academicJournals

Vol. 8(11), pp. 1001-1008, 28 March, 2013
DOI: 10.5897/AJAR12.2172
ISSN 1991-637X ©2013 Academic Journals
http://www.academicjournals.org/AJAR

African Journal of Agricultural Research

Full Length Research Paper

Genetic control of zinc and iron concentration in common bean seeds

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Accepted 18 March, 2013

The objective of this study was to obtain information regarding genetic control of zinc and iron levels in common bean seeds. For that purpose, four lines with high iron and zinc concentration and four with low concentration were crossed in a partial diallel design. Hybridizations were carried out in a greenhouse, as well as obtaining F_1, reciprocal F_1 and F_2 generations. The data obtained were submitted to analysis of variance for each generation. To verify the occurrence of maternal effects, the possible contrasts between parents and F_1 and reciprocal F_1 generations were tested for each cross. It was observed that an expressive part of the variation in zinc and iron concentrations among the lines used is due to the seed coat. In the case of zinc, the additive allelic interaction alone explained the variation. For iron, the occurrence of dominance is also important.

Key words: *Phaseolus vulgaris* L., maternal effect, combining ability, allelic interaction, nutritional quality.

INTRODUCTION

Micronutrient deficiency affects more than 3 billion people throughout the world (FAO, 2011). Among these deficient micronutrients, zinc and iron stand out. Zinc deficiency in the human body may cause delay in growth and in sexual maturity, hypogonadism, hypospermia, alopecia, skin rashes, slow healing of wounds, immunodeficiencies, behavioral disorders, night blindness and loss of appetite. That is because zinc exercises important structural, enzymatic and regulatory functions for live cells (Cozzolino, 2007). In general, 1.4% of deaths are attributed to a lack of zinc (WHO, 2011). Iron in human beings, for its part, is essential for preventing anemia and is active in many metabolic processes. Deficiency of this mineral in the human body is a serious public health problem in the world, affecting millions of people (Black, 2003). One and a half percent (1½%) of deaths occurring in the planet are attributed to iron deficiency (WHO, 2011). Foods that may overcome these nutritional deficiencies in the population are the subject of various studies (Akond et al., 2011; Blair et al., 2011; Zacharias et al., 2012). However, these foods, in addition to high nutritional quality must have good commercial and agronomic quality, besides being low cost. In this respect, one of the main options is common beans. This legume is the main nutritional component of the diet for more than 300 million people and has high nutritional and functional value (Beebe, 2010). However, Akond et al. (2011) drew attention to the fact that high concentration of phytic acid inhibit the availability of most minerals in common beans and should also be considered in improving the nutritional quality of food.

As genetic variability for the traits that provide nutritional quality to beans has been detected, especially for zinc and iron mineral concentration, it becomes possible to select lines with a high potential for participation in breeding programs for nutritional quality

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(Beebe et al., 2000; Bennink, 2010; Silva et al., 2012; Zacharias et al., 2012).

To begin a breeding program aiming to obtain cultivars with higher nutritional quality, it is important to have information on genetic control of the traits involved. In some occasions, studies were performed aiming to clarify the occurrence of maternal effect for zinc and iron concentrations in bean grains (Blair et al., 2009; Jost et al., 2009; Rosa et al., 2010). Nevertheless, in these studies, the number of parents used was small, which impedes generalization of the results.

In light of this, the purpose of the present study was to obtain information in regard to genetic control of zinc and iron concentrations in bean seeds.

MATERIALS AND METHODS

Based on previous assessment of the mineral composition in bean lines from the Germplasm Bank of the Universidade Federal de Lavras (UFLA) (Silva et al., 2010), four lines were selected that had high zinc and iron concentrations (P180, Linea 29, R1 and AN910523), and four lines with low concentrations (Paraná, Esal 543, BP28 and Esal 516). These lines were crossed following the partial diallel design in which one of the groups consisted of low concentration lines and the other group of high concentration lines.

Controlled hybridizations were carried out in a greenhouse located at the Biology Department of UFLA, as well as obtaining all the generations. The seeds of F_1 and reciprocal F_1 generations were obtained in the "wet season" 2009/2010. These seeds were sown in the winter of 2010 so as to obtain the F_2 generation. In this same crop season, so that seeds of the same age were obtained, the parents were also seeded for performance of crosses and, once more, obtaining of F_1 and reciprocal F_1 generations and seeds of the parents. For that reason, each parent was seeded in two pots with a capacity for 8 L of soil, with three seeds per pot for performance of the crosses and for obtaining the F_1 and reciprocal F_1 seeds. The F_1 seeds obtained in the previous crop season were also seeded, with two pots with three seeds per pot for each combination and left to self-pollinate for obtaining F_2 seeds.

In all the pots, fertilization with 22.4 g of the formula 8-28-16 of N, P_2O_5 and K_2O was used before seeding. Fifteen (15) days after seeding, cover fertilization was performed with ammonium sulfate and the quantity of fertilizer was the same for each pot (0.9 g). Irrigation was performed by sprinkling throughout the entire crop cycle.

Four samples from each parent and from each of the F_1 and reciprocal F_1 generations and eight replications for each F_2 generation were used for performance of chemical analyses of the minerals. The seeds were dried (65 to 70°C) for 48 h and the samples were ground in a micro cutting mill until obtaining particle size of less than 1 mm. They were then stored in small impermeable bags, duly sealed and labeled, and conserved in a cooler up to the time of performing the laboratory analyses. Analyses were performed in the Leaf Analysis Laboratory, located in the Chemistry Department/UFLA.

For analysis of the zinc and iron minerals, hot nitro perchloric digestion was performed with 0.5 g from each sample. At the end of digestion, the volume of the extract was completed to 15 ml with deionized water. In this digestion, there is the removal of the elements of the organic compounds of the sample or adsorbed to them. Analyses were performed by atomic absorption spectrophotometry using the apparatus model SpectrAA 110 (Varian INE), using the procedures described by Malavolta et al. (1997).

The data obtained were submitted to analysis of variance for each generation, considering the entirely randomized design with four replications for the parents and F_1 and reciprocal F_1 generations, and eight replications for the F_2 generation. To verify the occurrence of maternal effect, possible contrasts were tested among parents and F_1 and reciprocal F_1 generations for each cross. To identify the reciprocal crosses, a second number was used to identify the female parent, that is, F_{11} and F_{12}. Analyses were performed by means of the statistical program Statistical Analysis Systems (SAS) version 9.0 of Statistical Analysis Systems (2008). Using the mean data of the F_2 generation (seed), diallelic analysis was performed using method IV of Griffing (1956) through the model presented by Ferreira et al. (1992):

$$Y_{ij} = m + g_i + g_j + s_{ij} + e_{ij},$$

In which Y_{ij} is the mean of the population derived from crossing of the i-th line of group 1 (I = 1, 2, 3 and 4) with the j-th line of Group 2 (j = 1, 2, 3 and 4); m is the mean of the populations; g_i and g_j is the general combining ability (GCA) of the i-th and j-th line of Groups 1 and 2, respectively; s_{ij} is the specific combination ability between the i-th line of Group 1 and j-th line of Group 2; e_{ij} is the error associated with Y_{ij}.

RESULTS

Zinc concentration

Analysis of variance provided evidence that the precision in assessment the zinc concentration was high, with an accuracy estimate greater than 94%. Significant difference was observed ($P \leq 0.01$) for all the sources of variation, showing that there was variability among the populations obtained (Table 1). In decomposition of parent source of variation, significant difference was observed among the parents of Group 1, Group 2 and for the Group 1 versus Group 2 contrast.

The significance for the F_{11} versus F_{12} contrast indicates the possibility of occurrence of maternal effect for the trait. The mean of the F_{12} generation was significantly ($P = 0.0000$) greater than that of F_{11} and this was already expected since, in F_{12}, the parent used as female was that which had a high zinc concentration (Table 2).

It was observed that of the 16 F_{11} versus F_{12} contrasts, only 4 were not significant and, of these, 2 P_1 versus P_2 contrasts were also not significant (Table 3). The other two cases in which it was expected that the test would be significant, because the parents differed, this probably did not occur due to error Type 2. A similar result was obtained in the P_2 versus F_{12} contrasts. Thus, it may be inferred that the zinc concentration is concentrated mainly in the seed coat of the bean seeds.

Through diallelic analysis of the crosses performed, significant differences ($P \leq 0.01$) among the hybrids (Table 4) were detected. In the decomposition of the effects of crosses in GCA of Groups 1 and 2 and of the specific combining ability (SCA), a significant difference ($P \leq 0.01$) was found only for the source of variation GCA (Group 2). The GCA of Group 2 explained 85% of the variation obtained among the hybrids. In this condition, it

Table 1. Summary of analyses of variance of zinc and iron concentrations obtained in assessment of the eight parents, F_1's (F_{11}) and their reciprocals (F_{12}) and means of zinc and iron concentrations in mg kg^{-1} of dry matter.

SV	DF	Zinc		Iron	
		MS	Probability	MS	Probability
Populations	39	279.22	0.0000	3191.08	0.0000
Among parents	7	361.91	0.0000	1663.01	0.0000
Among parents Group 1	3	121.90	0.0060	164.20	0.4286
Among parents Group 2	3	213.80	0.0001	249.35	0.2376
Group 1 versus Group 2	1	1526.30	0.0000	10400.45	0.0000
F_{11}	15	76.26	0.0017	549.96	0.0002
F_{12}	15	75.20	0.0020	1781.23	0.0000
F_{11} versus F_{12}	1	5888.84	0.0000	75330.21	0.0000
Parents versus hybrids	1	195.59	0.0103	2513.02	0.0002
Error	120	28.77		174.96	
Mean populations		49.60		124.35	
$\hat{r}_{\hat{g}g}$ (%)		94.71		97.22	

DF, Degree of freedom; MS, mean square; SV, source of variation.

Table 2. Means of zinc and iron concentrations in mg kg^{-1} of dry matter of the parents and of the hybrids F_1's (F_{11}) and reciprocals (F_{12}).

Parents/hybrids	Zinc	Iron
Paraná	41.4	102.4
Esal 543	47.2	104.8
BP-28	39.3	90.9
Esal 516	33.9	95.4
Mean - Parents - Group 1	40.5	98.4
P-180	53.9	126.8
Linea 29	46.7	131.2
R-1	64.2	145.3
AN 910523	52.2	134.3
Mean - Parents - Group 2	54.3	134.5
Hybrids	50.2	126.3
F_{11}	43.4	102.1
F_{12}	56.9	150.6

may be inferred that in control of the trait, the additive allelic interaction predominates.

As the parents versus hybrids contrast was significant (P ≤ 0.01) (Table 1), it was expected that the SCA would also be. Comparing the mean of the 8 parents and the mean of the 16 hybrids, it is observed that the hybrid vigor was 5.9%, a value that in the context of analysis of variance is different from zero. Perhaps for this reason, coinciding results have not been obtained in the two cases. The most promising hybrid combination was from the R1 line with the BP-28 (Table 5). This combination obtained a mean zinc concentration of 50.18 mg kg^{-1} of dry matter, being the highest among the crosses (Table 6). Thus, this population is most recommended for selection of lines with a high zinc level. This population furthermore presents the advantage of the two parents having "carioca" type grains, which is preferred by the consumer, which should facilitate the selection.

Iron concentration

The precision in assessment of the iron concentration was also high, with an accuracy estimate greater than 97%. A significant difference (P ≤ 0.01) was also verified for all the sources of variation, showing that there is variability among the populations obtained. When decomposition of the parent source of variation was performed, it was possible to observe that among the parents of Group 1, as well as those of Group 2, there was no significant difference (Table 1). This may be verified through the means of the parents of each group, which were very near (Table 2). Nevertheless, the Group 1 versus Group 2 contrast was significant, showing that the groups differ in regard to iron concentration.

In diallelic analysis, a significant difference (P ≤ 0.01) was observed among the crosses assessed, with mean iron concentration ranging from 95.46 to 181.10 mg kg^{-1} (Tables 4 and 8).

In decomposition of the effects of crosses on GCA of Groups 1 and 2 and of the SCA, a significant difference (P ≤ 0.01) was found for all the sources of variation (Table 4). The SCA explained more than 50% of the variation obtained among the hybrids, indicating the occurrence of dominance for the trait. The significant SCA and the parents versus hybrids contrast, likewise significant (Table 1), indicate the occurrence of heterosis

Table 3. Significance obtained by the F test for zinc concentration (mg kg^{-1}) in comparison of the different contrasts of the 16 hybrid combinations.

Hybrid	P_1 versus P_2	F_{11} versus F_{12}	P_1 versus F_{11}	P_2 versus F_{12}
Paraná × P-180	**	**	NS	NS
Paraná × Linea 29	NS	**	NS	**
Paraná × R-1	**	**	NS	NS
Paraná × AN 910523	**	**	NS	NS
Esal 543 × P-180	NS	**	NS	NS
Esal 543 × Linea 29	NS	NS	NS	*
Esal 543 × R-1	**	NS	NS	*
Esal 543 × AN 910523	NS	NS	NS	NS
BP 28 × P-180	**	**	NS	NS
BP 28 × Linea 29	*	**	NS	NS
BP 28 × R-1	**	**	NS	NS
BP 28 × AN 910523	**	**	NS	NS
Esal 516 × P-180	**	**	**	*
Esal 516 × Linea 29	**	**	NS	**
Esal 516 × R-1	**	**	**	NS
Esal 516 × AN 910523	**	NS	**	NS

**, Significant at 1% by the F-test; *, significant at 5% probability, by the F-test; NS, not significant at 1% probability, by the F-test.

Table 4. Summary of diallel analysis of zinc and iron concentration of F_2 bean seeds derived from partial diallel cross among four lines selected for low nutrient concentrations (Group 1) and four with high concentration (Group 2).

SV	DF	Zinc		Iron	
		MS	R^2 (%)	MS	R^2 (%)
Hybrids	15	55.09**		3913.95**	
GCA (G1)	3	14.28^{NS}	5	2673.93**	14
GCA (G2)	3	234.09**	85	6323.69**	32
SCA (1 × 2)	9	9.02^{NS}	10	3524.05**	54
Residue	112	17.56		354.07	

DF, Degree of freedom; MS, mean square; SV, source of variation; **, significant at 1% probability by the F-test; ^{NS}, not significant at 1% probability, by the F-test.

Table 5. Effects of GCA (g_i e g_j) and SCA (s_{ij}) of bean lines selected for low and high zinc concentrations (mg kg^{-1}) obtained in assessment of F_2 seeds of the partial diallel.

Parent	P 180	Linea 29	R 1	AN 910523	$\hat{g}_j$ (low)
Paraná	1.16	0.43	-1.44	-0.16	-0.20
Esal 543	-0.43	-0.29	-0.39	1.12	0.99
BP 28	-1.29	0.15	1.47	-0.33	-0.37
Esal 516	0.56	-0.29	0.36	-0.63	-0.42
$\hat{g}_i$ (high)	1.48	-2.02	3.05	-2.52	

for iron concentration in bean seeds. This heterosis may be observed through the mean of F_1 generation, which was greater than the mean of the parents (Table 2). The effects of GCA of the two groups are presented in Table 9. Even within Group 1 (parents with low iron concentration), lines were found, such as ESAL 516, with a high concentration of favorable alleles in relation to the parent group. In Group 2 (parents with high iron concentration), the P 180 line was that which presented the highest $\hat{g}_i$. This line should contribute to an 18.55 mg kg^{-1} increase

Table 6. Means of zinc concentrations (mg kg^{-1}) obtained in assessment of the F_2 generation of the partial diallel.

Parent	P 180	Linea 29	R 1	AN 910523
Paraná	48.48[a1]	44.25[b]	47.45[a]	43.15[b]
Esal 543	48.08[a]	44.72[b]	49.69[a]	45.62[b]
BP 28	45.86[b]	43.80[b]	50.18[a]	42.81[b]
Esal 516	47.66[a]	43.31[b]	49.03[a]	42.47[b]

[1]Means followed by the same letter belong to the same group by the Scott and Knott (1974) test, at 5% probability.

in iron in the crosses in which it participates.

The most promising hybrid was Paraná × P180, which presented the greatest effect of SCA (Table 9). This combination obtained a mean of 181.10 mg kg^{-1} of dry matter, being the highest among the crosses (Table 8). It is worth highlighting that the two parents presented high values of positive $\hat{g}_j$ and $\hat{g}_i$.

DISCUSSION

Zinc concentration

When a hybrid seed is produced, the seed coat is maternal tissue, and therefore does not depend on the cross. The embryo and cotyledons, for their part, in being products of fertilization, are in generation F_1 (Ribeiro et al., 2006). Therefore, if the F_{11} and F_{12} contrast is assessed, in which the second number identifies the parent used as female, the effect of the reciprocal cross is assessed. If the contrast is not significant, it implies that the information refers to the embryo and cotyledon, which in reciprocal cross, for obvious reasons, is the same. If it is significant, a hypothesis for explanation would be that this difference could be attributed to the cytoplasm. Nevertheless, there is no information that the DNA of the mytochondria or of the cytoplasm could have an influence on the chemical composition of the seeds. Thus, the explanation for this difference may only be attributed to the tegument, that is, the presence of the maternal effect. In this case, the P_1 versus F_{11} or P_2 versus F_{12} contrasts must be non-significant.

The significant difference observed among the parents of Groups 1, 2 and for the Group I versus Group 2 contrast indicate, as was expected, that the parents differ in regard to zinc concentration between the groups and also within each group. This may be verified in Table 2, where the means of the groups and of all the parents within each group are presented. The significance for the F_{11} versus F_{12} contrast indicates the possibility of occurrence of maternal effect for the trait. The mean of the F_{12} generation was significantly (P = 0.0000) greater than that of F_{11} and this was already expected since, in F_{12}, the parent used as female was that which had a high zinc concentration (Table 2).

The most contrasts is F_{11} versus F_{12}; these parents did not differ in regard to zinc concentration and, therefore, the composition of the F_{11} and F_{12} seeds should not differ either (Table 3).

In the literature, there are some results that contradict those reported here (Moraghan et al., 2002; Rosa et al., 2010). A probable discrepancy in these results may be attributed to the methodology used in obtaining the information. In these studies, the number of lines used was small and the seed coat was separated from the rest of the seed. This process, in addition to being very laborious, is of questionable accuracy because it is difficult to remove the seed coat without taking part of the cotyledons with it. The reason is that the lines tested were different from those used in this study. Another argument which may reinforce the probable localization of part of the zinc in the seeds is the fact that this nutrient is positively correlated with iron and, as will be commented on afterwards, in the case of this nutrient, there seems to be no doubt that it is concentrated in the seed coat (Moraghan et al., 2002; Jost et al., 2009).

In light of the above, in interpretation of the diallel, the generation of reference will be that of the seed coat and not that of the embryo; in other words, although the seed is F_2, the plant that originated it is in generation F_1 and the seed coat will be F_1.

The GCA of Group 2 explained 85% of the variation obtained among the hybrids. In this condition, it may be inferred that in control of the trait, the additive allelic interaction predominates.

Therefore, only the lines assessed in Group 2, which represent the parents with a high zinc level, differ in concentration of loci with fixed favorable alleles, contributing differently to the crosses in which they are involved. That way, it is possible to identify lines that contribute to increasing the zinc concentration of the populations in which they participate as parents. This result may be better seen in Table 5 in which the effects of the GCA of the two groups are presented. It may be observed that the R1 line of Group 2 (high zinc concentration), is that which should present a higher concentration of fixed favorable alleles. This line should contribute to an increase of 3.05 mg kg^{-1} in the zinc concentration of the crosses in which it participates.

Dominance in control of the trait also occurs; however,

Table 7. Significance obtained by the F test for iron concentration (mg kg^{-1}) in comparison of the different contrasts of the 16 hybrid combinations.

Hybrid	P_1 versus P_2	F_{11} versus F_{12}	P_1 versus F_{11}	P_2 versus F_{12}
Paraná × P-180	**	**	NS	NS
Paraná × Linea 29	**	**	NS	**
Paraná × R-1	**	**	NS	NS
Paraná × AN 910523	**	**	NS	NS
Esal 543 × P-180	*	**	NS	*
Esal 543 × Linea 29	**	*	NS	NS
Esal 543 × R-1	**	**	NS	NS
Esal 543 × AN 910523	**	*	NS	NS
BP 28 × P-180	**	**	NS	**
BP 28 × Linea 29	**	**	NS	**
BP 28 × R-1	**	**	NS	**
BP 28 × AN 910523	**	**	NS	NS
Esal 516 × P-180	**	**	NS	**
Esal 516 × Linea 29	**	*	*	NS
Esal 516 × R-1	**	**	*	*
Esal 516 × AN 910523	**	**	**	**

**, Significant at 1% by the F-test; *, significant at 5% probability, by the F-test; NS, not significant at 1% probability, by the F-test

Table 8. Means of iron concentrations (mg kg^{-1}) obtained in assessment of the F_2 generation of the partial diallel.

Parent	P 180	Linea 29	R 1	AN 910523
Paraná	181.10^{a1}	104.20^{e}	106.70^{e}	102.30^{e}
Esal 543	119.90^{d}	111.00^{d}	123.20^{c}	120.80^{d}
BP 28	106.10^{e}	126.80^{c}	105.60^{e}	95.46^{e}
Esal 516	148.10^{b}	135.50^{c}	137.20^{c}	100.00^{e}

[1]Means followed by the same letter belong to the same group by the Scott and Knott (1974) test at 5% probability.

with a smaller effect than the additive. It is important to highlight that part of the effect of the GCA must be attributed to heterosis of the parental (Bernardo, 2002). The authors report that considering only one locus with two alleles, the GCA is obtained through the expression: GCA = $(p_i - \bar{p})$ [a + (1 - 2t) d], in which: $\bar{p}$ is the mean allelic frequency of a determined locus of the n parents assessed; p_i is the frequency of the favorable allele of the parent i; t is the allelic frequency of the tester used; a is the deviation of the homozygotes in relation to the mean (additive effect) and d is the deviation of the heterozygotes in relation to the mean, also denominated as the dominance effect of the genes. Therefore, it is observed that the GCA also depends on the dominance effect of the alleles.

Iron concentration

The significant difference verified for the F_{11} versus F_{12} contrast indicates the possibility of occurrence of maternal effect for iron concentration. The mean of F_{12} generation was greater than that of F_{11}, which was expected if there was maternal effect for iron concentration since, in F_{12}, the parent used as female was that which had high iron concentration (Table 2).

Seeking to verify if the occurrence of maternal effect for iron concentration could vary depending on the genotype, the different contrasts among the possible crosses between the two groups of parents were obtained (Table 7). It was verified that in all the crosses, there was significance for the F_{11} versus F_{12} contrast, indicating that the iron concentration in beans is dependent on the seed coat. In the literature, there are reports that agree with that presented here, showing that in genetic control of iron concentration, there is the presence of maternal effect (Jost et al., 2009). Nevertheless, it is important to mention that the iron proportion found in the seed coat may vary. In an assessment performed by Moraghan et al. (2002), it was verified that from 11 to 36% of the iron is concentrated in the seed coat of the bean seeds. Thus, part of the nutrient has maternal effect and part is

Table 9. Effects of GCA (g_i and g_j) and SCA (s_{ij}) of bean lines selected for low and high iron concentrations (mg kg^{-1}) obtained in assessment of F_2 seeds of the partial diallel.

Parent	P 180	Linea 29	R 1	AN 910523	$\hat{g}_j$ (low)
Paraná	38.97	-18.50	-14.80	-5.67	3.33
Esal 543	-17.38	-6.85	6.55	17.68	-1.52
BP 28	-20.94	19.18	-0.82	2.58	-11.76
Esal 516	-0.65	6.17	9.07	-14.59	9.95
$\hat{g}_i$ (high)	18.55	-0.87	-2.07	-15.61	

concentrated in the cotyledons, just as verified for zinc, which makes the selection process more difficult because the seed coat is in one generation and the embryo and cotyledons in another.

In some cases, it was observed that the proportion of iron found in the seed coat may also vary according to its color (Moraghan et al., 2002; Silva et al., 2012). Moraghan et al. (2002) observed that bean cultivars with black grains had greater iron concentration in the seed coat (35 to 40%), while in cultivars with white grains, the concentration is from 17 to 20% of iron. The authors attributed this difference to the tannin concentration, which is greater in cultivars with black grains, and the tannins may complex iron (Moraghan et al., 2002), and phytates (Akond et al., 2011). Thus, the occurrence of maternal effect will not always be detected, with the results being dependent on the cross that is, of the lines used in the hybridizations.

In diallelic analysis, it is important to observe that combinations were obtained with mean iron concentration greater than the mean of the parents (Table 8). This may be an indicative of the occurrence of transgressive segregation, which is the appearance of individuals with phenotypes more extreme than those of the parents in segregating generations. This fact may occur in the case of traits controlled by various genes in which the parents used in the hybridizations complement each other for the favorable alleles of these genes. Beebe et al. (2000), working with three bean populations for studying iron and zinc minerals, also observed transgressive segregation for iron concentration and suggested that from 4 to 7 genes are involved in genetic control of this mineral.

The significant difference for GCA and SCA indicate thus, parents assessed differ in concentrations of loci with fixed favorable alleles, contributing differently to the crosses in which they are involved, and certain combinations proved to be relatively better or worse than that which could be expected as based on mean performance of the two parents of the hybrid in question.

Conclusions

An expressive part of variation in zinc and iron concentrations among the lines used is due to the seed coat. In the case of zinc, the additive allelic interaction alone explained the variation. For iron, the occurrence of dominance is also important.

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