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Research Article

Grain micronutrients, yield and their components in pearl millet: A genetic study

Mithlesh Kumar[1,2]*, M. P. Patel[1,3], Kirti Rani[4] and M. S. Patel[5,3]

[1]Department of Genetics & Plant Breeding, C. P. College of Agriculture, S.D. Agricultural University, S.K.Nagar -385 506 (Gujarat), India
[2]Present Address: AICRN on Potential Crops, ARS Mandor, Agriculture University, Jodhpur -342 304 (Rajasthan), India
[3]Pulses Research Station, S.D. Agricultural University, S.K.Nagar, Gujarat 385 506, India
[4]ICAR-National Bureau of Plant Genetic Resources (NBPGR), Regional Station Jodhpur -342 003 (Rajasthan), India
[5]Centre for Crop Improvement (CCI), S.D. Agricultural University, Sardarkrushinagar-385 506 (Gujarat), India
***E-Mail:** mithleshgenetix@gmail.com

Abstract

The biofortification of pearl millet, a prime staple crop around the world with increased grain iron (Fe) and zinc (Zn) concentrations is part of continuing attempts to fight micronutrient deficiency. The goal of the current study was to examine heterosis, heritability, genetic advancement and inbreeding depression (ID) for yield, and associated features in pearl millet or bajra [*Pennisetum glaucum* (L.) R. Br.]. The majority of crosses with days to 50% flowering, maturity, and plant height showed negligible inbreeding depression and significant heterosis in the desired direction. Yield and other associated characteristics demonstrated significant average heterosis and heterobeltiosis, along with severe inbreeding depression. The presence of additive gene effects for grain Fe and Zn content was shown by the lower value of better parent and relative heterosis in F_1^s and the absence of inbreeding depression in F_2. Majority of the characteristics had moderate to high heritability and low to average genetic advance. Crosses, 30127 x J 2556 for maturity; 30725 x ICMB 05333, J 2454 x 30348 and 30843 x ICMB 98222 for height of plants; 30727 x J 2523, ICMB 99222 x ICMB 08222, 30127 x J 2556, and 30843 x ICMB 98222 for panicle diameter; 30727 x J 2523 and 30725 x ICMB 05333 for seed yield/plant; J 2372 x 30610, ICMB 99222 x ICMB 08222, and 30843 x ICMB 98222 for test weight/1000 grain weight; 30843 x ICMB 98222 and ICMB 99222 x ICMB 08222 for Fe content; 30727 x J 2523, J 2372 x 30610, J 2454 x 30348, 30127 x J 2556, 30843 x ICMB 98222, ICMB 99222 x ICMB 08222, and ICMB 10444 x ICMB 97222 for Zn content showed average to high heritability (broad sense) associated with high to medium genetic advance (GA) that can be improved through selection.

Keywords. Biofortification, pearl millet, heterosis, heritability, inbreeding depression

INTRODUCTION

Pearl millet, often known as bajra, is a C_4 plant in the poaceae family that having excellent photosynthetic efficiency and hence produces a lot of dry matter. It is primarily a cross-pollinated crop with higher outcrossing percentage (Kumar *et al*., 2021b). It is grown as food, feed, and fodder crop in different continents *viz.,* Asia, South and North America, Australia and Africa (Yadav *et al*., 2012a). The crop is cultivated chiefly in the tropical dry and semi-dry zones of Africa and Asia on more than 26 million hectares. India is the world's largest producer, producing 8.61 million tonnes of grain from an area of 6.93 million ha (Kumar *et al*., 2021b). Pearl millet is more adapted to hot and drier semi-arid regions compared to other cereals. It also has better water use efficiency (WUE) under the stressed growing conditions (Zegada-Lizarazu and Iijima, 2005). Pearl millet is well adapted to high temperatures (Gupta *et al*., 2015) and also grows well in high saline condition (Yadav *et al*., 2012a, 2012b).

In addition to being a reliable source of energy, pearl millet is also regarded as a nutri-cereal and an excellent provider of vitamins and dietary proteins. According to Khairwal *et al*. (1999), bajra grains provide roughly 70% carbohydrates, 5% fat, 12–14% protein, and 360 Kcal of energy per 100 g. As a result, millions of people's access to food and nourishment depends significantly on pearl millet. Fe (14 to 135 parts per million (ppm) and Zn (11.5 to 92 ppm) in pearl millet germplasm have shown a wide range of variation, and several researchers have reported in their breeding materials (Velu *et a*l., 2008a, 2008b; Rai *et al*., 2012; Govindaraj *et al*., 2013; Kumar *et al*., 2020a, 2020b; Kumar *et al*., 2021a, 2021b). Micronutrient deficiencies, also known as "hidden hunger," are recognised as a serious health issue on a global scale. A deficiency of one or more micronutrients might affect 70% of the world's population, with Fe and Zn deficiencies being the most notable (Stein, 2010). Anemia brought on by iron deficiency is a global issue that affects both developed as well as developing nations. Despite the fact that it can happen at any age, it is more prevalent in young children and pregnant women (WHO, 2008). These micronutrients deficit deteriorate growth and mental development, weakens immunity, irritability, fatigue, hair loss, sterility, weakening of muscles, high morbidity rate and fatality in severe situations (Pfeiffer and McClafferty, 2007; Stein, 2010).

Several steps have been taken to combat micronutrient deficiencies in human being *viz*., dietary diversification supplementation and food fortification but long period efficacy of such implications rely on ongoing financing, quality inputs and satisfactory delivery system (White and Broadley, 2009). If not, a stronger, affordable and long-lasting way to address micronutrient deficiencies is biofortification. It combines traditional breeding with more advanced biotechnologies to increase the accumulation of micronutrients in edible parts of staple food crops, and it has a significant impact on improving the health and nutritional security for underprivileged populations in developing nations (Pfeiffer and McClafferty, 2007).

The most effective breeding strategy for enhancing yield and quality attributes in bajra has been the development of hybrids and the utilization of heterosis. In pearl millet, substantial effort has been done on hybrid breeding for yield and attributes relevant to yield (Ramamoorthi and Nadarajan, 2001; Yadav *et al*., 2012b; Yadav & Rai, 2013; Kumar *et al*., 2021a). Considering this, the current study was conducted to investigate heterosis, heritability, genetic advancement, and inbreeding depression for the various attributes in pearl millet.

MATERIALS AND METHODS

Materials and locations for experiments: The experimental material included 18 parental lines from various sources or pedigree. These lines were used to F_1 and F_2 generations from nine crosses. Experiment was conducted at CCI, SDAU, S. K. Nagar (Gujarat) which is situated at 24°19'26" north (N) latitude and 72°18'53" east (E) longitude with an elevation of 172 meters above sea level. The pH of the soil at the test site was 7.5, and it had a loamy sand texture. Iron levels in the soil ranged from 4-5 ppm, whereas Zn concentrations were between 0.2 and 0.3 ppm. The semi-arid climate was marked by annual rainfall amounts of less than 400 mm.

Field evaluation, data collection and grain micronutrients analysis: The compact family block design, or CFBD, was adopted to sow a set of nine crosses, under three replications. Nine blocks made out of one particular cross each were divided up into three replications. Each unique block consisted of four plots, one for each of the four distinct populations or generations. Every plot had one row for the F_1, one row for each parent, and four rows for the F_2. There were 40 plants in each 4 m long row, with 10 cm and 45 cm between each plant and row, respectively. To raise a healthy crop, the suggested package of practices were adopted. The data were recorded from 10 competitive individual plants for homogeneous populations *viz*., P_1 and P_2 and 40 plants for heterogeneous F_2 population in each replication for ten parameters including yield and component traits of yield *viz*., height of the plant, length of the panicle, quantity of productive tillers/plant, panicle diameter and test weight (1000 grain weight), phenological features such as days for flower initiation and days to maturity, and the amount of micronutrients in the grain. The samples were prepared as per the methodology described by Kumar *et al*. (2021a, 2021b), for estimation of grain micronutrients content with a diacid mixture and it was analyzed for Fe and Zn in an atomic absorption spectrophotometer (AAS) at the CBRL, SDAU, S. K. Nagar, Gujarat. The parental lines used in this study were obtained in 2015 from the Millets Research Station, JAU Jamnagar, and the Centre for Crop Improvement (CCI), SDAU, S. K. Nagar Gujarat, and their grain Fe and Zn levels were subsequently examined. The crossing took place in the summer of 2016, the generation advanced in the following *Kharif,* and all of the generation was then evaluated in the field in the following summer of 2017. The analysis of grain micronutrients was completed in 2018–19, and data analysis started in 2019 and continued through 2020.

Statistical analysis: Mid-parent heterosis (MPH) and heterobeltiosis (BPH) were calculated and significance was determined using the F probabilities at P ≤ 0.05 (5% level) and 0.01 (1% level). Inbreeding depression (ID) was measured from F_1 and F_2 mean values and calculated "t" value (Tcal) and tabulated "t" value (Ttab) was compared at error degree of freedom at 5 % and 1 % significance level. Broad-sense heritability was calculated as per the formula proposed by Falconer (1989) and the same was categorised as low = 0-30%, moderate = 30-60%, and high = 60% and above, as proposed by Robinson *et al*. (1949). Genetic advance as percent of mean was calculated as per the formula proposed by Johnson *et al.* (1955) and they were categorised as low = (<10%), moderate = (10%–20%), and high = (> 20%), as per Falconer (1989). Using Indostat 8.5, software, grain micronutrient data and agro-morphological traits were analysed.

RESULTS AND DISCUSSION

Heterosis: For different traits with varying degrees of significance for each cross, mid and better parent heterosis estimations were calculated (**Tables 1 to 5**). The results of the estimates for heterosis revealed that, in addition to positive heterosis, or heterosis in the desired direction, all crosses displayed significant negative heterosis over mid-parent value and better parent for days to flowering, some crosses for days to attaining maturity, girth of panicle and 1000 grain weight, and the majority of crosses for grain iron and zinc content. The parents manifesting high and positive heterotic values in F_1s for subjective characters were considered promising for different traits, except plant height, days to flowering and maturity for which negative values were preferred. The role of non-fixable interallelic epistasis and/or overdominance in the expression of characteristics was indicated by significant mid-parent/average heterosis and heterobeltiosis in the desired direction. The amount of heterosis estimated for yield and its various traits revealed that the parental lines had a huge diversity. With very few exceptions, the degree of heterosis did not significantly alter between crosses, which may be the result of the parents' high gene-combination harmony. Interestingly, there was enough consistency in the hybrids' performance over the crosses. Low and negative heterosis may result from significant epistatic gene effects or insufficient dominant gene effects. We may also infer that the close resemblance of the parents employed in this study is a result of the low heterosis values for particular traits in a few crosses.

For days to flowering all the crosses showed notable negative heterosis over mid parent value and better parent. Two best crosses that showed highly significant negative heterobeltiosis were J-2372 x 30610 (-17.79%) and ICMB-10444 x ICMB-97222 (-8.88%). For days to maturity, five out of nine hybrids exhibited highly significant negative relative heterosis *viz*., ICMB-99222 x ICMB-08222 (-1.17%), J-2372 x 30610 (-2.63%), J-2340 x 30291 (-36.72%), 30727 x J-2523 (-2.44%) and ICMB-10444 x ICMB-98222 (-6.17%). Two best crosses that showed significant heterobeltiosis were J-2340 x 30291 (-36.61%) and ICMB-10444 x ICMB-97222 (-6.12%). Plant height is an important growth parameter that is directly linked to the plant's productive potential in terms of yield. For plant height, all nine crosses showed highly significant relative heterosis. However, only one cross, J-2454 x 30348 exhibited negative heterosis. Pragmatically, superiority over better parent is more desirable. More productive tillers per plant are greatly desired to increase productivity because they are a key factor for higher production. In all the crosses, highly significant and positive relative heterosis and heterobeltiosis were detected except 30843 x ICMB-98222 (0.0%) for number of productive tillers per plant. Two best crosses that showed positive heterobeltiosis were J-2372 x 30610 (83.33%) and ICMB-99222 x ICMB-08222 (66.67%). Panicle length is an important character for grain yield and therefore, might be useful selection criteria for high yield. All the nine crosses exhibited highly significant relative heterosis for panicle length. Most of the crosses, except J-2340 x 30291 (-7.86%) and 30843 x ICMB-98222 (20.93%) exhibited highly significant positive heterobeltiosis. Two best crosses that evinced positive heterobeltiosis for panicle length were ICMB-10444 x ICMB-97222 (43.53%) and 30725 x ICMB-05333 (39.76%). Another criterion established as a selection index for good parental lines and segregants in a breeding programme for pearl millet is panicle girth. Significant positive relative heterosis for panicle girth was observed in all the crosses. The estimates of relative heterosis ranged from -4.92 per cent in cross J-2454 x 30348 to 24.50 per cent in cross 30725 x ICMB-05333. Three best crosses with highly significant positive heterobeltiosis for panicle girth were, 30725 x ICMB-05333 (18.40%), 30843 x ICMB-98222 (16.89%) and ICMB-99222 x ICMB-08222 (13.79%). All of the F_1s showed the highly significant positive relative/mid-parent heterosis for grain yield per plant. The estimates of relative heterosis ranged from 17.05 per cent in cross 30127 x J-2556 to 87.03 per cent in cross ICMB-99222 x ICMB-08222. Two best crosses exhibiting highly significant positive heterobeltiosis were ICMB-99222 x ICMB-08222 (59.51%) and ICMB-10444 x ICMB-97222 (39.07). Six out of the nine crosses exhibited highly significant relative heterosis for 1000 grain weight namely*,* 30843 x ICMB-98222 (88.78%), 30127 x J-2556 (32.48%), 30725 x ICMB-05333 (20.22%), 30727 x J-2523 (17.14%), J-2372 x 30610 (16.09%) and ICMB-99222 x ICMB-08222 (15.02%). The heterobeltiosis ranged from -13.70 per cent in cross J-2340 x 30291 to 71.13 per cent in cross 30843 x ICMB-98222 for test weight. Three crosses exhibited highly significant relative heterosis for grain iron content *viz*., ICMB-10444 x ICMB-97222 (2.46%), 30127 x J-2556 (1.13%) and 30727 x J-2523 (0.80%). Moreover, all crosses exhibited non significant heterobeltiosis for grain iron content. The estimates of heterobeltiosis ranged from -35.72 per cent in 30127 x J-2556 to -0.26 per cent in ICMB-99222 x ICMB-08222 cross. For grain zinc concentration, five out of the nine crosses displayed considerable positive relative heterosis *viz*., J-2454 x 30348 (5.13%), 30843 x ICMB-98222 (2.86%), J-2340 x 30291 (2.69%), ICMB-10444 x ICMB-97222 (2.58%) and 30725 x ICMB-05333 (2.23%). For grain zinc concentration, all of the crosses had highly significant negative heterobeltiosis except ICMB-10444 x ICMB-97222 (-1.92%). The estimates of heterobeltiosis ranged from -32.44 per cent in cross 30127 x J-2556 to

Table 1. Magnitude of relative heterosis (RH), heterobeltiosis (BP), inbreeding depression (ID), broad sense heritability (h^2_{bs}) and genetic advance as per cent of means (GA %) for flowering and maturity duration in crosses of pearl millet

Cross	Days to flowering				
	RH (%)	BP (%)	ID (%)	H^2_{bs} (%)	GA (%)
ICMB-99222 x ICMB-08222	-5.60**	-5.13**	6.41**	0.00	0.55
J-2372 x 30610	-18.06**	-17.79**	-9.49**	33.77	2.54
J-2340 x 30291	-5.80**	-1.29**	1.82**	45.08	0.24
30127 x J-2556	-9.85**	-7.82**	1.44**	44.21	0.00
J-2454 x 30348	-4.36**	-0.36*	-0.73	69.31	0.00
30725 x ICMB-05333	-3.63**	-3.17**	-1.97**	0.00	0.00
30727 x J-2523	-7.11**	-0.91**	-2.91**	71.81	5.09
ICMB-10444 x ICMB-97222	-8.88**	-8.88**	-2.17**	0.00	0.00
30843 x ICMB-98222	-5.40**	-2.05**	-1.62**	0.00	0.74
Designation	**Maturity duration**				
ICMB-99222 x ICMB-08222	-1.17**	-0.34	1.35**	40.74	4.38
J-2372 x 30610	-2.63**	-0.58	-0.44	86.71	6.97
J-2340 x 30291	0.058	0.234	-0.35	83.16	6.85
30127 x J-2556	-0.06	0.33	-0.75*	43.46	13.07
J-2454 x 30348	0.46	1.27**	-1.40**	63.28	1.10
30725 x ICMB-05333	-0.21	1.38**	-0.94**	40.95	0.63
30727 x J-2523	-2.44**	2.27**	0.17	70.05	0.00
ICMB-10444 x ICMB-97222	-6.17**	-6.12**	-2.98**	39.91	6.91
30843 x ICMB-98222	0.28	1.83**	-0.67*	0.00	1.30

*, ** Significant at 5 and 1 % levels, respectively

-1.92 per cent in cross ICMB-10444 x ICMB-97222. The aforementioned findings were consistent with earlier research by Jethva *et al.* (2012), Singh *et al.* (2015), Jog *et al.* (2016), Nandaniya *et al.* (2016) and Badhe *et al.* (2018) in pearl millet.

Inbreeding depression: Estimates of inbreeding depression were calculated based on the F_2 generation of all crosses (**Tables 1 to 5**). An increase in vigour that is only seen in the F_1 generation and a significant decrease from the F_1 to the F_2 and later generations are the two hallmarks of true heterosis. For each of the characteristics in nine crosses, inbreeding depression was often of a similar intensity. However, for days to 50% flowering, days to reach maturity, height of the plant, grain iron and zinc content, low in breeding depression was recorded in the majority of the crosses. The number of effective tillers per plant, spike length, spike girth, yield of grains per plant, and 1000 grain weight all showed severe inbreeding depression. The estimates of inbreeding depression for days to flowering in F_2 ranged from -9.49 per cent in J-2372 x 30610 to 6.41 per cent in cross ICMB-99222 x ICMB-08222. There were three out of the nine crosses *viz*., ICMB-99222 x ICMB-08222 (6.41%), J-2340 x 30291 (1.82%) and 30127 x J-2556 (1.44%) that exhibited highly significant positive inbreeding depression. The estimates of inbreeding depression ranged from -2.98 percent (ICMB-10444 x ICMB-97222) to 1.35 per cent (ICMB-99222 x ICMB-08222). Only one hybrid *i.e.* ICMB-99222 x ICMB-08222 showed significant positive heterosis for days to maturity. The significant heterotic gains for plant height were reflected with higher estimates of inbreeding depression in F_2 generation that varied from -27.66 per cent (ICMB-10444 x ICMB-97222) to 16.51 per cent (30725 x ICMB-05333). All the crosses showed significant positive inbreeding depression for number of effective tillers/plants. The inbreeding depression ranged from 15.48 per cent in cross, J-2454 x 30348 to 46.97 per cent in cross J-2340 x 30291. The inbreeding depression in F_2 generation ranged from -8.61 per cent in cross J-2372 x 30610 to 19.44 per cent in cross ICMB-99222 x ICMB-08222 for panicle length. All the crosses except J-2372 x 30610 exhibited significant positive inbreeding depression. The inbreeding depression in F_2 generation ranged from -12.54 per cent in cross ICMB-10444 x ICMB-97222 to 13.81 per cent in cross 30725 x ICMB-05333 for panicle girth. All of the crosses showed highly significant inbreeding depression for panicle diameter, with the exception of ICMB-10444 x ICMB-97222. The inbreeding depression in F_2 generations proved to be significant for all the crosses and positive for the grain yield per plant. The inbreeding depression ranged from 14.52 per cent in

Table 2. Magnitude of relative heterosis (RH), heterobeltiosis (BP), inbreeding depression (ID), broad sense heritability (h^2_{bs}) and genetic advance as percent of means (GA%) for plant-height and number of effective/ productive tillers per plant in crosses of pearl millet

Cross	Plant-height				
	RH (%)	BP (%)	ID (%)	H^2_{bs} (%)	GA (%)
ICMB-99222 x ICMB-08222	10.57**	15.15**	-1.78**	6.22	0.00
J-2372 x 30610	5.17**	6.11**	0.21	57.51	0.00
J-2340 x 30291	15.94**	36.01**	11.84**	38.93	0.00
30127 x J-2556	27.75**	37.54**	4.77**	29.73	16.43
J-2454 x 30348	-1.12**	0.58**	-9.70**	82.85	11.95
30725 x ICMB-05333	35.82**	83.18**	16.51**	91.67	34.46
30727 x J-2523	20.09**	27.77**	2.68**	0.00	0.00
ICMB-10444 x ICMB-97222	38.01**	84.12**	-27.66**	71.79	0.00
30843 x ICMB-98222	19.68**	21.89**	-3.14**	69.49	22.49
Designation	**Number of effective/productive tillers per plant**				
ICMB-99222 x ICMB-08222	70.73**	66.67**	32.86**	29.33	0.00
J-2372 x 30610	94.12**	83.33**	32.58**	29.11	5.48
J-2340 x 30291	60.98**	50.00**	46.97**	0.00	0.00
30127 x J-2556	33.33**	30.00**	33.65**	1.32	0.00
J-2454 x 30348	31.25**	31.25**	15.48*	0.00	0.00
30725 x ICMB-05333	57.14**	50.00**	35.61**	20.47	23.40
30727 x J-2523	46.67**	26.92**	42.42**	0.00	0.00
ICMB-10444 x ICMB-97222	40.00**	34.62**	32.14**	0.00	0.00
30843 x ICMB-98222	0.00	0.00	33.70**	0.00	0.00

*, ** Significant @ 5 and 1 % respectively

cross J-2372 x 30610 to 58.60 per cent in cross J-2454 x 30348. The inbreeding depression in F_2 generation was positive and highly significant in crosses 30843 x ICMB-98222 (42.87%), J-2372 x 30610 (28.26%), ICMB-99222 x ICMB-08222 (17.24%), 30127 x J-2556 (11.31%), 30727 x J-2523 (10.77%) and J-2340 x 30291 (4.73%) while negative in other crosses for 1000-grain weight. Inbreeding depression ranged from -7.97 per cent in cross 30725 x ICMB-05333 to 42.87 per cent in cross 30843 x ICMB-98222. Inbreeding depression in F_2 generation for grain iron content ranged from -3.04 per cent in cross 30727 x J-2523 to 0.0 per cent in cross J-2454 x 30348. Inbreeding depression in F_2 generation ranged from 10.68 per cent in cross 30127 x J-2556 to 4.54 per cent in cross J-2454 x 30348 for zinc content in grain. The highly significant positive inbreeding depression was reported in 2 crosses *viz*., J-2454 x 30348 (4.54%) and J-2372 x 30610 (3.27%) for grain zinc content. While the incidence of low or negligible relative and better parent heterosis in F_{1s} and absence of inbreeding depression in F_2s suggested additive gene action for Fe and Zn content. Govindaraj *et al.* (2013), Nandaniya *et al.* (2016), Jeeterwal *et al.* (2017), Rai *et al.* (2017), Badhe *et al.* (2018) and Kumar *et al.* (2021a) in pearl millet also showed non-significant negative and very low positive heterosis for grain iron and zinc concentration.

High inbreeding depression was a reflection of high heterosis as reported earlier for other characters in bajra (Jog *et al*., 2016). Negative and significant value of inbreeding depression indicated possibilities of obtaining transgressive segregants with increased expression of traits in the segregating populations. Both heterosis and inbreeding depression are the results of dominance type of gene action and heterosis is absent where the traits are governed only by additive gene action (Jog *et al*., 2016). When hybrid combinations show high heterosis followed by high inbreeding depression in the F_2 generation, non-additive gene effect might be the cause of such characteristics (Jain and Bharadwaj (2014). Therefore, it can be inferred from strong heterosis (even if it isn't substantial in some cases) and high inbreeding depression that the parents of such crosses have dominant genes for the traits being studied. In most crosses, days to flower, days to maturity and plant height showed high heterosis and low inbreeding depression, indicating additive and /or additive × additive variance that can be fixed in segregating generations. Superior inbred lines that may be employed in hybridization programmes could be created through such crossings. The continuous inbreeding depression and the varying ways that different crosses expressed heterosis provided a

Table 3. Magnitude of relative heterosis (RH), heterobeltiosis (BP), inbreeding depression (ID), broad sense heritability (h^2_{bs}) and genetic advance as per cent of means (GA%) for panicle length and panicle girth in crosses of pearl millet

Cross	Panicle length				
	RH (%)	BP (%)	ID (%)	H^2_{bs} (%)	GA (%)
ICMB-99222 x ICMB-08222	29.04**	15.51**	19.44**	65.67	20.97
J-2372 x 30610	15.19**	7.63**	-8.61**	48.96	0.00
J-2340 x 30291	4.69**	-7.86**	1.99*	15.85	0.00
30127 x J-2556	34.91**	32.09**	18.15**	35.43	17.14
J-2454 x 30348	13.71**	11.92**	13.37**	39.13	4.69
30725 x ICMB-05333	47.13**	39.76**	12.06**	29.24	34.87
30727 x J-2523	13.11**	11.55**	7.99**	44.77	20.67
ICMB-10444 x ICMB-97222	56.21**	43.53**	3.92**	17.02	51.36
30843 x ICMB-98222	30.62**	20.93	11.20**	75.71	40.32
Designation	**Panicle girth/diameter**				
ICMB-99222 x ICMB-08222	16.47**	13.79**	9.28**	49.73	0.00
J-2372 x 30610	3.07**	-0.15	-9.30**	36.45	27.52
J-2340 x 30291	-0.83*	-3.40**	2.84**	57.78	0.00
30127 x J-2556	12.16**	6.74**	3.17**	76.38	22.82
J-2454 x 30348	-4.92**	-11.82**	3.43**	22.20	0.35
30725 x ICMB-05333	24.50**	18.40**	13.81**	80.76	0.00
30727 x J-2523	10.52**	6.78**	9.34**	24.78	0.00
ICMB-10444 x ICMB-97222	3.18*	-2.50	-12.54**	0.00	0.00
30843 x ICMB-98222	22.70**	16.89**	8.74**	0.00	10.38

*, ** Significant @ 5 and 1 % respectively

clue as to which parental lines should be chosen for the creation of hybrids.

Further proof that grain Fe (R^2=0.999) and Zn (R^2=0.992) contents are primarily under additive gene action was provided by highly significant and positive relationships between hybrid performance *per se* and mid-parental values (**Fig. 1a and 1b**). Similar findings in pearl millet for additive genetic control have been reported in earlier researches (Velu *et al*., 2011; Govindaraj *et al*., 2013; Kumar *et al*., 2021a). If additive genetic control predominated, recurrent selection (RS) would be especially successful for intrapopulation improvement and the production of open pollinated varieties (OPV). The production of hybrids that have elevated grain Fe and Zn density would require the incorporation of the same genes for Fe and Zn density into each of the hybrids' parental lines, nevertheless, as no hybrid was created transgressing the parents for higher Fe and Zn density. About 33% of the hybrids had significant mid-parent heterosis for Fe density, but 55% of the hybrids had significant mid-parent heterosis for Zn density, indicating that additive gene action for Zn occurs predominantly. The remaining crosses exhibited negative MPH for both micronutrients revealed that additional genes, besides those with additive gene action, in which the alleles driving reduced Fe and Zn concentrations are partially dominant, were at play. Additionally, it is likely that the additive effects of the genes controlling the densities of Fe and Zn are largely influenced by genetic backgrounds, simulating low degrees of partial dominance. The *Iniadi* germplasm, which has so far been found to be the best source for high Zn and Fe density (Velu *et al*., 2011; Rai *et al*., 2012; Govindaraj *et al*., 2013), was used to generate high grain iron and zinc parental lines for the present investigation. Given the additive gene action, it is anticipated that the genetic variance or genetic distance between the male and female parents for other traits in heterosis breeding will be reduced if the same source is utilised to introgress the genes responsible for Fe and Zn density in both parents. There may be less heterosis in grain yield and other agronomic and economic traits that are primarily influenced by non-additive gene influences. Breeding high-yielding hybrids with higher Fe and Zn densities could be accomplished using genomic techniques for selective introgression of high Fe and Zn genes in the parents without impacting genetic diversity for other traits.

Heritability and Genetic advance: In many crosses of pearl millet, high to low broad sense heritability and high to low genetic advance for yield and associated traits were reported. The heritability estimates alone are unable

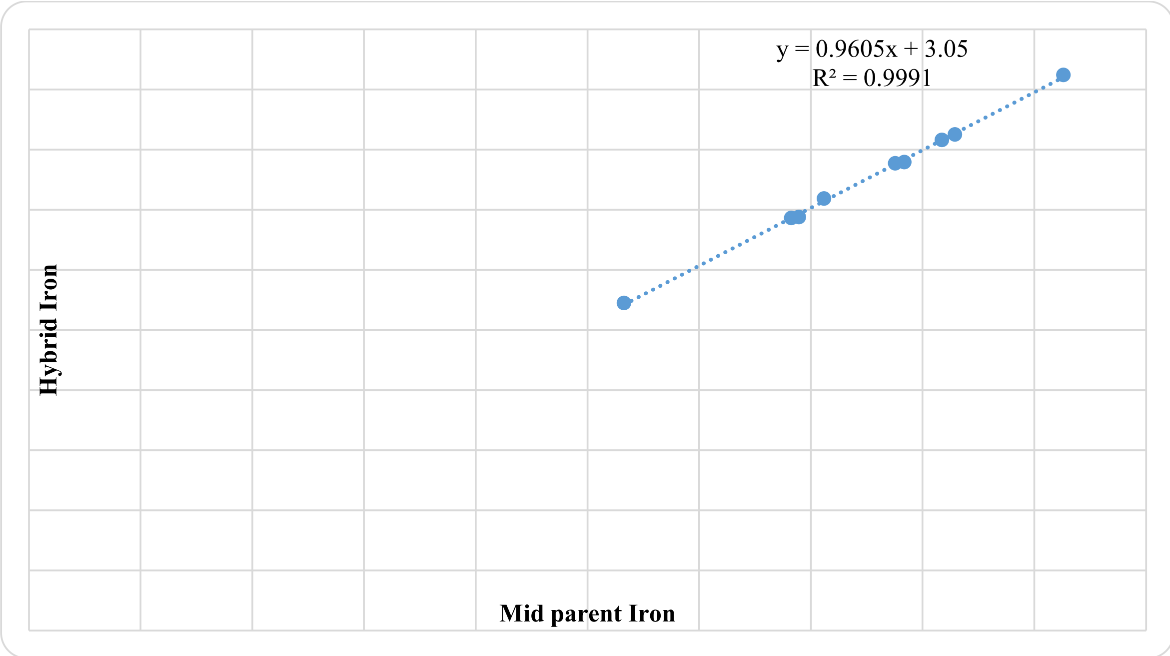

Fig. 1a. Relationship between hybrid and mid-parental values for the iron content of the pearl millet grain

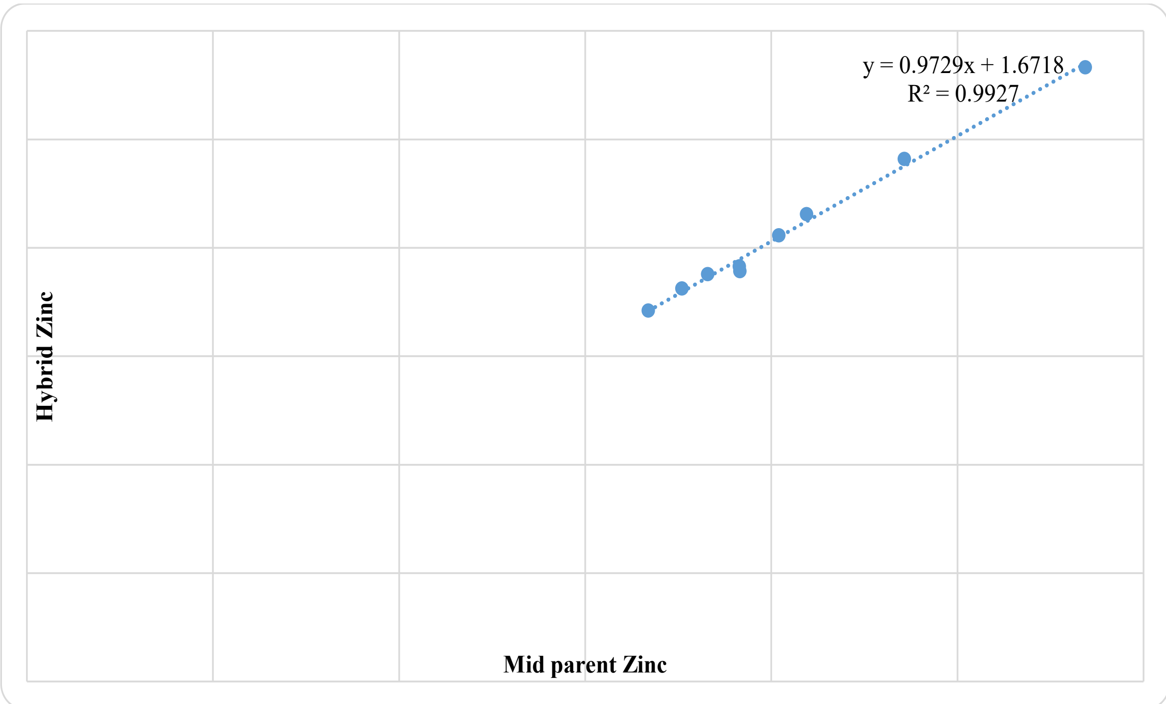

Fig. 1b. Pearl millet grain zinc content in relation to mid-parental and hybrid values

Table 4. Magnitude of relative heterosis (RH), heterobeltiosis (BP), inbreeding depression (ID), broad sense heritability (h^2_{bs}) and genetic advance as per cent of means (GA%) for grain yield per plant and 1000 grain weight in crosses of pearl millet

Cross	Grain or seed yield/plant				
	RH (%)	BP (%)	ID (%)	H^2_{bs} (%)	GA (%)
ICMB-99222 x ICMB-08222	87.03**	59.51**	23.13**	38.64	0.00
J-2372 x 30610	17.79**	8.65**	14.52**	0.00	0.00
J-2340 x 30291	50.50**	14.34**	40.69**	43.83	0.00
30127 x J-2556	17.05**	2.49**	39.63**	0.00	24.66
J-2454 x 30348	44.62**	14.98**	58.60**	2.31	5.18
30725 x ICMB-05333	28.26**	14.55**	50.78**	51.60	17.11
30727 x J-2523	35.38**	13.26**	42.60**	64.89	15.05
ICMB-10444 x ICMB-97222	61.50**	39.07**	55.96**	75.88	9.24
30843 x ICMB-98222	22.42**	15.19**	26.06**	5.87	0.00
Designation	**1000-grain weight (test weight)**				
ICMB-99222 x ICMB-08222	15.02**	14.51*	17.24**	99.87	100.00
J-2372 x 30610	16.09**	11.50**	28.26**	81.22	16.66
J-2340 x 30291	-7.24**	-13.70**	4.73**	32.63	0.04
30127 x J-2556	32.48**	22.24**	11.31**	3.48	0.00
J-2454 x 30348	4.17	1.25	-21.49	1.47	0.00
30725 x ICMB-05333	20.22**	8.89**	-7.97**	0.00	2.71
30727 x J-2523	17.14**	2.79	10.77**	12.17	4.90
ICMB-10444 x ICMB-97222	-10.30	-17.66*	-13.24	47.46	0.00
30843 x ICMB-98222	88.78**	71.13**	42.87**	99.33	100.00

*, ** Significant @ 5 and 1 % respectively

to accurately pinpoint the gene regulating the expression of a particular trait and are unable to account for the genetic benefit that would result from selection. Kumar *et al.*(2020b) in pearl millet noted that heritability estimates in combination with genetic progress were more helpful than heritability estimates alone when attempting to predict response to selection. The estimates of the broad sense heritability (h^2bs) and genetic advance as per cent of mean (GA%) for various traits under study are furnished in the **Tables 1 to 5**. Heritability estimations of days to flowering were shown to be high in the crosses 30727 x J-2523 (71.81%) and J-2454 x 30348 (69.31%). On the other hand, out of nine crosses, 30127 x J-2556 (13.07%) was shown to have a moderate genetic advance as a percentage of the mean. In four crosses, J-2372 x 30610 (86.71%), J-2340 x 30291 (71.81%), 30727 x J-2523 (70.05%), and J-2454 x 30348 (63.28%), high heritability in a broad sense for days to maturity was reported. For days to maturity, the genetic advance as a percentage of mean was determined to be moderate in 30127 x J-2556 (13.06%). For phenological features in pearl millet, strong heritability together with high to low genetic advance as a percentage of mean was reported. Moderate to high broad sense heritability coupled with low to moderate genetic advance in pearl millet for days to flowering was also reported by Drabo *et al.* (2013), Subi and Idris (2013), Salih *et al.* (2014), Singh *et al.* (2015), Solanki *et al.* (2017) and Subbulakshmi *et al.* (2018). Four crossings, namely 30725 x ICMB-05333 (91.67%), J-2454 x 30348 (82.85%), ICMB-10444 x ICMB-97222 (71.79%), and 30843 x ICMB-98222 (69.49%), had strong broad sense heritability for plant height. Both 30725 x ICMB-05333 (34.46%) and 30843 x ICMB-98222 (22.49%) revealed substantial levels of genetic advance as a percentage of the mean. However, in all nine crosses, there was low heredity in the broad sense for the number of effective tillers per plant. For one cross between 30725 and ICMB-05333, the genetic advance as a percentage of the mean was determined to be modest (23.40%). For panicle length, crosses 30843 x ICMB-98222 (75.71%) and ICMB-99222 x ICMB-08222 (65.67%) showed higher heritability overall. In crosses such as ICMB-10444 x ICMB-97222 (51.36%), 30843 x ICMB-98222 (40.32%), 30725 x ICMB-05333 (34.87%), ICMB-99222 x ICMB-08222 (20.97%), and 30727 x J-2556 (17.14%), the genetic advance as a percentage of the mean was considerable. For panicle girth, two crosses namely 30725 x ICMB-05333 (80.76%) and 30127 x J-2556 (76.38%) exhibited strong heritability in the broad sense. In crosses J-2372 x 30610 (27.52%) and 30127 x J-2556 (22.82%), the genetic advance as a percentage of the mean was considerable. Grain yield per plant had a high heritability in the broad sense in the

Table 5. Magnitude of relative heterosis (RH), heterobeltiosis (BP), inbreeding depression (ID), broad sense heritability (h^2_{bs}) and genetic advance as per cent of means (GA%) for grain iron and zinc content in crosses of pearl millet

Cross	Grain iron (Fe) content				
	RH (%)	BP (%)	ID (%)	H^2_{bs} (%)	GA (%)
ICMB-99222 x ICMB-08222	0.45	-0.26	-0.87**	86.34	13.87
J-2372 x 30610	-0.64**	-25.67**	-2.12**	32.47	3.59
J-2340 x 30291	0.14	-32.68**	-0.87	0.00	0.00
30127 x J-2556	1.13**	-35.72**	-0.10	41.66	0.00
J-2454 x 30348	-0.48	-22.90**	0.00	3.17	0.00
30725 x ICMB-05333	-0.49	-16.24**	-0.92	20.80	3.20
30727 x J-2523	0.80**	-19.49**	-3.04**	70.09	0.00
ICMB-10444 x ICMB-97222	2.46**	-11.58**	-2.21**	68.65	8.54
30843 x ICMB-98222	-0.43*	-2.84**	-1.54**	97.45	34.82
Designation	**Grain zinc (Zn) content**				
ICMB-99222 x ICMB-08222	-1.57**	-2.93**	-1.55**	84.70	28.92
J-2372 x 30610	-0.78	-25.54**	3.27**	84.17	30.57
J-2340 x 30291	2.69**	-23.78**	-2.70**	15.91	8.97
30127 x J-2556	-2.20*	-32.44**	-10.68**	68.08	22.61
J-2454 x 30348	5.13**	-8.70**	4.54**	62.88	11.22
30725 x ICMB-05333	2.23*	-12.50**	-3.09**	77.81	7.47
30727 x J-2523	3.47	-21.14**	-6.77**	85.06	22.54
ICMB-10444 x ICMB-97222	2.58*	-1.92	-3.91**	88.61	33.22
30843 x ICMB-98222	2.86**	-2.41**	0.57	84.41	24.21

*, ** significant @ 5 and 1 % respectively

crosses ICMB-10444 x ICMB-97222 (75.88%) and 30727 x J-2523 (64.89%). Cross 30127 x J-2556 had the most genetic advance as a percentage of the mean (24.66%). For test weight, crosses ICMB-99222 x ICMB-08222 (99.87%), 30843 x ICMB-98222 (99.33%), and J-2372 x 30610 (81.22%) had high heritability in the broad sense. In the crosses of ICMB-99222 x ICMB-08222 (100.00%) and 30843 x ICMB-98222 (100.00%), the genetic advance as a percentage of the mean was considerable. Subi & Idris (2013), Dapke *et al.* (2014), Salih *et al.* (2014), Singh *et al.* (2015), Solanki *et al.* (2017), and Subbulakshmi *et al.* (2018) have all reported on similar estimations of heritability for different traits in bajra. Four crossings were found to have high heritability in the broad sense for grain Fe content: 30843 x ICMB-98222 (97.45%), ICMB-99222 x ICMB-08222 (86.34%), 30727 x J-2523 (70.09%), and ICMB-10444 x ICMB-97222 (68.65%). In the cross 30843 x ICMB-98222, genetic advance as a percentage of the mean was considerable (34.82%), while in cross ICMB-99222 x ICMB-08222 it was moderate (13.87%) and in others, it was low. Except for J-2340 x 30291, all the crosses demonstrated strong heritability in the broad sense for Zn content. Two crosses, 30843 x ICMB-98222 and ICMB-99222 x ICMB-08222, showed high heritability in the broad sense and high to medium genetic advance for Fe content, indicating the presence of substantial additive variance for grain iron content. Other crosses with high to moderate broad sense heritability but poor grain iron content genetic advance had an increased amount of nonadditive variance. These crosses could be utilised in heterosis breeding to create hybrid pearl millet plants that are iron-enriched. The current findings from the majority of crosses strongly suggested that the genetic additive variance, which supports phenotypic selection to increase zinc concentration, was influencing grain zinc content. Only one hybrid, 30725 x ICMB-05333, showed high heritability and low genetic advance, which indicated the existence of nonadditive gene activity and suggested that selection may not be advantageous to increase the zinc content of pearl millet grains in this cross. In support to the present findings, Arulselvi *et al.* (2007), Gupta *et al.* (2009), Govindaraj *et al.* (2011), Chaudhary *et al.* (2012) and Subbulakshmi *et al.* (2018) in pearl millet reported the low to high genetic advance together with low to high heritability for grain zinc and iron content.

The most effective and promising breeding strategy for enhancing pearl millet's yield and quality features has been the development of hybrids. The biofortification in pear millet is considered as sustainable, cost effective and a novel approach to reduce micronutrient malnutrition among the population in developing world. As a result, investigations on heterosis, inbreeding depression, heritability, and genetic progress for several traits were conducted in pearl millet. The predominance of non-additive gene action was supported by the preponderance of high magnitude heterosis and severe inbreeding depression for yield and related attributes. So, utilising heterosis can result in a big improvement. In most of the crosses for phonological attributes, high heterosis and low inbreeding depression indicated the presence of additive and /or additive x additive variation. These crosses might be used to create early hybrids or superior inbred lines that might then be further utilised in hybridization programmes for heat and water stressed conditions. The lack of inbreeding depression in F_2s and low level of heterosis for Fe and Zn content in F_1 revealed that additive and partial dominance gene effects are the main determinants of the character. Therefore, enhancing grain micronutrients in pearl millet is anticipated to be most successful when assisted by high volume crossing techniques including biparental mating, diallel selective mating, and reciprocal recurrent selection. On the other hand, creating hybrids with high Fe and Zn densities will require introducing these elements into both parental lines, a procedure that genomics approaches might facilitate.

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