Original article

Heterosis and combining ability for grain Fe and Zn concentration and agronomic traits in sorghum [*Sorghum bicolor* (L.) Moench]

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ABSTRACT

Studies on genetics and trait relationships with grain yield and other agronomic traits are critical for improving the micronutrients content in the grain and it forms an effective strategy for breeding bio fortified sorghum. It greatly contributes to addressing micronutrient malnutrition in poor people who are dependent on sorghum as a staple food. Development of hybrids with high grain Fe and Zn and higher yield enables delivery of commercial products that address both food and nutrition while bringing profits to farmers. The present study was aimed at developing suitable breeding strategy and improving breeding products using gene action, heterosis and combining ability analysis for improving the grain Iron (Fe) and Zinc (Zn) concentration and grain yield in sorghum. This study was conducted in Line × Tester mating design involving seven parents. A total of 12 new hybrids were developed by mating three lines with four testers. The combining ability of the crosses indicated predominance of dominance variance than additive variance for the agronomic traits such as days to 50% flowering, grain yield, grain Fe and Zn concentrations except for plant height and 100 seed weight. Higher magnitude of SCA than GCA variance for grain iron and zinc concentrations indicated the importance of non-additive gene action in the improvement of nutritional traits. Hybrids exhibited heterosis for agronomic traits and for grain Fe concentration and grain Zn. Most of the traits showed significant positive heterosis over mid parent value indicating the predominance of dominant gene action except the trait 100 seed weight. Significant positive mid-parent heterosis for grain iron indicated that there would be an opportunity to exploit heterosis in improving for grain Fe. But for Zn concentration, there is a limited possibility for exploitation of heterosis. This study suggested that simple selection will improve plant height and 100 seed weight in sorghum but heterosis breeding is more useful for improving grain yield. While both parents need to be improved for improving grain Zn concentration, there is good scope for exploiting heterosis for improving grain Fe concentration in sorghum.

1. Introduction

Micronutrient malnutrition is a major health problem worldwide. Iron (Fe) and zinc (Zn) deficiencies are one of the major risk factors among the micronutrients. Biofortification is a trending plant breeding approach to increase the Fe and Zn density in staples, to tackle the micronutrient malnutrition in low-income group population globally. It is a cost effective and sustainable method without an additional cost to consumers (Ashok Kumar et al., 2012). It has an advantage for improving the nutrient content of the food and health of the low-income group people in developing countries (Kanatti et al., 2014). *Sorghum bicolor* is among the top five major cereal crops in the world, occupying 44.7 m ha area and serves as food for 500 million people globally (FAO STAT, 2016). It is grown mostly in semi-arid regions of Asia and Africa. India is one of the major sorghum producers with 5.65 million ha area with a production of 4.4 million tons of sorghum grain (FAO

STAT, 2016). Apart from being used as grain for food purpose, sorghum is also gaining importance as a feed, fodder and biofuel feedstock. It is the second cheapest source of energy (63.4–72.5% starch) and micronutrients and it supplies more than 50% micronutrient needs in the low-income group populations in predominantly sorghum eating areas (Parthasarathy Rao et al., 2006; Ashok Kumar et al., 2011).

Knowledge of genetic variability, gene action, heterosis and combining ability are critical for improving grain Fe and Zn concentrations in sorghum. Ashok Kumar et al. (2013) and Phuke et al. (2017) reported large heritable genetic variability for Fe and Zn densities in sorghum. Combining ability is the most important for the quality traits in hybrid development programs. It helps the breeder to select the parents with good general combining ability (GCA) and cross combinations with good specific combining ability (SCA) and the appropriate breeding methodology to achieve the objective quickly and reliably (Gayathri, 2012). Extent of heterosis will have a direct bearing on devising effective hybrid breeding strategies for Fe and Zn density. Negative heterosis for grain iron was reported earlier in pearl millet by Rai et al. (2007) and in maize by Chakraborti et al. (2009). However, there is a limited information on gene action, combining ability and heterosis for Fe and Zn density in sorghum.

In view of this, present study was undertaken to examine the nature of genetic variability in relation to heterosis and combining ability for Fe and Zn density in sorghum lines for improving grain quality and agronomic traits.

2. Materials and methods

The experiments were conducted initially using six female (A lines), six male (R lines) lines and 36 hybrids in two years. Based on the restoration of lines, 12 hybrids were used for the analysis which include three maintainer lines (B lines i.e. ICSB 11, ICSB 17 high for Fe and Zn, ICSB 88,005 moderate Fe and Zn) which were used as female parents (L), four restorer lines (R lines i.e. ICSR-12, 89011, low for Fe and Zn and ICSR 89051, ICSR 89056 moderate for Fe and Zn as male parents (T)], and 12 hybrids produced by mating in L × T design during the rainy season of 2013. Parents used for hybrid making were diverse for Fe and Zn density and agronomic traits (Table 1). Parents and hybrids were evaluated in single trial. The trial was conducted during the rainy seasons of 2014 and 2015 at ICRISAT, Patancheru, Hyderabad located at an altitude of 545 m above mean sea level and at 17.53° N latitude and 78.27° E longitude, Rain fall 40–101 mm, temperature 19.730c–32.250c, 3–65% humidity and the soil Fe 2.7 to 4.3 mg kg^{-1} and Zn 0.7 to 1.0 mg kg^{-1}. The trials were conducted in randomized complete block design (RBD) with three replications. Each entry was planted in two rows of 2 m length, with a spacing of 75 cm between rows and 10 cm between plants. The parents were kept together as one set and hybrids as another set in the trials to avoid shading effect. Two seeds were planted per hill and thinned later to a single seedling per hill to obtain a population stand of 20 plants per plot. The crop was supplied with a fertilizer dose of 80 kg N and 40 kg P_2O_5 per hectare and nitrogen was applied in three doses. Recommended cultural practices were adopted to raise a good and healthy crop. Data were recorded for the following traits viz., days to 50% flowering, plant height, grain yield per plant, 100 grain weight, and grain Fe and Zn concentration.

Sorghum panicles were harvested at maturity and grains were thrashed manually without any metal and dust contamination. The cleaned seeds were collected in cloth bags for micronutrient analysis. Fe and Zn were analyzed at the Charles Reynard Analytical Laboratory, ICRISAT, Patancheru, India following the method described by Wheal et al. (2011). Sorghum grain samples were finely ground (0.2 g), transferred to 25 ml polypropylene PPT tubes; digestion was initiated by adding 2 ml of concentrated nitric acid (HNO$_3$) and 0.5 ml of 30% hydrogen peroxide (H$_2$O$_2$). Tubes were vortexed to ensure the entire sample was wetted, and then predigested overnight at room temperature. Tubes were vortexed again before placing them into the digestion block and initially heated at 80 °C for 1 h, followed by digestion at 120 °C for 2 h. After digestion, the volume of the digest was made to 25 ml using distilled water; and the content was agitated for 1 min by vortex mixer. The digests were filtered and Fe and Zn densities were determined using ICP-OES.

2.1. Statistical analysis

The data were analyzed using SAS version 9.2 (SAS institute Inc.2004). ANOVA was performed for two environments and individual environments. Pooled ANOVA for two environments were performed using Generalized Linear Model procedures following a random effects model (McIntosh, 1983). Line × tester model for female × male hybrid (Kempthorne, 1957) was used to obtain estimates of GCA for parents as well as SCA effects for hybrids. The estimates of mid-parent heterosis (MPH) and better-parent heterosis (BPH) were derived for individual environments as well as for mean of two environments following Hallauer and Miranda (1988). The tests of significance for MPH and BPH were performed via "t" test. The Pearson correlation coefficient among the traits was calculated using the PROC CORR procedure.

3. Results and discussion

3.1. Mean performance and variability for parental lines and hybrids

Parental lines were highly significant (P < 0.01) for the traits studied, and also parent and environment interaction (P × E) for days to 50% flowering (Table 1). The contribution of P × E interaction to variability was smaller relative to those due to genetic differences among the parental lines. Hence, it is necessary to improve grain Zn content simple section, by using pure-line varieties or use of both parents with high Zn concentration in hybrid development considering the additive variance of the trait. Low interaction indicates improving genetics is key. Similar interaction

Table 1
. Mean square for days to 50% flowering (DTF), plant height (PHT), grain yield (GY), 100 seeds weight (GW0, grain Fe and Zn density of parental lines across 2014 and 2015 rainy seasons carried out ICRISAT, Patancheru.

Source of variation	Df	Mean Square					
		DTF	PHT (cm)	GYtha^{-1}	GW(g)	Fe mg kg^{-1}	Zn mg kg^{-1}
Environment	1	184.38**	729.16	3.41**	0	156.38**	4.91
Replication (ENV)	4	7.16*	1334.52	0.57*	0.04	25.07	0.39
Parents	6	105.43**	3585.31	6.39**	0.6**	124.18**	33.88**
ENV *Parents	6	17.65**	16.66	0.16	0.04	7.05	7.54
Error	24	2.08*	1391.46	0.14	0.03	12.19	5.27

*, ** Significant at the P < 0.05 and 0.01 probability level, respectively.

was observed in pearl millet by Kanatti et al. (2014). The parental mean performance of two environments showed large variation for Fe and Zn. The days to 50% flowering varied from 62 to 66 in females and 68 to 75 in males. While plant height ranged from 131.66 to 189.16 cm in females and 151.66 to 201.66 in males, grain yield varied from 1.62 to 3.92 t ha^{-1} and 3.88 to 4.08 t ha^{-1} in females and males respectively. The range of Fe content in females (L) was 34.45 to 37.04 mg kg^{-1} and 26.00 to 33.21 mg kg^{-1} in males (T), while Zn ranged from 20.92 to 24.14 mg kg^{-1} among females and 17.79 to 23.12 mg kg^{-1} in males (Table 3). The mean performance of hybrids in two environments for the days to 50% flowering varied from 58 to 73 and for plant height from 153.33 to 205.83 cm. The grain yield ranged from 2.78 to 5.75 t ha^{-1} and 100-grain weight ranged from 2.97 to 4.26 g. The variation for Fe and Zn concentration ranged from 33.31 to 45.24, and 24.09 to 32.8 mg kg^{-1} respectively (Table 4). The variance due to SCA was about 3 to 12-folds higher than variance due GCA for Fe and Zn density, and twice for days to 50% flowering and grain yield whereas GCA was twice higher than the SCA for plant height. The predictability ratio was higher for 100-grain weight (0.80) compared to other traits. It was slightly lower for plant height (0.79) and much lower for days to 50% flowering (0.47), grain yield (0.56), grain Fe (0.36) and Zn (0.11) (Table 2). There were significant positive, and moderate correlations between mid-parental values and hybrid performance per se for days to 50% flowering (r = 0.37) and 100-grain weight (0.19), grain Fe (r = 0.26), Zn (r = 0.33), very low correlation for grain yield (r = 0.05) and plant height (Table 6).

Combining ability: Among three female lines, ICSB11 exhibited significant positive GCA for Fe density (37.04) mg kg^{-1}, while

ICSB88005 displayed significant negative GCA for the same (35.45 mg kg^{-1}). In contrast, for the same character, non-significant results were observed in ICSB 17. Among 4 male parents, ICSR 27 displayed significant negative GCA and 27.88 mg kg^{-1} Fe density, while reaming three male parents showed non-significant results, and most of these contained >28.92 mg kg^{-1} Fe density. ICSB 11 showed the best general combiner character with 37.04 mg kg^{-1} Fe density. When female and male lines were considered together, there was significant and highly positive correlation between Fe density of parental lines per se and their GCA for this trait (r = 0.26; p < 0.01). For Zn density, similar patterns were observed. Thus, none of the female parents revealed significant grain Zn density. Among the 4 male parents, one line displayed significant and positive GCA with grain Zn density at 33.21 mg kg^{-1}, but the other three male lines were non-significant for the same trait.

Two female parents showed significantly positive, while one exhibited negative GCA values for days to 50% flowering. Among the 4 male parents, two parents showed significantly positive GCA except days to 50% flowering (Table 3). Parental lines revealed significant and large differences for days to 50% flowering, grain Fe and Zn, grain yield and 100-grain weight, except plant height. Hybrids produced from both the parents (female × male) showed highly significant differences. The ratio of GCA to SCA variances for days to 50% flowering suggested that this trait was under the control of non-additive gene action. Predictability ratio (0.47) supported the role of non-additive gene action in controlling the trait. Similar results have been reported in sorghum earlier (Mohammed et al., 2015). Contrarily, importance of additive gene action for days to 50% flowering was reported by Al-Aaref et al. (2016) who found

Table 2
. Mean square for hybrids and genetic components.

Source of variation	Mean Square						
	DF	DTF	PHT (cm)	GYtha^{-1}	GW(g)	Fe mg kg^{-1}	Zn mg kg^{-1}
Environment	1	561.12**	1653.12	0.47	0.01	2.01	0.57
REP(ENV)	4	5.69	1066.66	0.14	0.03	3.97	3.8
Hybrid	11	130.92**	1563.73*	5.31**	1.02**	105.18**	39.42**
LINE	2	103.72**	262.5	0.75**	4.53**	223.69**	5.62
TESTER	3	190.6**	3739.23*	11.46**	0.17**	35.23	27.63*
LINE*TESTER	6	110.14**	909.72	3.76**	0.27**	100.66**	56.58**
ENV*HYBRID	11	14.88**	46.3	0.37**	0.04	18.38	19.42
LINE*ENV	2	8.66	112.5	0.05	0.01	1.37	20.83
TESTER*ENV	3	1.71	54.97	0.68**	0.08	40.72*	29.77**
LINE*TESTER*ENV	6	23.53**	19.9	0.32*	0.04	12.88	13.77
ERROR	44	4.83	601.51	0.13	0.04	13.74	10.29
Genetic components							
SCA		17.55	51.36	0.60	0.03	14.49	7.71
GCA		7.84	98.94	0.38	0.07	4.21	0.50
Predictability ratio		0.47	0.79	0.56	0.80	0.36	0.11

*, ** Significant at the P < 0.05 and 0.01 probability level, respectively.

Table 3
. Mean performance of parental lines and their general combining ability (GCA) effects across 2014 and 2015 rainy seasons carried out at ICRISAT, Patancheru.

Parents	Mean performance						GCA					
	DTF	PHT (cm)	GY tha^{-1}	GW (g)	Fe mg kg^{-1}	Zn mg kg^{-1}	DTF	PHT (cm)	GY tha^{-1}	GW (g)	Fe mg kg^{-1}	Zn mg kg^{-1}
Female Parents												
ICSB11	65.33	131.66	1.62	3.39	37.04	20.92	−2.36**	3.75NS	−0.03NS	0.42**	2.57**	−0.3NS
ICSB17	66.33	162.5	2.1	3.1	36.59	23.4	1.55**	−1.25NS	0.19**	0.02NS	0.79NS	0.55NS
ICSB88005	62.33	189.16	3.92	3.02	35.45	24.14	0.8*	−2.5NS	−0.15*	−0.44**	−3.37**	−0.25NS
Male Parents						S.Em	0.44	5	0.07	0.04	0.75	0.65
ICSR-12	68.33	188.33	4.08	2.98	26	19.12	−1.79**	−15.62**	−0.42**	0.11*	0.73NS	0.24NS
ICSR-27	69.66	165.83	3.94	2.69	27.88	22.47	−3.62**	7.15NS	0.33**	0.04NS	−1.98*	−0.73NS
ICSR-89011	70.16	151.66	3.88	3.38	28.6	17.79	2.09**	−7.84NS	−0.85**	−0.09*	0.06NS	−1.15NS
ICSR-89056	75.5	201.66	3.96	3.63	33.21	23.12	3.31**	16.31**	0.94**	−0.06NS	1.18NS	1.63*
S.Em	0.96	24.86	0.25	0.11	2.32	1.53	0.51	5.78	0.08	0.05	0.87	0.75

Table 4

. Mean performance of hybrids and their (SCA) effects across 2014 and 2015 rainy seasons carried out ICRISAT, Patancheru.

Hybrids	Hybrids Mean Performance						SCA hybrids					
	DTF	PHT (cm)	GY tha^{-1}	GW (g)	Fe mg kg^{-1}	Zn mg kg^{-1}	DTF	PHT (cm)	GY tha^{-1}	GW (g)	Fe mg kg^{-1}	Zn mg kg^{-1}
ICSA11A-1 × ICSR-12	62	187.5	3.37	4.26	35.35	24.09	1.74*	17.08*	0.05NS	0.08NS	−6.03**	−2.79*
ICSA11A-1 × ICSR-27	64	193.33	4.99	3.97	40.31	25.09	0.66NS	−6.25NS	−0.47**	0.24**	4.88**	3.3**
ICSA11A-1 × ICSR-89011	63	175.83	3.01	4.01	41.71	24.58	−2.41**	−10.83NS	0.41**	−0.33**	1.15NS	−0.5NS
ICSA11A-1 × ICSR-89056	60	187.5	3.59	3.98	45.24	32.8	5.08**	0.13NS	0.9**	−0.13NS	1.64NS	−0.82NS
ICSA17A-1 × ICSR-12	65	159.16	3.07	4.02	44.49	31.05	−1.5NS	3.47NS	−0.22NS	−0.07NS	−3.49*	−0.96NS
ICSA17A-1 × ICSR-27	61	191.66	4.08	3.62	33.4	25.81	−3.58**	−3.61NS	−0.68**	0.2*	1.84NS	1.78NS
ICSA17A-1 × ICSR-89011	68	167.5	2.95	3.48	39.42	26.16	−0.97NS	−2.36NS	0.12NS	0.05NS	0.98NS	−0.9NS
ICSA17A-1 × ICSR-89056	71	205.83	5.75	3.49	38.19	27.00	−0.55NS	−5.69NS	−0.15NS	−0.07NS	0.47NS	−0.19NS
ICSA88005A-1 × ICSR-12	61	153.33	3.61	2.97	36.59	26.43	1.52*	8.05NS	0.02NS	0.01NS	−1.46NS	1.1NS
ICSA88005A-1 × ICSR-27	58	183.33	3.26	3.43	34.57	27.74	−5.86**	−14.86NS	−1.09**	−0.01NS	3.4*	4.52**
ICSA88005A-1 × ICSR-89011	69	180	2.78	3.10	33.31	26.65	1.38NS	8.47NS	0.84**	−0.1NS	−1.86NS	−2.14NS
ICSA88005A-1 × ICSR-89056	73	202.5	4.80	3.24	34.35	25.95	4.47**	6.38NS	0.24NS	0.11NS	−1.53NS	−2.38*

Table 5

. *Per se* of hybrids and parental lines, and GCA of parents ranking hybrids, across 2014 and 2015 rainy seasons carried out ICRISAT, Patancheru.

Fe (mg kg^{-1})						Zn (mg kg^{-1})				
Hybrids[a]	Performance *per se*[b]			GCA[c]		Performance per se[b]			GCA[c]	
	F1	P1	P2	P1	P2	F1	P1	P2	P1	P2
ICSA11A-1 × ICSR-89056	45.24	37.04	33.21	2.57**	1.18NS	32.8	20.92	23.12	−0.3NS	1.63*
ICSA17A-1 × ICSR-12	44.49	36.59	26	0.79NS	0.73NS	31.05	23.4	19.12	0.55NS	0.24NS
ICSA11A-1 × ICSR-89011	41.71	37.04	28.6	2.57**	0.06NS	24.58	20.92	17.79	−0.3NS	−1.15NS
ICSA11A-1 × ICSR-27	40.31	37.04	27.88	2.57**	−1.98*	25.09	20.92	19.12	−0.3NS	−0.73NS
ICSA17A-1 × ICSR-89011	39.42	36.59	28.6	0.79NS	0.06NS	26.16	23.4	17.79	0.55NS	−1.15NS
ICSA17A-1 × ICSR-89056	38.19	36.59	33.21	0.79NS	1.18NS	27	23.4	23.12	0.55NS	1.63*
ICSA88005A-1 × ICSR-12	36.59	35.45	26	−3.37**	0.73NS	26.43	24.14	19.12	−0.25NS	0.24NS
ICSA11A-1 × ICSR-12	35.35	37.04	26	2.57**	0.73NS	24.09	20.92	19.12	−0.3NS	0.24NS
ICSA88005A-1 × ICSR-27	34.57	35.45	27.88	−3.37**	−1.98*	27.74	24.14	19.12	−0.25NS	−0.73NS
ICSA88005A-1 × ICSR-89056	34.35	35.45	33.21	−3.37**	1.18NS	25.95	24.14	23.12	−0.25NS	1.63*
ICSA17A-1 × ICSR-27	33.4	36.59	27.88	0.79NS	−1.98*	25.81	23.4	19.12	0.55NS	−0.73NS
ICSA88005A-1 × ICSR-89011	33.31	35.45	28.6	−3.37**	0.06NS	26.65	24.14	17.79	−0.25NS	−1.15NS

[a] Grain iron (Fe) and zinc (Zn) density, 100 grain weight (TW) and grain yield (GY); b: Values outside the parentheses are phenotypic correlations for performance *per se* and values within the parentheses are correlations between GCA effects in parents and between SCA effects in hybrids; *, **Significant at 0.05 and 0.01 probability level respectively; NS = Non-significant.

[b] Mean performance of grain Fe and Zn density.

[c] GCA General combining ability effects; *, **Significant at 0.05 and 0.01 probability level, respectively; NS Non-significant.

Table 6

Correlation coefficient among traits in hybrids (above diagonal) and parents (below diagonal).

Trait	DTF	PHT	Gytha^{-1}	Tw (g)	Fe mg kg^{-1}	Zn mg kg^{-1}
DTF	1(1)	0.32(0.64*)	0.38(0.72**)	−0.34(0.05)	−0.16(0.34)	−0.2(−0.6)
PHT	0.33(0.16)	1(1)	0.71*(0.46)	0.11(0.18)	−0.28(0.85)	−0.18(−0.71)
Gy	0.39(0.12)	0.7(0.87)	1(1)	−0.06(−0.51)	−0.09(−0.34)	−0.14(−0.75)
Tw	0.43(−0.51)	−0.03(0.05)	−0.2(0.05)	1(1)	0.57(0.13)	0.1(0.29)
Fe	−0.41(0.07)	−0.12(0.08)	−0.66(0.09)	0.4(0.8)	1(1)	0.59*(0.77**)
Zn	−0.19(0.03)	0.37(−0.22)	−0.13(0.4)	−0.15(0.12)	0.61(0.26)	1(1)

the importance of both additive and non-additive components of genetic variances for days to 50% flowering. The negative estimates of GCA and SCA are considered as favorable for days to 50% flowering development for early duration hybrids. Hence, they can be used as good general combiners to attain early maturity. Our results corroborate what has been observed earlier in sorghum by many researchers (Akbari et al., 2013; Tariq et al., 2014; Soujanya et al., 2017).

For plant height, the values for all female parents were found non-significant. Among 4 male parents, the results for two were highly significant with opposite sign GCA and the rest non-significant for plant height. Two female parents revealed significant GCA values for grain yield with opposite signs. Contrary to it, there was no significant variation among the crosses. For plant height, GCA variance was higher than SCA variance, suggesting

the operation of additive gene action in controlling the trait. Further, predictability ratio (0.79) obtained for this trait revealed the predominant role of additive gene action. These results are in line with the earlier reports noticed in sorghum (Gayathri, 2012; Chikuta et al., 2017). Among seven parents taken for the trait plant height, one showed positive values which can be used as parents for fodder improvement. Rest of the lines exhibited negative GCA and hence are of value as parents (general combiners) for grain yield and can be utilized in hybrid programs where especially short statured plants are preferred.

Since grain yield is the most desirable trait for the hybrids, high grain yield has become the prime objective in majority of the plant breeding programs. In the present study, all parents showed highly significant variance for grain yield. Among the 3 female parents, one exhibited positive values, one negative and among 4 male par-

ents, two showed positive and two negative values for GCA variance. The magnitude of SCA variance was larger in proportion, which suggests the predominance of non-additive gene action in controlling grain yield. The results inferred the possibility of grain yield improvement through heterosis breeding. The predictability ratio observed (0.56) across the seasons is reasonable. Similar results were reported earlier by Tariq et al. (2014), Kumar and Chand (2015), and Mohammed et al. (2015), who observed the preponderance of non-additive gene action in controlling grain yield. The study reveals if at least one good combiner is included in hybrid combinations as one of the parents, one can get better hybrids; hence these crosses provide scope for obtaining transgressive segregants that could be utilized for improvement of grain yield in sorghum. These results were in line with Khadi (2013), and Justin et al. (2015). For 100 grain weight, two female parents showed significant GCA, one with positive and another with negative GCA variance. Higher GCA variance than SCA variance indicated that 100 seed weight was largely under the control of additive gene action. Present findings are in agreement with that of the results obtained by Tariq et al. (2014), and Chikuta et al. (2017). Among the hybrids, two showed significant positive SCA and one negative effect.

Among the parents, since one of them (ICSB 11) exhibited significant positive GCA effects for grain Fe, this could be considered as the best. Contrary to this, ICSB 88,005 recorded the highest significant negative GCA effects. Among male parents, three showed non-significant but ICSR 27 negative GCA variance. Two hybrids recorded significant positive SCA and two negative SCA effects with the predictability ratio of 0.36, indicating the predominant non-additive gene effects. These results endorse the results obtained earlier by Hariprasanna et al. (2014) (Table 4). For Zn, among all male and female parents, only one parent portrayed significant positive GCA and all other non-significant values. Moreover, SCA variance was higher than the GCA which indicated non-additive gene action for the trait. This suggests that Zn accumulation was governed by non-additive gene action due to lower predictability ratio (0.11). Among the 12 hybrids, two displayed significant positive SCA effects and two negative, indicating that non-additive gene effects play a critical role. These results were in confirmation with Hariprasanna et al. (2014) (Table 3).

4. Heterosis

Among the hybrids, Fe density varied from 33.31 to 45.24 mg kg^{-1}, and two hybrids showed significant positive better-parent heterosis (Table 5). However, 6 hybrids portrayed positive mid-parent heterosis. Heterosis over mid-parent ranged from 0.05% to 42.16% for grain Fe. Among 12 hybrids, 6 of them showed significant positive mid-parent heterosis. Similar results were reported by Gayathri (2012), Ravi Kiran (2013), and Hariprasanna et al. (2014). The results indicate that opportunity exists to exploit heterosis for grain Fe. Zn density ranged from 24.09 to 32.80 mg kg^{-1}, and among 12 hybrids, 2 hybrids showed significant positive better-parent heterosis. Nine hybrids represented significant positive mid-parent heterosis. While heterosis for mid-parents ranged from 9.81% to 48.95%, for better-parents, it ranged from 7.49% to 41.9%. Among 12 hybrids, only two depicted significant positive heterosis for mid- and better-parent heterosis. These results indicate that there is a limited possibility for exploitation of heterosis for improving grain Zn concentration (Ashok et al., 2013; Hariprasanna et al., 2014).

The grain yield among the hybrids varied from 2.78 to 5.75 t ha^{-1}, three hybrids showed significant positive better-parent heterosis. Eight hybrids exhibited significant mid-parent heterosis, of which 6 were positive and 2 negative. Heterosis over mid-parent varied from −28.71% to 89.76%, and heterosis over better-parent ranged from −29% to 45.2% for grain yield. More than 50% of hybrids recorded significant positive heterosis over mid-parents. Similar results were reported earlier by Jadhav and Deshmukh (2017), Gayathri (2012), and Ravi Kiran (2013) in sorghum. Three hybrids displayed positive better-parent heterosis. Patterns for 100-grain weight among hybrids varied from 2.97 to 4.26 g, seven of these hybrids exhibited significant better-parent heterosis. Eight hybrids showed significant positive heterosis. Heterosis over mid-parent ranged from −3.11% to 38.27%, and better-parent heterosis ranged from −11% to 29.7%. Among 12 hybrids, 8 hybrids exhibited significant positive heterosis over mid-parent for 100 grain weight. Earlier studies reported greater magnitude of heterosis for grain yield in sorghum (Chikuta et al., 2017; Gayathri, 2012; Ravi Kiran, 2013; Ashok Kumar et al., 2013). Nearly 50% of hybrids exhibited heterosis over both mid- and better-parents. Significant positive heterosis for 100-grain weight was also evidenced earlier by Lokapur (1997) and Rao et al. (1993).

Days to 50% flowering of hybrids varied from 58 to 73-days for heterosis over better-parent which ranged from −20.52 to −2.64%. Nine hybrids displayed significant mid-parent heterosis, of which 2 were positive and seven negative. None of the hybrids exhibited like better-parent heterosis. Heterosis over mid-parent ranged from −11.36% to 6.65%. Among 12 hybrids, 9 showed negative heterosis over mid-parent for days to 50% flowering. Earliness as indicated by negative heterosis is perhaps desirable. These results are in line with that of Khadi (2013), Hussien (2015), and Tag El-Din (2015). Two hybrids showed positive heterosis over mid-parent but all hybrids portrayed negative but non-significant better-parent heterosis for days to 50% flowering (Gayathri, 2012; Tiwari et al., 2003). Heterosis for mid-parent varied from −9.26% to 24.11%, and for better-parent −19% to 16.6%. For plant height, only two hybrids were found significant, one positive, and another negative. None of the hybrids exhibited significant better-parent heterosis. Similar kind of results were also reported earlier by Naik et al. (1994), and Khadi (2014) in sorghum.

5. Conclusions

Genetic variability exists in elite sorghum lines for grain Fe and Zn concentrations and agronomic traits which can be exploited for improving these traits. Higher magnitude of SCA than GCA variance for grain Fe and Zn concentrations indicated the importance of non-additive gene action in the nutritional trait improvement. Hybrids displayed heterosis not only for agronomic traits but also for grain Fe concentration, implying that intra-population improvement for the micronutrients is likely to be highly effective. Limited heterosis for grain Zn breeding hybrids with high levels of Fe and Zn densities will require incorporation of both the parental lines, and application of genomic tools may significantly accelerate this activity. Significant positive mid-parent heterosis for grain Fe concentration indicated that there would be an opportunity to exploit heterosis for improving grain Fe. For Zn concentration, possibility for exploitation of heterosis is however limited. This study reported that simple selection will improve plant height and 100-grain weight in sorghum but heterosis breeding is more useful for improving grain yields. While both the parents need to be improved for refining grain Zn concentration, there is good scope for exploiting heterosis for enhancing grain Fe concentration in sorghum. The experiments suggested that wide variability exists for grain Fe and Zn, and grain yield traits in advanced breeding lines can be exploited as future parents. Accessibility and use of these parental lines in future will be of immense help to the public and private sectors involved in sorghum breeding programs. Such

programs might benefit the nutritional trait introgression and mainstreaming for commercial hybrid breeding in the years to come. Developing improved commercial hybrids that address both food and nutrition security while giving profits to farmers adopting them.

Authors contributions

Planning experiments, supporting and monitoring of research - AAK; Performance of experiments – AG, RP, JJ, SG; Data analysis was carried out by AG, RP; and manuscript development and review – AG, RP, AAK, PK, PBK.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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