Research Square

Preprints are preliminary reports that have not undergone peer review.
They should not be considered conclusive, used to inform clinical practice,
or referenced by the media as validated information.

Fe, Zn & Protein content in grain, per se performance, heterosis, combining ability of grain yield in bread wheat (Triticum aestivum) under normal & late sowing condition.

Gita R. Chaudhari (geetchaudhary89@gmail.com)
Anand Agricultural University
D. A. Patel
Anand Agricultural University
D. J. Parmar Parmar
Anand Agricultural University
K. C. Patel
Anand Agricultural University

Research Article

Keywords:

Posted Date: February 9th, 2022

DOI: https://doi.org/10.21203/rs.3.rs-1338914/v1

License: This work is licensed under a Creative Commons Attribution 4.0 International License.
Read Full License

Fe, Zn & Protein content in grain, per se performance, heterosis, combining ability of grain yield in bread wheat (*Triticum aestivum*) under normal & late sowing condition.

Gita R. Chaudhari[1], D. A. Patel[2], D. J. Parmar[3] and K. C. Patel[4]

1, 2, 3 & 4 Anand Agricltural University, Anand, Gujarat, India.

[1]email: geetchaudhary89@gmail.com

The aim of this study was to understand the inheritance of grain iron (Fe), zinc (Zn) and protein concentrations in bread wheat (*Triticum aestivum* L.*)* under normal & late sown condition. The half diallel cross were made, using ten parents. The crosses and parents were evaluated in replicated trials for two conditions and to assess the possibility of exploiting heterosis to improve these micronutrients. The perusal of results revealed that hybrid GW 451 × GW 173 was consistent for both better parent (BH) and standard heterotic effects (SH) in all the environments. In both the sowing condition, General Combining Ability (GCA) effects of parents and Specific Combining Ability (SCA) effects of hybrids were observed to be contrasting for the micronutrient & protein content. However, σ^2_A/σ^2_D greater than unity confirmed the preponderance of additive gene action for only protein content and GW 173 was identified as good general combiners for these characters under both environments.

Wheat is one of the major staple food crops in the world, being consumed from ancient times by human beings[1]. Wheat is being cultivated on more than 17 % of cultivable land consumed by nearly 40 % of the global population occupying about 32% of the total land under cereals in the world. Wheat fulfills 21% of the protein requirements of more than 4.5 billion people in developing countries[1]. Micronutrients malnutrition is of great public health importance in several parts of the world, especially the developing and underdeveloped countries[2]. It has been estimated that about 2 billion people, about one third of the world's population, are deficient in one or more mineral elements[3]. Although required in traces, these mineral elements are involved in many vital metabolic functions[4]. It is estimated that over 60% of the world's population are anaemic due to iron (Fe) deficiency and over 30% are zinc (Zn) deficiency, which is referred as hidden hunger[2]. In India 80% of the pregnant women, 52% of the non-pregnant women and 74% of the children (6–35 months) are suffering from Fe deficiency-induced anaemia (IDA)[5].

Fortifying such wheat's with high and essential micronutrients will be right step to eliminate "hidden hunger" and significant positive health outcomes for millions of people[6]. Micronutrient deficiencies in humans can be remedied through food diversification, mineral supplementation, food fortification and biofortification[7]. Biofortification is one of the most effective approaches to alleviate malnutrition[8]. Biofortification is the strategy of increasing

the content of bioavailable nutrients in the edible parts of staple food crops for better human nutrition[9]. However, staple crop based diets fall far short in providing the required amounts of micronutrients and heavy reliance on staple food is the root cause of micronutrient malnutrition[10]. The use of these biofortified cultivars is expected to mitigate micronutrient malnourishment in large populations especially in Africa[11]. Crop breeding, genetic manipulation, and application of mineral fertilizers are the bases of biofortification strategies and have enormous potential to address micronutrient malnourishment[12]. Biofortification is a proven strategy to combat micronutrient deficiency in large populations, particularly for those living in developing countries[6,13,14]. However, to make it more effective, efficient, and acceptable for people, better planning, implementation, monitoring, and evaluation of biofortification programs are needed to produce cost-effective and socially acceptable biofortified food crops[6,13,14].

Different sowing dates affect the growth of wheat mainly due to the effects of temperature and day length. Temperature and short winter growing season in central India are main reasons for low yield in wheat. High temperature increases the rate of grain filling but, the duration of grain filling is reduced considerably and grain weight is decreased[15,16]. Early sowing of wheat may escape from high temperature during grain filling but high temperature at the time of sowing affects germination and early vegetative growth. Therefore, identification of wheat genotypes suitable for specific sowing conditions is of great importance for achieving higher yield.

In this regard, understanding the relationship between grain yield, grain protein and grain micronutrient content under normal and late sown conditions will make a best use of heterosis breeding/hybrid wheat technology. Although wheat grain is known to have low Fe and Zn content, it seems to provide requisite micronutrient supplement to the deprived populace who solely depend on rice and who lack a balanced nutritive diet regularly[17,18]. Thus, to combat the micro- nutrient deficiencies among wheat eaters, efforts are to be made to enhance the grain micronutrient content (particularly Fe and Zn) along with sustainable crop yield potential [18,19,20]. The present investigation was executed to study the combining ability and heterosis in hybrid wheat parental lines and their derived hybrid crosses characterized for grain protein and grain Fe and Zn content under normal and late sown conditions.

		Male Parents									
		P1	P2	P3	P4	P5	P6	P7	P8	P9	P10
Female Parents	P1	GW 451	P1× P2	P1 × P3	P1 × P4	P1 × P5	P1 × P6	P1 × P7	P1 × P8	P1 × P9	P1 × P10
	P2		GW 496	P2 × P3	P2 × P4	P2 × P5	P2 × P6	P2 × P7	P2 × P8	P2 × P9	P2 × P10
	P3			LOK 1	P3 × P4	P3 × P5	P3 × P6	P3 × P7	P3 × P8	P3 × P9	P3 × P10
	P4				GW 322	P4 × P5	P4 × P6	P4 × P7	P4 × P8	P4 × P9	P4 × P10
	P5					GW 366	P5 × P6	P5 × P7	P5 × P8	P5 × P9	P5 × P10
	P6						HI 1544	P6 × P7	P6 × P8	P6 × P9	P6 × P10
	P7							GW 173	P7 × P8	P7 × P9	P7 × P10
	P8								GW 11	P8 × P9	P8 × P10
	P9									HD 2864	P9 × P10
	P10										USA 385
Standard check varieties	1.	MASC 6222 – TS									
	2.	HD 2932 – LS									

Table 1. Crossing pattern in 10 × 10 half diallel crosses in normal and late environments.

Environments	Sowing time	Season & Year
E_1	Normal	*Rabi* 2018-19
E_2	Late	

Table 2: Environments under study

Source	Df	Normal				Late			
		GYP	PC	Fe	Zn	GYP	PC	Fe	Zn
Replications	2	2.38	0.01	0.65	0.05	9.48	0.25	0.10	0.16
Genotypes	56	57.87**	1.67**	37.51**	4.88**	89.86**	0.56**	31.36**	5.92**
Parents	9	26.56**	2.33**	49.72**	4.51**	71.70**	0.58**	32.59**	1.46**
Hybrids	44	67.93**	0.78**	33.27**	4.86**	82.67**	0.51**	32.36**	4.38**
Parents v/s Hybrids	1	7.35	31.90**	11.77**	18.63**	485.7**	1.73**	7.99**	93.52**
Check v/s Hybrids	1	2.14	0.005	91.09**	0.07	262.76**	1.42**	33.14**	40.63**
Bet. Checks	1	3.68	5.73**	79.62**	0.03	58.28**	0.68*	0.54	1.48**
Error	112	3.35	0.01	0.65	0.14	4.19	0.13	0.89	0.21
Proportional contribution of Parents and Hybrids									
Replications	2	3.00	0.011	0.88	0.050	7.64	0.23	0.05	0.30
Parents	9	48.88**	6.56**	10.55**	3.51**	25.58**	0.25**	6.71**	2.59**
Hybrids	45	14.19**	0.51**	12.13**	1.32**	30.20**	0.16**	11.43**	1.70**
Genetic components									
σ^2 GCA		2.89**	0.50**	-0.13	0.18**	-0.39	0.01	-0.39	0.07
σ^2 SCA		13.09**	0.51**	11.93**	1.28**	28.80**	0.12**	11.13**	1.64**
σ^2_A		5.78	1.01	-0.26	0.37	-0.77	0.02	-0.79	0.15
σ^2_D		13.09	0.51	11.93	1.28	28.80	0.12	11.13	1.64
$(\sigma^2_A/\sigma^2_D)^{0.5}$		0.44	1.98	0.021	0.28	0.026	0.16	0.070	0.09

Table 3. Mean squares and genetic components for GYP,PC, Grain Fe and Zn densities in half diallel mating design in Normal and late conditions. df—Degrees of freedom; *P < 0.05;P < 0.01. GYP— Grain yield per plant; PC— protein content; Fe—Grain Fe content; Zn—Grain Zn content.**

Entries	Normal				Late			
	GYP	PC	Fe	Zn	GYP	PC	Fe	Zn
Parents								
GW 451 (P1)	15.0	11.5	22.2	11.5	20.3	10.4	24.8	14.9
GW 496 (P2)	14.2	11.2	28.7	11.1	21.1	10.5	26.3	14.0
LOK 1 (P3)	21.7	12.1	27.8	11.5	26.8	11.3	28.2	12.7
GW 322 (P4)	17.2	11.4	23.6	11.5	24.4	10.8	24.2	12.9
GW 366 (P5)	17.3	10.9	22.9	10.9	32.2	10.5	33.3	13.4
HI 1544 (P6)	23.1	11.9	25.4	13.9	24.7	11.3	27.3	12.5
GW 173 (P7)	14.5	13.4	28.7	12.9	19.0	11.8	31.3	13.3
GW 11 (P8)	16.6	12.9	31.4	11.8	16.7	11.3	28.8	13.7
HD 2864 (P9)	16.5	12.2	34.4	10.7	20.1	10.9	33.2	13.6
USA 385 (P10)	15.6	10.6	23.2	9.4	16.4	10.9	31.3	13.7
Mean	17.2	11.8	26.8	11.5	22.2	11.0	28.8	13.5
Min.	14.2	10.6	22.2	9.4	16.4	10.4	24.2	12.5
Max.	23.1	13.4	34.4	13.9	32.2	11.8	33.3	14.9

Hybrids								
GW 451 × GW 496 (H1)	20.0	10.7	25.9	11.2	16.1	11.5	27.3	10.4
GW 451 × LOK 1(H2)	29.8	10.4	21.7	9.8	20.2	11.9	29.6	10.5
GW 451 × GW 322(H3)	32.9	10.2	24.4	9.3	23.0	11.9	33.5	11.1
GW 451 × GW 366(H4)	15.8	10.2	24.2	8.8	16.4	11.6	30.1	11.0
GW 451 × HI 1544(H5)	20.4	10.0	29.1	9.5	18.1	12.3	32.2	10.9
GW 451 × GW 173(H6)	22.9	10.1	23.2	9.8	23.8	11.5	31.0	11.5
GW 451 × GW 11(H7)	17.2	9.9	27.1	9.0	13.6	11.2	31.2	10.7
GW 451 × HD 2864(H8)	16.4	10.3	30.0	10.5	32.1	11.6	35.5	11.2
GW 451 × USA 385(H9)	15.3	10.0	26.3	10.6	25.9	10.6	34.9	12.0
GW 496 × LOK 1(H10)	13.6	10.5	23.7	9.9	12.8	11.2	33.7	11.8
GW 496 × GW 322(H11)	12.5	11.3	27.2	10.2	21.6	11.0	26.3	12.1
GW 496 × GW 366(H12)	16.6	10.3	23.2	9.7	20.3	11.6	26.0	12.0
GW 496 × HI 1544(H13)	13.2	10.3	21.9	10.0	19.3	11.5	30.0	10.4
GW 496 × GW 173(H14)	12.9	10.2	41.5	14.1	13.4	11.2	26.9	10.8
GW 496 × GW 11(H15)	19.1	10.9	25.2	9.3	22.2	11.2	28.3	9.6
GW 496 × HD 2864(H16)	17.3	11.1	24.9	9.4	15.6	11.4	32.3	10.3
GW 496 × USA 385(H17)	16.4	10.9	27.8	10.7	16.0	11.2	26.9	10.9
LOK 1 × GW 322(H18)	21.8	11.2	26.2	10.2	13.8	11.4	26.9	9.5
LOK 1 × GW 366(H19)	21.3	9.9	27.2	10.3	13.2	11.1	25.9	10.0
LOK 1 × HI 1544(H20)	22.1	11.1	30.5	10.7	17.0	11.5	27.2	9.4
LOK 1 × GW 173(H21)	16.7	11.3	28.8	10.4	16.2	11.3	27.5	12.3
LOK 1 × GW 11(H22)	13.3	10.9	25.2	10.3	10.5	12.4	28.0	11.6
LOK 1 × HD 2864(H23)	12.4	11.5	25.6	11.0	23.3	11.6	26.1	11.1
LOK 1 × USA 385(H24)	14.6	11.0	25.1	10.0	35.4	10.6	26.7	12.3
GW 322 × GW 366(H25)	18.0	11.3	26.3	10.3	13.8	10.7	26.3	11.6
GW 322 × HI 1544(H26)	25.4	11.7	24.5	12.3	16.2	10.7	32.5	12.4
GW 322 × GW 173(H27)	18.7	10.8	25.2	10.2	9.4	11.3	29.6	13.6
GW 322 × GW 11(H28)	19.9	10.9	28.1	10.0	14.4	11.0	31.1	10.2
GW 322 × HD 2864(H29)	14.5	11.2	24.5	10.5	17.5	11.0	31.6	11.9
GW 322 × USA 385(H30)	14.5	11.6	27.8	10.6	20.3	11.1	29.1	11.6
GW 366 × HI 1544(H31)	16.6	11.3	25.0	10.5	12.1	11.4	32.3	13.0
GW 366 × GW 173(H32)	10.7	10.8	31.8	11.2	17.1	10.9	31.8	12.9
GW 366 × GW 11(H33)	13.9	10.9	23.1	12.2	17.4	10.9	26.3	11.4
GW 366 × HD 2864(H34)	17.1	11.0	22.8	10.2	23.3	11.1	22.3	12.5
GW 366 × USA 385(H35)	14.2	10.3	25.2	9.9	14.9	11.4	33.4	12.1
HI 1544 × GW 173(H36)	11.6	10.9	30.8	15.4	22.3	11.8	35.1	10.9
HI 1544 × GW 11(H37)	12.4	10.0	25.0	8.8	17.9	10.8	36.0	9.7
HI 1544 × HD 2864(H38)	15.8	10.5	28.1	11.2	17.3	11.1	23.0	10.7
HI 1544 × USA 385(H39)	15.7	10.2	25.7	11.1	14.5	11.0	28.0	10.9
GW 173 × GW 11(H40)	12.7	10.8	23.3	11.8	14.2	11.2	28.7	12.1
GW 173 × HD 2864(H41)	12.0	10.7	22.4	12.1	15.2	10.8	28.4	13.4
GW 173 × USA 385(H42)	11.1	10.7	25.8	12.4	10.0	11.0	29.4	14.3
GW 11 × HD 2864(H43)	14.9	9.9	25.3	11.7	15.2	11.1	32.1	12.4
GW 11 × USA 385(H44)	13.7	10.1	24.9	10.6	13.9	10.6	26.9	12.3
HD 2864 × USA 385(H45)	10.0	10.8	24.4	11.8	20.2	10.6	25.9	14.6
Mean	16.6	10.7	26.1	10.6	17.7	11.2	29.4	11.5
Min.	10.0	9.9	21.7	8.8	9.4	10.6	22.3	9.4

Max.	32.9	11.7	41.5	15.4	35.4	12.4	36.0	14.6
Standard checks								
MASC 6222 –TS	16.5	11.7	25.8	10.8	21.4	11.1	27.3	14.7
HD 2932 –LS	18.0	9.7	18.5	10.7	27.6	10.4	26.7	13.7
Mean	17.2	10.7	22.2	10.8	24.5	10.7	27.0	14.2
Grand Mean	16.7	10.9	26.1	10.8	18.7	11.2	29.2	11.9
S.Em. ±	**1.06**	**0.07**	**0.47**	**0.22**	**1.18**	**0.21**	**0.55**	**0.27**
C.D. (5%)	**2.96**	**0.18**	**1.30**	**0.61**	**3.31**	**0.59**	**1.52**	**0.74**
C.V.%	**10.9**	**1.03**	**3.09**	**3.51**	**10.9**	**3.27**	**3.23**	**3.84**

Table 4. Performance of F_1 progenies (Hybrids), parent lines and checks for GYP, PC, grain Fe and Zn concentration in Normal and Late condition. GYP— Grain yield per plant; PC—protein content; Fe—Grain Fe content; Zn—Grain Zn content.

Results

Performance of hybrids and parental lines. The performance of hybrids and parental lines is presented in Table 3. The results of ANOVA indicates that mean squares due to genotypic effects for the traits under study are significant ($P < 0.01$) in both the sowing conditions.

The per se performance of parental lines, hybrids and checks are presented in **Table** 4. The coefficient of variation (CV) values for the evaluated traits was < 10%, thereby indicating acceptable and effective experiment precision (Table 4).

The GYP in hybrids ranged 10.0 g (H45) to 32.9 g (H3) in E_1 and 9.4 g (H27) to 35.4 g (H24) in E_2. Standard check HD 2932 had highest GYP compared with MASC 6222 in both environments. The PC in hybrids it ranged from 9.9 % to 11.7 % in E_1 and 10.6% to 12.4% in E_2. In case of standard checks, MASC 6222 recorded higher protein content compared to HD 2932 in both environments.

The Fe content hybrids showed variation of 21.7 ppm (H2) to 41.5 ppm (H14) in E_1 & 22.3 ppm (H34) to 36.0 (H37) in E_2. In case of standard check, MASC 6222 recorded higher iron content compared to HD 2932 in both environments. Zn content in hybrids, H36 (15.4 ppm) and H14 (14.1 ppm) in E_1 and H45 (14.6 ppm) in E_2 recorded higher zinc content. Standard check MASC 6222 had highest zinc content compared with HD 2932 in both environments.

Heterosis. Two categories of heterosis, viz., standard heterosis (SH) and Better parent heterosis (BH) exhibited significant variation in both the sowing methods (Table 5 and 6). In the present study, several crosses exhibited conspicuous heterotic response over better parent

(heterobeltosis) and over standard check varieties (standard heterosis). *i.e*. MASC 6222 for normal sown and HD 2932 for late sown.

For GYP**,** four F_1 progenies recorded significant positive estimates for both environments. Among these, H3 and H6 were observed with higher BPH in normal condition. In addition, H6 had consistent significant positive estimates for BPH (Normal-52.69%; Late- 17.41%).H3 and H24 had highest positive SH for E_1 (99.41%) and E_2 (65.64%).

However, the higher percentage of crosses showed positive BPH in late than normal condition for PC. Although one F_1 progenies-H30 for normal and eight F_1 progenies for late showed significant positive BPH. Specially, late condition had high significant positive crosses SH than normal.

For Fe content, H5, H9 and H36 had consistent positive significant heterosis for BPH in both condition. H5, H7, H8, H28, H30, H32 and H36 found significant positive SH for both checks in all environments. Interestingly, H5 recorded significant consistent positive BPH & SH estimates for Fe content in both environments as well as GYP in normal (SH).

For Zn content, H45 had consistent significant positive BPH in both environments and also found significant positive SH over checks except SH_1 in E_1. In addition, H36 recorded highest significant positive estimates of SH for grain Zn in normal. Although nine F_1 progenies for normal and late condition showed significant positive SH.

Combining ability. The ANOVA for the diallel design was summarized in Table 3. The analysis of variance for combining ability in (E_1 and E_2) all the environments revealed that mean squares due to parents and hybrids were significant ($P< 0.01$) for all the characters.

Sr. No.	Hybrids	Normal				Late			
		Heterobeltosis							
		GYP	PC	Fe	Zn	GYP	PC	Fe	Zn
1	GW 451 × GW 496 (H1)	32.85**	-7.34**	-9.88**	-2.45	-24.00**	9.81**	3.87	-29.76**
2	GW 451 × LOK 1(H2)	37.45**	-14.53**	-22.03**	-15.01**	-24.54**	5.25*	4.96*	-29.60**
3	GW 451 × GW 322(H3)	**91.15****	-11.71**	3.31	-19.51**	-5.68	10.50**	**35.39****	-25.12**
4	GW 451 × GW 366(H4)	-8.59	-11.30**	5.79*	-23.24**	-49.01**	**10.76****	-9.64**	-26.15**
5	GW 451 × HI 1544(H5)	-11.51	-15.46**	14.50**	-31.64**	-26.65**	8.98**	18.08**	-26.69**
6	GW 451 × GW 173(H6)	52.69**	**-24.81****	-19.06**	-24.54**	17.41*	-2.63	-0.88	-22.63**
7	GW 451 × GW 11(H7)	3.17	-23.44**	-13.60**	-23.76**	-32.88**	-1.52	8.25**	-28.01**
8	GW 451 × HD 2864(H8)	-0.68	-15.58**	-12.98**	-8.47**	**58.49****	6.11*	7.08**	-24.89**
9	GW 451 × USA 385(H9)	-1.89	-13.44**	13.66**	-7.48**	27.52**	-2.70	11.71**	-19.29**
10	GW 496 × LOK 1(H10)	-37.27**	-13.54**	-17.47**	-14.17**	-52.27**	-0.48	19.43**	-15.61**
11	GW 496 × GW 322(H11)	-27.49**	-0.79	-5.31**	-11.82**	-11.41	2.01	-0.09	-13.76**
12	GW 496 × GW 366(H12)	-4.00	-8.80**	-19.35**	-12.62**	-36.77**	10.17**	-21.78**	-14.68**
13	GW 496 × HI 1544(H13)	-42.99**	-13.12**	-23.84**	-27.63**	-21.79**	1.82	10.20**	-25.75**
14	GW 496 × GW 173(H14)	-10.95	-24.25**	**44.63****	8.87**	-36.79**	-5.21*	-14.13**	-22.93**
15	GW 496 × GW 11(H15)	14.67	-15.83**	-19.56**	-21.34**	5.35	-1.51	-1.79	**-31.74****

16	GW 496 × HD 2864(H16)	4.68	-9.01**	-27.56**	-15.48**	-26.16**	4.22	-2.71	-26.63**
17	GW 496 × USA 385(H17)	5.53	-2.91**	-3.33	-3.96	-24.41**	2.66	-13.99**	-22.59**
18	LOK 1 × GW 322(H18)	0.27	-7.28**	-5.67**	-11.87**	-48.47**	1.08	-4.41	-26.51**
19	LOK 1 × GW 366(H19)	-1.71	-18.44**	-2.06	-10.46**	-59.10**	-1.00	-22.04**	-25.24**
20	LOK 1 × HI 1544(H20)	-4.17	-8.14**	9.80**	-22.90**	-36.61**	2.35	-3.41	-25.72**
21	LOK 1 × GW 173(H21)	-22.99**	-15.69**	0.23	-19.41**	-39.33**	-4.50	-12.05**	-9.94**
22	LOK 1 × GW 11(H22)	-38.60**	-15.36**	-19.50**	-12.93**	-60.74**	9.39**	-2.71	-15.55**
23	LOK 1 × HD 2864(H23)	-42.89**	-5.68**	-25.54**	-4.66	-12.99*	2.91	-21.34**	-18.29**
24	LOK 1 × USA 385(H24)	-32.64**	-9.57**	-9.57**	-13.19**	32.46**	-5.69*	-14.48**	-9.90**
25	GW 322 × GW 366(H25)	4.18	-0.11	11.41**	-11.09**	-57.22**	-0.71	-20.90**	-13.31**
26	GW 322 × HI 1544(H26)	9.98	-1.65**	-3.62	-11.58**	-34.29**	-4.69	19.40**	-3.96
27	GW 322 × GW 173(H27)	8.35	-19.29**	-12.12**	-21.28**	-61.59**	-4.54	-5.49**	-0.34
28	GW 322 × GW 11(H28)	15.73	-15.54**	-10.47**	-15.29**	-40.74**	-3.06	8.09**	-25.10**
29	GW 322 × HD 2864(H29)	-15.60	-8.50**	-28.73**	-8.70**	-28.04**	1.00	-4.87*	-12.44**
30	GW 322 × USA 385(H30)	-15.51	**2.50****	18.12**	-8.32**	-16.70**	1.05	-6.89**	-15.64**
31	GW 366 × HI 1544(H31)	-28.07**	-4.47**	-1.55	-24.32**	**-62.50****	1.30	-2.92	-2.84
32	GW 366 × GW 173(H32)	-38.37**	-19.33**	10.84**	-13.02**	-46.82**	-7.98**	-4.47*	-5.85*
33	GW 366 × GW 11(H33)	-19.40*	-16.07**	-26.46**	2.85	-46.02**	-4.09	-20.96**	-16.98**
34	GW 366 × HD 2864(H34)	-0.89	-10.08**	-33.85**	-6.72*	-27.69**	2.08	**-33.08****	-7.67**
35	GW 366 × USA 385(H35)	-17.64*	-5.37**	8.61**	-9.38**	-53.83**	4.02	0.25	-11.80**
36	HI 1544 × GW 173(H36)	**-49.62****	-18.57**	7.48**	**10.67****	-9.58	-0.27	12.05**	-20.54**
37	HI 1544 × GW 11(H37)	-46.17**	-22.67**	-20.32**	**-36.74****	-27.58**	-5.13*	25.08**	-29.22**
38	HI 1544 × HD 2864(H38)	-31.45**	-14.53**	-18.40**	-19.37**	-29.86**	-1.05	-30.59**	-21.39**
39	HI 1544 × USA 385(H39)	-32.22**	-13.84**	1.12	-19.65**	-41.14**	-2.29	-10.37**	-20.63**
40	GW 173 × GW 11(H40)	-23.45**	-19.36**	-25.76**	-9.10**	-25.38**	-4.74	-8.21**	-11.74**
41	GW 173 × HD 2864(H41)	-27.53**	-20.22**	**-34.91****	-6.11**	-24.29**	**-8.26****	-14.36**	-1.88
42	GW 173 × USA 385(H42)	-28.42**	-20.52**	-10.08**	-4.28	-47.23**	-7.07**	-6.02**	4.09
43	GW 11 × HD 2864(H43)	-10.50	-23.76**	-26.65**	-0.87	-24.56**	-1.77	-3.30	-9.23**
44	GW 11 × USA 385(H44)	-17.51*	-22.23**	-20.45**	-10.47**	-16.39	-6.16*	-13.82**	-10.46**
45	HD 2864 × USA 385(H45)	-39.67**	-11.83**	-29.22**	10.60**	0.55	-3.23	-21.91**	**6.64****
	Max.	91.15	2.50	44.63	10.67	58.49	10.76	35.39	6.64
	Min.	-49.62	-24.81	-34.91	-36.74	-62.50	-8.26	-33.08	-31.74
	S.E. ±	1.43	0.08	0.56	0.30	1.57	0.30	0.65	0.32
Number of significant crosses		24	43	38	38	39	15	34	39
Significant positive crosses		4	1	10	3	4	8	12	1
Significant negative crosses		20	42	28	35	35	7	22	38

Table 5. Estimates of heterobeltosis in individual environments for Grain yield per plant, protein content, iron content and zinc content.

*, ** Significant at 5 % and 1 % levels, respectively; Highest and lowest values are indicated by bold; HB = Heterobeltosis ; SH_1 = Standard heterosis over check variety MASC 6222 (TS) ; SH_2 = Standard heterosis over check variety HD 2932 (LS)

The estimate of σ^2_{GCA} and σ^2_{SCA} revealed that both additive and non-additive gene effects were involved for inheritance of GYP and Zn content in E_1. Whereas, the estimates of only σ^2_{SCA} were significant for all the characters in both environments, which suggested importance of only non-additive gene effect for inheritance of these characters.

The value of average degree of dominance was less than one for the characters GYP in (E_1), protein content in (E_2) and zinc content in (E_1), it revealed partial dominance behaviour of interacting alleles for these characters. Whereas, for the character iron content in (E_1 and E_2) and zinc content in (E_2), the value of average degree of dominance was close to zero or zero, it revealed absence of dominance for both the characters.

GCA effect of parents. No any parent that concurrently had positive GCA effects for all the studied traits in both environments (Table 7). For GYP & PC, P1 had significant positive GCA effect in both environments; Whereas, P7 had highest & significant positive effects for all environments except GYP in E_1. Hence, this parent is considered as a good general combiner. P10 & P4 was considered as poor general combiner as it possessed significant negative GCA effect in all the environments (Table 7). While for Zn content, the numbers of parents' depicted significant and positive GCA effect were 2 in E_1 and 4 in E_2. Here, parents with negative GCA effect for yield traits had positive GCA effect for micronutrient traits in both environments. Likewise, Parents maintain the same (positive or negative) in both environments.

SCA effect of crosses. Similar to the results noticed for GCA effects of parents, there was no hybrid cross that concurrently attained positive SCA effects for all of the studied traits (Table 8). For Fe and Zn content the percentage of crosses with positive SCA effects remain constant in both environments, though the individual crosses showed differential response. For GYP, the hybrid combinations H15 and H34 had showed positive significant SCA effect in both environments.

The hybrids (H3>H2>H6>H26) had showed significant ($P<0.01$) positive SCA effect for GYP in E_1. Moreover, H3 had highest positive SCA effect for GYP (10.73**) in E_1 and (2.71**) in E_1, conversely in PC (0.69**) & Fe content (3.78**), it had positive SCA effect in E_2. A few hybrid combinations with negative SCA effect in E_1 showed positive SCA effect in E_2.For instance, the hybrid combinations- H2, H16, H17, H19 & H26 for GYP; H24, H25 & H26 for PC; H14, H17, H19 & H20 for Fe content; H1, H9 & H14 for Zn content showed positive SCA effect in E_1, hence, these crosses were considered as good specific combiners and negative effect in E_2, therefore considered as poor specific combiners. For Fe & Zn content, H43 had significant positive SCA effect in both environments but in reverse order for GYP & PC. H14 had highest positive significant for Fe & Zn content in E_1. For iron content 16 each in E_1 & E_2 hybrids recorded significant positive SCA effects. For Zn content Out of 45 hybrids, the number of crosses depicted significant and positive SCA effects were 8 each in E_1 and E_2. For

Zn content, H36 had highest significant and positive SCA effects in E_1 (2.66**) as well as significant positive in both environments for Fe content. In addition, the variance due to SCA (σ^2_{SCA}) was greater than GCA (σ^2_{GCA}) for all studied (Table 3).

Correlation between phenotype, heterosis and combining ability. The association between phenotype, heterosis and combining ability effects for yield components, PC, Fe & Zn content in both environments was represented in supplementary table 2. GCA did not have any significant correlation with SCA effects, BPH, SH and phenotype for all traits in both environment.

Sr. No.	Hybrids	Normal								Late							
		Standard Heterosis 1				Standard Heterosis 2				Standard Heterosis 1				Standard Heterosis 2			
		GYP	PC	Fe	Zn	GYP	PC	Fe	Zn	GYP	PC	Fe	Zn	GYP	PC	Fe	Zn
1	GW 451 × GW 496 (H1)	20.94*	-8.95**	0.34	3.43	10.86	9.82**	39.93**	4.39	-25.00**	3.59	0.00	-28.98**	-41.85**	10.56**	2.25	-23.80**
2	GW 451 × LOK 1(H2)	80.87**	-11.43**	**-16.04****	-9.44**	65.80**	6.83**	**17.10****	-8.60**	-5.64	6.76*	8.33**	-28.82**	-26.84**	13.95**	10.76**	-23.63**
3	GW 451 × GW 322(H3)	**99.41****	-13.24**	-5.60**	-14.04**	**82.79****	4.65**	31.65**	-13.24**	7.39	7.35**	22.84**	-24.29**	-16.73**	14.58**	25.61**	-18.76**
4	GW 451 × GW 366(H4)	-4.20	-12.84**	-6.05**	-18.62**	-12.18	5.13**	31.02**	-17.86**	-23.33**	4.94	10.11**	-25.33**	-40.56**	12.01**	12.58**	-19.88**
5	GW 451 × HI 1544(H5)	23.89**	-14.38**	12.76**	-12.19**	13.57	3.28**	57.26**	-11.37**	-15.30*	10.60**	17.86**	-25.87**	-34.32**	18.04**	20.51**	-20.46**
6	GW 451 × GW 173(H6)	39.00**	-13.78**	-9.97**	-9.66**	27.42**	3.99**	25.55**	-8.82**	11.25	3.45	13.57**	-21.77**	-13.74*	10.42**	16.12**	-16.06**
7	GW 451 × GW 11(H7)	4.07	-15.36**	4.99*	-16.60**	-4.60	2.10**	46.42**	-15.83**	-36.40**	0.68	14.25**	-27.21**	-50.69**	7.46**	16.82**	-21.90**
8	GW 451 × HD 2864(H8)	-0.46	-11.74**	16.15**	-2.96	-8.76	6.45**	61.98**	-2.06	50.17**	4.38	30.12**	-24.06**	16.44**	11.41**	33.05**	-18.52**
9	GW 451 × USA 385(H9)	-7.54	-14.94**	2.13	-1.91	-15.24	2.60**	42.43**	-1.00	20.83**	-4.08	27.89**	-18.39**	-6.32	2.38	30.76**	-12.43**
10	GW 496 × LOK 1(H10)	-17.45*	-10.40**	-8.11**	-8.56**	-24.33**	8.07**	28.15**	-7.70**	-40.31**	0.95	23.26**	-19.46**	-53.72**	7.74**	26.03**	-13.58**
11	GW 496 × GW 322(H11)	-24.36**	-3.75**	5.43*	-5.83*	-30.66**	16.10**	47.04**	-4.95	0.87	-0.90	-3.81	-17.69**	-21.79**	5.77*	-1.65	-11.68**
12	GW 496 × GW 366(H12)	0.62	-12.37**	-10.21**	-10.06**	-7.76	5.70**	25.22**	-9.22**	-4.92	4.38	-4.69*	-18.57**	-26.28**	11.41**	-2.55	-12.63**
13	GW 496 × HI 1544(H13)	-20.18*	-12.01**	-15.21**	-7.04*	-26.84**	6.14**	18.25**	-6.17*	-9.69	3.33	10.00**	-29.14**	-29.98**	10.28**	12.47**	-23.97**
14	GW 496 × GW 173(H14)	-21.88*	-13.15**	**61.03****	30.34**	-28.39**	4.76**	**124.58****	31.56**	-37.62**	0.72	-1.61	-26.44**	-51.63**	7.50**	0.60	-21.07**
15	GW 496 × GW 11(H15)	15.67	-6.93**	-2.24	-13.96**	6.03	12.25**	36.33**	-13.15**	3.97	0.68	3.65	-34.85**	-19.39**	7.46**	5.98*	-30.10**
16	GW 496 × HD 2864(H16)	4.91	-4.88**	-3.31	-13.00**	-3.83	14.74**	34.84**	-12.19**	-27.13**	2.53	18.22**	-29.98**	-43.50**	9.44**	20.87**	-24.87**
17	GW 496 × USA 385(H17)	-0.55	-6.71**	7.64**	-1.14	-8.83	12.52**	50.11**	-0.22	-25.40**	1.21	-1.54	-26.12**	-42.16**	8.03**	0.67	-20.73**
18	LOK 1 × GW 322(H18)	31.95**	-3.91**	1.59	-5.89*	20.95**	15.90**	41.67**	-5.01	-35.56**	2.53	-1.34	-35.56**	-50.04**	9.43**	0.87	-30.85**
19	LOK 1 × GW 366(H19)	29.34**	-15.48**	5.47*	-4.60	18.56*	1.95*	47.09**	-3.71	-38.50**	0.42	-5.01*	-31.84**	-52.31**	7.18*	-2.87	-26.86**
20	LOK 1 × HI 1544(H20)	34.17**	-4.80**	18.24**	-0.96	22.99**	14.82**	64.90**	-0.03	-20.73**	3.87	-0.31	**-35.94****	-38.54**	10.86**	1.94	**-31.27****
21	LOK 1 × GW 173(H21)	1.33	-3.32**	11.49**	-3.52	-7.11	16.61**	55.48**	-2.62	-24.13**	1.47	0.77	-16.19**	-41.18**	8.30**	3.03	-10.07**
22	LOK 1 × GW 11(H22)	-19.20*	-6.42**	-2.17	-4.76	-25.94**	12.88**	36.43**	-3.87	-50.91**	**11.83****	2.69	-21.41**	-61.93**	**19.35****	4.99*	-15.67**
23	LOK 1 × HD 2864(H23)	-24.85**	-1.40*	-0.61	1.57	-31.11**	18.93**	38.61**	2.52	8.80	4.38	-4.42	-24.65**	-15.64**	11.41**	-2.27	-19.15**
24	LOK 1 × USA 385(H24)	-11.36	-6.29**	-2.62	-7.51	-18.75*	13.03**	35.81**	-6.65	**65.64****	-4.34	-2.10	-16.01**	**28.43****	2.10	0.10	-9.88**
25	GW 322 × GW 366(H25)	9.19	-3.09**	1.80	-5.06	0.09	16.89**	41.98**	-4.17	-35.67**	-3.54	-3.61	-20.95**	-50.12**	2.95	-1.45	-15.18**
26	GW 322 × HI 1544(H26)	53.99**	**-0.39**	-5.08*	13.58**	41.16**	**20.15****	32.37**	14.64**	-24.13**	-3.28	19.18**	-15.78**	-41.17**	3.23	21.86**	-9.64**
27	GW 322 × GW 173(H27)	13.03	-7.45**	-2.26	-5.76*	3.61	11.63**	36.31**	-4.88	**-56.26****	1.42	8.29**	-7.26**	**-66.09****	8.25**	10.72**	-0.49
28	GW 322 × GW 11(H28)	20.73*	-6.62**	8.80**	-7.35**	10.67	12.63**	51.73**	-6.48*	-32.52**	-0.90	14.08**	-30.29**	-47.68**	5.77*	16.64**	-25.21**

29	GW 322 × HD 2864(H29)	-11.95	-4.34**	-4.87*	-2.50	-19.29*	15.38**	32.67**	-1.59	-18.07*	-0.64	15.59**	-19.25**	-36.47**	6.05*	18.19**	-13.36**
30	GW 322 × USA 385(H30)	-11.86	-0.56	7.93**	-2.10	-19.20*	19.95**	50.52**	-1.18	-5.16	-0.37	6.59**	-21.36**	-26.46**	6.33*	8.99**	-15.62**
31	GW 366 × HI 1544(H31)	0.71	-3.24**	-3.04	-2.78	-7.68	16.71**	35.22**	-1.87	-43.61**	2.80	18.30**	-11.41**	-56.28**	9.72**	20.96**	-4.94*
32	GW 366 × GW 173(H32)	-35.41**	-7.50**	23.28**	4.14	-40.79**	11.57**	71.93**	5.11	-20.03**	-2.22	16.41**	-12.38**	-38.00**	4.36	19.03**	-5.99**
33	GW 366 × GW 11(H33)	-15.53	-7.20**	-10.63**	12.50**	-22.57**	11.93**	24.64**	13.55**	-18.83*	-1.96	-3.69	-22.74**	-37.07**	4.64	-1.52	-17.10**
34	GW 366 × HD 2864(H34)	3.87	-6.00**	-11.71**	-5.68*	-4.78	13.38**	23.13**	-4.80	8.73	0.42	**-18.45****	-14.85**	-15.70**	7.18*	**-16.62****	-8.64**
35	GW 366 × USA 385(H35)	-13.68	-11.91**	-2.40**	-8.37**	-20.87**	6.25**	36.11**	-7.52**	-30.58**	2.55	22.16**	-17.78**	-46.17**	9.46**	24.91**	-11.78**
36	HI 1544 × GW 173(H36)	-29.46**	-6.63**	19.55**	**42.16****	-35.34**	12.62**	66.72**	**43.49****	4.41	5.97*	28.39**	-26.05**	-19.04**	13.10**	31.27**	-20.66**
37	HI 1544 × GW 11(H37)	-24.63**	-14.50**	-3.17	**-18.73****	-30.91**	3.13**	35.04**	**-17.98****	-16.37*	-3.02	**32.01****	-34.13**	-35.16**	3.51	**34.98****	-29.32**
38	HI 1544 × HD 2864(H38)	-4.02	-10.65**	8.91**	3.58	-12.02	7.77**	51.89**	4.55	-19.00**	0.42	-15.65**	-27.51**	-37.20**	7.18*	-13.76**	-22.21**
39	HI 1544 × USA 385(H39)	-5.10	-12.74**	-0.42	3.21	-13.01	5.26**	38.87**	4.17	-32.03**	-0.84	2.61	-26.01**	-47.30**	5.83*	4.92*	-20.61**
40	GW 173 × GW 11(H40)	-22.78**	-7.53**	-9.78**	8.83**	-29.21**	11.53**	25.82**	9.84**	-33.85**	1.21	5.18*	-17.87**	-48.71**	8.03**	7.54**	-11.87**
41	GW 173 × HD 2864(H41)	-27.38**	-8.52**	-13.12**	12.41**	-33.43**	10.34**	21.17**	13.46**	-28.89**	-2.52	4.07	-8.68**	-44.87**	4.04	6.40**	-2.02
42	GW 173 × USA 385(H42)	-32.54**	-8.87**	0.02	14.60**	-38.16**	9.92**	39.49**	15.67**	-53.22**	-1.26	7.68**	-2.97	-63.73**	5.39	10.10**	4.11
43	GW 11 × HD 2864(H43)	-9.72	**-15.71****	-2.10	8.43**	-17.24*	**1.67***	36.53**	9.44**	-29.14**	0.42	17.51**	-15.53**	-45.06**	7.18*	20.15**	-9.37**
44	GW 11 × USA 385(H44)	-16.79	-14.01**	-3.32	-2.07	-23.72**	3.72**	34.82**	-1.15	-34.92**	-4.07	-1.34	-16.53**	-49.54**	2.38	0.87	-10.44**
45	HD 2864 × USA 385(H45)	**-39.54****	-7.82**	-5.52*	9.14**	**-44.58****	11.18**	31.76**	10.16**	-5.56	**-4.60**	-5.10*	**-0.59**	-26.78**	**1.82**	-2.97	**6.67****
	Max.	99.41	-0.39	61.03	42.16	82.79	20.15	124.58	43.49	65.64	11.83	32.01	-0.59	28.43	19.35	34.98	6.67
	Min.	-39.54	-15.71	-16.04	-18.73	-44.58	1.67	17.10	-17.98	-56.26	-4.60	-18.45	-35.94	-66.09	1.82	-16.62	-31.27
	S.E. ±	1.43	0.08	0.56	0.30	1.43	0.08	0.56	0.30	1.57	0.30	0.65	0.32	1.57	0.30	0.65	0.32
Number of significant crosses		22	43	29	27	28	45	45	23	32	5	29	42	44	34	30	42
Significant positive crosses		10	0	14	9	7	45	45	9	3	5	24	0	2	34	28	1
Significant negative crosses		12	43	15	18	21	0	0	14	29	0	5	43	42	0	2	41

Table 6. Estimates of standard heterosis in individual environments for grain yield per plant, protein content, iron content and zinc content.

Characters		GYP		PC		IC		ZC	
S. N.	Parents	E_1	E_2	E_1	E_2	E_1	E_2	E_1	E_2
1	GW 451 (P1)	**3.06****	**2.17****	**-0.42****	0.16**	-1.05**	**1.03****	**-0.63****	-0.12
2	GW 496 (P2)	-1.17**	-0.35	-0.10**	-0.04	0.83**	-1.03**	-0.18*	-0.34**
3	LOK 1 (P3)	2.10**	1.02**	0.20**	**0.20****	0.07	**-1.20****	-0.28**	-0.55**
4	GW 322 (P4)	2.39**	-0.41	0.27**	-0.12*	-0.62**	-0.59**	-0.20**	-0.05
5	GW 366 (P5)	-0.42	0.75*	-0.16**	-0.11	**-1.19****	-0.13	-0.33**	0.23**
6	HI 1544 (P6)	1.29**	0.05	0.01	0.13*	0.21	0.70**	0.70**	**-0.61****
7	GW 173 (P7)	-2.14**	-2.01**	**0.29****	0.11	**1.79****	0.70**	**1.19****	**0.66****
8	GW 11 (P8)	-1.12**	**-2.59****	0.04*	0.01	0.08	0.33*	-0.14*	-0.27**
9	HD 2864 (P9)	-1.70**	1.35**	0.14**	-0.07	0.67**	0.09	0.07	0.39**
10	USA 385 (P10)	**-2.28****	0.02	-0.25**	**-0.26****	-0.78**	0.11	-0.21**	0.65**
Range	**Min.**	-2.28	-2.59	-0.42	-0.26	-1.19	-1.20	-0.63	-0.61
	Max.	3.06	2.17	0.29	0.20	1.79	1.03	1.19	0.66
S.E. (gi) ±		0.29	0.32	0.02	0.06	0.12	0.15	0.06	0.07
Number of significant parents		9	6	9	5	7	7	9	8
Significant and positive parents		4	4	5	3	3	4	2	4
Significant and negative parents		5	2	4	2	4	3	7	4

Table 7. Estimates of general combining ability (GCA) effect of parents for Grain yield per plant, protein content, iron content and zinc content.

*, ** Significant at 5 % and 1 % levels, respectively; Highest and lowest values are indicated by bold.

Characters		GYP		PC		IC		ZC	
S. N.	Hybrids	E_1	E_2	E_1	E_2	E_1	E_2	E_1	E_2
1	GW 451 × GW 496 (H1)	1.33	-4.29**	0.29**	0.19	-0.15	-2.02**	1.18**	-0.96**
2	GW 451 × LOK 1(H2)	7.95**	-1.51	-0.30**	0.30	-3.61**	0.43	-0.11	-0.73**
3	GW 451 × GW 322(H3)	**10.73****	2.71*	-0.58**	0.69**	-0.23	3.78**	-0.69**	-0.55*
4	GW 451 × GW 366(H4)	-3.56**	-5.03**	-0.10*	0.41*	0.22	-0.15	-1.05**	-1.00**
5	GW 451 × HI 1544(H5)	-0.65	-2.61*	-0.44**	0.80**	3.67**	1.13*	-1.38**	-0.23
6	GW 451 × GW 173(H6)	5.29**	5.13**	-0.66**	0.03	-3.77**	-0.04	-1.61**	-0.90
7	GW 451 × GW 11(H7)	-1.50	-4.49**	-0.59**	-0.17	1.80**	0.52	-1.03**	-0.77**
8	GW 451 × HD 2864(H8)	-1.66	10.10**	-0.28**	0.31	4.09**	5.09**	0.24	-0.97**
9	GW 451 × USA 385(H9)	-2.26*	5.15**	-0.26**	-0.44*	1.93**	4.46**	0.63**	-0.39
10	GW 496 × LOK 1(H10)	-4.04**	-6.41**	-0.50**	-0.15	-3.45**	**6.56****	-0.47*	0.87**
11	GW 496 × GW 322(H11)	**-5.46****	3.83**	0.21**	-0.03	0.74	-1.44**	-0.26	0.64**
12	GW 496 × GW 366(H12)	1.47	1.43	-0.37**	0.54**	-2.73**	-2.13**	-0.58**	0.22
13	GW 496 × HI 1544(H13)	-3.68**	1.11	-0.49**	0.19	-5.42**	1.04**	-1.28**	-0.49*
14	GW 496 × GW 173(H14)	-0.53	-2.80*	-0.91**	-0.08	**12.67****	-2.13**	2.26**	-1.37**
15	GW 496 × GW 11(H15)	4.65**	6.67**	0.07	0.02	-1.95**	-0.32	-1.19**	-1.68**
16	GW 496 × HD 2864(H16)	3.46**	-3.93**	0.20**	0.29	-2.81**	3.90**	-1.30**	-1.62**
17	GW 496 × USA 385(H17)	3.13**	-2.22*	0.38**	0.33	1.47**	-1.51**	0.26	-1.31**
18	LOK 1 × GW 322(H18)	0.56	-5.33**	-0.11*	0.11	0.51	-0.59	-0.17	**-1.78****
19	LOK 1 × GW 366(H19)	2.93**	-7.12**	-1.03**	-0.14	2.08**	-2.04**	0.11	-1.52**
20	LOK 1 × HI 1544(H20)	2.02*	-2.62*	0.06	0.01	3.97**	-1.60**	-0.53**	-1.28**
21	LOK 1 × GW 173(H21)	0.03	-1.28	-0.06	-0.24	0.65	-1.30*	-1.30**	0.35
22	LOK 1 × GW 11(H22)	-4.38**	-6.44**	-0.17**	**1.02****	-1.17**	-0.40	-0.10	0.51*
23	LOK 1 × HD 2864(H23)	-4.72**	2.40*	0.31**	0.27	-1.35**	-2.10**	0.37	-0.63**
24	LOK 1 × USA 385(H24)	-1.92*	**15.89****	0.13**	-0.52**	-0.42	-1.49**	-0.33	0.38
25	GW 322 × GW 366(H25)	-0.68	-5.09**	0.35**	-0.25	1.82**	-2.27**	-0.02	-0.42

26	GW 322 × HI 1544(H26)	5.00**	-1.91	0.51**	-0.46**	-1.36**	3.11**	0.96**	1.19**
27	GW 322 × GW 173(H27)	1.68	-6.73**	-0.61**	0.08	-2.21**	0.14	-1.62**	1.17**
28	GW 322 × GW 11(H28)	1.93*	-1.07	-0.26**	-0.07	2.35**	2.10**	-0.46*	-1.29**
29	GW 322 × HD 2864(H29)	-2.88**	-1.92	-0.10*	0.03	-1.76**	2.75**	-0.15	-0.33
30	GW 322 × USA 385(H30)	-2.29*	2.17*	**0.73****	0.25	3.00**	0.27	0.17	-0.90**
31	GW 366 × HI 1544(H31)	-0.98	**-7.25****	0.60**	0.20	-0.27	2.41**	-0.67**	1.54**
32	GW 366 × GW 173(H32)	-3.51**	-0.14	-0.18**	-0.34	4.95**	1.90**	-0.42*	0.13
33	GW 366 × GW 11(H33)	-1.25	0.69	0.10*	-0.20	-2.09**	-3.21**	1.81**	-0.47*
34	GW 366 × HD 2864(H34)	2.54**	2.64*	0.13**	0.13	-2.96**	-7.00**	-0.36	0.03
35	GW 366 × USA 385(H35)	0.22	-4.44**	-0.17**	0.56**	0.89*	4.06**	-0.37	-0.66**
36	HI 1544 × GW 173(H36)	-4.24**	5.79**	-0.25**	0.33	2.58**	4.33**	**2.66**	-1.04**
37	HI 1544 × GW 11(H37)	-4.46**	1.92	-0.92**	**-0.56****	-1.57**	5.70**	**-2.59**	-1.30**
38	HI 1544 × HD 2864(H38)	-0.48	-2.59*	-0.57**	-0.10	0.96*	**-7.08****	-0.39	-0.98**
39	HI 1544 × USA 385(H39)	-0.08	-4.04**	-0.43**	-0.06	0.00	-2.11**	-0.15	-1.03**
40	GW 173 × GW 11(H40)	-0.72	0.24	-0.39**	-0.07	-4.85**	-1.63**	-0.11	-0.18
41	GW 173 × HD 2864(H41)	-0.90	-2.64*	-0.61**	-0.41*	**-6.30****	-1.69**	0.07	0.51*
42	GW 173 × USA 385(H42)	-1.18	-6.52**	-0.26**	-0.08	-1.46**	-0.72	0.59**	1.09**
43	GW 11 × HD 2864(H43)	1.00	-2.12	**-1.20****	0.02	1.75**	2.36**	0.97**	0.43
44	GW 11 × USA 385(H44)	0.40	-2.03	-0.60**	-0.29	-0.62	-2.81**	0.12	0.03
45	HD 2864 × USA 385(H45)	-2.77**	0.31	0.00	-0.28	-1.77**	-3.60**	1.12**	**1.71****
Range	**Min.**	-5.46	-7.25	-1.20	-0.56	-6.30	-7.08	-2.59	-1.78
	Max.	10.73	15.89	0.73	1.02	12.67	6.56	2.66	1.71
S.E. (sij) ±		0.96	1.09	0.05	0.20	0.41	0.51	0.20	0.22
Number of significant crosses		25	31	41	11	35	35	27	32
Significant and positive crosses		11	11	12	6	16	16	8	8
Significant and negative crosses		14	20	29	5	19	19	19	24

Table 8. Estimates of specific combining ability (SCA) effect of $F_{1's}$ for Grain yield per plant, protein content, iron content and zinc content.

*, ** Significant at 5 % and 1 % levels, respectively; Highest and lowest values are indicated by bold

Discussion

Wheat is an important and most widely cultivated food crop in the world. This crop played a central role in combating hunger and improving the global food security[16]. Wheat is ranked second in total cereal production behind corn, with rice being the third[21]. The grains of this plant provide about 20% of all calories and proteins consumed by people on the globe[22]. In recent years, demand for wheat has significantly increased as a result of the global population growth, and thus wheat production has a strategic role in food security and the world economy. As a result, horizontal expansion of wheat production has arisen in recent years by moving wheat into nontraditional areas formerly considered unacceptable for production. However, the global warming introduced various abiotic stresses such as drought, temperature extremes, and salinity that adversely affect the yield and grains quality of wheat[23].

The intergovernmental panel on climatic change has projected the temperature increase by the end of this century will likely to be in the range 1.8 to 4.0°C. Global climatic change will affect agriculture through their direct and indirect effects on crops, soils,

livestock and pests[24]. This will lead to heat stress at different growth stages of various crops, which can reduce crop duration, increase crop respiration rates, and alter photosynthetic partitioning to economic products[25,26]. Thus need to take some remedial measures like development of hybrids, high stress tolerance and use of conventional and non-conventional approaches. Different sowing dates affect the growth of wheat mainly due to the effects of temperature and day length. Temperature and short winter growing season in central India are main reasons for low yield in wheat. High temperature increases the rate of grain filling but, the duration of grain filling is reduced considerably and grain weight is decreased [27,28]. In this regard, understanding the relationship between grain yield, grain protein and grain micronutrient content under normal and late sown conditions will make a best use of heterosis breeding/hybrid wheat technology. To combat the micro- nutrient deficiencies among wheat eaters, efforts are to be made to enhance the grain micronutrient content (particularly Fe and Zn) along with sustainable crop yield potentials[29]. Biofortified varieties like HD 3298, WB 02, HPBW 01, Pusa Tejas (HI 8759) Pusa Ujala (HI 1605) HD 3171, HI 8777, MACS 4028, PBW 752, PBW 757, Karan Vandana (DBW 187), DBW 173, UAS 375, DDW 47, PBW 771, HI 8802, HI 8805, HD 3249, MACS 4058, HI 1633, DBW 303 and DDW 48 with high PC, Fe & Zn content were released for commercial cultivation in different countries[30]. Several studies are available on PC, Fe & Zn Bio-fortification in wheat. However, little progress in yield improvement and Bio-fortification has been made under both environments.

In the present study a total of 45 hybrids were developed by following half diallel mating design by using 10 parental genotypes under normal & late environments. The hybrids, parental genotypes and two standard checks, MASC 6222 – TS and HD 2932 – LS were evaluated for GYP, grain protein, Fe and Zn content under normal and late sown condition. The parents P9 & P5 were found to be good general combiners for all the studied traits in both environments. For Fe & Zn traits, hybrids H14 in normal & H37 for late. In our study, some hybrids performed better for GYP than their parents and check variety & exhibited the marked hybrid vigour in both the environments. The hybrids showed less mean value for protein content compared to parents. In the present study, several crosses exhibited conspicuous heterotic response over better parent (heterobeltosis) and over standard check varieties (standard heterosis). *i.e*. MASC 6222 for normal sown and HD 2932 for late sown. Among the two categories of heterosis, SH is the most appropriate than BPH. SH elucidated the acceptance yield advantage of hybrid varieties over the best checks. The hybrids in the

present study are observed with negative heterosis for all the studied traits in both environments.

For protein content, the magnitude of HB was low to high in negative and low in positive directions. While magnitude of SH was moderate in positive and low to high in negative directions. The findings were in accordance with the results of [31-33] for HB. The findings of SH were in accordance with[34]. For Fe content, the magnitude of HB was moderate in negative and low in positive directions. While magnitude of SH was moderate in both directions. The results contradicted the finding of[35]. For Zn content, the magnitude of HB and SH was high in negative and low in positive directions.

The GCA elucidates the average performance of a line in an array of hybrid crosses and it can be used to differentiate the parental lines. In our study the GCA effect of parental lines for protein content is varied with environment. The P1 had the highest significant positive GCA effect in E_2 (0.20). Another good general combiner was P7 in E_1 (0.29). P10 was considered as poor general combiner as it possessed significant negative GCA effect in all the environments. In our study, the GCA effect of parents (except P7) for grain Fe content is in contrasting manner with the both environments. In E_1, the GCA effect of GYP and grain Fe and Zn contents were observed in contrasting manner. Negative correlation and negative GCA effect was observed between grain yield and Fe & Zn content under E_1 and E_2 indicates the need for Fe and Zn content improvement of parental materials with grain yield. These parents, therefore, may be used in combination breeding for isolating desirable types in bread wheat.

The present findings also revealed high degree of correspondence between *per se* performance of parents and their GCA effect for majority of the traits studied, which indicated that *per se* performance can be used as a reliable criterion for selection of parents for hybridization. The success in crop improvement lies in isolating superior gene combinations in terms of the genotypes with high combing ability. The genotypes with good general combining ability can be further exploited in development of new variety.

SCA is mainly associated with non-additive gene action resulting from dominance, over dominance and epistatic effects[36-38]. Analysis of the hybrids revealed that no specific combination obtained significant positive SCA values for all of the estimated traits simultaneously**.** This result is in agreement with those from previous studies in rice[39,40] as well as in maize[41], bread wheat[42]. However, the crosses H3, H2 & H6 [significant ($P < 0.01$)

for GYP] and H43 [significant ($P < 0.01$) for grain Fe and Zn content] showed positive SCA values for all the traits in normal conditions. Conversely, in late condition—H3 (significant for SPY, PC and grain Fe content), H26 for grain Fe and Zn content showed positive SCA values. These results were in agreement with previous studies in rice[39,40], pearl millet[43,44] and maize[45,46] indicating that the grain micronutrient concentrations are mostly under additive genetic control.

The parents of cross combination with significant SCA effect for a particular trait, may not possess significant GCA effects. For instance, the cross H15 had significant positive SCA effect for yield traits in E1 and its parents had significant negative GCA effects. There were no significant SCA effects in all crosses for the estimated traits, suggesting that the values for these traits are within the limits of the parent's averages.

In Reverse case, parents with significant GCA effects did result the best hybrids with significant SCA like parents of H2, H3 and H26 showed positive GCA effects as well as hybrids were observed with positive SCA effects for GYP in normal condition. This observation could be attributed to different combination of dominant and recessive genes or alleles from one of the parents; it further substantiates the operation of non-additive gene action (additive × dominance, dominance × dominance and epistatic interactions). The hybrid H3 was observed with highest significant positive SCA effect for GYP in normal condition; GYP, PC and grain Fe content in late condition. For grain Fe and Zn content, the hybrid H43 had significant positive SCA effect in both the environments. Generally, the hybrids with high SCA effects are recommended for heterosis breeding. Thus, these crosses could be exploited in breeding programme to isolate desirable segregants in subsequent generations and hence, it would be worthwhile to use them for improvement in grain yield as well as micronutrients.

Thus, the GCA effects of parents are inadequate to predict the SCA effects of respective hybrids. Conversely, the significant correlation between SCA effects and heterosis was observed for all studied traits in both envrionments. In common, heterosis breeding targeted for particular traits on the basis of the GCA effects of parents can be taken as for the hybrid combinations.

The crosses which involved at least one good general combiner parent would produce transgressive segregants. However, for full exploitation of existing genetic variance in these crosses intermating of elite plants in early segregating generations would be profitable to

built up elite population of parents with high grain yield & micronutrients. Whereas, the cross combinations with high specific combining ability estimates can be exploited in heterosis breeding. The analysis of variance for combining ability to partitioning the total genetic variance into general combining ability representing additive type of gene action and specific combining ability as measure of non-additive gene action.

Positive correlation between grain Fe and Zn concentration was observed in parents as well as in the hybrids in irrigated method. Similar associations between these grain micronutrient concentrations have been reported previously in rice[47-49], maize[50-52], wheat [53-55], sorghum [56,57] pearl millet [58,59-61] and finger millet[62]. To the best of our knowledge, this is the first report on evaluation of wheat parental lines, hybrids under normal and late sown conditions for grain micronutrient content.

Conclusions

The study elucidated variation in GYP, protein content, Fe and Zn content under normal and late sown condition. Though many studies are not available in estimation of micronutrient content under normal and late sown condition, the present findings clearly indicate that the hybrids exhibited higher mean micronutrient content along with protein content under late sown condition than normal sown condition. The study paved way for further improvement of Fe and Zn content under late sown condition. However, breeding hybrids with high levels of Fe and Zn densities will require incorporating them in both parental lines, and application of genomics tools may significantly accelerate this process. Highly significant and high positive correlation between performance per se of parental line and their general combining ability (GCA) both for Fe and Zn densities showed that parental lines of potential hybrids with high GCA can be effectively selected based on their performance per se, thus enhancing the breeding efficiency. Lack of correlation of Fe and Zn densities with grain yield in inbred lines, but significant negative (although low) correlation in hybrids merits further investigation as these results have direct bearing on the efficiency of breeding high-yielding hybrids with high levels of Fe and Zn densities.

Materials and methods

Plant materials and field performance evaluation. The experimental material consisted of a total 55 entries comprising of 45 hybrids were developed by following diallel mating design[63,64,65] by using 10 parental genotypes by excluding reciprocal crosses (Table 1). The 10 parental genotypes, 45 hybrids and two standard checks, MASC 6222 – TS and HD 2932

– LS were evaluated at Regional Research Station, Anand Agricultural University, Anand, India (22° 35' N, 72° 55' E) during *Rabi* 2018-19 under normal and late sown conditions (Table 2). All the parental genotypes were provided by the Centre of Excellence for Research on Wheat, SDAU, Vijapur. The details of the parental genotypes, checks and hybrid crosses are given in Table 1.

The experimental design was laid out in randomized complete block design (RCBD) with three replications. Plot size consist of single row of 3.0 m length with 20 cm inter row spacing and 10 cm intra row spacing for normal (E_1), whenever, 18 × 10 cm for late ($E_{2)}$ conditions.

Environments study represented in Table 2. The soil of experimental site is sandy loam, alluvial in origin, deep, well drained and had fairly good moisture holding capacity. This is typically "Goradu" soil, prevalent in the "Charotar" region of Gujarat. This area has tropical and semi-arid climate. Weather data recorded at the Observatory, Department of Meteorology, B. A. College of Agriculture, A.A.U., Anand,

Grain Protein. This parameters estimated using Fourier Transform-Near Infrared Reflectance Spectroscopy (FT-NIRS) at the Centre of Excellence for Research on Wheat, Sardarkrushinagar Dantiwada Agricultural University, Vijapur. FT-NIRS is a rapid and non-destructive technique, which is being used largely in food and feed industry.

Grain Fe and Zn analysis. All the samples of wheat grain were determined for the micronutrients (Fe and Zn) using an inductively coupled plasma (ICP-OES), Model Optima 7000 DV, Perkin Elmer, USA and reliability of data was ensured by analyzing blanks at the Micronutrient Research Scheme (ICAR), Anand Agricultural University, Anand.

Statistical analysis. The data recorded on studied traits in parenys and hybrids were subjected to analysis of variance (ANOVA) using a general linear model as implemented in SPAR01. In addition, variances attributed to general combining ability (GCA) (σ^2 GCA) and specific combining ability (SCA) (σ^2 SCA) were calculated.

Estimation of heterosis and combining ability. For each hybrid cross combination, the better parent heterosis and standard heterosis were estimated.

REFERENCES

1. Patricia Giraldo, Elena Benavente, Francisco Manzano-Agugliaro & Estela Gimenez. Worldwide research trends on wheat and barley: A Bibliometric Comparative Analysis. *Agronomy* **9**, 352 (2019).
2. Shridhar Ragi. *et al.* Genetic and molecular characterisation of subtropically adapted low-phytate genotypes for utilisation in mineral biofortification of maize (Zea mays). *Crop & Pasture Science*. https ://doi.org/10.1071/CP21104. (2021)
3. Global Nutrition Report. Availble online at: https://www.globalnutritionreport.org. (2017).
4. Bouis, H.E. & Welch, R.M. Biofortification: a sustainable agricultural strategy for reducing micronutrient malnutrition in the global south. *Crop Sci.* **50**, S20–S32 (2010).
5. Sharma, D., Chhabra, R., Muthusamy, V., Zunjare, R.U. & Hossain, F. Molecular characterization of elite maize (*Zea mays* L.) inbreds using markers associated with iron and zinc transporter genes. *Genetic Resources and Crop Evolution* **68**, 1545–1556 (2021).
6. Bouis, H. E., & Saltzman, A. Improving nutrition through biofortification: a review of evidence from Harvest Plus, 2003 through 2016. Glob. Food Sec. **12**, 49–58 (2017).
7. Gupta, H.S., Hossain, F. & Muthusamy, V. Biofortification of maize: an Indian perspective. *Indian Journal of Genetics and Plant Breeding* **75**, 1–22 (2015).
8. Heck S. *et al.* Resilient agri-food systems for nutrition amidst COVID-19: evidence and lessons from food-based approaches to overcome micronutrient deficiency and rebuild livelihoods after crises. *Food Security* **12**, 823–830 (2020).
9. Prasanna, B.M. *et al.* Molecular breeding for nutritionally enriched maize: status and prospects. *Frontiers in Genetics* **10**, 1392 (2020).
10. Wakeel, b., Farroq, M., Bashir, K. & Ozturk, L. Micronutrient Malnutrition and Biofortification: Recent Advances and Future Perspectives. *Molecular and Genomic Perspectives in Crop Plants*, 225-243 (2018).
11. Sofield, I., Evans, L. T., Cook, M. G. & Wardlow, I. F. Factors influencing the rate and duration of grain filling in wheat. *Aust. J. Pl. Physiol.* **4**, 785-797 (1977).
12. Garg M, Sharma N, Sharma S, Kapoor P, Kumar A, Chunduri V and Arora P. Biofortified Crops Generated by Breeding, Agronomy, and Transgenic Approaches Are Improving Lives of Millions of People around the World. *Front. Nutr.* 5:12 (2018). doi: 10.3389/fnut.2018.00012.
13. Bouis, H. E., Saltzman, A., & Birol, E. Improving nutrition through biofortification. In Agriculture for improved nutrition: Seizing the momentum. Chapter 5. Fan, Shenggen; Yosef, Sivan; Pandya-Lorch, Rajul (Eds.). Wallingford, UK: International Food Policy Research Institute (IFPRI) and CABI (2019). http://ebrary.ifpri.org/cdm/ref/collection/p15738coll2/id/133096.
14. Birol, E. & Bouis, H. E. Leveraging biofortified crops and foods: R4D perspective. *In Encyclopedia of Food Security and Sustainability* **2**,181-188 (2019).
15. Wardlaw, I. F., Dawson, I. A. & Munibi, P. The tolerance of wheat to high temperatures during reproductive growth. II Grain development. *Aust. J. Agric. Res.* **40**,15-24 (1989).

16. Noha I. A. *et al*. Effect of environment and genotypes on the physicochemical quality of the grains of newly developed wheat inbred lines. *Food Science & Nutrition*, (2015). doi: 10.1002/fsn3.313.
17. Michael R La Frano, Fabiana F de Moura, Erick Boy, Bo Lönnerdal, and Betty J Burri. Bioavailability of iron, zinc, and provitamin A carotenoids in biofortified staple crops. *Nutrition Reviews* **72** (5), 289–307 (2014).
18. Welch RM and Graham RD. A new paradigm for world agriculture: meeting human needs-productive, sustainable, nutritious. *Field Crops Res.* **60**, 1–10 (1999).
19. Welch RM, Graham RD. Breeding for micronutrients in staple food crops from a human nutrition perspective. *J Exp Bot*. **55**, 353–64 (2004).
20. Nestel P, Bouis HE, Meenakshi JV. & Pfeiffer W. Biofortification of staple food crops. *J Nutr*. **136**, 1064–7 (2006).
21. FAO. 2020. FAO statistical yearbook 2020. World Food and Agriculture. Food and agriculture organization of the united nations, Rome, Italy.
22. Shiferaw, B. *et al*. Crops that feed the world 10. Past successes and future challenges to the role played by wheat in global food security. *Food Security* **5**, 291–317 (2013).
23. Huseynova, I. M. and Rustamova, S. M. Screening for drought stress tolerance in wheat genotypes using molecular markers. *Proc. ANAS* (*Biol. Sci.*) **65**, 132–139 (2010).
24. Abenezer Abebe Tefera. Review Article: Climate Change Impact on Farming Components. *International Journal of Research in Agricultural Sciences* **8**(4), 2348 – 3997 (2021).
25. Farooq, M., Wahid, A., Kobayashi, N., Fujita, D. & Basra, S. M. A. Plant drought stress: effects, mechanisms and management. *Agron. Sustain. Dev*. **29**, 185–212. (2009). doi: 10.1051/agro:2008021.
26. Praba, M. L., Cairns, J. E., Babu, R. C. & Lafitte, H. R. Identification of physiological traits underlying cultivar differences in drought tolerance in rice and wheat. *J. Agron. Crop Sci.* **195**, 30–46 (2009). doi: 10.1111/j.1439-037X.2008.00341.x.
27. Sofield, I., Evans, L. T., Cook, M. G. & Wardlow, I. F. Factors influencing the rate and duration of grain filling in wheat. *Aust. J. Pl. Physiol*. **4**, 785-797 (1977).
28. Wardlaw, I. F., Dawson, I. A. & Munibi, P. The tolerance of wheat to high temperatures during reproductive growth. II Grain development. *Aust. J. Agric. Res.* ***40***,15-24 (1989).
29. Yadava D.K., Hossain F. & Mohapatra T.. Nutritional security through crop biofortification in India: Status & future prospects. *Indian J. Medical Research* **148**, 621-631 (2018).
30. Yadava D.K., Choudhury P.R., Hossain F., Kumar D. & Mohapatra T. Biofortified Varieties: Sustainable Way to Alleviate Malnutrition (Third Edition). Indian Council of Agricultural Research, New Delhi. 84p (2020).
31. Kumar, R. Genetic architecture of seed yield and quality parameters in bread wheat (*Triticum aestivum* L.) Over Environments" Ph.D. thesis submitted to Anand Agricultural University, Anand (2012).

32. Desale, C. S. & Mehta, D. R. Heterosis and combining ability analysis for grain yield and quality traits in bread wheat (*Triticum aestivum* L.). *Electronic Journal of Plant Breeding* **4** (3), 1205-1213 (2013).
33. Ekhlaque, A., Kamar, A. & Jaiswal, J. P. Identifying heterotic combinations for yield and quality traits in bread wheat (*Triticum aestivum* L.). *Electronic Journal of Plant Breeding* **7** (2), 352-361 (2016).
34. Kumar, A., Razdan, AK, Sharma, V., Kumar, N. & Kumar, D. Study of heterosis and inbreeding depression for economic and biochemical traits in bread wheat (*Triticum aestivum* L.). *Journal of Pharmacognosy and Phytochemistry* **7** (4), 558-564 (2018).
35. Younas, A., Ahmad, H., Kashif, M., Ahmed, N. & Farooq, M. Combining ability and heterosis for grain iron biofortification in bread wheat. *J Sci Food Agric*. **100**, 1570–1576 (2019).
36. Sprague, G. F. & Tatum, L. A. General vs. specific combining ability in single crosses of corn 1. *Agron. J*. **34** (10), 923–932 (1942).
37. Yussouf Saleem, M., Mirza, I. & Haq, M. A. Combining ability analysis for yield and related traits in basmati rice (*Oryza sativa* L.). *Pak. J. Bot*. **42**, 1 (2010).
38. Griffing, B. Concept of General and Specific Combining Ability in Relation to Diallel Crossing Systems. *Aust. J. Biol. Sci*. **9**, 463 (1956).
39. Gramaje, L. V. *et al.* Heterosis and combining ability analysis in CMS hybrid rice. *Euphytica* **216**, 1 (2020)
40. Tiwari, D. K., Pandey, P., Giri, S. P. & Dwivedi, J. L. Heterosis studies for yield and its components in rice Hybrids using CMS system. *Asian J. Plant Sci*. **10**, 29–42 (2011).
41. Kahriman, F., Egesel, C. Ö., Orhun, G. E., Alaca, B. & Avci, F. Comparison of graphical analyses for maize genetic experiments: Application of biplots and polar plot to line × tester design. *Chil. J. Agric. Res.* **76**, 285–293 (2016).
42. Fellahi, Z. E. A., Hannachi, A., Bouzerzour, H. & Boutekrabt, A. Line × tester mating design analysis for grain yield and yield related traits in bread wheat (*Triticum aestivum* L.). *Int. J. Agron.* **2013**, 1–9 (2013).
43. Velu, G., Rai, K. N., Muralidharan, V., Longvah, T. & Crossa, J. Gene effects and heterosis for grain iron and zinc density in pearl millet (*Pennisetum glaucum* (L.) R. Br). *Euphytica* **180**, 251–259 (2011).
44. Govindaraj, M. *et al.* Combining ability and heterosis for grain iron and zinc densities in pearl millet. *Crop Sci*. **53**, 507–517 (2013).
45. Long, J. K., Bänziger, M. & Smith, M. E. Diallel analysis of grain iron and zinc density in Southern African-adapted maize inbreds. *Crop Sci*. **44**, 2019–2026 (2004).
46. Chen, F., Chun, L., Song, J. & Mi, G. Heterosis and genetic analysis of iron concentration in grains and leaves of maize. *Plant Breed*. **126**, 107–109 (2007).
47. Gramaje, L. V. *et al.* Heterosis and combining ability analysis in CMS hybrid rice. *Euphytica* **216**, 1 (2020).
48. Stangoulis, J. C. R., Huynh, B. L., Welch, R. M., Choi, E. Y. & Graham, R. D. Quantitative trait loci for phytate in rice grain and their relationship with grain micronutrient content. *Euphytica* **154**, 289–294 (2007).

49. Anandan, A., Rajiv, G., Eswaran, R. & Prakash, M. Genotypic variation and relationships between quality traits and trace elements in traditional and improved rice (*Oryza sativa* L.) genotypes. *J. Food Sci*. **76**, 1 (2011).
50. Arnold, J. M., Bauman, L. F. & Aycock, H. S. Interrelations among protein, lysine, oil, certain mineral element concentrations, and physical kernel characteristics in two maize populations. *Crop Sci*. **17**, 421–425 (1977).
51. Oikeh, S. O., Menkir, A., Maziya-Dixon, B., Welch, R. & Glahn, R. P. Assessment of concentrations of iron and zinc and bioavail- able iron in grains of early-maturing tropical maize varieties. *J. Agric. Food Chem*. **51**, 3688–3694 (2003).
52. Oikeh, S. O. *et al.* Environmental stability of iron and zinc concentrations in grain of elite early-maturing tropical maize genotypes grown under field conditions. *J. Agric. Sci.* 142, 543–551 (2004).
53. Garvin, D. F., Welch, R. M. & Finley, J. W. Historical shifts in the seed mineral micronutrient concentration of US hard red winter wheat germplasm. *J. Sci. Food Agric.* **86**, 2213–2220 (2006).
54. Peleg, Z. *et al.* Quantitative trait loci conferring grain mineral nutrient concentrations in durum wheat × wild emmer wheat RIL population. Theor. *Appl. Genet*. **119**, 353–369 (2009).
55. Velu, G., Ortiz-Monasterio, I., Singh, R. P. & Payne, T. Variation for grain micronutrients concentration in wheat core-collection accessions of diverse origin. *Asian J. Crop Sci*. **3**, 43–48 (2011).
56. Kumar, A. A., Reddy, B. V. S., Sahrawat, K. L. & Ramaiah, B. Combating micronutrient malnutrition: identification of commercial sorghum cultivars with high grain iron and zinc. *SAT eJournal* **8**, 5 (2010).
57. Ashok Kumar, A., Reddy, B. V. S., Ramaiah, B., Sahrawat, K. L. & Pfeiffer, W. H. Gene effects and heterosis for grain iron and zinc concentration in sorghum [*Sorghum bicolor* (L.) Moench]. *F. Crop. Res*. **146**, 86–95 (2013).
58. Govindaraj, M. *et al.* Combining ability and heterosis for grain iron and zinc densities in pearl millet. *Crop Sci*. **53**, 507–517 (2013).
59. Velu, G., Rai, K., Sahrawat, K. & Sumalini, K. Variability for grain iron and zinc contents in pearl millet hybrids. *J. SAT Agric. Res*. **6**, 4 (2008).
60. Rai, K. N., Govindaraj, M. & Rao, A. S. Genetic enhancement of grain iron and zinc content in pearl millet. *Qual. Assur. Saf. Crop. Foods* **4**, 119–125 (2012).
61. Kanatti, A. *et al.* Grain iron and zinc density in pearl millet: combining ability, heterosis and association with grain yield and grain size. *Springerplus* **3**, 1–12 (2014).
62. Upadhyaya, H. D. *et al.* Genetic diversity for grain nutrients contents in a core collection of finger millet (*Eleusine coraca*na (L.) Gaertn.) germplasm. *F. Crop. Res*. **121**, 42–52 (2011).
63. Hayman, B. I. The theory and analysis of diallel crosses. *Genetics* **39**, 789-809 (1954).
64. Hayman, B. I. Interaction, heterosis and diallel crosses. *Genetics* **42**, 336-355 (1957).
65. Hayman, B. I. The theory and analysis of diallel crosses III. *Genetics* **45**, 155-172 (1960).