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Research Paper

Improvement of restorer lines for strengthening pearl millet (*Pennisetum glaucum* L.) hybrid breeding in West and Central Africa

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Abstract. Little information was available on the genetics of pearl millet restorers available in West and Central Africa. Hence, diallel analysis was carried out using six parents and 30 F1's, to identify the nature of gene action, and improve the restorer gene pool. The genotype ICMR 157004 is early flowering with high biomass yield. The cross ICMX 1770192 (2.19 t/ha) ICMX 1770197 (2.14 t/ha) and ICMX 1770193 (2.08 t/ha) exhibited high grain yield with early days to 50% flowering and medium plant height. Grain Fe content is positively associated with grain Zn content (r = 0.93**) but exhibited negative association with other agronomic traits indicating proper care should be taken for breeding these traits. Mean sum of squares for panicle circumference, grain yield and biomass yield exhibited significant probabilities for the maternal effects indicating the influence of maternal factors in inheritance of these traits. The estimates of narrow sense heritability for days to 50% flowering, panicle length, plant height, panicle circumference, biomass yield and grain Fe and Zn content was high indicating the predominance of additive gene action in inheritance of these traits. ICMX 1770193, ICMX 1770194, ICMX 1770197, ICMX 1770204 and ICMX 1770208 exhibited significant negative *sca* effects for days to 50% flowering. Positive and significant *sca* effects for grain Fe and Zn contents were expressed by crosses ICMX 1770197, and ICMX 1770204. Identified genotypes with good GCA and crosses with good SCA, were useful in improving the restorer lines of pearl millet to promote the hybrid pearl millet breeding in West and Central Africa.

Keywords: Pearl millet, restorers, diallel mating design, general and specific combining abilities (GCA & SCA), heritability.

INTRODUCTION

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is a diploid, C_4 photosynthetic plant that is extensively cultivated for grain and fodder in the semi-arid tropics of Africa and Asia. It is the sixth most important staple cereal, next to maize (*Zea mays* L.), rice (*Oryza sativa* L.), wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), and sorghum [*Sorghum bicolor* (L.) Moench] (FAOSTAT, 2017; Bidinger and Hash, 2004). It is the staple food for millions of people living in semi-arid tropics (Haussmann *et al*., 2012; Gulia *et al*., 2007). It is drought tolerant and can withstand high temperatures, saline conditions, and can grow under poor soil conditions (Yadav *et al*., 2012), where other crops fail to grow. Pearl millet is also a good source of higher nutritional value than other cereals, and are supplying 80 to 90% of the calories for millions of poor people living in semi-arid regions (Govindaraj *et al*., 2009; Muthamilarasan *et al*., 2016).

Pearl millet is a major source of food, feed, fodder and fuel in West and Central Africa (WCA). World millet production is about 30 million tonnes, of which 35% is produced in Africa. Nearly, 70% of pearl millet in Africa, is grown in WCA (FAO, 2013). In WCA, Niger stands first with 7.0 M ha of land under pearl millet cultivation, followed by Nigeria (5.0 M ha), Chad (3.0 M ha), Burkina Faso (1.5 M ha), Mali (1.5 M ha), and Senegal (1.0 M ha) (FAOSTAT, 2017; Andrews *et al*., 1993). Despite the clear importance of pearl millet in WCA agriculture, the production and productivity are very low (500 to 800 kg/ha), when compared to rest of the world.

Innovation has played a major role in increasing production and productivity of many agricultural commodities, to sustain food wealth and cattle production. The concept of hybrid cultivars was one such innovation that has revolutionized the productivity and production of pearl millet in India, making it a largest pearl millet producer worldwide (Gowda *et al*., 2006; Pucher *et al*., 2015; Varshney *et al*., 2017). Hybrids had been reported to have about 20 to 50% or more grain yield advantage over varieties (Reddy *et al*., 2004).

The development of an effective hybrid breeding program depends on the stability of male sterility, frequency of maintainers in a wide range of breeding materials, nature of character association, inheritance of male sterility and its fertility restorers (Gowda *et al*., 2006). The low frequency of restorers (10% specially A_4 and A_5 cytoplasm) observed in several WCA bred pearl millet was a big challenge for hybrid breeding and point towards the need for restorer development research, for breeding commercial hybrids (Gowda *et al*., 2006; Pucher *et al*., 2015). Few inbred lines that restore male fertility of two or more CMS systems are useful for genetic improvement to meet the need of farmers. Nevertheless, in hybrid breeding, identified restorers do not seem constructive, but needs to be best combining parents.

Restorer lines must produce good amounts of pollen and should remain viable at high temperatures of 42 to 44°C, which is common at Sahel of WCA (Yadav *et al*., 2012). Also, restorer parents must produce high yielding fertile hybrids, which confers some degree of protection from biotic (ergot and smut infection) and abiotic stresses (Yadav *et al*., 2012). It also depends on the magnitude of genetic variability and the extent to which desirable characters are heritable from parents (Allard, 1960). It is desirable to breed pollinators of medium (150 to 180 cm) height, with long panicle, medium maturity and high productive tillering attributes that will be preferred by farmers in the hybrids (Pucher *et al*., 2018; Yadav *et al*., 2012). Improving the restorers for diverse cytoplasmic male sterile sources will open up the new avenues in hybrid breeding. Most of the restorers from WCA are photoperiod sensitive and medium maturity and is a need to breed them for earliness and non-photoperiod sensitive. There are several techniques for evaluating the varieties or lines in terms of their combining abilities and genetic makeup. Among these, diallel analysis proposed by Griffing (1956) has been extensively used to assess the combining ability of parents and their crosses for different quantitative and qualitative characters. Hence, the present study was carried out to improve the gene pool of restorer lines and forward them for strengthening the pearl millet hybrid breeding program in West and Central Africa.

MATERIALS AND METHODS

Experimental material

Six diverse restorer lines of pearl millet available at ICRISAT, Sadore were utilised as parents (ICMR 157001, ICMR 157002, ICMR 157003, ICMR 157004, ICMR 157005 and ICMR 167011), and crossed in a full diallel mating design, which generated thirty F_1 progenies, during the off season 2016-17. Thirty F_1's along with six parents (Annexure 1) were evaluated in randomized complete block design (RCBD) in three replications, during the rainy season 2017 at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Sadore, Niger (latitude 13.238, longitude 2.280, altitude 235, average rainfall 591 mm, sandy soil and the temperature ranging from 14.2 to 43.13°C). The test material was sown in 2 row plot of 4.2 m length with 0.75 m distance between rows and 0.80 m in between plants, with seven hills per row. Experimental plots were thinned to two plants per hill. A basal dose of fertilizer @100 kg/ha was applied to the experimental field. Micro dosing of the crop with urea @2 g per hill was carried out at 30 days after seedling emergence (DAE). Hand weeding was carried out when necessary.

Data were recorded for days to 50% flowering, plant height, panicle length, panicle circumference, grain yield, and dry biomass yield. Grain iron (Fe) and zinc (Zn) contents were estimated under lab conditions for which the grain samples were collected from the field and analysed using X-Ray Fluorescence (XRF) machine following the method of Govindaraj *et al*. (2016).

Statistical analysis

Data recorded for morphological and agronomic traits, were subjected to analysis of variance (ANOVA) using GenStat® 18th edition (GenStat 2015). Significance of the differences between the genotypes was judged by F-test, while the genotypic means were compared by least significant difference (LSD) at $P \leq 0.05$. The general combining ability (GCA) and specific combining ability (SCA) effects were calculated as per Method I, and Model 1 of Griffing (1956), using AGD-R (Analysis of

Genetic Designs in R), Version 5.0 (Francisco *et al.*, 2015). Heritability estimates were calculated according to Johnson *et al*. (1955).

RESULTS

Mean performance of pearl millet restorer lines and their crosses for agronomic and morphological traits

Analysis of variance revealed significant differences ($P \leq 0.05$) among the genotypes for all the traits examined (Table 1) indicating presence of significant variability in the restorer lines tested and can be exploited through selection. The overall mean was 66.53 days (ranging from 47 to 88 days) for number of days to 50% flowering. ICMR 157003 exhibited early flowering of 65 days. Thirteen F_1 progenies also exhibited early flowering. The cross ICMX 1770217 showed early flowering of 47 days, whose parents were ICMR 167011 and ICMR 157003.

Parents ICMR 157001, ICMR 157005, and ICMR 167011 exhibited medium plant height along with twelve hybrids (Table 1). Twenty crosses exhibited longer length of panicles, when compared to the mean of 39 cm and fourteen crosses exhibited higher panicle circumference of >8 cm. The cross ICMX 1770192 (2.19 t/ha), ICMX 1770197 (2.14 t/ha) and ICMX 1770193 (2.08 t/ha) exhibited high grain yield with early days to 50% flowering and medium plant height. The parents ICMR 157004 (9.87 t/ha) and ICMR 157002 (8.50 t/ha) produced high biomass yield. Eighteen hybrids showed high grain yield along with the biomass yield. All the parental genotypes used in the study had low to medium grain Fe content ranging between 34-47 ppm but, the crosses ICMX 1770206 (Fe = 70.00 ppm; Zn = 63.00 ppm) and ICMX 1770217 (Fe = 69.00 ppm and Zn = 53.00 ppm) showed high grain Fe and Zn contents.

Association of agronomic and morphological traits

Association of agronomic and morphological traits revealed presence of significant and positive (r = 0.93**) correlation of grain Fe content with grain Zn content (Table 2). Plant height (r = -0.43**; -0.48**), panicle length (r = -0.52**; -0.53**) and grain yield (r = -0.58**; -0.52**) exhibited significant negative correlation with grain Fe and Zn contents, respectively. Plant height (r = 0.66**; 0.89**) and panicle length (r = 0.65**; 0.63**) exhibited significant and positive correlation with grain yield and biomass yield.

Combining ability studies

Analysis of variance for combining ability

The mean sum of squares for general combining ability (GCA) of parents and specific combining ability (SCA) for the crosses showed significant ($P \leq 0.01$) probabilities for all the studied traits (Table 3). The mean sum of squares for the reciprocal crosses was significant at $P \leq 0.01$ for all the traits. The magnitude of mean sum of squares of GCA for days to 50% flowering, plant height, panicle length, panicle circumference, biomass yield and grain Fe content was high. Mean sum of squares for panicle circumference, grain yield and biomass yield exhibited significant probabilities for the maternal effects indicating the influence of the maternal factors in inheritance of these traits.

The variance due to SCA (σ^2SCA) was higher in magnitude than the variance due to GCA (σ^2GCA) for all the studied traits (Table 3). The ratio of σ^2GCA to σ^2SCA is less than one, indicating predominance of dominant gene action in inheritance of these traits. The predictability ratio is less than one for all the traits. The narrow sense heritability was high for days to 50% flowering (76%) and panicle length (71%), medium for plant height (53%), panicle circumference (60%), biomass yield (59%), and grain Fe content (48%).

Estimates of *gca*, *sca* and reciprocal effects of parents and hybrids

Estimates of general combining ability (gca) effects

Estimates of *gca* effects of parent ICMR 157001 exhibited positive and significant *gca* effects for panicle length (Table 4). ICMR 157002 showed significant and positive *gca* effects for all the traits studied except for panicle circumference, grain yield and grain Zn content. The parent ICMR 157005 exhibited positive and significant *gca* effects for panicle circumference. The *gca* effects of ICMR 157001, ICMR 157004 and ICMR 167011 is positive but not significant for grain yield. The *gca* effects of ICMR 157003 and ICMR 157004 are positives but not significant for grain Fe and Zn content.

Estimates of specific combining ability (sca) effects

The estimates of *sca* effects of crosses for traits examined revealed that most of the crosses exhibited significant and positive *sca* effects (Table 5). The crosses ICMX 1770192, ICMX 1770198, and ICMX 1770209 exhibited significant and positive *sca* effects for days to 50% flowering, whereas ICMX 1770193, ICMX 1770194, ICMX 1770197, ICMX 1770204 and ICMX 1770208 exhibited significant negative *sca* effects. The crosses ICMX 1770192, ICMX 1770193, ICMX 1770198, ICMX 1770199, ICMX 1770203, and ICMX 1770209 exhibited significant and positive *sca* effects for plant height.

Good specific combiners for panicle length were ICMX 1770190, ICMX 1770194, ICMX 1770199, ICMX 1770202, ICMX 1770203, and ICMX 1770209 (Table 5).

Table 1. Mean performance of restorer lines (parents) and their F1's for morphological and agronomic traits of pearl millet (*Pennisetum glaucum* L.).

Genotype	Days to 50% flowering	Plant height (cm)	Panicle length (cm)	Panicle circumference (cm)	Grain yield (t/ha)	Biomass yield (t/ha)	Grain Fe content (ppm)	Grain Zn content (ppm)
Direct crosses								
ICMX 1770190	76.00	231.00	54.00	7.00	1.13	8.60	41.00	33.00
ICMX 1770191	55.00	209.00	50.00	8.00	1.98	6.70	37.00	33.00
ICMX 1770192	62.00	204.00	44.00	8.00	2.19	7.52	39.00	38.00
ICMX 1770193	58.00	212.00	44.00	8.00	2.08	5.94	38.00	36.00
ICMX 1770194	58.00	199.00	47.00	8.00	1.88	5.43	35.00	32.00
ICMX 1770196	75.00	229.00	46.00	9.00	1.78	12.57	42.00	37.00
ICMX 1770197	63.00	211.00	48.00	9.00	2.14	5.98	34.00	30.00
ICMX 1770198	77.00	237.00	40.00	8.00	1.35	13.77	43.00	34.00
ICMX 1770199	74.00	245.00	42.00	9.00	1.65	12.48	42.00	40.00
ICMX 1770202	68.00	124.00	43.00	7.00	0.68	1.84	41.00	32.00
ICMX 1770203	69.00	135.00	41.00	7.00	0.71	2.19	43.00	37.00
ICMX 1770204	67.00	177.00	24.00	9.00	0.97	2.36	38.00	34.00
ICMX 1770208	52.00	129.00	21.00	9.00	0.67	1.86	46.00	41.00
ICMX 1770209	71.00	204.00	40.00	8.00	1.92	7.39	37.00	32.00
ICMX 1770214	63.00	188.00	30.00	9.00	0.89	2.41	34.00	27.00
Reciprocals								
ICMX 1770195	74.00	238.00	55.00	7.00	1.37	9.11	38.00	34.00
ICMX 1770200	66.00	153.00	37.00	8.00	0.57	2.60	46.00	41.00
ICMX 1770201	64.00	135.00	38.00	8.00	0.57	1.45	46.00	42.00
ICMX 1770205	73.00	239.00	40.00	9.00	1.51	10.28	43.00	33.00
ICMX 1770206	52.00	113.00	19.00	10.00	0.10	0.47	70.00	63.00
ICMX 1770207	61.00	214.00	42.00	9.00	1.61	6.83	39.00	31.00
ICMX 1770210	61.00	196.00	32.00	9.00	1.06	3.55	43.00	33.00
ICMX 1770211	77.00	251.00	42.00	9.00	1.26	11.67	43.00	36.00
ICMX 1770212	65.00	229.00	43.00	9.00	1.71	6.06	32.00	29.00
ICMX 1770213	70.00	175.00	32.00	8.00	1.06	5.09	36.00	31.00
ICMX 1770215	60.00	210.00	46.00	8.00	1.89	5.98	38.00	31.00
ICMX 1770216	76.00	240.00	51.00	7.00	1.44	9.03	44.00	34.00
ICMX 1770217	47.00	117.00	20.00	9.00	0.14	1.43	69.00	53.00
ICMX 1770218	67.00	212.00	42.00	8.00	1.75	6.68	41.00	37.00
ICMX 1770219	67.00	157.00	19.00	10.00	0.42	1.50	41.00	36.00
Parents								
ICMR 157001	71.00	138.00	40.00	6.00	0.46	1.44	34.00	30.00
ICMR 157002	88.00	243.00	45.00	8.00	0.32	8.50	47.00	37.00
ICMR 157003	65.00	198.00	39.00	8.00	0.78	4.39	42.00	39.00
ICMR 157004	66.00	216.00	47.00	9.00	1.68	9.87	40.00	34.00
ICMR 157005	71.00	131.00	27.00	9.00	0.33	1.08	43.00	40.00
ICMR 167011	67.00	147.00	39.00	8.00	1.48	2.93	41.00	35.00
Fpr	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001
Vr	24.54	25.86	18.75	4.16	6.70	10.49	8.63	5.50
Mean	66.53	191.00	39.00	8.00	1.21	5.75	42.00	36.00
SE	1.68	8.40	2.20	0.40	0.24	1.16	2.60	2.80
LSD	4.73	23.70	6.30	1.20	0.68	3.26	7.40	7.90
CV (%)	4.40	7.60	9.90	8.70	34.40	34.80	10.90	13.50

Table 2. Association of agronomic and morphological traits of crosses of pearl millet (*Pennisetum glaucum* L.) restorer lines.

Traits	Days to 50% flowering	Plant height	Panicle length	Panicle circumference	Grain yield	Biomass yield	Grain Fe content	Grain Zn content
Days to 50% flowering	1.00							
Plant height	0.51**	1.00						
Panicle length	0.41**	0.67**	1.00					
Panicle circumference	-0.35*	-0.10	-0.63**	1.00				
Grain yield	0.00	0.66**	0.65**	-0.12	1.00			
Biomass yield	0.55**	0.89**	0.63**	-0.14	0.61**	1.00		
Grain Fe content	-0.31	-0.43**	-0.52**	0.30	-0.58**	-0.24	1.00	
Grain Zn content	-0.36*	-0.48**	-0.53**	0.32*	-0.52**	-0.29	0.93**	1.00

*,** Correlation coefficient significant at P 0.05 and 0.01, respectively.

ICMX 1770197 and ICMX 1770214 showed positive and significant *sca* effects for panicle circumference. Significant positive *sca* effects by the crosses ICMX 1770192, ICMX 1770198, and ICMX 1770199 were recorded for biomass yield. Positive and significant *sca* effects for grain Fe and Zn contents were expressed by crosses ICMX 1770197, and ICMX 1770204.

Estimates of reciprocal effects

Estimates of reciprocal effects of the crosses for the traits examined showed that ICMX 1770201, ICMX 1770206, ICMX 1770207, and ICMX 1770217 exhibited significant negative reciprocal effects for days to 50% flowering (Table 5). ICMX 1770207, ICMX 1770212 and ICMX 1770213 exhibited significant and positive reciprocal effects for plant height. The crosses ICMX 1770200, ICMX 1770201, ICMX 1770206, and ICMX 1770210 exhibited significant negative reciprocal effects for grain yield. The cross ICMX 1770207 for biomass yield; ICMX 1770206 and ICMX 1770217 for grain Fe and Zn contents exhibited significant positive reciprocal effects.

Mid parent and better parent heterosis

The degree and significance of mid-parent and better parent heterosis varied from cross to cross and from trait to trait for the traits examined (Table 6). Nine crosses exhibited significant positive mid parent heterosis (MPH) and better parent heterosis (BPH), while six crosses exhibited significant positive MPH for grain yield. The crosses ICMX 1770202, ICMX 1770206, and ICMX 1770217 exhibited significant negative MPH and BPH for grain yield. For biomass yield, six crosses showed significant positive heterosis simultaneously over MPH and BPH and seven crosses exhibited significant positive MPH. The crosses ICMX 1770206 and ICMX 1770217 had significant positive MPH and BPH for both grain Fe and Zn content. The cross ICMX 1770200 exhibited significant positive MPH for both grain Fe and Zn content. The crosses ICMX 1770205 and ICMX 1770192 had significant positive MPH for grain Fe and Zn, respectively.

DISCUSSION

Results emanating from the present study showed extensive genetic variability for all the studied traits among the parents and crosses of pearl millet, indicating presence of significant variability and can be exploited through selection. This variability can be explored for the development of new high yielding restorers with good pollen capacity for desirable hybrid production. Due to the fact that the probability of selecting superior genotypes immensely dependent on the existing genetic diversity in the genotypes, which is also a function of the influence of the additive variance (Ramalho *et al*., 1993). The high variability, suggested a good potential and raw material for restorer's improvement in WCA. The results can also be of broader interest for the WCA pearl millet breeding community, especially the national agriculture research services that initiated hybrid breeding programs and seek for new restorers' parents.

Association of agronomic and morphological traits revealed presence of significant and positive correlation of grain Fe content with grain Zn content. Similar results were reported by Pucher *et al.* (2014), and Govindaraj *et al.* (2013). This showed that the underlying physiological processes determining both micronutrients were largely associated and improvement of one trait can improve the other. This would imply that recurrent selection can be effectively used for intra population improvement of Fe and Zn densities (Govindaraj *et al*., 2013). Plant height, panicle length, and grain yield exhibited significant negative correlation with grain Fe and Zn contents. Similar findings were reported by Kanatti *et al*. (2014). Plant height and panicle length exhibited significant and positive correlation with grain yield and biomass yield. This would imply likely effectiveness of simultaneous selection for plant height, panicle length and grain yield, which is very important for breeding farmer desirable hybrids (Govindaraj *et al*., 2013). Presence of significant

Table 3. Analysis of variance (ANOVA) showing the mean sum of squares of general, specific, and reciprocal combining abilities of R × R diallel of pearl millet (*Pennisetum glaucum* L.).

Sources of variation	df	Days to 50% flowering	Plant height	Panicle length	Panicle circumference	Grain yield	Biomass yield	Grain Fe content	Grain Zn content
Due to GCA	5	476.96**	7962.39**	626.97**	3.85**	1.28**	80.81**	145.42**	87.60**
Due to SCA	15	190.75**	5415.98**	277.82**	1.90**	1.05**	45.62**	99.78**	87.46**
Due to reciprocals	15	132.81**	4721.40**	159.74**	1.47**	1.22**	25.38**	263.68**	187.70**
Maternal effect	5	139.28	7344.41	220.66	2.53*	2.19**	55.08**	347.58	180.76
Maternal interaction	10	129.58**	3409.89**	129.29**	0.93	0.74**	10.54**	221.73**	191.17**
Error	70	8.43	211.01	15.25	0.63	0.17	4.00	21.09	23.85
Variance components									
σ^2GCA		58.57	968.92	76.47	0.40	0.14	9.60	15.54	7.97
σ^2SCA		182.32	5204.97	262.57	1.27	0.88	41.62	78.69	63.61
σ^2GCA/σ^2SCA		0.32	0.19	0.29	0.32	0.16	0.23	0.20	0.13
Predictability ratio		0.39	0.27	0.37	0.39	0.24	0.32	0.28	0.20
Narrow sense heritability (h_{ns})		0.76	0.53	0.71	0.60	0.42	0.59	0.48	0.31

*,** F probability significant at P 0.05 and 0.01, respectively. σ^2GCA, variance due to general combining ability; σ^2SCA, variance due to specific combining ability.

GCA and SCA mean squares for traits indicates that both additive and non-additive genetic effects were important in determining these traits as averred by Griffing (1956) and there is the probability of obtaining new varieties (Silva *et al*., 2004). The negative correlations among grain yield and grain Fe and Zn can be improved though identification of high yield and high Fe and Zn QTL and pyramiding them in the parental lines using marker-assisted selection (Govindaraj *et al*., 2013; Yadav and Rai, 2013).

The predominance of GCA mean squares over SCA mean squares and higher magnitude of SCA variance to the GCA variance for the studied traits suggested that, both additive and non-additive gene interactions are important in controlling the inheritance of these traits. These findings are in agreement with Singh and Sharma (2014).

The significant SCA effects and *per se* performance for grain yield displayed by ICMX 1770198, and ICMX 1770199 and high SCA effects and *per se* performance for grain Fe and Zn contents displayed by ICMX 1770197, and ICMX 1770204 further confirm the preponderance of non-additive gene action in these crosses. The high SCA effects of crosses for grain yield, grain Fe and Zn contents might be due to complementation of combining loci (Raut *et al*., 2017). Parents of these crosses can be used for bi-parental mating or reciprocal recurrent selection for developing superior varieties or hybrids (Azad *et al*., 2014).

Reciprocal effects are important because they can detect a desirable female seed parent base in hybridization program, particularly for producing commercial F_1 hybrids. The significance of the reciprocal mean squares for all the studied traits and significance of mean squares of maternal effects for panicle circumference, grain yield and biomass yield indicates proper care should be taken for choosing parents in breeding for improvement of these traits.

The significant and ample genetic variation, as well as sufficiently high narrow sense heritability were observed for most of the traits indicated that, genotype plays a most important role than the environment in determining the phenotype and suggesting predominance of additive gene effects in the inheritance of the studied traits (Govindaraj *et al*., 2011) and the feasibility of restorer improvement, for breeding farmer preferred pearl millet hybrids (Pucher *et al*., 2014). Therefore, progeny performance can be predicted based on the GCA for the traits.

Presence of high magnitude of heterosis for most of the studied traits suggested enough diversity among the parental lines. This showed the existence of great potential for improved pearl millet restorers' lines because of the high level of heterosis and genetic diversity observed (Satyavathi *et al*., 2009; Yadav, 2007; Mather and Jinks, 1971; Fonseca and Patterson, 1968). The presence of depicted significant positive heterosis over their mid parent and better parent values for all morphological and agronomic traits studied showed that these traits were most heterotic

Table 4. Estimates of general combining ability effects of agronomic and morphological traits of parents of pearl millet (*Pennisetum glaucum* L.).

Genotype/Traits	Days to 50% flowering	Plant height	Panicle length	Panicle circumference	Grain yield	Biomass yield	Grain Fe content	Grain Zn content
ICMR 157001	-1.06	6.08	5.02**	-0.59**	0.17	-0.03	-2.88*	-2.28
ICMR 157002	7.14**	26.63**	4.45**	-0.11	-0.09	2.76**	2.85*	2.10
ICMR 157003	-2.69*	-14.66**	-0.53	-0.01	-0.19	-1.35*	1.30	1.26
ICMR 157004	-2.31*	-3.30	-0.45	0.26	0.21	0.39	0.26	0.31
ICMR 157005	0.17	-10.37*	-5.95**	0.42*	-0.22*	-1.07*	-1.49	-0.82
ICMR 167011	-1.25	-4.38	-2.54*	0.03	0.12	-0.70	-0.04	-0.57
SE±	0.76	3.83	1.03	0.21	0.11	0.53	1.21	1.29

*, ** t test significant at P 0.05 and 0.01, respectively.

Table 5. Estimates of specific and reciprocal combining ability effects of agronomic and morphological traits of F1 crosses of pearl millet (*Pennisetum glaucum* L.).

Genotype/Traits	Days to 50% flowering	Plant height	Panicle length	Panicle circumference	Grain yield	Biomass yield	Grain Fe content	Grain Zn content
Direct crosses								
ICMX 1770190	2.39	10.52	5.79*	-0.28	-0.04	0.38	-2.20	-2.23
ICMX 1770191	-2.28	-1.69	0.32	0.17	0.08	0.28	1.25	1.71
ICMX 1770192	4.67**	27.56**	-1.82	0.47	0.26	2.79*	2.29	1.52
ICMX 1770193	-6.14**	17.19*	-0.27	0.52	0.41	0.10	2.99	1.73
ICMX 1770194	-5.22**	11.58	5.10*	-0.20	0.39	0.69	-2.46	-1.51
ICMX 1770196	-1.47	-20.79*	-1.21	0.41	0.24	-0.15	-1.85	0.18
ICMX 1770197	-13.86**	-52.93**	-9.96**	0.93*	-0.21	-5.68**	6.96*	8.02**
ICMX 1770198	3.17*	36.09**	3.21	-0.40	0.41	5.27**	-0.61	-2.14
ICMX 1770199	2.58	29.03**	5.35*	-0.35	0.31	2.95*	-1.33	-0.61
ICMX 1770202	2.81	-4.26	4.62*	-0.34	-0.09	-0.45	-3.50	-5.90*
ICMX 1770203	2.67	15.82*	9.46**	-0.34	0.40	0.79	-3.79	-3.33
ICMX 1770204	-5.58**	-25.18*	-13.84**	0.72	-0.58*	-1.80	10.44**	6.80*
ICMX 1770208	-3.39*	-25.65**	-6.29**	-0.48	-0.33	-1.60	0.23	0.76
ICMX 1770209	6.03**	24.12**	4.97*	-0.54	0.30	1.60	-3.29	-1.27
ICMX 1770214	-0.44	-3.75	-6.26*	0.96*	-0.45*	-2.03	-2.48	-3.05
SE±	1.74	8.73	2.35	0.48	0.25	1.20	2.76	2.93
Reciprocals								
ICMX 1770195	-0.67	3.22	0.56	-0.11	0.12	0.25	-1.60	0.52
ICMX 1770200	5.17*	-27.72**	-6.56*	-0.11	-0.70*	-2.05	4.53	4.02
ICMX 1770201	-5.17*	-47.06**	-4.22	-0.50	-0.61*	-5.56**	2.00	2.27
ICMX 1770205	5.50**	17.33	-2.17	0.33	-0.34	1.38	2.00	-2.35
ICMX 1770206	-5.17*	-48.94**	-14.56**	0.61	-1.02**	-2.75*	18.30**	16.70**
ICMX 1770207	-3.67*	44.89**	-0.61	0.89	0.46	2.50*	-0.65	-0.20
ICMX 1770210	1.50	-8.33	-6.00*	0.56	-0.51*	-1.20	2.88	-1.30
ICMX 1770211	0.33	7.00	0.78	0.44	-0.04	-1.05	-0.02	0.82
ICMX 1770212	-2.00	47.33**	1.06	0.94	0.50	1.94	-5.38	-3.88
ICMX 1770213	9.00**	23.33*	5.17*	-0.72	0.19	1.61	-5.00	-4.83
ICMX 1770215	1.33	5.72	-0.22	0.00	0.00	0.28	1.55	-0.70
ICMX 1770216	1.00	-2.94	4.44	-0.67	-0.11	-1.72	0.85	-2.62
ICMX 1770217	-10.33**	-30.11**	-2.06	-0.17	-0.42	-0.46	15.03**	9.42**
ICMX 1770218	-2.33	4.00	0.83	0.06	-0.09	-0.36	1.80	2.70
ICMX 1770219	2.33	-15.50	-5.67*	0.39	-0.23	-0.46	3.67	4.33
SE±	2.05	10.27	2.76	0.56	0.29	1.41	3.25	3.45

*, ** t test significant at P 0.05 and 0.01, respectively.

traits (Kumar *et al.*, 2016).

Grain yield is the character and an attribute of economic importance for which considerable positive magnitude of heterosis is needed. Number of crosses was registered considerable magnitude in desirable sense for this trait over MPH and BPH. Such a situation

Table 6. Estimates of relative and better parent heterosis for morphological and agronomic traits of pearl millet (*Pennisetum glaucum* L.) 6 x 6 diallel, ICRISAT, Sadore, Niger.

Genotype	Days to 50% flowering		Plant height		Panicle length		Panicle circumference		Grain yield		Biomass yield		Grain Fe content		Grain Zn content	
	MPH	BPH	MPH	BPH	MPH	BPH	MPH	BPH	MPH	BPH	MPH	BPH	MPH	BPH	MPH	BPH
Direct crosses																
ICMX 1770190	-4.82*	6.58*	21.43**	-4.70	26.87**	20.10**	4.68	-4.29	191.73**	146.51*	73.07**	1.20	2.03	-11.52	-1.58	-10.55
ICMX 1770191	-18.63**	-14.88**	24.15**	5.40	28.23**	26.10**	13.39*	4.34	218.36**	152.17**	130.11**	52.84	-2.82	-11.71	-5.71	-16.38
ICMX 1770192	-8.79**	-5.09	15.37**	-5.38	1.53	-5.72	6.57	-7.60	104.86**	30.32	33.03	-23.78	6.96	-0.40	18.94*	13.13
ICMX 1770193	-18.31**	-18.31**	57.92**	53.69**	30.37**	9.73	5.80	-8.75	427.34**	354.80**	371.75**	312.78**	-2.10	-11.69	1.74	-11.06
ICMX 1770194	-16.22**	-13.50**	39.56**	35.51**	19.21**	17.23*	6.26	-2.85	94.21**	27.22	148.89*	85.71	-7.01	-14.60	-0.11	-6.29
ICMX 1770196	-2.39	14.88**	4.13	-5.44	10.25	2.72	17.98**	17.14*	223.45**	126.91**	95.20**	47.96**	-4.71	-9.52	-1.97	-4.61
ICMX 1770197	-18.44**	-4.57	-8.12*	-13.19**	4.25	2.14	6.04	0.00	114.31**	27.29	-34.93*	-39.44**	-22.08**	-27.85**	-15.62	-19.58*
ICMX 1770198	-3.56	7.99**	26.73**	-2.47	10.94	-10.67	-6.67	-12.50*	316.05**	306.02**	187.49**	62.01**	-4.37	-8.51	-11.26	-15.02
ICMX 1770199	-4.31*	10.99**	26.07**	1.15	0.40	-6.45	10.00	10.00	84.38**	11.92	118.47**	46.83**	-2.86	-8.81	10.62	6.92
ICMX 1770202	4.08	4.62	-40.02**	-42.49**	1.55	-7.16	-10.82	-16.46*	-44.93*	-59.63**	-74.18**	-81.35**	-0.56	-3.18	-12.17	-18.43*
ICMX 1770203	0.99	5.65	-18.07**	-31.97**	24.24**	6.03	-10.07	-16.26*	27.42	-9.31	-20.04	-50.17	2.45	1.65	-6.88	-8.42
ICMX 1770204	2.27	3.58	2.76	-10.56*	-37.37**	-37.37**	19.42**	18.57*	-13.84	-34.06	-35.38	-46.13	-6.92	-8.03	-7.38	-12.80
ICMX 1770208	-23.90**	-20.82**	-25.79**	-40.41**	-42.65**	-54.53**	4.40	3.75	-33.27	-60.05**	-65.96**	-81.12**	11.53	7.76	11.23	1.73
ICMX 1770209	7.80**	8.62**	12.39*	-5.61	-5.74	-13.82*	-3.36	-8.86	21.75	14.33	15.61	-25.06	-8.20	-9.55	-6.56	-7.91
ICMX 1770214	-8.96**	-6.00*	35.64**	28.29**	-9.09	-22.42**	11.99*	4.99	-1.82	-39.88*	20.40	-17.57	-18.08*	-19.69*	-27.29**	-32.60**
Reciprocals																
ICMX 1770195	-6.50**	4.69	24.84**	-2.02	29.49**	22.58**	1.56	-7.15	253.75**	198.91**	83.24**	7.14	-5.90	-18.40*	1.49	-7.76
ICMX 1770200	-3.43	1.03	-8.86	-22.63**	-5.10	-6.68	10.24	1.45	-7.73	-26.91	-10.73	-40.71	21.05**	9.97	17.46*	4.17
ICMX 1770201	-15.91**	-1.03	-38.58**	-44.23**	-9.98	-16.12*	5.03	4.28	3.27	-27.55	-77.52**	-82.96**	4.35	-0.92	9.94	6.99
ICMX 1770205	7.31**	11.66**	34.97**	10.70*	-8.46	-15.00*	15.33*	0.00	40.93	-10.34	81.76**	4.15	17.80*	9.69	4.19	-0.90
ICMX 1770206	-31.89**	-20.31**	-50.83**	-53.54**	-59.41**	-60.23**	20.80**	13.92*	-90.39**	-94.29**	-94.84**	-95.20**	62.88**	50.81**	79.17**	70.76**
ICMX 1770207	-7.14*	-6.66*	3.38	-0.88	-1.31	-9.77	10.81	3.79	30.33	-4.46	-4.09	-30.73*	-3.76	-6.29	-13.27	-19.45*
ICMX 1770210	-14.08**	-14.08**	45.58**	41.68**	-5.27	-20.28**	20.29**	3.75	168.10*	131.22*	181.51	146.32	12.95	1.88	-5.62	-17.50*
ICMX 1770211	-2.73	8.92**	34.23**	3.30	15.27*	-7.19	4.00	-2.50	288.27**	278.92**	143.62**	37.29*	-4.46	-8.60	-7.02	-10.97
ICMX 1770212	-4.90	-0.51	39.48**	15.81**	30.64**	11.48*	12.74*	4.99	205.56**	117.47**	121.88*	38.27	-23.09**	-23.69**	-26.44**	-27.65**
ICMX 1770213	2.44	6.59*	1.10	-18.81**	-14.70*	-32.38**	-11.95*	-12.50*	4.87	-37.22*	-7.02	-48.42**	-12.82	-15.76*	-14.94	-22.20*
ICMX 1770215	-12.36**	-9.51**	47.56**	43.29**	18.06**	16.10*	6.26	-2.85	95.14**	27.83	174.14**	104.55*	1.25	-7.00	-4.43	-10.35
ICMX 1770216	-1.73	13.99**	23.09**	-1.24	21.70**	13.40*	-7.15	-7.15	60.51*	-2.57	58.15*	6.30	1.03	-5.16	-4.02	-7.22
ICMX 1770217	-29.11**	-28.20**	-32.17**	-40.96**	-48.00**	-48.00**	15.11*	14.28*	-87.88**	-90.72**	-60.77	-67.30*	65.81**	63.83**	43.81**	35.40**
ICMX 1770218	0.76	1.52	16.80**	-1.90	-1.83	-10.24	-2.02	-7.60	10.86	4.10	4.45	-32.29*	0.75	-0.73	9.32	7.74
ICMX 1770219	-2.19	0.99	13.30*	7.16	-43.42**	-51.72**	21.33**	13.75*	-53.34	-71.43**	-25.19	-48.79	-0.47	-2.42	-4.14	-11.14

*, ** t test significant at P 0.05 and 0.01, respectively, MPH, mid parent heterosis; BPH, better parent heterosis.

of heterosis in pearl millet has also been reported by Bhasker *et al*. (2017), Nandaniya *et al*. (2016), Chotaliya *et al*. (2009) and Vetriventhan *et al*. (2008). Also, desirable significant positive heterosis was found over MPH and BPH for traits plant height, panicle length, panicle circumference and biomass yield. These characteristics have high value as grain yield for West and Central Africa pearl millet farmers (Pucher *et al*., 2018). Positive significant estimates of MPH and BPH were also recorded by some crosses for grain Fe and Zn content. This further supports the fact that the physiological processes determining Fe and Zn densities in grains were partially under additive genetic control, but it also indicates some degree of over dominance of genes responsible for high Fe and Zn densities over those responsible for low Fe and Zn densities (Govindaraj *et al*., 2013).

CONCLUSIONS

Identification and improvement of superior restorers from variability generated *via* hybridization are crucial for pearl millet hybrid breeding program in West and Central Africa. This study elucidated the inheritance of grain yield, its related traits and grain Fe and Zn contents in pearl millet using a diallel mating design. ICMR 157002 was good general combiner for days to 50% flowering, plant height, panicle length, biomass yield, grain Fe and Zn contents, and other parents with good combining ability, could be exploited as donor parents in improving the restorer gene pool.

The superior and promising cross combinations having high *per se* performance; GCA and significant positive SCA effects for most of the agronomic and morphological traits can be utilised in developing new restores. ICMX 1770192, ICMX 1770198, ICMX 1770200, ICMX 1770205, ICMX 1770209 and ICMX 177213 were early flowering and yielding high, therefore recommended that, these genotypes should be included in the restorer improvement program in that, the likelihood of obtaining transgressive segregants from segregating generations of these crosses is high and should therefore be exploited. The crosses ICMX 1770197, ICMX 17720204, ICMX 1770206 and ICMX 1770217 showed high grain Fe and Zn content. All the superior crosses identified in this study should be further tested on a wide range of environments for stability and adaptation. Reciprocal effects revealed the careful selection of parents as male or female depending on the trait of inheritance. Narrow sense heritability estimates in general were high for all the characters studied, hence, these characters need to be given more importance while selecting the breeding lines as they were controlled by additive genes. Selection criteria to improve the restorer lines should focus on plants with early maturity, medium plant height, long panicle, as these traits have high genetic correlation with grain yield and grain Fe and Zn content.

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Annexure I. Pedigree information of the parents utilised and crosses generated in R × R diallel of pearl millet (*Pennisetum glaucum* L.), ICRISAT, Sadore, Niger.

Genotype	Pedigree
Parents	
ICMR 157001	PE00397_B_B_1_1_B
ICMR 157002	PE00349_B_2_1_B
ICMR 157003	PE11291_B_2_1_B
ICMR 157004	PE11322_B_B_3_1_B
ICMR 157005	PE11322_B_B_4_1_B
ICMR 167011	3/4Exborno_P30_1_1_1_B
Direct crosses	
ICMX 1770190	ICMR 157001 × ICMR 157002
ICMX 1770191	ICMR 157001 × ICMR 157003
ICMX 1770192	ICMR 157001 × ICMR 157004
ICMX 1770193	ICMR 157001 × ICMR 157005
ICMX 1770194	ICMR 157001 × ICMR 167011
ICMX 1770196	ICMR 157002 × ICMR 157003
ICMX 1770197	ICMR 157002 × ICMR 157004
ICMX 1770198	ICMR 157002 × ICMR 157005
ICMX 1770199	ICMR 157002 × ICMR 167011
ICMX 1770202	ICMR 157003 × ICMR 157004
ICMX 1770203	ICMR 157003 × ICMR 157005
ICMX 1770204	ICMR 157003 × ICMR 167011
ICMX 1770208	ICMR 157004 × ICMR 157005
ICMX 1770209	ICMR 157004 × ICMR 167011
ICMX 1770214	ICMR 157005 × ICMR 167011
Reciprocal crosses	
ICMX 1770195	ICMR 157002 × ICMR 157001
ICMX 1770200	ICMR 157003 × ICMR 157001
ICMX 1770205	ICMR 157004 × ICMR 157001
ICMX 1770210	ICMR 157005 × ICMR 157001
ICMX 1770215	ICMR 167011 × ICMR 157001
ICMX 1770201	ICMR 157003 × ICMR 157002
ICMX 1770206	ICMR 157004 × ICMR 157002
ICMX 1770211	ICMR 157005 × ICMR 157002
ICMX 1770216	ICMR 167011 × ICMR 157002
ICMX 1770207	ICMR 157004 × ICMR 157003
ICMX 1770212	ICMR 157005 × ICMR 157003
ICMX 1770217	ICMR 167011 × ICMR 157003
ICMX 1770213	ICMR 157005 × ICMR 157004
ICMX 1770218	ICMR 167011 × ICMR 157004
ICMX 1770219	ICMR 167011 × ICMR 157005