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Intra-population genetic variance for grain iron and zinc contents and agronomic traits in pearl millet

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ARTICLE INFO

Article history:
Received 29 July 2015
Received in revised form
9 November 2015
Accepted 27 November 2015
Available online 3 December 2015

Keywords:
Genetic variance
Iron
Micronutrient malnutrition
Pearl millet
Zinc

ABSTRACT

Crop biofortification is a sustainable approach for fighting micronutrient malnutrition in the world. The estimation of variance components in genetically broad-based populations provides information about their genetic architecture, allowing the design of an appropriate biofortification breeding method for cross-pollinated crops such as pearl millet. The objective of this study was to estimate intra-population genetic variance using self (S_1) and half-sib (HS) progenies in two populations, AIMP92901 and ICMR312. Field trials were evaluated in two contrasting seasons (2009 rainy and 2010 summer; otherwise called environments) in Alfisols at ICRISAT, Patancheru. Analyses of variance showed highly significant variation for S_1s and HS progenies, reflecting high within-population genetic variation for both micronutrients and other key traits. However, the HS showed narrow ranges and lower genetic variances than the S_1 for all of the traits. The micronutrients were highly positively correlated in S_1 (r = 0.77 to 0.86; $P < 0.01$) and HS (r = 0.74 to 0.77; $P < 0.01$) progenies of both populations, implying concurrent genetic improvement for both micronutrients. The genetic variance component was different among populations for Fe and Zn contents across environments, with AIMP92901 showing a greater proportion of dominance and ICMR312 greater additive variance for these micronutrients. The estimates of variance (additive and dominance) were specific for each population, given their dependence on the additive and dominance effects of the segregating loci, which also differ among populations. The possible causes for such differences were discussed. The results showed that the expression of these micronutrients in pearl millet shows largely additive variance, so that breeding high-iron hybrids will require incorporation of these micronutrient traits into both parental lines.

1. Introduction

Micronutrient malnutrition has emerged as a major health challenge, mostly to resource-poor families in the developing world. It is largely associated with reliance on a diet of cereals as a staple food. Currently, over 60% and 30% of the world's population are deficient in iron (Fe) and zinc (Zn), respectively [1]. Pearl millet [*Pennisetum glaucum* (L.) R. Br.] contains higher

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Peer review under responsibility of Crop Science Society of China and Institute of Crop Science, CAAS.

http://dx.doi.org/10.1016/j.cj.2015.11.002

(by 6–8 fold) levels of nutrients including Fe and Zn contents than rice and wheat and is a staple food for millions of people in Asia and Africa. Because it is a cross-pollinated crop, open-pollinated varieties (OPVs) and hybrids are the two cultivar options. The development of OPVs is the main research area in Africa, whereas development of hybrids is the primary focus in India, with OPV development as a second priority for dry areas receiving <400 annual rainfall. Intra-population improvement is pursued to support a hybrid–parent development program and such population is a reservoir of variation for several traits that will be tapped for future hybrid–parent breeding. Phenotypic variance (σ^2_P) of a population is the sum of genetic (σ^2_G) and environmental (σ^2_E) variances. The σ^2_G is made up of additive (σ^2_A), dominance ($\sigma^2_{D)}$, and epistatic components [2,3]. Progeny testing of half-sib (HS), full-sib (FS), or selfed (S_1) families is widely used for improving population performance per se [4–7]. HS progenies are produced by crossing a common female line with a set of male lines (often unknown), whereas in FS both male and female lines are different (mostly known). Progeny obtained by self-pollinating an individual in a population is known as S_1 progeny. It is reasonable to expect that S_1 progeny performance will reflect mainly additive genetic effects, while HS performance reflects more non-additive effects such as dominance or epistatic relationships between the parents [8].

Given that information on the genetic architecture of populations is necessary to the formulation of efficient breeding methods, it is essential to estimate the relative magnitude of additive and dominance variance in traits of concern to breeders. Selection within populations is advisable if gene action is mainly additive, whereas the presence of dominance or epistasis justifies the use of a hybrid program [9]. The importance of additive genetic variance in grain Zn has been reported for common bean [10] and that for grain weight has been reported for pearl millet [11–14]. The equal importance of additive and dominance components has been reported for grain yield and ear length and girth in pearl millet [15,16]. In pearl millet, negative estimates of dominance have been observed for days to flowering [12] and grain weight [14]. The results of earlier studies under the HarvestPlus project showed large variability for Fe (30–75 mg kg^{-1}) and Zn (25–65 mg kg^{-1}) in several mainstream breeding populations, including released open-pollinated varieties [17,18]. Genetic improvement of these populations for grain Fe and Zn contents, if grain yield and other agronomic traits are uncompromised, can make valuable contributions to the nutritional security of pearl millet farmers and consumers. Development of improved populations (composites) is a natural step in OPV development and also provides base materials for deriving potential progenies for hybrid parent breeding. Although there have been many estimates of the additive and dominance components of genetic variance for quantitative traits, estimates of these genetic parameters in broad-based populations have not been reported for micronutrients in pearl millet. This study was conducted to estimate additive and dominance genetic variances for both micronutrients and key agronomic traits using population progenies in two released OPVs.

2. Materials and methods

2.1. Experimental materials

Two OPV, AIMP92901 and ICMR312, were selected. Both populations are early-maturing and show large seed size with high variations for grain Fe and Zn contents. AIMP92901 was jointly developed by ICRISAT and Marathwada Agricultural University (MAU), National Agricultural Research Project (NARP) Station, Aurangabad, Maharashtra, by random mating of Bold-seeded Early Composite (BSEC) progenies and showed resistance to downy mildew [*Sclerospora graminicola* (Sacc.) Schroet.] in disease screening nurseries at ICRISAT. AIMP92901 was released in 2001 for cultivation in Peninsular India. ICMR312 was developed at ICRISAT by mass selection in BSEC with further progeny testing to improve its male fertility restoration ability and resistance to downy mildew. ICMR312 is a pollen parent of a topcross hybrid, ICMH312, that was developed at ICRISAT and released in 1993 for cultivation in Peninsular India.

2.2. Seed production and evaluation of population progenies

Both populations were sown in the 2009 summer season, in 20 rows at 4 m long, to produce selfed (S_1) and half-sib (HS) progenies. The HS seeds were produced by collecting bulk pollen from each population and sib mating within the population, whereas S_1 seeds were produced by selfing. Sixty S_1 and sixty HS from each population were sown in single rows of 2 m length with a spacing of 15 cm between plants and 75 cm between rows, during the 2009 rainy season. To eliminate field variation, S_1 and HS progenies of each population were randomized together in a randomized complete block design with two replications; thus, both S_1 and HS progenies experienced both low and high fertility in the experimental field. Agronomic practices were adopted to raise healthy crops free of moisture stress throughout crop season. The same trial (using remnant seed of the original S_1 and HS) was repeated for second-season evaluation during the 2010 summer season. Grain samples for 1000-grain weight (TGW) and grain Fe and Zn contents were harvested in both seasons from 5–8 self-pollinated main panicles per plot. Days to 50% flowering was recorded on a plot basis.

2.3. Sampling and micronutrient estimation

The selfed panicles were hand-harvested at or after physiological maturity (85–90 days after sowing) and sun-dried to <12% post-harvest grain moisture. The sun-dried panicles were threshed with a well-cleaned single head thresher (Wintersteiger-ID780ST4), and grains were manually separated from glumes, panicle chaff, and debris. Ten-gram grain samples were taken from the grain of each plot and transferred to new metal-free envelopes for grain Fe and Zn estimation. Care was taken at each step to avoid any contamination of the grains with dust particles or other extraneous matter. All the grain samples from both population progeny trials were subjected to grain Fe and Zn contents estimation and both micronutrients were expressed in mg kg^{-1}.

Fe and Zn were determined by the triacid mixture method [19] as described below. The grain samples were finely ground (<60 mesh) in a cyclone mill and oven-dried at 60 °C for 48 h before estimation. Ground and dried grain samples of 0.5 g were transferred to 125-ml conical flasks. Twelve ml of a mixture of nitric, sulfuric, and perchloric acids (9:2:1, v/v) was added to the flasks. The samples were digested at room temperature for 3 h followed by 2–3 h on a hot plate until the digest was clear and colorless. The flasks were allowed to cool and the solutions were diluted to an appropriate volume. These clear digests were used for Fe and Zn estimation using atomic absorption spectrophotometry in the central analytical laboratory at ICRISAT, Patancheru.

2.4. Statistical analyses

S_1 and HS progeny data were subjected to analysis of variance [20] using the GenStat version 12 statistical package [21] for individual seasons as well as across seasons (hereafter referred to as environments). For genetic variance estimates, additive and dominance genetic variances were estimated from the observed mean squares using the expected genetic variance following Hallauer et al. [22] and also as described earlier by Jan-orn et al. [23]. All variance estimates were performed under the assumption of no epistasis. σ^2_{HS} was calculated as 1/4 σ^2_A and σ^2_{S1} as σ^{2*}_A + 1/4 σ^2_D, where σ^{2*}_A is the distribution of genetic variance among and within lines estimated under selfing (S_1) when allelic frequency, $p = q = 0.5$ [22]. Where, p = frequency of the dominant allele in the population and q = frequency of the recessive allele in the population.

3. Results and discussion

3.1. Genetic variance and environmental interaction

Analyses of variance showed highly significant genotypic variance for grain Fe and Zn contents within and among populations in both environments, as the variances due to S_1s, HS, and S_1s versus HS (S_1s against HS) were significantly different (Table 1). Although genotype × environments (G × E) interaction was significant, the genetic variance was twice that due to G × E for all traits in both populations. The low σ^2_{ge}/σ^2_g ratio (<1) in both AIMP92901 and ICMR312 indicates the presence of low G × E interaction, accounting for 1/3 of total variation and suggesting that variation in the population was due largely to genetic factors with negligible effect of G × E interaction for these micronutrients. The values of σ^2_{ge} were only 0.5 for Fe and Zn contents and 0.6 and 0.4 respectively for 1000-grain weight (TGW) and days to 50% flowering in AIMP92901. Similarly, σ^2_{ge} was 0.7 for grain Fe, Zn, and TGW and 0.4 for days to 50% flowering in ICMR312. The low σ^2_{ge}/σ^2_g ratio further indicates a low contribution of environmental interaction to total phenotypic variation, meaning that broadly adapted genotypes may be identified.

High broad-sense heritability (h^2_{bs}) of S_1 progenies for grain Fe (72–86%) and Zn (66–84%) in the two populations in individual environments as well as across environments revealed that both Fe and Zn contents are highly heritable, suggesting that simple selection will be effective for improvement of both micronutrients (data not presented). In contrast, HS progenies showed moderate to high h^2_{bs} for Fe (39–64%) and Zn (42–75%) contents in individual environments and

Table 1 – Combined analysis of variance for Fe and Zn contents, 1000-grain weight (TGW), and days to 50% flowering in S_1 and half-sib progeny trials of AIMP92901 and ICMR312 across two environments.

Source of variation	*df*	Mean square							
		Fe (mg kg^{-1})		Zn (mg kg^{-1})		TGW (g)		Days to 50% flowering	
		AIMP92901	ICMR312	AIMP92901	ICMR312	AIMP92901	ICMR312	AIMP92901	ICMR312
Environments (E)	1	35,383.9**	76,197.2**	18,258.3**	28,330.0**	0.6	16.4**	49.4**	15.4**
Replications/E	2	100.3	148.4	43.2	150.8**	1.9	0.2	1.7	0.8
Genotypes (G)	119	314.1**	284.5**	152.2**	127.0**	6.7**	6.6**	15.7**	11.6**
S_1 progenies (S_1)	59	452.8**	364.1**	233.8**	148.4**	6.8**	7.3**	15.7**	13.1**
Half-sib progenies (HS)	59	132.7**	152.7**	64.7**	90.9**	4.0**	3.7**	8.4**	7.2**
S_1 vs HS	1	2838.2**	3363.9**	504.3**	991.9**	150.7**	140.4**	444.7**	185.0**
G × E	119	120.7**	140.0**	67.1**	62.7**	2.6**	3.0**	3.6**	3.1**
S_1 × E	59	181.5**	175.3**	92.1**	55.0**	2.9**	4.0**	4.7**	3.4**
HS × E	59	51.9	101.6**	41.0	71.1**	2.2**	1.9**	2.5**	2.9**
S_1 vs HS × E	1	588.3**	321.0*	134.6	29.2	7.6**	0.5	10.2**	0.5
Error	238	63.0	62.9	37.3	31.3	0.8	1.0	0.9	0.8
C.D. (5%)		11.1	11.1	8.5	7.8	1.3	1.4	1.3	1.2
CV (%)		14.9	14.5	12.2	11.8	7.7	8.0	2.1	1.9
σ^2_g		62.8	55.4	28.7	23.9	1.5	1.4	3.7	2.7
σ^2_p		78.5	71.1	38.1	31.7	1.7	1.7	3.9	2.9
σ^2_{ge}		28.8	38.5	14.9	15.7	0.9	1.0	1.4	1.2
σ^2_{ge}/σ^2_g		0.5	0.7	0.5	0.7	0.6	0.7	0.4	0.4

* Significant at $P \leq 0.05$.
** Significant at $P \leq 0.01$.

across environments. Similar findings have been reported for Fe and Zn contents in pearl millet [18,24,25], while moderate h^2_{bs} for Fe and Zn contents have been reported in common bean [10] and rice [26]. In the summer season, HS progenies showed lower h^2_{bs} than in the rainy season and across environments for both Fe (21%) and Zn (13–24%) contents. Such variable estimates of h^2_{bs} between environments have been reported, from 52% (summer) to 81% (rainy) for Fe content and from 44% (summer) to 70% (rainy) for Zn content [17]. Both S_1 and HS progenies showed high h^2_{bs} for days to 50% flowering (82–94%) and TGW (69–89%), indicating that these traits can be improved by deliberate selection and that the results are consistent with those of earlier studies in pearl millet [18,24]. Considering the large variability and high heritability together, genetic improvement for Fe and Zn contents will be effective in pearl millet. However, the breeding risk is that heritability estimates may differ between populations or its progenies. The reason for such deviation could be that (i) the soil environment is likely to affect micronutrient uptake and thereby alter heritability estimates, as observed in sweet potato [27]; (ii) h^2_{bs} is based on total genetic variance, which includes fixable (additive) and non-fixable (dominance and epistatic) variances and does not reliably indicate the magnitude of additive genetic variance. However, it could be the best indicator of genetic variance amenable to mass selection where highly heritable traits can be maintained by simple selection in the population.

3.2. S_1 and HS performance per se and interrelationship

The mean Fe among S_1 progenies ranged from 26.7 to 74.7 mg kg^{-1} in the rainy season, from 32.1 to 118.4 mg kg^{-1} in the summer season, and from 29.4 to 87.9 mg kg^{-1} across seasons in AIMP92901. In ICMR312 progenies, it ranged from 27.1 to 73.3 mg kg^{-1} in the rainy season, from 49.9 to 112.5 mg kg^{-1} in the summer season, and from 42.1 to 89.2 mg kg^{-1} across environments (Table 2). In HS progenies, Fe varied from 31.9 to 58.6 mg kg^{-1} in the rainy season, from 42.7 to 75.5 mg kg^{-1} in the summer season, and from 42.0 to 64.7 mg kg^{-1} across environments in AIMP92901, while in ICMR312 Fe varied from 29.5 to 74.5 mg kg^{-1} in the rainy season, from 42.4 to 81.2 mg kg^{-1} in the summer season, and from 39.8 to 71.2 mg kg^{-1} across environments. Similar patterns were observed for Zn content in the S_1s and HS progenies of the two populations. Thus, the performance per se of the two types of progenies shows that the Fe and Zn contents of S_1 were higher than those of HS progenies, indicating the importance of simple mass selection or progeny selection for improvement of Fe and Zn and key agronomic traits such as TGW and days to 50% flowering. As expected, HS progenies displayed a narrower range of variability for Fe and Zn contents than did S_1 progenies for Fe and Zn contents (Table 2), with similar results for TGW and days to 50% flowering in both populations. This finding was in agreement with an earlier report for pearl millet [13]. The correlation between Fe and Zn contents was highly significant and highly positive in both S_1s and HS progenies of two populations. For instance, the correlation coefficients in S_1s varied from $r = 0.77$ to 0.86 ($P < 0.01$) and from $r = 0.74$ to 0.77

Table 2 – Mean and range among S1 and half-sib progenies for Fe and Zn contents, 1000-grain weight (TGW) and days to 50% flowering in two populations across two environments.

Variance components	Fe (mg kg^{-1})			Zn (mg kg^{-1})			TGW (g)		Days to 50% flowering		
	Rainy 2009	Summer 2010	Combined	Rainy 2009	Summer 2010	Combined	Rainy 2009	Summer 2010	Combined	Rainy 2009	Summer 2010	Combined
AIMP92901												
S_1 mean	45.9	65.3	55.6	44.5	57.9	51.2	11.3	11.0	11.2	46.9	46.0	46.5
S_1 range	26.7–74.7	32.1–118.4	29.4–87.9	28.1–60.1	33.9–92.5	32–70.6	8.5–15.8	7.6–14	8.8–14.1	42–51	42–51	42–50
HS mean	43.3	58.2	50.7	43.5	54.8	49.2	12.2	12.4	12.3	44.7	44.4	44.5
HS range	31.9–58.6	42.7–75.5	42–64.7	31.7–54.9	42.8–64.3	41.7–59.4	8.9–16.4	9.9–14.7	9.4–14.9	41–49	41–49	41–47
ICMR312												
S_1 mean	43.83	70.66	57.24	41.06	56.76	48.91	12.02	11.58	11.80	48.23	48.66	48.45
S_1 range	27.1–73.3	49.9–112.5	42.1–89.2	29.1–61.9	44.4–77.5	36.8–69.7	8.5–17.4	8.6–15.3	9.4–16.2	41–53	45–54	43–53
HS mean	40.17	63.73	51.95	38.52	53.39	45.96	13.03	12.73	12.88	47.06	47.35	47.20
HS range	29.5–74.5	42.4–81.2	39.8–71.2	27.9–84.6	43.8–67.1	37.3–68.7	10.7–16.6	10.9–15.1	11.2–15.3	44–51	45–54	45–50

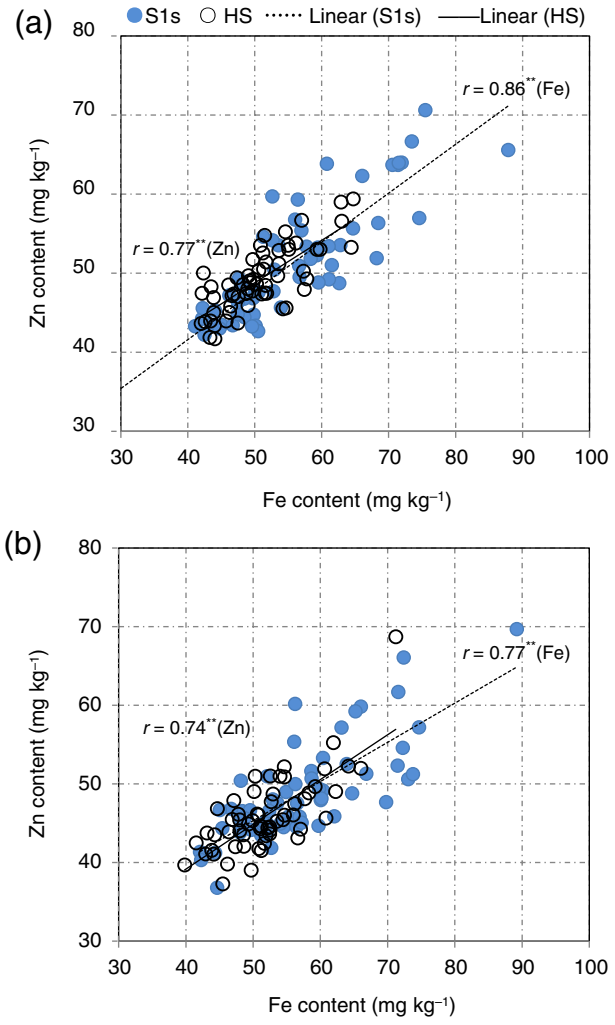

Fig. 1 – Association between iron and zinc contents in S_1 and HS progenies of the broad-based populations AIMP92901 (a) and ICMR312 (b), means of two environments.
** **Significant at P ≤ 0.01.**

(P < 0.01) in HS progenies across environments (Fig. 1). These two micronutrients were not correlated with TGW or days to 50% flowering. This result indicates that simultaneous improvement of both micronutrient in pearl millet without compromising seed size and maturity is feasible, in accord with recent findings in pearl millet [28,29].

3.3. *Intra-population genetic variance components*

The variance of S_1 progenies (σ^2_{S1}) exceeded that of HS (σ^2_{HS}) for all four traits (Table 3). This finding was in agreement with those reported for pearl millet [12]. Additive and dominance genetic variances were estimated assuming the absence of epistasis. The additive genetic variance was higher than the dominance variance for TGW and days to 50% flowering in both populations. The genetic variance component differed among populations for Fe and Zn contents across environments. For instance, population AIMP92901 showed a larger proportion of dominance than of additive variance for Fe and

Table 3 – Estimates of progeny (S1 and HS) variances and genetic components of variances for Fe and Zn contents, 1000-grain weight (TGW), and days to 50% flowering in two populations in individual and across two environments.

Variance component	Fe (mg kg^{-1})			Zn (mg kg^{-1})			TGW (g)			Days to 50% flowering		
	Rainy 2009	Summer 2010	Combined	Rainy 2009	Summer 2010	Combined	Rainy 2009	Summer 2010	Combined	Rainy 2009	Summer 2010	Combined
AIMP92901												
σ^2_{S1}	61.12	193.02	97.45	44.23	81.40	49.11	1.95	2.10	1.51	6.04	3.27	3.70
σ^2_{HS}	18.87	10.39	17.41	12.09	3.44	6.85	1.43	0.88	0.80	2.67	1.91	1.89
σ^2_A	75.50	41.56	69.66	48.36	13.75	27.41	5.71	3.54	3.21	10.67	7.64	7.57
σ^2_D	−57.51	605.84	111.16	−16.53	270.63	86.81	−15.06	−5.73	−6.81	−18.52	−17.47	−15.48
σ^2_D/σ^2_A	−0.76	14.58	1.60	−0.34	19.68	3.17	−2.64	−1.62	−2.12	−1.74	−2.29	−2.05
ICMR312												
σ^2_{S1}	55.88	150.96	75.31	29.57	40.86	29.28	2.73	1.92	1.57	4.46	3.02	3.09
σ^2_{HS}	37.31	26.94	22.45	44.66	5.06	14.91	1.43	0.39	0.67	2.11	2.14	1.60
σ^2_A	149.25	107.74	89.81	178.65	20.26	59.63	5.72	1.55	2.68	8.45	8.57	6.39
σ^2_D	−373.51	172.89	−57.98	−596.35	82.40	−121.39	−11.96	1.47	−4.47	−15.99	−22.22	−13.21
σ^2_D/σ^2_A	−2.50	1.60	−0.65	−3.34	4.07	−2.04	−2.09	0.95	−1.67	−1.89	−2.59	−2.07

σ^2_{S1} and σ^2_{HS} are variances of S_1 and half-sib progenies, respectively; σ^2_A and σ^2_D are additive and dominance genetic variances, respectively.
σ^2_A variance in S_1 progenies is valid only when allelic frequency $p = q = 0.5$.

Zn contents, in contrast to previous genetic findings [28–30]. However, ICMR312 showed greater σ^2_A for these two traits across environments (Table 3), in agreement with the earlier results of line × tester studies [28–30]. The dominance variances were negative for both Fe and Zn contents in ICMR312 and for TGW and days to 50% flowering in both populations. These results indicate the greater role of additive genetic variance for TGW and days to 50% flowering, whereas both additive and dominance genetic variances were important for Fe and Zn contents. A predominance of additive genetic variance suggests the importance of a population-improvement strategy such as mass selection, recurrent selection for general combining ability (GCA), or synthetic and composite breeding for improvement of these traits, whereas a predominance of dominance genetic variance indicates the importance of heterosis or recombination breeding and recurrent selection for specific combining ability (SCA). If both genetic variances (additive and dominance) play large roles in the expression of characters, population improvement by reciprocal recurrent selection is indicated. The significant role of additive genetic variance has been reported for grain Zn content inheritance in common bean [10] and for grain weight in pearl millet populations [11–13]. Equal importance of additive and dominance components has been reported for grain yield and ear length and girth in pearl millet populations [15,16]. In some cases of studies in pearl millet, negative estimates of dominance have been observed for days to 50% flowering and TGW [12,14].

In view of the expectations of variance components in the two types of progenies, it should be possible to draw some conclusions about the kinds of gene effects operating. The variances estimated from this study are based entirely on several genetic assumptions that are necessary for the adequate interpretation of the genetic composition of variance reported by various studies [22,23]. For instance, estimates of σ^2_A will be valid only when epistasis is absent in a population or when $p = q = 0.5$ (equilibrium population). The dominance variance components were negative for TGW and days to 50% flowering and in some cases for Fe and Zn contents. These negative estimates of dominance variance could arise from inadequate sampling [31,32]. The random errors in sampling could arise from the number of pollinators (males) used in half-sib progeny development in the present study, which is expected to be very small (10–20 plants, depending on flowering) and these male plants could have contained more dominance variance [23]. Another explanation for the negative dominance variance could be lack of random mating in constructing half-sib progenies. For instance, the flowering characteristics of each plant in a population could lead to assortative mating in the production of HS. Mating involving early-flowering (first anthesis) males could be restricted largely to early-flowering females and vice versa. This situation would lead to upward bias in estimates of additive variance and underestimate dominance variance [31]. The best solution in such a situation would be to assign these variances as zero and re-estimate other components [32]. In the present study, the negative estimates have been assumed due to either random errors in sampling (i.e., assortative mating) or inflate of self-seed set (reduction of seed set will elevate Fe content) thus such negative sign genetic components is assumed to be a zero, thus variable estimates of genetic variance might be due to incorrectness of some of the genetic assumptions (such as gene interaction) and use of self-pollinated seed. Across two environments, the relative importance of dominance (σ^2_D/σ^2_A) showed a high degree of dominance for Fe and Zn in AIMP92901, while Fe and Zn contents in ICMR312 and TGW and days to 50% flowering in both populations showed either high additive or negative estimates owing to the negative values of dominance variance.

4. Conclusion

The estimates of genetic components of variance (additive and dominance) reported in this study are specific for each population because they depend on the additive and dominance effects of segregating loci, which differ among populations. Also suggesting that use of open-pollinated grain sample for micronutrient analysis to avoid any seed set effect on these micronutrients. However, additive genetic variances were important for the expression of grain Fe and Zn contents, TGW, and days to 50% flowering. Thus, high-Fe and high-Zn OPVs can be developed by deliberate selection for Fe and Zn contents as a target trait, whereas breeding for a high-Fe/Zn hybrid would require incorporation of these micronutrients into both parental lines to achieve a higher degree of average heterosis for these micronutrients.

Acknowledgments

The research reported here forms part of the Ph.D. Dissertation of M. Govindaraj, Tamil Nadu Agricultural University, Coimbatore 641003, India. It was supported by a grant (HP No. 5203) from the HarvestPlus Challenge Program of the CGIAR.

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