years (2004 and 2005).

S/No.	Hybrids	Pedigree	Days to 50% flowering	No. of tillers/ plant	No. of leaves/ plant	Downy mildew incid (%)	Plant height (cm)	Panicle length (cm)	No. of leaves/ plant	1000-grain weight (g)	Threshing (%)	Grain yield/ plant (g)	Grain yield (kg ha^{-1})
1	1×2	ACC-1022-1-2SPT×BONKOK SHORT	2.138	-0.135	1.852	-3.407	9.381	9.484**	551.663	-1.291	-2.412	-0.175	56.882
2	1×3	ACC-1022-1-2SPT×D2P29	-0.679	-0.130	0.663	2.022	-3.770	-0.173	296.124	0.113	4.382	1.054	39.316
3	1×4	ACC-1022-1-2SPT×DMR43	1.684	0.297	-0.074	1.598	0.993	-5.216	328.678	0.146	7.877	-0.733	16.378
4	1×5	ACC-1022-1-2SPT×DMR22	-0.977	-0.168	1.707	-3.244	1.405	-2.471	108.084	-0.774	2.907	-2.999	-79.982
5	1×6	ACC-1022-1-2SPT×E×-BORNO	-2.334	0.208	-2.289	-3.444	-7.464	1.174	-264.897	0.440	-0.572	0.237	59.409
6	1×7	ACC-1022-1-2SPT×IMV11-3-3SPT	-0.114	-0.460	-1.325	-2.971	7.392	-0.953	187.958	0.544	-0.744	0.079	67.821
7	1×8	ACC-1022-1-2SPT×LCIC9702	0.164	-0.017	2.042	0.559	8.850	-1.251	-274.796	0.168	-7.103	-4.826	-103.297
8	1×9	ACC-1022-1-2SPT×LCIC9703-27	0.725	-0.307	-2.263	-2.677	-14.920	-1.826	119.975	0.163	2.535	0.414	33.405
9	1×10	ACC-1022-1-2SPT×SOSAT-C88	0.219	0.131	-1.064	8.977	1.765	0.750	-372.441	0.478	-3.495	2.862	26.508
10	2×3	BONKOK SHORT×D2P29	-0.008	0.065	0.857	1.633	-15.778	-6.521**	-302.712	0.657	4.366	-1.485	-57.477
11	2×4	BONKOK SHORT×DMR43	-0.887	0.057	-0.477	1.295	0.346	-5.917*	-243.346	3.206**	1.150	-5.133	-195.950
12	2×5	BONKOK SHORT×DMR22	-1.646*	0.263	0.622	5.381	6.807	-4.161	-189.608	0.829	1.951	4.341	161.930
13	2×6	BONKOK SHORT×E×-BORNO	-4.355**	-0.055	0.025	1.175	9.574	-1.362	-185.882	0.906	5.295	2.536	168.873
14	2×7	BONKOK SHORT×IM11-3-3SPT	-2.238	0.522	2.209	-5.683	0.983	-1.977	-202.212	-0.031	-4.483	1.321	155.554
15	2×8	BONKOK SHORT×LCIC9702	-1.832	0.099	-1.110	7.188	3.672	0.706	36.229	-0.386	4.577	-2.231	-14.627
16	2×9	BONKOK SHORT×LCIC9703-27	-0.484	0.083	0.595	-2.501	1.692	-0.130	-53.049	-0.434	0.735	-0.396	146.244
17	2×10	BONKOK SHORT×SOSAT-C88	4.493**	-0.326	-1.813	-3.383	-0.960	5.644	294.032	-1.803	-8.331	3.057	-118.092
18	3×4	D2P29×DMR43	-1.828	0.057	-0.238	4.504	1.340	-3.858	-227.768	-0.046	2.975	1.266	203.408
19	3×5	D2P29×DMR22	-0.114	0.207	1.015	-1.606	-1.186	-3.998	18.745	-0.103	-3.636	-2.637	32.124
20	3×6	D2P29×E×-BORNO	-0.503	-0.056	-0.801	-2.192	-0.289	2.416	122.804	0.142	-1.297	2.502	224.263
21	3×7	D2P29×IMV11-3-3SPT	0.277	-0.233	-3.134	0.483	7.684	2.364	508.728	-0.231	5.428	3.004	154.678
22	3×8	D2P29×LCIC9702	0.645	0.249	1.833	-1.871	19.656	3.770	111.666	-0.080	-1.252	6.545	154.204
23	3×9	D2P29×LCIC9703-27	-1.286	0.455	2.641	-1.943	14.803	4.105	-55.946	0.525	-1.663	4.897	51.732
24	3×10	D2P29×SOSAT-C88	-2.293	-0.181	-0.729	-0.954	-5.593	2.011	-354.140	-0.904	-8.775	-10.600	-495.727*
25	4×5	DMR43×DMR22	-1.262	0.327	2.759	-3.219	-29.480	1.780	215.399	0.358	-0.079	2.923	114.661
26	4×6	DMR43×E×-BORNO	0.025	0.485	1.152	-1.766	16.968	1.575	-268.784	0.121	-7.602	1.490	64.578
27	4×7	DMR43×IMV11-3-3SPT	2.100	-0.316	-1.353	-7.634	0.387	9.306**	248.965	-0.114	2.753	6.808	168.614
28	4×8	DMR43×LCIC9702	1.054	-0.300	-0.414	-1.167	11.328	3.433	192.583	-0.431	-8.375	3.826	249.875
29	4×9	DMR43×LCIC9703-27	-2.203	0.271	1.300	5.605	2.641	1.176	85.218	-0.573	0.532	2.841	-36.553
30	4×10	DMR43×SOSAT-C88	3.228	-0.577	-1.743	0.032	6.500	1.198	177.130	-1.421	-0.937	-8.211	-288.399
31	5×6	DMR22×E×-BORNO	1.022	-0.240	0.324	-1.334	3.912	-1.861	513.244	-0.361	3.462	-0.296	21.467
32	5×7	DMR22×IMV11-3-3SPT	1.580	0.392	2.758	-0.900	17.139	-0.645	-42.695	0.347	-5.365	2.607	62.935
33	5×8	DMR22×LCIC9702	0.408	-0.091	-0.803	-1.599	27.256	0.596	460.298	-0.138	-2.093	5.290	299.555
34	5×9	DMR22×LCIC9703-27	0.652	-0.272	0.285	-0.917	12.068	3.926	318.309	0.329	7.914	4.359	232.658
35	5×10	DMR22×SOSAT-C88	0.333	-0.257	-6.079*	2.850	-22.466	4.589	-650.767	-0.107	-3.071	-7.458	-606.422**
36	6×7	E×-BORNO×IMV11-3-3SPT	-1.346	0.414	2.858	8.173	-12.493	-4.200	-78.459	0.669	4.735	-1.107	87.452
37	6×8	E×-BORNO×LCIC9702	-0.402	0.299	0.342	-1.325	-2.083	-2.400	-192.990	0.246	-2.239	-2.316	44.156
38	6×9	E×-BORNO×LCIC9703-27	0.961	-0.505	-3.050	0.527	11.812	0.503	-79.731	-0.374	-3.467	-4.575	-43.550
39	6×10	E×-BORNO×SOSAT-C88	3.481	-0.146	1.926	0.814	-0.133	1.646	167.269	-1.001	1.408	0.033	-272.978
40	7×8	IMV11-3-3SPT×LCIC9702	-0.135	-0.027	2.345	7.320	18.570	3.525	109.866	-0.289	-0.234	3.204	-118.275
41	7×9	IMV11-3-3SPT×LCIC9703-27	0.058	0.144	-0.713	0.557	9.166	0.827	2.616	-0.462	-5.766	-3.098	-68.348
42	7×10	IMV11-3-3SPT×SOSAT-C88	-0.777	-0.369	-1.377	-0.659	-20.843	-3.883	-217.381	-0.096	1.999	-4.831	-182.011
43	8×9	LCIC9702×LCIC9703-27	-3.728*	0.187	0.851	2.261	-5.824	-0.886	-191.243	0.983	3.993	1.832	62.939
44	8×10	LCIC9702×SOSAT-C88	0.745	-0.240	-3.708	-7.631	-49.552**	-5.215	-51.632	0.163	9.413	-4.889	-220.158
45	9×10	LCIC9703-27×SOSAT-C88	2.237	0.104	1.008	-2.066	-17.972	-5.040	-4.630	0.069	0.755	-2.364	-155.682
		LSD (0.05)	4.806	0.954	6.133	12.245	39.419	7.221	1187.260	2.769	15.443	15.940	552.487
		LSD (0.01)	6.317	1.252	8.061	16.094	51.808	9.491	1560.400	3.626	20.296	20.950	726.126
		r (SCA & Means)	0.425**	0.008	0.693**	0.470**	0.315*	0.306*	0.379*	0.200	0.481**	0.461**	0.425**

*: Significant; **: Highly sig significant; Ns: Non-significant

grain weight. The result indicated that there is a significant and positive correlations existing between GCA effects and the parental performance *per se* in all the traits except in number of tillers/plant, grain yield/plant and total grain yield/ha.

The results indicated that ACC-1022-1-2SPTx BONKOK-SHORT exhibited the highest, positive significant SCA effect in panicle length. In contrast however, BONKOK-SHORTxD2P29, exhibited the highest and significant negative SCA effect also in panicle length. The hybrids BONKOK-SHORTxSOSAT-C88 and BONKOK-SHORTxEX-BORNO exhibited highest significant positive SCA effect and the highest significant negative SCA effect respectively in days to 50 flowering

(Table 3). Similarly, highest and negative significant SCA effect for total grain yield was recorded by D2P29x SOSAT-C88. No positive and significant SCA effects were observed among all the hybrids in total grain yield and in yield/plant.

The best performing parents and the hybrids on the basis of *per se* performance and their combining abilities for certain traits are presented in Table 4. The result revealed that the best hybrids in SCA effects did not always involved one or both of the best general combiners. The hybrids with high SCA effects in most cases involved at least one or two of the good general combiners as parents, namely BONKOK-SHORT, DMR43, DMR22, LCIC9702 and D2P29. The result reveals a good general parallelism between GCA effects and *per se* performance of parents for most of the traits. A similar trend of good general parallelism was also observed between SCA effects and the *per se* performance of hybrids (Table 4).

Positive higher parent heterosis ranging between 1.69 to 114.05 for total grain yield was recorded in forty-two out of the forty-five hybrids. The result also revealed high level of higher parent heterosis in grain yield/plant (Table 5). Higher parent heterosis of 85.13, 82.46 and 64.83 percentages in the hybrids IMV11-3-3SPT×LCIC9702, DMR22×LCIC9702 and D2P29×LCIC9702 in yield/plant was recorded. The result revealed that hybrids, DMR22×LCIC9702, EX-BORNO×IMV11-3-3SPT, D2P29×DMR43, EX-BORNO×LCIC9702, BONKOK-SHORT×IMV11-3-3SPT and D2P29×EX-BORNO as having the best higher parent heterosis level for total grain yield. Of all the hybrids, D2P29×EX-BORNO, BONKOK-SHORT×D2P29,BONKOK-SHORT×IMV11-3-3SPT,DMR22×IMV11-3-3SPTandEX-BORNO×IMV11-3-3SPT exhibited the highest higher parent heterosis in tiller number. The result also revealed, LCIC9703-27×SOSAT-C88, DMR43×IMV11-3-3SPT, LCIC9702×SOSAT-C88, ACC-1022-1-2SPT×BONKOK-SHORT and BONKOK-

Table 4: Best performing parents and crosses on the basis of *per se* performance and combining ability for certain characters in a diallel cross

Characters	Parents (*per se*)	General combiners	Specific combiners	Crosses (*per se*)
Days to 50 flowering	ACC-1022-1-2SPT	BONKOK-SHORT	BONKOK-SHORT×E×-BORNO	BONKOK-SHORT×E×-BORNO
Number of tillers	ACC-1022-1-2SPT	E×-BORNO	DMR43×E×-BORNO	BONKOK-SHORT×IMV11-3-3SPT
Number of leaves	SOSAT-C88	DMR43	IMV11-3-3SPT×LCIC9702	E×-BORNO×IMV11-3-3SPT
Downy mildew incidence	D2P29	D2P29	LCIC9703-27×SOSAT-C88	DMR43×IMV11-3-3SPT
Plant height	DMR43	DMR22	DMR43×SOSAT-C88	DMR22×LCIC9702
Panicle length	DMR22	DMR43	DMR43×IMV11-3-3SPT	ACC-1022-2SPT×BONKOK-SHORT
Number of seeds/panicle	SOSAT-C88	DMR43	DMR43×SOSAT-C88	ACC-1022-2SPT×BONKOK-SHORT
1000-grain weight	BONKOK-SHORT	BONKOK-SHORT	ACC-1022-2SPT×BONKOK-SHORT	BONKOK-SHORT×DMR43
Threshing	LCIC9702	BONKOK-SHORT	D2P29×IMV11-3-3SPT	LCIC9702×SOSAT-C88
Grain yield per plant	E×-BORNO	DMR43	DMR43×E×-BORNO	DMR43×IMV11-3-3SPT
Grain yield per hectare	ACC-1022-1-2SPT	DMR43	D2P29×DMR43	DMR22×LCIC9702

Table 5: Heterosis of crosses over high parent for yield and yield component of pearl millet, combined across locations and years

S/No.	Cross	Pedigree	Days to 50% flowering	No. of tillers/ plant	No. of leaves/ plant	Downy mildew incid (%)	Plant height (cm)	Panicle length (cm)	No. of leaves/ plant	1000-grain weight (g)	Threshing (%)	Grain yield/ plant (g)	Grain yield (kg ha^{-1})
1	1×2	ACC-1022-1-2SPT×BONKOK SHORT	-6.60	15.58	-3.37	-81.02	-11.00	-35.39	19.62	18.59	-9.47	-12.77	21.14
2	1×3	ACC-1022-1-2SPT×D2P29	-4.26	-8.67	3.50	-58.45	3.57	-2.41	4.23	0.78	-5.61	10.23	52.20
3	1×4	ACC-1022-1-2SPT×DMR43	-3.66	-7.65	-6.47	9.42	3.53	-6.14	-11.78	12.77	-2.63	-8.27	30.47
4	1×5	ACC-1022-1-2SPT×DMR22	-0.43	-12.24	11.78	-72.73	4.85	-9.91	1.41	-2.23	-0.44	-19.08	9.38
5	1×6	ACC-1022-1-2SPT×E×-BORNO	-6.50	1.02	-8.35	-78.25	1.00	-9.98	-26.07	7.29	1.82	10.55	28.27
6	1×7	ACC-1022-1-2SPT×IMV11-3-3SPT	-3.45	-4.59	-4.01	-64.13	3.81	-6.77	-32.24	-2.05	-8.98	-4.19	27.37
7	1×8	ACC-1022-1-2SPT×LCIC9702	-5.45	-5.61	8.80	-33.66	-7.81	-18.35	-16.90	-5.33	-19.56	-32.17	-3.35
8	1×9	ACC-1022-1-2SPT×LCIC9703-27	-2.58	-9.05	-18.63	-75.02	-1.55	-14.23	-0.56	2.38	6.41	-12.08	-1.69
9	1×10	ACC-1022-1-2SPT×SOSAT-C88	-7.78	-1.53	-7.42	-54.43	4.27	-6.80	-22.48	6.27	-5.91	-5.30	35.34
10	2×3	BONKOK SHORT×D2P29	-8.32	49.18	36.24	-68.09	-4.11	-38.68	-43.04	-16.95	-2.80	37.77	39.86
11	2×4	BONKOK SHORT×DMR43	-6.33	6.10	0.84	-13.34	1.31	-28.08	-31.18	13.10	-5.09	-21.62	5.93
12	2×5	BONKOK SHORT×DMR22	-6.06	27.33	22.72	-37.01	3.95	-37.04	-13.38	-12.61	-2.56	60.54	85.28
13	2×6	BONKOK SHORT×E×-BORNO	-13.55	11.18	10.57	-29.67	9.12	-34.02	-48.79	-7.07	-0.78	-0.67	88.81
14	2×7	BONKOK SHORT×IM11-3-3SPT	-6.88	41.67	17.25	-77.18	10.78	-21.00	-27.98	-12.48	-6.73	36.82	93.45
15	2×8	BONKOK SHORT×LCIC9702	-7.65	-11.73	-8.81	221.80	12.11	-14.44	-23.46	-13.78	2.55	1.15	50.68
16	2×9	BONKOK SHORT×LCIC9703-27	-10.33	-3.02	4.26	-69.05	-1.83	-19.41	-24.65	-19.98	-2.34	-15.42	78.75
17	2×10	BONKOK SHORT×SOSAT-C88	-9.21	24.54	9.29	-79.91	15.88	-9.86	-36.40	-12.76	-11.45	16.96	55.87
18	3×4	D2P29×DMR43	-2.75	-11.59	1.75	126.41	10.66	3.15	1.80	9.03	2.03	16.58	96.90
19	3×5	D2P29×DMR22	-0.23	-27.33	18.62	-35.45	10.50	-8.31	16.19	2.90	0.58	12.06	60.34
20	3×6	D2P29×E×-BORNO	-5.56	-3.11	-7.75	23.97	7.51	-5.13	3.22	6.19	2.94	1.74	89.29
21	3×7	D2P29×IMV11-3-3SPT	-3.90	-17.61	-13.63	91.16	6.94	-0.49	21.09	-3.46	7.41	22.02	81.35
22	3×8	D2P29×LCIC9702	-7.03	-10.71	6.25	-13.74	3.17	-1.92	9.44	1.67	5.59	64.83	80.07
23	3×9	D2P29×LCIC9703-27	-6.73	-17.59	0.70	-12.34	11.35	-1.25	-7.09	13.49	7.77	16.08	49.85
24	3×10	D2P29×SOSAT-C88	-4.41	-8.59	-3.20	-24.73	10.69	-6.50	-11.17	-5.02	-2.48	-37.95	18.69
25	4×5	DMR43×DMR22	-3.11	18.29	19.78	-50.10	-4.49	2.88	-7.41	10.16	0.63	13.06	42.09
26	4×6	DMR43×E×-BORNO	-3.23	53.05	18.94	-32.52	8.75	-6.03	-6.02	10.28	-10.91	60.71	65.62
27	4×7	DMR43×IMV11-3-3SPT	-1.38	-7.93	-1.04	-91.01	3.51	11.22	2.84	3.22	-2.12	42.65	58.33
29	4×9	DMR43×LCIC9703-27	-7.89	5.03	6.23	3.09	7.78	-9.94	-10.16	6.58	-1.41	30.64	23.92
30	4×10	DMR43×SOSAT-C88	-3.37	3.05	-2.29	-61.70	13.83	3.06	12.78	6.21	-7.89	1.07	53.22
31	5×6	DMR22×E×-BORNO	-1.02	6.21	9.06	-54.67	7.76	-22.25	3.22	7.29	11.73	-6.01	48.59
32	5×7	DMR22×IMV11-3-3SPT	-2.26	37.33	9.41	-13.91	10.25	-7.92	0.87	-2.79	-15.45	54.49	73.25
33	5×8	DMR22×LCIC9702	-4.40	-10.20	2.76	-63.87	11.20	-15.06	28.32	0.00	-4.31	82.46	114.05

Table 5: Continued

S/No.	Cross	Pedigree	Days to 50% flowering	No. of tillers/ plant	No. of leaves/ plant	Downy mildew incid (%)	Plant height (cm)	Panicle length (cm)	No. of leaves/ plant	1000-grain weight (g)	Threshing (%)	Grain yield/ plant (g)	Grain yield (kg ha^{-1})
34	5X9	DMR22 X LCIC9703-27	-4.04	-17.59	0.57	-47.65	12.97	-3.67	9.32	5.44	7.45	28.13	63.13
35	5X10	DMR22 X SOSAT-C88	-4.39	17.18	-22.33	-77.44	2.66	-8.25	-11.03	5.44	-3.67	-12.78	-16.62
36	6X7	EX-BORNO X IMV11-3-3SPT	-7.28	34.16	19.63	66.05	5.22	-8.26	-18.33	5.64	-12.51	-0.34	107.23
37	6X8	EX-BORNO X LCIC9702	-9.17	2.04	5.84	29.2	-0.63	-12.84	-21.95	6.41	-9.64	-16.69	91.63
38	6X9	EX-BORNO X LCIC9703-27	-7.16	-18.59	-14.18	-16.59	7.98	-4.48	-21.95	3.31	0.69	-26.42	69.79
39	6X10	EX-BORNO X SOSAT-C88	-4.31	19.63	-3.2	-59.97	17.97	-10.34	2.36	1.1	-9.16	-17.83	37.83
40	7X8	IMV11-3-3SPT X LCIC9702	-5.08	2.04	24.59	-20.26	21.67	20.88	7.32	-0.78	1.99	85.13	67.10
41	7X9	IMV11-3-3SPT X LCIC9703-27	-5.65	-0.5	-5.85	-41.85	-1.66	7.2	-5.56	-8.63	-9.77	1.19	15.97
42	7X10	IMV11-3-3SPT X SOSAT-C88	-9.85	19.63	-0.6	-68.62	13.83	11.17	-7.01	3.98	-5	20.75	49.84
43	8X9	LCIC9702 X LCIC9703-27	-11.29	1.51	5.34	-22.37	-2.83	0.69	-4.07	15	-1.44	36.4	88.81
44	8X10	LCIC9702 X SOSAT-C88	-10.77	6.12	-7.6	-86.67	6.8	2.55	-2.06	3.22	1.63	6.32	50.56
45	9X10	LCIC9703-27 X SOSAT-C88	-7.72	15.58	4.95	-99.42	6.21	1.07	-10.66	3.18	1.9	12.39	27.98
		r (Heterosis & SCA)	0.300*	0.087	0.711**	0.537**	0.207	0.25	0.545**	0.194	0.523**	0.663**	0.648**

*: Significant, **: Highly significant

SHORT×SOSAT-C88 as having the highest and negative levels of higher parent heterosis for downy mildew incidence. A positive higher parent heterosis of up to 221.8 of downy mildew incidence was recorded in the hybrid BONKOK-SHORT×LCIC9702. Generally, tremendous level of higher parent heterosis was observed among the population, except in days to 50 flowering, plant height and 1000-grain weight. The result also indicated significant and positive correlations between higher parent heterosis and SCA effects for all the traits, except in number of tillers/plant, plant height, panicle length and 1000-grain weight (Table 5).

DISCUSSION

The presence of significant difference among the parental lines and the hybrids of pearl millet population studied have been observed in all the traits. The presence of these differences indicated that an appreciable level of genetic variability exist in the pearl millet population. Falconer (1989) reported that the genetic improvement that can be obtained by selection among a number of parental lines and hybrids are dependent on the amount of variation existing between the population and the amount of selection applied. This therefore implies that the population generated would respond to selection.

The combining ability analysis of variance revealed the presence of additive and non-additive genetic effects as important in the control of the traits investigated. However, the ratio of GCA to SCA indicated that the major part of the total genetic variability for most of the traits were mainly due to non-additive genetic effects, except for panicle length, number of seeds per/panicle and 1000-grain weight, suggesting the traits were predominantly under the control of additive genetic effects. Contrasting results were reported by Nwasike *et al.* (1992), Chawdhary and Singh (1978) and Rao and Joshi (1979). The over all breeding implication of these results suggest that few of the traits of the pearl millet population could be improved through selection programs such as recurrent selection, which would necessitate the maintenance of heterozygosity in the population. Doggett and Eberhart (1968), Ahmad *et al.* (1979) and Kadams (2000) made similar recommendation in other self-pollinated crops. Panicle length, number of seeds/panicle and 1000-grain weight were at variance with this conclusion as they were under an additive genetic control. These traits could therefore, be improved through selection schemes such as the pedigree method or single seed descent method or any other modified selection capable of exploiting the fixable genetic variance. Under such a situation, the simultaneous exploitation of additive and non-additive components of genetic effects is advocated. Nwasike and Oyejola (1989) recommended the use of recurrent selection for population improvement in that respect.

Since the variance due to GCA was lower than that due to SCA, it also means that non-additive genetic effects were more stable than additive genetic effects over the environments suggesting that more than one test environment is not necessary to get any reliable information on the characters involved among these populations. Similar results were reported by Nwasike *et al.* (1992).

The general combining ability effects helps in identifying desirable parents in order to isolate desirable homozygotes from a segregating population. Highly significant and negative GCA effects displayed by BONKOK-SHORT and LCIC9702 in days to 50 flowering, implies that these two parents when crossed together would produce early or extra-early maturing hybrids. Kimbeng and Nwasike (1994) and Kukadia *et al.* (1983) reported similar results. The parent D2P29 that is a good general combiner for downy mildew tolerance, because of its negative and significant GCA effect for downy mildew incidence could be suitable for incorporation into a breeding program for downy mildew disease tolerance. The parental line EX-BORNO reported by Ouendeba *et al.* (1993) to be tolerant to downy mildew disease however did not appear to show any significant and negative GCA effect for downy mildew incidence in this study. This could be due in part to difference in the environments in which the two different studies were carried out. It could also be because; downy mildew disease strain in Nigeria that was reported to be the most virulent (Anaso *et al.*, 1998) is at work.

High level of correlations existing between GCA effects of parents and the parental line *per se* performance for most of the traits has a serious implication on crop improvement. Singh *et al.* (1982) reported that crossing two parents having a high general combining ability effects produced best performing hybrids. Some authors however expressed reservation and reported that the performance of a variety *per se* is not always a good indicator of their superior general combining abilities. Therefore in most cases parents could not be selected easily based on their GCA effects purely on the basis of their performance as varieties.

Specific combining ability effects are used to identify the best cross-combinations for hybrid production. The means (*per se* performances) of the best eleven hybrids as well as the correlation coefficients between the *per se* performance and the SCA effects shows that the best hybrids in terms of SCA effects, involved one or both of the best general combiners, namely BONKOK-SHORT, EX-BORNO, DMR43, DMR22 and D2P29. However, other poor general combiners frequently gave good cross-combinations, when they were crossed with best general combiners. Srivastava *et al.* (1978) and Kadams (2000) suggested that when parents with high and low GCA effects are crossed, the poor parent could throw up desirable transgressive segregates giving rise to a new population. However, this is only possible if the additive genetic system present in the good combiner and the complimentary epistasis present in the hybrids act in a complimentary fashion to maximize the desirable plant attributes which could be further exploited in further breeding programs. The corresponding means of the best hybrids as well as the existence of high levels of correlation between means and SCA effects for all the traits except, number of tillers/plant and 1000-grain weight connotes that the *per se* performance could be used to predict the best hybrids, eliminating the cumbersome calculations of SCA effects.

The presence of heterosis for the different traits of pearl millet has been reported in a number of studies. Virk (1988) and Presterl and Weltzien (2003) gave a detailed review. Most estimates of heterosis were obtained by using diallel with inbred parents as in this study and therefore comparable. Ouendeba *et al.* (1993) investigated heterosis and combining ability among five African pearl millet landraces in contrast to this study where heterosis were investigated among ten parental lines. Barker (1978) reported that estimate of heterosis and combining ability becomes effective only when the parental lines are not less than ten in a diallel. Negative heterosis for downy mildew incidence in pearl millet is very desirable, implying a possibility of breeding downy mildew tolerant cultivars. Hybrids producing higher and negative heterosis in downy mildew incidence were among those that recorded higher negative SCA effects. Chawdhry and Singh (1978) reported similar results where higher SCA effects were reflected in higher heterotic responses among hybrids. SCA effects could therefore be used in some cases to predict or identify high level of heterosis among hybrids. However, in some instances high heterotic response of a hybrid does not always mean high performance of the hybrid as well. This is because high heterosis of a hybrid may be due to relatively poor performance of one of the parents.

Plant height and panicle length in addition to grain yield are traits local farmers consider in choosing pearl millet cultivars in northern Nigeria. Longer plants are useful because the straws are used for bedding, building and thatching. Shorter plants are also desirable in this particular environment because of their tolerance to strong windy conditions that could cause lodging. The choice of a cultivar therefore depends on the farmer's priority. The present study identified the hybrids, EX-BORNO×SOSAT-C88 and IMV11-3-3SPT×LCIC9702, as having the longest plant height with high levels of higher parent heterosis, while ACC-1022-1-2SPT×BONKOK-SHORT as having the shortest plant height. However, DMR43×IMV11-3-3SPT, IMV11-3-3SPT×LCIC9702 and IMV11-3-3SPT×SOSAT-C88 could be the most desired cross combinations for developing varieties with longer panicle length, because they exhibited high level of higher parent heterosis in panicle length.

The hybrids ACC-1022-1-2SPT×BONKOK-SHORT, D2P29×LCIC9703-27 and LCIC9702×LCIC9703-27, recorded high levels of higher parent heterosis in 1000-grain weight and could be recommended for increased total grain yield. Significant and positive level of heterosis for 1000-grain weight was reported by Nwasike *et al.* (1992) in pearl millet, but this not match the levels reported in this study.

This study concludes that the SCA variance was greater than the GCA variance for most of the traits among the pearl millet population, indicating non-additive genetic effects as the most important in the control of the traits studied. Since non-additive gene action was more important for grain yield, simple recurrent selection that emphasizes selection for SCA could be employed in the breeding program. The study also concludes that an astounding level of variability existed in the population because of the enormous level of high parent heterosis among the hybrids, indicating a possibility for the production of pearl millet hybrid varieties.

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