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Inheritance pattern of zinc (Zn) concentration in Middle American and Andean common bean (*Phaseolus vulgaris* L.) seeds

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Abstract

The development of common bean cultivars biofortified for zinc meets the global demand for food which may help minimize nutritional deficiencies. The objectives of this research were to investigate the distribution of zinc in the four different Middle American and Andean common bean (*Phaseolus vulgaris*) seeds, to estimate the genetic parameters for zinc concentration in seeds, and to select recombinants biofortified for zinc. Thus, controlled crossings were carried out between the Middle American lines CNFP 10104 and CHC 01-175, and the Andean cultivars Cal 96 and Hooter. Seeds from F_1, F_1 reciprocal, F_2, F_2 reciprocal, and backcross (BC_{11} and BC_{12}) generations were obtained. Parents and segregating generations were evaluated in two field experiments performed in Brazil. In the parents evaluated, from 57.01 to 68.47% of zinc was accumulated in the seeds embryo. Zinc concentration in Middle American and Andean common bean seeds had no significant maternal effect. Zinc concentration in common bean seeds ranged from 11.59 to 49.84 mg kg^{-1} of DM in F_2 generation, and showed a continuous distribution, which is characteristic of quantitative inheritance. Broad-sense heritability of zinc concentration in common bean seeds is of high magnitude (h^2b= 67.21 to 90.03%) and from 17.32 to 27.80% of gain with selection is expected. From the tested hybrid combinations 112 recombinants with high zinc concentration in the seeds can be selected. Inheritance pattern of zinc concentration in Middle American and Andean common bean seeds is quantitative.

Keywords: frequency distribution; gain with selection; heritability; maternal effect; *Phaseolus vulgaris.*
Abbreviations: DM_ dry matter.

Introduction

Bean biofortification for zinc is a promising strategy to minimize nutritional deficiency problems that affect particularly children under five years old from nations where zinc absorbed from food does not meet the daily nutritional need (WHO, 2009). Zinc deficiency in humans alters the immune system and growth, and causes diarrhea, dermatitis and other disorders (Martínez-Ballesta et al., 2010; Gibson, 2012). Zinc concentration ranged from 19 to 56 mg kg^{-1} of DM in common bean cultivars from several countries (Blair et al., 2010a; Tryphone and Nchimbi-Msolla 2010; Silva et al., 2012; Ribeiro et al., 2014a). Due to the natural genetic variability, it is possible to select common bean cultivars with zinc concentration equal or superior to 31 mg kg^{-1} DM, i.e., with high zinc concentration (Cichy et al., 2005; Tryphone and Nchimbi-Msolla, 2010) to be used in food. Bean (*Phaseolus vulgaris* L.) is native to the American continent, and has two domestication centers, the Middle American and the Andean (McClean et al., 1993). Common bean germplasm of the Middle American gene pool presents higher zinc concentration in the seeds than those of Andean origin (Islam et al., 2002; Blair et al., 2010a). However, lines with high zinc concentration have been obtained both in Middle American (Gelin et al., 2007; Blair et al., 2010b; Teixeira et al., 2015) and in Andean (Cichy et al., 2009) common bean seeds. Therefore, it is possible to develop common bean cultivars with high zinc concentration in the seeds in both gene pools. The potential of beans for biofortification for zinc has been evaluated, and results obtained by classic breeding (Mukamuhirwa et al., 2015; Teixeira et al., 2015; Maziero et al., 2016) and molecular methods (Blair et al., 2009; Cichy et al., 2009; Blair et al., 2010b; Blair and Izquierdo, 2012) are promising. Backcross has been used to transfer high zinc concentration from wild beans to cultivated beans, and biofortified recombinants have been identified by molecular marker analysis (Blair and Izquierdo, 2012). Quantitative trait loci for zinc and iron concentrations were found in specific linkage groups (Cichy et al., 2009; Blair et al., 2010b), suggesting the possibility of developing common bean cultivars biofortified for both minerals. Another factor that needs to be further investigated in common bean is the distribution of zinc in the embryo and seed coat. Previous studies have reported high zinc concentration in the embryo of common bean seeds (Moraghan and Grafton, 2002; Moraghan et al., 2002; Ribeiro et al., 2012). This fact influences the zinc bioavailability to the human body (Ariza-Nieto et al., 2007), and the decision of when to start the selection of superior recombinants for zinc concentration by the breeding program (Rosa et al., 2010).

Middle American common bean seeds presented high broad-sense heritability zinc concentration (Cichy et al., 2005; Rosa et al., 2010; Teixeira et al., 2015). Middle American (Cichy et al., 2005; Rosa et al., 2010) and Andean common bean seeds (Mukamuhirva et al., 2015) presented high magnitude narrow-sense heritability estimates for zinc concentration in indicating prevalence of additive effects in the expression of this character. Thus, the selection can be facilitated, since segregation is not expected for zinc concentration with the advance of generations. However, the comparison of the similarities and differences in inheritance pattern of zinc concentration in Middle American and Andean common bean seeds is not found in the literature. This is because no studies have been carried out in which the genetic parameters estimates were obtained using the same methodology and uniform environment conditions for both gene pools. Such studies are fundamental to the obtainment of new common bean cultivars, with the grains types of better acceptance for consumption in several countries. Thus, the objectives of this research were to investigate the distribution of zinc in the four different Middle American and Andean common bean seeds, to estimate the genetic parameters for zinc concentration in seeds, and to select recombinants biofortified for zinc.

Results and Discussion

Genetic variability for zinc concentration in seeds

In the hybrid combinations CNFP 10104 x CHC 01-175 and Cal 96 x Hooter, parents (P_1 and P_2) did not differ significantly for zinc concentration in the seeds (Table 1). Therefore, parents did not contrast for zinc, unlike the results obtained by Ribeiro et al. (2013, 2014a). Silva et al. (2013), similarly, pre-selected contrasting parents for zinc concentration in the seeds. However, the authors verified that the P_1 *vs* P_2 contrast was not significant for zinc concentration in some hybrid combinations. This is justified by the fact that zinc concentration in common bean seeds varies according to the genotype, to the environment, and to the genotype x environment interaction (Ribeiro et al., 2008; Cichy et al., 2009; Silva et al., 2012; Pereira et al., 2014; Teixeira et al., 2015). The mean values of zinc obtained in the 2013 dry season for the parents CNFP 10104 and CHC 01-175, and for the early generations, were lower than those observed in the 2012 rainy season (Table 1). Since the experiments were performed in a homogeneous soil area for physical and chemical properties, using the same management practices, the differences verified between the growing seasons for zinc concentration in the seeds may be justified by meteorological data. In the 2013 dry season, the average minimum and maximum air temperatures, and the rainfall previous to the harvest were lower than those observed in the 2012 rainy season, resulting in less zinc accumulation in the seeds. Silva et al. (2012) also observed that the mean zinc concentration of 20 lines evaluated in the dry season (sowing on February) was lower than the mean values obtained in other growing seasons. In the 2012 rainy season, not enough seeds were obtained for the Andean cultivars and their generations for the determination of zinc concentration. Therefore, mean and variances data were not shown in the crosses between Cal 96 x Hooter carried in the 2012 rainy season. The hypothesis is that the high average maximum temperatures in the months from December to February contributed to increase the percentage of abortion of flowers and pods of the Andean germplasm. According to Debouck (1993), the Andean germplasm is more adapted to cultivation in regions of milder temperatures. In the present study, using the same converging crosses for zinc concentration in the seeds, great segregation was observed for the mineral in the F_2 generation, ranging from 11.59 to 49.84 mg kg^{-1} of DM (Figure 1A, 1B and 1C). This variation range was very close to that observed by Rosa et al. (2010) in recombinants obtained in the controlled crossing between the common bean cultivars TPS Nobre x Guapo Brilhante, which did not significantly differ for zinc concentration in the seeds. Therefore, from the hybrids tested in this study, genetic variability for zinc concentration was obtained in Middle American and Andean common bean seeds, and it allows selecting of recombinats for biofortification program.

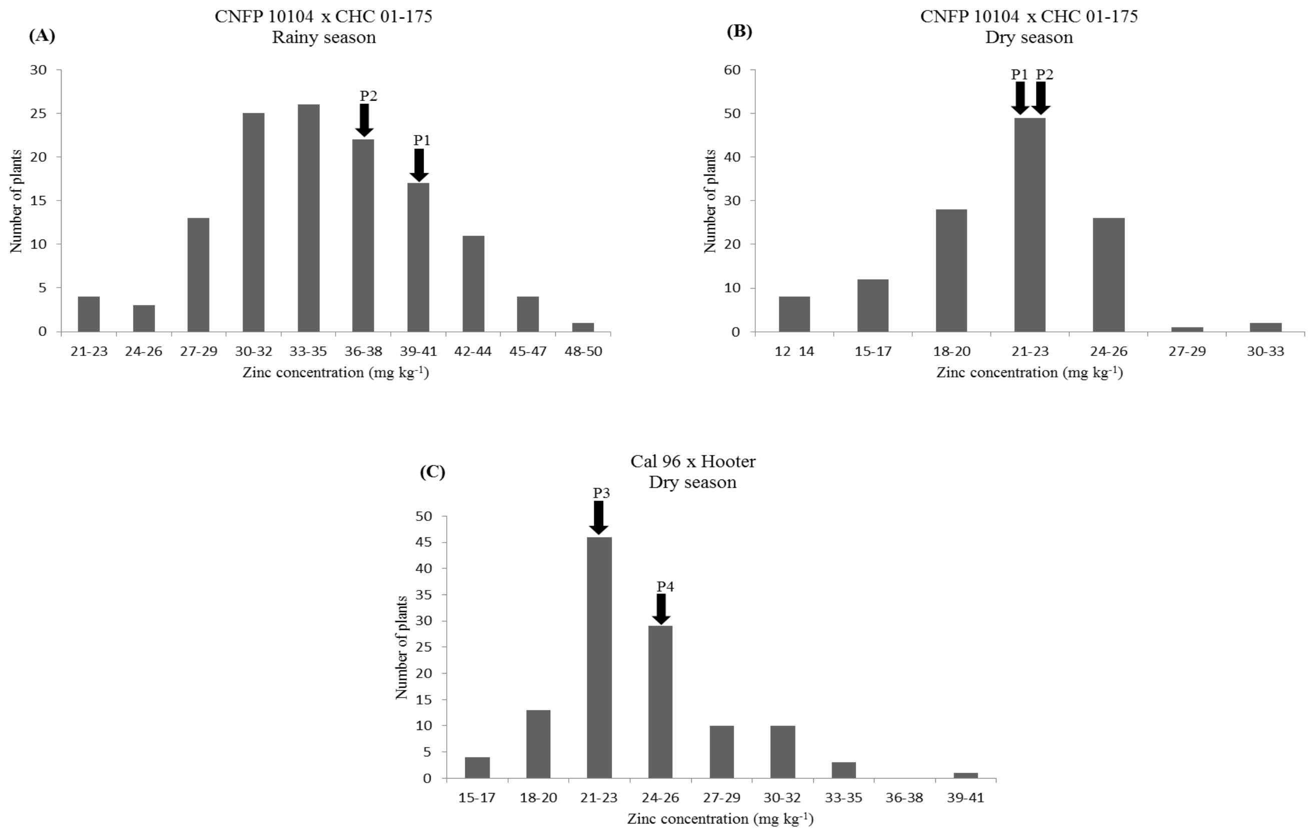
Maternal effect and distribution of zinc in the seeds

For the CNFP 10104 x CHC 01-175 (rainy and dry seasons) and Cal 96 x Hooter (dry season) crosses, F_1 *vs* F_1 reciprocal contrast was not significant, indicating no maternal effect for the zinc concentration in Middle American and Andean common bean seeds (Table 1). Thus, F_1 generation seeds represented the product of fertilization between parents in both gene pools, since embryo seeds presented more zinc accumulation (Table 2). Similarly, Rosa et al. (2010) did not observe significant maternal effect for zinc concentration in common bean hybrids obtained from crosses between cultivars of the Middle American gene pool. However, Mukamuhirva et al. (2015) found significant maternal effect for zinc concentration in common bean hybrids derived from the crosses Andean x Andean and Middle American x Andean. If the F_1 *vs* F_1 reciprocal contrast was significant, the cytoplasm could be justify this result. No previous results have indicated that the DNA of the mitochondria or cytoplasm could influence the chemical composition of the seeds (Silva et al., 2013). In present study, no significant maternal effect was discovered for zinc concentration in beans. Thus, selection should start with the seeds of the F_2 generation, when the maximum genetic variability can be assessed in both gene pools. In the parents evaluated in this study, the embryo presented from 89.09 to 92.85% of the total dry matter of common bean seeds, and concentration ranged from 57.01% (Cal 96, dry season) to 68.47% (CHC 01-175, dry season) of the total zinc present in the seeds (Table 2). Therefore, higher zinc accumulation was observed in the embryo of Middle American and Andean common bean seeds, which is in agreement with previous results reported by Moraghan and Grafton (2002), Moraghan et al. (2002), and Ribeiro et al. (2012). In the embryo of common bean seeds, great accumulation of phytate was observed (Ariza-Nieto et al., 2007). Phytates are zinc absorption inhibitors in leguminous plants (Gibson, 2012). Since zinc is accumulated mostly in the embryo of Middle American and Andean common bean seeds, it is expected that this mineral is less bioavailable for the human body. However, Ramírez-Cárdenas et al. (2010) observed that cooked bean grains of Ouro Branco cultivar, which has high zinc

Table 1. Number of plants (NP), mean zinc concentration in the seeds, and respective standard deviations obtained in the parents (P_1 and P_2) and in the F_1, F_1 reciprocal, F_2, and F_2 reciprocal generations in the crossing of CNFP 10104 (P_1) x CHC 01-175 (P_2) lines (rainy and dry seasons) and of Cal 96 (P_1) x Hooter (P_2) lines (dry season), and probability by the t test for the contrasts P_1 vs P_2, P_1 vs F_1, P_2 vs F_1 reciprocal, F_1 vs F_1 reciprocal, and F_2 vs F_2 reciprocal.

Zinc concentration (mg kg^{-1} dry matter)						
Parents and generations	NP	CNFP 10104 x CHC 01175 Rainy season	NP	CNFP 10104 x CHC 01175 Dry season	NP	Cal 96 x Hooter Dry season
P_1	10	39.62±1.11	10	22.06±0.12	10	22.24±0.68
P_2	10	36.98±1.00	10	22.90±0.10	10	24.27±0.16
F_1	6	37.58±0.61	6	21.06±0.43	5	22.62±0.02
F_1 reciprocal	6	36.73±3.44	6	23.62±0.97	5	22.47±1.50
F_2	63	36.08±0.43	63	20.31±0.25	58	21.94±0.15
F_2 reciprocal	63	33.51±0.56	63	21.74±0.15	58	23.80±0.32
Probability (%)						
P_1 vs P_2		8.28^{ns}		8.39^{ns}		3.75*
P_1 vs F_1		19.48^{ns}		15.42^{ns}		74.86^{ns}
P_2 vs F_1 reciprocal		89.43^{ns}		58.06^{ns}		9.51^{ns}
F_1 vs F_1 reciprocal		68.14^{ns}		5.36^{ns}		89.82^{ns}
F_2 vs F_2 reciprocal		1.04*		2.43*		0.72*

*Significant at 0.01 probability by *t* test. ^{ns}Non-significant.



* The arrows refer to the parents: P_1, CNFP 10104; P_2, CHC 01-175; P_3, Cal 96; and P_4, Hooter.

Fig 1. Frequency distribution for zinc concentration in F_2 plants obtained from the crossing of CNFP 10104 x CHC 01-175 lines in the rainy (A) and dry seasons (B), and from the crossing of Cal 96 x Hooter lines in the dry season (C).

Table 2. Percentage of dry matter, percentage of zinc, and zinc concentration in the embryo and seed coat of the common bean seeds of the Mesoamerican lines CNFP 10104 and CHC 01-175 (rainy and dry seasons), and of the Andean cultivars Cal 96 and Hooter (dry season).

Fraction	Inbred lines	Dry matter (%)	Zinc (%)	Zinc (mg kg^{-1})
Mesoamerican inbred lines, rainy season				
Embryo	CNFP 10104 (a)	89.15	64.58	29.32
	CHC 01-175 (b)	91.26	61.22	33.18
	a – b	- 2.11*	3.36^{ns}	-3.86^{ns}
Seed coat	CNFP 10104 (a)	10.85	35.42	16.50
	CHC 01-175 (b)	8.74	38.78	21.10
	a – b	2.11*	-3.36^{ns}	-4.60^{ns}
Mesoamerican inbred lines, dry season				
Embryo	CNFP 10104 (a)	89.09	57.32	25.74
	CHC 01-175 (b)	91.09	68.47	24.22
	a – b	- 2.00*	-11.15*	1.52^{ns}
Seed coat	CNFP 10104 (a)	10.91	42.68	19.11
	CHC 01-175 (b)	8.91	31.53	11.26
	a – b	2.00*	11.15*	7.85*
Andean inbred lines, dry season				
Embryo	Cal 96 (c)	92.24	57.01	28.31
	Hooter (d)	92.85	60.26	26.50
	c – d	- 0.61^{ns}	-3.25^{ns}	1.81^{ns}
Seed coat	Cal 96 (c)	7.76	42.99	21.34
	Hooter (d)	7.15	39.74	17.60
	c – d	0.61^{ns}	3.25^{ns}	3.74^{ns}

*Significant at 0.05 probability by *t* test. ^{ns}Non-significant.

Table 3. Estimates of means, genetic parameters, and predicted gains with selection for zinc concentration in common bean seeds in the crossing of CNFP 10104 x CHC 01-175 lines (rainy and dry seasons) and in the crossing of Cal 96 x Hooter lines (dry season).

Parents and generations	Zinc concentration (mg kg^{-1} dry matter)		
	CNFP 10104 x CHC 01-175 Rainy season	CNFP 10104 x CHC 01-175 Dry season	Cal 96 x Hooter Dry season
Mean	36.75	21.95	22.89
Phenotypic variance (σ^2_P)	26.84	15.87	8.61
Environmental variance (σ^2_E)	8.27	1.58	2.82
Genetic variance (σ^2G)	18.57	14.29	5.79
Additive variance (σ^2A)	7.82	-	-
Broad-sense heritability (h^2b)	69.20	90.03	67.21
Narrow-sense heritability (h^2n)	29.15	-	-
Minimum value in parentes	32.49	20.48	19.01
Maximum value in parentes	45.68	24.33	25.61
Minimum value in F_2	20.96	11.59	14.73
Maximum value in F_2	49.84	31.70	38.88
Selected plant in F_2	25, 119, 6, 11, 35, 10, 3, 106, 105, 66, 27 and 44	78, 85, 49, 61, 73, 64, 65, 24, 92, 43, 41 and 10	100, 97, 99, 62, 74, 102, 96, 53, 47, 80 and 113
Original mean in F_2	34.79	21.03	22.87
Mean of selected plants	45.03	26.74	30.80
Selection differential (SD)	10.23	5.72	7.93
Selection gain (ΔG)	6.03	5.02	6.36
Selection gain (ΔG%)	17.32	23.89	27.80
Predicted mean after the first selection cycle	40.82	26.05	29.22

which has high zinc and phytate concentrations, had the highest zinc bioavailability among the evaluated cultivars. Therefore, it is possible to select common bean lines with high zinc and phytates concentrations, without compromising the bioavailability of this mineral.

Frequency distribution

In the cross CNFP 10104 x CHC 01-175, greater variation was obtained for zinc concentration in F_2 plants, ranging from 11.59 to 49.84 mg kg^{-1} DM (Figure 1A and 1B). A more restricted variation range was observed for the zinc concentration in segregating populations obtained from biparental crossings between common bean lines in F_2 generation (Rosa et al., 2010) and F_3 generation (Mukamuhirwa et al., 2015). However, continuous distribution, close to normal, was observed in both hybrid combinations evaluated in the study, characterizing quantitative inheritance for zinc concentration in Middle American and Andean common bean seeds (Figure 1A, 1B and 1C). Continuous distribution for zinc concentration in common bean seeds was previously described for segregating populations obtained from crosses between parents of Middle American x Middle American (Blair et al., 2010b; Teixeira et al., 2015), Andean x Andean (Cichy et al., 2009), and Middle American x Andean gene pool (Blair et al., 2009). Therefore, the inheritance pattern of zinc concentration in Middle American and Andean common bean seeds is quantitative, contrary to the initial hypothesis of Cichy et al. (2005) of monogenic control for zinc concentration in Middle American common bean seeds. The present results suggest that zinc concentration in common bean grains is multigenically controlled, agreeing with previous results of Blair et al. (2009).

Transgressive segregation for zinc concentration in common bean seeds was verified in two gene pools (Figures 1A, 1B and 1C). Thus, it was possible to obtain recombinants with zinc concentration lower and higher than the values found in the parents, as previously reported by Gelin et al. (2007), Blair et al. (2009), and Mukamuhirwa et al. (2015). The cross CNFP 10104 x CHC 01-175 presented 106 plants (rainy season) and 2 plants (dry season) with zinc concentration in the seeds superior to 31 mg kg^{-1} of DM, which is considered high for common bean lines (Cichy et al., 2005; Tryphone and Nchimbi-Msolla, 2010). Conversely, the cross Cal 96 x Hooter (dry season) presented four common bean plants with high zinc concentration in the seeds. The 112 recombinant identified with high zinc concentration in the seeds will be selected by the zinc biofortification program of UFSM. The advance of segregating generations obtained in this study may result in the development of common bean cultivars biofortified for zinc, which could contribute to minimize zinc deficiency in the human body wich according to Gibson et al. (2012), alters the immune system, and causes diarrhea, respiratory diseases, dermatitis, and other disorders.

Heritability and predicted gain with selection

Broad-sense heritability estimates varied from 67.21 (Cal 96 x Hooter, dry season) to 90.03% (CNFP 10104 x CHC 01-175, dry season) (Table 3). High magnitude broad-sense heritability was also described for zinc concentration in Middle American common bean seeds (Cichy et al., 2005; Rosa et al., 2010; Teixeira et al., 2015.). High broad-sense heritability values indicate greater contribution of genetic variance in the expression of zinc concentration in common bean seeds, and therefore selection is expected to be easier.
Narrow-sense heritability of zinc concentration was determined only in the cross CNFP 10104 x CHC 01-175 in the rainy season, and presented low magnitude (h^2n = 29.15%). However, high magnitude narrow-sense heritability estimates were obtained for zinc concentration in Middle American (Cichy et al., 2005; Rosa et al., 2010) and Andean common bean seeds (Mukamuhirwa et al., 2015). In the present study, the additive variance did not make up for the most part of the genetic variance. Effects of dominance and overdominance were also significant for the expression of zinc concentration, suggesting difficulties for the fixation of this character with the advance of generations. In the presence of predominance of additive effects for zinc concentration in common bean seeds, as observed in the hybrid combinations obtained by Cichy et al. (2005), Rosa et al. (2010), Mukamuhirwa et al. (2015), selection is expected to be easier, since segregation for the character is not expected with the advance of generations. Therefore, narrow-sense heritability should be estimated in different hybrid combinations. Based on the magnitudes of these estimates, breeders should decide whether or not perform selection in the population.

Considering the predicted gains with selection from 17.32 to 27.80% for zinc concentration in Middle American and Andean common bean seeds (Table 3), common bean lines biofortified for zinc from the selection of superior recombinants obtained in the F_2 generation are expected. Due to the direct relationship between zinc concentration in common bean seeds and zinc bioavailability (House et al., 2002), biofortification for zinc increases in beans nutritional value. In a scenario where 89% of children under five years old that live in nations where the zinc absorbed from food is insufficient to meet the daily nutritional requirements (WHO, 2009), beans biofortified for zinc is a low-cost strategy, and can be very efficient to tackle problems of nutritional deficiencies reported by Gibson (2012) and Martínez-Ballesta et al. (2010).

Materials and Methods

Plant material

Four common bean genotypes were used for the study of the inheritance pattern of zinc concentration in the seeds, being two lines of the Middle American gene pool (CNFP 10104 and CHC 01-175) and two cultivars of the Andean gene pool (Cal 96 and Hooter). Parents were selected based on the zinc concentration in the seed, in agronomic value and cooking quality of accession maintained in the Bean Germplasm Bank of the Federal University of Santa Maria (UFSM), Brazil (Ribeiro et al., 2013, 2014a). CNFP 10104 and CHC 01-175 represent the most consumed types of beans in Brazil, the black and carioca (beige seed coat with brown streaks), respectively. Cal 96 presents dark red seed coat with cream coloured stripes, and Hooter has cream seed coat with red coloured stripes, classified as cranberry type. These cultivars have great demand for exports, although they are not very popular in Brazil. The controlled crossings between the lines CNFP 10104 and CHC 01-175 and between the cultivars Cal 96 and Hooter were carried out using the interlacing method with previous emasculation of floral bud (Peternelli et al., 2009). Thus, the cultivation of the parent plants was performed in a greenhouse at the Plant Science Department of UFSM, located in the city of Santa Maria, state of Rio Grande do Sul, Brazil (29°42'S lat, 53°49'W long, and 95m asl.). F_1 seeds (♀ P_1 × ♂ P_2) and F_1 reciprocal (♀ P_2 × ♂ P_1) were obtained during the summer-fall season of 2012 for each hybrid combination. Afterwards, seeds of F_2, F_2 reciprocal, backcross 1 (BC_{11}: ♀ F_1 × ♂ P_1) and backcross 2

(BC_{12}: ♀ F_1 × ♂ P_2) were generated, in the winter-spring season of 2012. Pods obtained in the experiment were individually harvested at maturity, and were manually threshed. Seeds were dried in an oven (65-70°C) until reaching to 13% average humidity.

Generations evaluated

The generations (F_1, F_1 reciprocal, F_2, F_2 reciprocal, BC_{11} and BC_{12}) obtained for each hybrid combination and the parents (CNFP 10104, CHC 01-175, Cal 96 and Hooter) were evaluated in two field experiments carried out in the experimental area of the Bean Breeding Program of UFSM. Sowing was carried out on November 9th, 2012 and on June 3rd, 2013, which corresponded to the traditional growing season for common bean in southern Brazil (rainy and dry seasons). The experiments were performed in a homogeneous soil area for physical and chemical properties. The soil is classified as typical alitic Argisol, Hapludalf and presented the following chemical composition at the time of the installation of the experiments: pH (H_2O): 6.1; organic matter: 50 g kg^{-1}; phosphorus: 13.5 mg dm^{-3}; potassium: 60 mg dm^{-3}; calcium: 6.0 $cmol_c$ dm^{-3}; and magnesium: 2.9 $cmol_c$ dm^{-3}. Soil was prepared in conventional manner, and fertility correction was made according to the soil chemical analysis. Fertilization was carried out by applying 250 kg ha^{-1} of the formula N-P_2O_5-K_2O 5-30-20 (urea: 45% nitrogen, superphosphate: 18% P_2O_5, and potassium chloride: 60% K_2O) at sowing, and 20 kg ha^{-1} of urea (45% nitrogen) at the first trifoliate leaf stage. Soil and leaves received no micronutrients application. Sowing was carried out in 1 m long rows, spaced 0.5 m apart. Fifteen seeds were evenly distributed in one row for each of the parents. For F_1, F_1 reciprocal, BC_{11} and BC_{12} generations, 10 seeds/meter were used in the row. On the other hand, for F_2 and F_2 reciprocal generations, 15 rows were sown, with 8 seeds/meter. This adjustment was performed due to the availability of seeds and to the differences in relation to genetic variability. In the two growing seasons, similar and uniform management practices were used. Irrigation was carried out before water deficit was reported, as recommended by CTSBF (2010). Weed control was performed by hand hoeing, and insects were eliminated using Engeo™ Pleno (Thiamethoxam and Lambda-cyhalothrin) insecticide, at a dose of 125 ml ha^{-1}. Disease control was not carried out. Plants were harvested at maturity and pods were threshed by hand in order to avoid the contamination of seeds by metal. After the removal of broken seeds and of impurities, seeds were dried in an oven (65-70 ºC) until reaching 13% average humidity. 10 g random samples of seeds of each parent and of the generations obtained in the experiment were individually milled in a micromill in order to get particles smaller than 1 mm. A 0.5 g sample of this raw bean flour was used for nitric-perchloric digestion (HNO_3 + $HClO_4$), which was carried out as described by Ribeiro et al. (2014b). Zinc concentration was determined using an atomic absorption spectrophotometer, with 213.9 nm wavelength.

Estimates of the genetic parameters

The bilateral *t* test was used to compare the means of contrasts P_1 *vs* P_2, P_1 *vs* F_1, P_2 *vs* F_1 reciprocal, F_1 *vs* F_1 reciprocal, and F_2 *vs* F_2 reciprocal, for each hybrid combination and in each growing season, in order to test the maternal effect hypothesis. Zinc distribution in the seeds, in embryo and seed coat fractions, was determined in the parents in order to confirm the maternal effect hypothesis. Thus, 25 seeds of the Middle American line (CNFP 10104 and CHC 01-175), and 15 seeds of the Andean line (Cal 96 and Hooter), were collected at random in three seed sub-samples. The removal of the seed coat was performed according to Ribeiro et al. (2012). The determination of the zinc concentration present in the embryo and seed coat was carried out by nitric-perchloric digestion and by atomic absorption spectrophotometer reading, as preliminarily described by Ribeiro et al. (2014b). The *t* test was used to evaluate embryo *vs* seed coat contrast in each growing season. Zinc concentration values in the embryo and seed coat were transformed to mg%, because these seed fractions represent different percentages of the total seed dry matter. Data obtained for the F_2 plants were subjected to the Lilliefors test to check the type of distribution (continuous or discontinuous) observed for zinc concentration in common bean seeds. The number of classes used in the frequency distribution was calculated by the expression $\sqrt{n}$, where *n* is the number of observations.

Genetic parameters were obtained from the variances of the parents (P_1 and P_2) and of the generations F_1, F_2, BC_{11} and BC_{12} for each hybrid combination, and in each growing season. Broad-sense and the narrow-sense heritability were estimated by the backcrossing method, described by Warner (1952). For the prediction of gains with selection, selection of 10% of the F_2 plants with the highest zinc concentration in seeds was considered, regardless of the parent used as pollen donor. The predicted gain with selection, considering the selection and recombination of the superior F_2 plants was estimated by the expressions: $\Delta G = DS \times h_b^2$, considering the broad-sense heritability; $\Delta G = DS \times h_n^2$ considering the narrow-sense heritability; and $\Delta G(\%) = (\Delta G x 100)/\overline{F}_2$. In these cases, DS is the selection differential, expressed by $\overline{X}_s - \overline{X}_0$, where $\overline{X}_s$ is the mean of the selected F_2 plants, and $\overline{X}_0$ is the mean of F_2 plants. Statistical analyses were carried out using the Office Excel spreadsheet, and the Genes software (Cruz, 2013).

Conclusion

No maternal effect for zinc concentration is observed in Middle American and Andean common bean seeds, and from 57.01 to 68.47% of the zinc concentration is found in seeds embryo. In early generation, broad-sense heritability of zinc concentration in common bean seeds is of high magnitude (h^2b = 67.21 to 90.03%), and the predicted gains with selection are from 17.32 to 27.80%. Zinc concentration in Middle American and Andean common bean seeds presents continuous distribution in the F_2 generation, ranging from 11.59 to 49.84 mg kg^{-1} of dry matter, which is a characteristic of quantitative inheritance. From the tested hybrid combinations, 112 recombinants with high zinc concentration in the seeds can be selected.

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