



Genetic control and estimation of genetic parameters for seed-coat darkening of carioca beans

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ABSTRACT. The maintenance of the light color of the grains of carioca beans is a requirement for the development of new cultivars of common beans because it enables the storage of grains for long periods so that they may be traded at a proper opportunity. Crosses of cultivar BRSMG Madrepérola, which presents slow grain darkening, were made to 10 elite lines presenting normal darkening to obtain information about the genetic control of the trait and estimates of phenotypic and genotypic parameters. Progenies at the tegument generations F_3 and F_4 and their parents were evaluated at the locations of Santo Antônio de Goiás and Ponta Grossa at 71, 106, and 155 days of storage for seed-coat darkening using a rank of scores ranging from 1 (very light colored grains) to 5 (very dark colored grains). Genotypic and phenotypic variances and broad-sense heritabilities were estimated for each population. The segregation ratios were subjected to the chi-square test to establish the genetic control. Some populations did not present consistent patterns of genetic control, while others presented monogenic or double-recessive digenic segregation, indicating that the trait is controlled by few genes. Six segregant populations were identified

with both low means for darkening and high expected gain under selection. Despite the strong environmental influence on the expression of the traits and the occurrence of the genotype by environment interaction, the estimates of genotypic and phenotypic parameters indicate the possibility of successful selection to develop lines with slow seed-coat darkening.

Key words: *Phaseolus vulgaris* L.; Storage, Slow darkening; Genotype by environment interaction

INTRODUCTION

Common beans of the carioca group are cultivated throughout Brazil, representing 70% of the total crop area (Del Peloso and Melo, 2005). In the 2011 growing season, 2.7 million metric tons of common beans were harvested in Brazil, which is one of the world's greatest producers (Feijão, 2013). Because of the great market demand, Brazilian breeding programs have given a greater emphasis to the development of cultivars of this group.

After harvesting, common beans rapidly lose their commercial value because of chemical changes that occur during grain storage that modify seed-coat color, depreciating their quality and market value. In Brazil, a dark seed coat is associated with old grains with prolonged time for cooking, which induces low acceptability by the consumer. Hence, great efforts are invested in the development of light-colored-grain cultivars that maintain their color for a greater period of storage time (Silva et al., 2008).

The elucidation of the genetic control of this trait is the basic requirement for the development of a breeding program that intends to develop cultivars with less seed-coat darkening during storage. There are very few studies about the subject, and those that exist have divergent and restricted conclusions. According to Basset (1996), seed-coat darkening is controlled by a single gene with alleles J and j, and the expression of the recessive allele j results in genotypes that are less susceptible to tegument darkening when compared with seeds of plants carrying the dominant allele. Results confirming that the trait is controlled by one gene with the dominance of the allele being responsible for seed-coat darkening were reported by Junk-Knievel et al. (2008), Silva et al. (2008), and Araújo et al. (2012) using different lines. On the other hand, Elsadr et al. (2011) described a model with two genes interacting under epistasis, leading to three phenotypic classes for seed-coat darkening. Under this model, the J gene, responsible for darkening (yes or no), interacts epistatically with a second gene *Sd*, that is responsible for the rate of darkening (slow or normal), where the latter recessive allele is responsible for the slow rate. Despite such discordant results and the paucity of information for such a characteristic, it is common knowledge that it is possible to select lines with slow seed-coat darkening (Faria et al., 2004; Junk-Knievel et al., 2008; Silva et al., 2008; Araújo et al., 2012; Carneiro et al., 2012).

The success of the selection process in breeding programs depends on the identification of promising segregant populations and the estimation of genetic and phenotypic parameters, which, in turn, assist in the decision-making process and allow the analyses of the structure and genetic potential of the germplasm under evaluation. Studies on the genetic variability of seed-coat darkening of common beans are important for the planning of breeding programs because the segregant populations may present low variability for the trait in question because of the similar genetic constitution of parental genotypes (Ramalho et al., 1993). Thus, variance estimates are widely utilized because they allow the estimation of heritabilities

and genetic gain under selection. Another aspect that has been observed is the occurrence of genotype by environment interactions (GxE) for the trait, which is frequently reported in the literature (Ribeiro et al., 2004; Filho et al., 2006; Junk-Knievel et al., 2007).

The objectives of this research were to study the genetic control of seed-coat darkening of common bean grains of the carioca type and to estimate phenotypic and genetic parameters in different populations that were evaluated in different environments.

MATERIAL AND METHODS

Parents and segregant populations

A line of common bean of the carioca type, BRSMG Madrepérola, which keeps its light grain color after storage (Carneiro et al., 2012), was crossed with 10 other elite lines that present normal seed-coat darkening (BRS Estilo, Pérola, BRS Cometa, BRS Pontal, BRSMG Majestoso, IAC Alvorada, IPR Saracura, IPR Siriri, CNFC 10429, and BRS Notável). Seeds of the F_1 and F_2 generations of each population were increased in a greenhouse. The F_3 generation was cultivated in the field; 720 seeds of each of the 10 populations together with the 11 parental genitors were cultivated in the winter season of 2010 at Santo Antônio de Goiás, GO (latitude 16°28'00"S, longitude 49°17'00"W, and altitude 823 m). At the harvest time, approximately 120 plants of each population were randomly harvested to give origin to $F_{3,4}$ progenies and parents. The remaining plants were harvested in bulk to attain populations in generation F_4 .

The same procedure was repeated with the F_4 generation during the 2010 rainfall season at Ponta Grossa, PR (latitude 25°05'42"S, longitude 50°09'43"W and altitude 969 m) using the bulked seed harvested in the previous generation to attain $F_{4,5}$ progenies of the 10 populations and the 11 parents.

Evaluation of seed-coat darkening

After harvesting, seeds of each progeny in both experiments were stored in polyethylene receptacles under uncontrolled temperature and humidity at Santo Antônio de Goiás, GO. $F_{3,4}$ and $F_{4,5}$ progenies were then evaluated for darkening, observing their seed tegument in the generations F_3 and F_4 because the tegument is composed of maternal tissue. In order to avoid confusion, references from this point on will be to the generation expressed by the tegument.

The evaluations were performed at 71, 106, and 155 days after harvest for both field trials. Grades were assigned relative to the tegument darkening of grains from the 120 progenies of each population according to a scale adapted from Silva et al. (2008), in which the grades were 1 (very light-colored grains), 2 (intermediate- to light-colored grains), 3 (intermediate-colored grains), 4 (intermediate- to dark-colored grains), and 5 (very dark-colored grains). The final mean score for each population was attained by calculating the average over the 120 progenies.

Statistical and genetic analyses

Initially, estimates of Pearson's correlations between evaluation trial periods (71, 106, and 155 days after harvest) were obtained for the F_3 and F_4 populations and parents for each generation as well as between the two generations. Analyses were performed using the

software GENES (Cruz, 2006).

In order to verify the genetic control of tegument darkening, progeny segregation was analyzed within each population. To attain a better discrimination of grades attributed to darkening, the evaluation at 155 days after harvesting was utilized because, at that time, the progenies showed the highest contrast between slow and normal grain darkening. Two phenotypic classes were established: slow darkening, which included progenies graded from 1 (very light-colored grains) to 3 (intermediate-colored grains), and normal darkening, which encompassed progenies graded 4 (intermediate- to dark-colored grains) and 5 (very dark-colored grains). The segregation ratios that were obtained for all populations were tested to define a genetic control model that would fit the observed frequencies.

At first, monogenic segregation based on dominance of the allele conferring normal darkening was tested, because this was the genetic model identified by Silva et al. (2008) and Araújo et al. (2012). Thus, the expected segregation in the F_2 generation would be three progenies with normal darkening (ND) to one progeny with slow darkening (SD). For the populations that did not adhere to the monogenic model, new hypotheses were formulated to better explain the results. On the basis of the model proposed by Elsadr et al. (2011), the hypothesis of digenic genetic control was tested through three assumptions: double recessive epistasis (9 SD:7 ND in F_2), double-dominant genes (15 ND:1 SD in F_2), and dominant by recessive interaction (13 ND:3 SD in F_2). The chi-square test was applied at the 5% probability level to verify the significance of the deviations. The expected segregation values were calculated for generations F_3 and F_4 because those were the actual generations used in this research.

The estimates of genetic parameters were obtained for each population at each environment using the sampled progenies. The method proposed by Melo et al. (1997), which estimates the environmental variance of each segregant population from the coefficients of environmental variation of the check treatments (parents), was utilized. Broad-sense heritability was attained using the genotypic and phenotypic variances that were also obtained according to the cited method. The expected selection gains (SG) were estimated upon the selection of the 10 best progenies in each population as described by Ramalho et al. (2008).

RESULTS

The occurrence of a highly significant positive correlation ($r \geq 0.87$, $P < 0.01$) was verified between evaluation periods (71, 106, and 155 days) and seed darkening within both the F_3 and F_4 generations (Table 1). When storage periods between generations were compared, the estimates were smaller, ranging from 0.58 to 0.80 ($P < 0.01$), although still considered to be a medium to high correlation. These are indications that seed darkening presents a similar outcome in different evaluation times so that it is not necessary to undergo several evaluations in the selection process. Hence, only one evaluation was utilized to determine the genetic control and estimate genetic parameters; the evaluation at 155 days was chosen for its high power of discrimination among grades of darkening.

The frequency distributions of seed-darkening grades of progenies at 155 days of storage indicated that 29.7 and 28.6% of the progenies evaluated at Santo Antônio de Goiás and Ponta Grossa, respectively, presented light-colored grains after storage, demonstrating the possibility of attaining genetic gain with the selection and validating studies related to the genetic control of the trait.

Table 1. Estimates of Pearson's correlation between storage time-periods for seed coat darkening within and between generations.

		Storage time-period (days)		
		106	155	-
Within F ₃	71	0.92**	0.87**	-
	106		0.92**	-
Within F ₄	71	0.90**	0.88**	-
	106		0.91**	-
Between (F ₃ and F ₄)		Storage time-period (days)		
		71	106	155
	71	0.67**	0.58**	0.59**
	106	0.75**	0.68**	0.72**
	155	0.80**	0.76**	0.80**

***t*-test significant at 1% probability.

Results of the segregation ratios that were tested from the 10 populations and evaluated at two environments are presented in Table 2. At Santo Antônio de Goiás, a monogenic segregation (3:1) was detected in four populations [BRSMG Madrepérola x (BRS Cometa, BRS Notável, BRS Pontal, and BRSMG Majestoso)]. Digenic segregation (double-recessive epistasis - 9:7) with a probability higher than 5% was detected in three populations [BRSMG Madrepérola x (Pérola, IPR Saracura, and IPR Siriri)]. The three other populations did not adhere to any of the segregation ratios tested. At Ponta Grossa, the populations that fit the monogenic segregation ratio at probabilities higher than 5% were [BRSMG Madrepérola x (Pérola, BRS Estilo, BRS Notável, and BRS Pontal)], one population (BRSMG Madrepérola x IAC Alvorada) showed digenic segregation, and five populations did not fit into any of the ratios tested. Only two populations (BRSMG Madrepérola x BRS Notável and BRSMG Madrepérola x BRS Pontal) obtained coincident results (monogenic segregation) at both locations.

The independent-gene segregation models (double-dominant genes and dominant by recessive interaction) were not identified for any of the populations at both environments; this indicates that such gene interactions are not part of the genetic control of seed-coat darkening in common beans.

The inconsistency in the rates of segregation observed in populations between environments did not allow accurate inferences in these cases. Probably, these discrepancies between the patterns of genetic control obtained at each location are due to the interaction effect of the environments.

It is worth noting that the segregation ratios of population BRSMG Madrepérola x BRSMG Majestoso, at Santo Antônio de Goiás, fit the monogenic inheritance. This result agrees with the findings of Silva et al. (2008), who evaluated progenies of this same cross at Lavras, Minas Gerais, and determined monogenic control in generations F₂ and F_{2,3}. This same population, however, when evaluated at Ponta Grossa, presented a segregation pattern that did not fit any of the working hypotheses tested in this research.

The only population that did not present any adherence to any of inheritance patterns that were tested at either of the two locations was BRSMG Madrepérola x CNFC 10429. Another important observation refers to the inconsistent outcome of the BRSMG Madrepérola x Pérola population. This population presented a segregation ratio that suggests a two-gene model with double recessive epistasis when it was evaluated at Santo Antônio de Goiás. However, when it was evaluated at Ponta Grossa, the results suggested a single gene model with dominance for the allele conferring normal grain darkening (Table 2).

Table 2. Segregation ratios for seed coat darkening, Chi-square test, expected, and observed frequencies for grains with slow darkening (SD) and normal darkening (ND) for the populations evaluated at Santo Antônio de Goiás and Ponta Grossa, at 155 days storage.

Populations	Segregation ratios in F ₂	Santo Antônio de Goiás-F ₃				Ponta Grossa-F ₄			
		OF	EF	χ ²	P (%)	OF	EF	χ ²	P (%)
		SD:ND	SD:ND			SD:ND	SD:ND		
1-BRSMG Madrepérola x Pérola	MCD-3SD:1ND	47:43	34:56	8.32	0.39	43:76	52:67	2.77	9.61
	DDRE-9SD:7ND	47:43	55:35	2.85	9.16	-	-	-	-
2-BRSMG Madrepérola x BRS Estilo	MCD-3SD:1ND	88:28	44:72	72.84	0.00	49:69	52:66	0.23	63.39
	DDRE-9SD:7ND	88:28	71:45	10.91	0.09	-	-	-	-
3-BRSMG Madrepérola x BRS Cometa	MCD-3EL:1EN	52:68	45:75	1.74	18.68	61:48	48:61	6.66	0.98
	DDRE-9EL:7EN	-	-	-	-	61:48	75:34	7.80	0.52
4-BRSMG Madrepérola x CNFC 10429	MCD-3EL:1EN	80:32	42:70	55.01	0.00	41:31	31:41	5.14	2.35
	DDRE-9EL:7EN	80:32	68:44	5.21	2.24	41:31	49:23	4.37	3.65
5-BRSMG Madrepérola x BRS Notável	MCD-3EL:1EN	49:71	45:75	0.57	45.07	39:41	35:45	0.83	36.25
	DDRE-9EL:7EN	-	-	-	-	-	-	-	-
6-BRSMG Madrepérola x BRS Pontal	MCD-3EL:1EN	45:57	38:64	1.90	16.74	47:66	49:64	0.20	65.16
	DDRE-9EL:7EN	-	-	-	-	-	-	-	-
7-BRSMG Madrepérola x BRSMG Majestoso	MCD-3EL:1EN	47:72	45:74	0.20	65.29	41:79	52:68	4.43	3.52
	DDRE-9EL:7EN	-	-	-	-	41:79	82:38	65.06	0.00
8-BRSMG Madrepérola x IAC Alvorada	MCD-3EL:1EN	91:27	44:74	79.02	0.00	59:21	35:45	29.36	0.00
	DDRE-9EL:7EN	91:27	72:46	13.03	0.03	59:21	55:25	1.06	30.33
9-BRSMG Madrepérola x IPR Saracura	MCD-3EL:1EN	58:31	33:56	29.07	0.00	62:51	49:64	5.73	1.67
	DDRE-9EL:7EN	58:31	54:45	0.68	40.92	62:51	77:36	9.57	0.20
10-BRSMG Madrepérola x IPR Siriri	MCD-3EL:1EN	66:38	39:65	29.61	0.00	65:55	52:68	5.34	2.08
	DDRE-9EL:7EN	66:38	63:41	0.29	59.24	65:55	82:38	11.25	0.08

MCD = monogenic inheritance with complete dominance. DDRE = digenic inheritance with double recessive epistasis.

The estimates of genetic parameters of the populations increased with the storage period, and the discrepancies among the progenies for seed-coat darkening were intensified over the storage time for both locations, Santo Antônio de Goiás and Ponta Grossa (Tables 3 and 4). The heritability estimates obtained reinforced the existence of genetic variability among progenies, indicating the possibility of successful selection for slow grain darkening. High magnitude values were detected in the populations, ranging from 74 to 82% at Santo Antônio de Goiás and 90 to 95% at Ponta Grossa (Table 4). These estimates were quite consistent; they were high for different locations, indicating the possibility of successful selection in both situations (Ramalho et al., 1993). However, it must be mentioned that these estimates refer to broad-sense heritabilities that contain the additive variance component and the dominance component, which could overestimate the genetic gains in new selected lines.

Table 3. Phenotypic variance estimates (σ_p^2), genetic variance (σ_G^2) and broad sense heritabilities (h^2) for the trait seed coat darkening of common beans in 10 segregant populations, evaluated over three time periods of storage at Santo Antônio de Goiás.

Populations	Time-period of storage								
	71 days			106 days			155 days		
	σ_G^2	σ_F^2	h^2	σ_G^2	σ_F^2	h^2	σ_G^2	σ_F^2	h^2
BRSMG Madrepérola x IAC Alvorada	0.28	0.41	0.69	0.29	0.46	0.62	0.54	0.71	0.75
BRSMG Madrepérola x BRS Estilo	0.17	0.31	0.55	0.31	0.47	0.67	0.66	0.85	0.77
BRSMG Madrepérola x IPR Saracura	0.32	0.44	0.72	0.60	0.82	0.73	0.85	1.07	0.79
BRSMG Madrepérola x Pérola	0.32	0.49	0.65	0.89	1.18	0.76	1.13	1.38	0.82
BRSMG Madrepérola x CNFC 10429	0.25	0.40	0.61	0.49	0.70	0.71	0.56	0.75	0.74
BRSMG Madrepérola x IPR Siriri	0.26	0.39	0.66	0.69	0.90	0.76	1.00	1.23	0.81
BRSMG Madrepérola x BRSMG Majestoso	0.31	0.47	0.66	0.53	0.78	0.68	1.02	1.33	0.77
BRSMG Madrepérola x BRS Cometa	0.07	0.25	0.30	0.83	1.11	0.75	1.07	1.36	0.79
BRSMG Madrepérola x BRS Pontal	0.25	0.39	0.63	0.25	0.49	0.52	1.08	1.38	0.78
BRSMG Madrepérola x BRS Notável	0.15	0.34	0.42	0.77	1.10	0.70	1.01	1.31	0.77
Average	0.24	0.39	0.59	0.56	0.80	0.69	0.89	1.14	0.78

Table 4. Phenotypic variance estimates (σ^2_P), genetic variance (σ^2_G), and broad sense heritabilities (h^2) for the trait seed coat darkening of common beans in 10 segregant populations, evaluated over three time periods of storage at Ponta Grossa.

Populations	Time-periods of storage								
	71 days			106 days			155 days		
	σ^2_G	σ^2_P	h^2	σ^2_G	σ^2_P	h^2	σ^2_G	σ^2_P	h^2
BRSMG Madrepérola x IAC Alvorada	0.06	0.17	0.35	0.13	0.30	0.44	0.71	0.79	0.90
BRSMG Madrepérola x BRS Estilo	0.05	0.17	0.31	0.40	0.62	0.65	1.10	1.19	0.92
BRSMG Madrepérola x IPR Saracura	0.15	0.28	0.52	0.68	0.88	0.77	1.04	1.11	0.93
BRSMG Madrepérola x Pérola	0.26	0.41	0.65	0.73	0.98	0.74	1.11	1.21	0.92
BRSMG Madrepérola x CNFC 10429	0.24	0.39	0.61	0.54	0.76	0.70	0.85	0.93	0.92
BRSMG Madrepérola x IPR Siriri	0.06	0.17	0.36	0.56	0.77	0.74	1.07	1.13	0.94
BRSMG Madrepérola x BRSMG Majestoso	0.18	0.36	0.50	0.46	0.68	0.67	1.37	1.47	0.93
BRSMG Madrepérola x BRS Cometa	0.30	0.44	0.68	0.79	0.99	0.80	1.68	1.76	0.95
BRSMG Madrepérola x BRS Pontal	0.35	0.53	0.66	0.77	1.01	0.76	1.32	1.42	0.93
BRSMG Madrepérola x BRS Notável	0.15	0.35	0.44	0.39	0.63	0.61	1.41	1.50	0.94
Average	0.18	0.33	0.51	0.54	0.76	0.69	1.17	1.25	0.93

In general, the expected SGs at Ponta Grossa were superior to those found at Santo Antônio de Goiás, despite their similar averages (Table 5). The greatest SGs were presented by populations BRSMG Madrepérola x BRSMG Majestoso, BRSMG Madrepérola x Pérola, BRSMG Madrepérola x BRS Pontal, BRSMG Madrepérola x BRS Notável, and BRSMG Madrepérola x BRS Cometa.

Table 5. Means for darkening of the 10 most lights (10+) broad sense heritabilities (h^2) and expected selection gain (SG) of the best families of the populations evaluated at Santo Antônio de Goiás and Ponta Grossa, at 155 days of storage.

Populations	Santo Antônio de Goiás				Ponta Grossa			
	Overall mean	h^2	Average (+10)	SG (%)	Overall mean	h^2	Average (+10)	SG (%)
BRSMG Madrepérola x IAC Alvorada	2.84 ^a	0.75	2.00	-22.29	3.42 ^a	0.90	2.00	-37.37
BRSMG Madrepérola x BRS Estilo	2.96 ^a	0.77	2.00	-25.12	3.62 ^a	0.92	2.00	-41.17
BRSMG Madrepérola x CNFC 10429	2.99 ^a	0.74	2.00	-24.65	3.35 ^a	0.92	2.00	-37.07
BRSMG Madrepérola x IPR Saracura	3.19 ^a	0.79	2.00	-29.55	3.28 ^a	0.93	2.00	-36.29
BRSMG Madrepérola x IPR Siriri	3.23 ^a	0.81	2.00	-31.01	3.24 ^a	0.94	2.00	-35.97
BRSMG Madrepérola x Pérola	3.37 ^a	0.82	2.00	-33.34	3.83 ^a	0.92	2.00	-43.96
BRSMG Madrepérola x BRS Cometa	3.62 ^b	0.79	2.00	-35.35	3.46 ^a	0.95	2.00	-40.09
BRSMG Madrepérola x BRS Notável	3.72 ^b	0.77	2.00	-35.59	3.62 ^a	0.94	2.00	-42.07
BRSMG Madrepérola x BRS Pontal	3.74 ^b	0.78	2.00	-36.28	3.77 ^a	0.93	2.00	-43.66
BRSMG Madrepérola x BRSMG Majestoso	3.75 ^b	0.77	2.00	-35.91	3.86 ^a	0.93	2.00	-44.81

Means followed by the same superscript letter in the same column do not differ statistically by the Scott-Knott test at 5 and 10% probability levels.

All of the generated populations presented potential for selection of lines with slow grain darkening. Nevertheless, segregant populations that showed low averages for darkening and associated with high SG were BRSMG Madrepérola x IAC Alvorada, BRSMG Madrepérola x BRS Estilo, BRSMG Madrepérola x CNFC 10429, BRSMG Madrepérola x IPR Saracura, BRSMG Madrepérola x IPR Siriri, and BRSMG Madrepérola x Pérola, and hence, are the most indicated for the selection of lines with slow seed-coat darkening. It is worth noting the superiority of these populations because they were always part of the group of populations with the best averages for slow seed-coat darkening and were associated with relevant SGs.

DISCUSSION

The elucidation of the genetic control of grain darkening is fundamentally important for the establishment of breeding programs that aim to develop cultivars with slow seed-coat darkening during the storage period. The results demonstrated that the inheritance of grain darkening is due to monogenic control in 40% of the situations that were analyzed in this research, with the allele conferring normal grain darkening being dominant. Such results were confirmed by other research presented in the literature. Junk-Knievel et al. (2008), upon evaluating pinto beans, verified that grain darkening was controlled by a single gene with dominance being conferred by the allele expressing normal darkening. Similar results were obtained by Silva et al. (2008) and Araújo et al. (2012), who described an analogous genetic control upon evaluation of progenies from a single carioca bean population. On the other hand, Elsadr et al. (2011) determined that two genes in recessive epistasis, expressing three phenotypic classes, controlled grain darkening in bean populations that originated from pinto beans, cranberry-like beans, and two genetic testers for the *j* allele. According to the authors, the *J* gene would be responsible for grain darkening and would also be epistatic to a second gene *Sd*, which would be responsible for the rate of darkening. In our research, however, two-gene control for seed-coat darkening was detected only in some populations.

Junk-Knievel et al. (2008) detected variability for grain darkening within phenotypic classes. A possible explanation could be related to differences in the maturity of the genotypes, which implicates variation in the degree of darkening before harvesting. The authors suggest further that modifier genes influence the complete extension of darkening for both phenotypic classes, suggesting a quantitative or environmental effect over such classes.

It is worth mentioning that, in our research, the effect of generations is confounded with the time of sowing because generations were obtained from different sowing times, and this is a factor of major importance for environmental characterization. At Santo Antônio de Goiás, the winter crop environment is dry, which is a favorable condition for harvest. On the other hand, at Ponta Grossa, the rainfall season is characterized by high humidity and high temperatures, with high rainfall incident during harvest. The variation of segregant proportions for seed-coat darkening demonstrates that the progenies were affected by environmental conditions; hence, part of the differences could be attributed to environmental effects.

Several factors that may affect grain darkening were already described. Park and Maga (1999) verified that darkening is accelerated by high grain humidity and light incidence. Ribeiro et al. (2004) reported a differential response of cultivars to years and growing seasons and reported that grain darkening is favored in rainy seasons. The same authors concluded that an excess of humidity, especially during grain filling, contributes to greater seed-coat darkening of carioca beans. Junk-Knievel et al. (2007) observed that beans that were produced under irrigation presented lighter seed coats than those grown under dry land conditions. Araújo et al. (2012) indicated that grain darkening is greatly influenced by the environment, growing season, and location. Other results demonstrated that the variability in rate of darkening was due to the sensibility of the genotypes to environmental variations and to the effects of GxE interactions upon the trait (Ribeiro et al., 2004; Filho et al., 2006; Junk-Knievel et al., 2007). These results denote the importance of the environmental conditions and the influence of the GxE interaction on the evaluation of the characteristic.

Some studies with common beans reported the great influence of the environment

on the determination of genetic control of several traits. Cunha et al. (2005), upon evaluating plant architecture, concluded that results obtained for progenies were not coincident over different generations/growing seasons. Similar result was observed by Collicchio et al. (1997), who evaluated plant architecture and seed size. Silva et al. (2008), in a study of genetic control of grain darkening, identified the inconsistent performance of progenies over generations/growing seasons.

Overall, there is strong evidence that grain seed-coat darkening is under oligogenic control because more than half of the populations evaluated in two environments presented genetic control governed by one or two genes. However, the inconsistency in the segregation patterns observed in populations in different environments does not allow for precise inferences. Such inconsistencies between patterns of genetic control in each location may be because of the interaction between progenies and environments. Hence, a more precise definition of the genetic control of grain darkening is not yet conclusive.

From these results, it is evident that further studies and evaluations in other populations that were preferably obtained from different genotypes with slow seed-coat darkening are required for a better definition of the genetic control of the trait because diverse populations do not show the same segregation pattern. Furthermore, the necessity of evaluating genetic control under distinct environments became clear because the GxE interaction may alter the performance of the progenies under evaluation and distort the conclusions. This is an important finding because research that utilizes several populations and distinct environments for genetic control studies of common beans traits are scarce. Evaluations at a single environment may lead to segregations specific to that environment, generating results of genetic control that may not be consistent in other environments.

The evaluation of the nature of the genetic effects that control a trait is of paramount importance because traits are descriptive parameters of the genetic control. Such parameters, in turn, are aids to the selection process and the prediction of the performance of segregation generations. The presence of genetic variability in seed-coat darkening makes the incorporation of the trait into new cultivars possible. The estimates of genetic variance among progenies increased with increasing storage time (Tables 3 and 4); this conclusion was also reported by Silva et al. (2008) and Araújo et al. (2012). This result becomes evident from the heritability estimates that were observed in both experiments. Despite these estimates ranging from 74 to 95%, one may foresee the possibility of successful selection in some of the populations even with the earliest evaluation. Silva et al. (2008) verified broad-sense heritability values ranging from 90.6 to 91.1% at 90 days of storage for generations F_2 and $F_{2,3}$, respectively. Araújo et al. (2012) obtained similar heritability estimates at 60 days of storage (85.9% in $F_{2,3}$ at Lavras and 87.2% in $F_{2,4}$ at Patos de Minas).

Furthermore, the high magnitude of the estimates of correlation between the average performance of the progenies and the evaluations for darkening indicate that the identification of favorable lines for the trait may occur at any time during storage and in accordance with the breeder interest. However, the estimates were quite high, especially in the evaluations at 106 and 155 days of storage considering the different generations (Table 4). Similar results were reported by Silva et al. (2008), who found that the greatest correlation indexes were detected between the latest evaluation periods that were utilized (60 and 90 days). In the generations F_2 and $F_{2,3}$, the estimates of correlations obtained were 0.99 and 0.92, respectively. An advantage of performing the evaluations at 155 days of storage is the possibility of associating them with

other traits, such as the cooking capacity of the grain after storage. This would make possible the identification of lines that would preserve both light-colored grains and short cooking time for a longer period of time.

Through oligogenic genetic control and genetic variability for grain darkening, it is possible to obtain lines that present slow darkening of the grains, which can be selected from the promising populations identified in this research.

CONCLUSIONS

Seed-coat darkening in common beans is under oligogenic genetic control. It is possible to select common bean lines of the carioca type with slow seed-coat darkening. The GxE interaction affects seed-coat darkening in common beans; therefore, it is necessary to evaluate the trait in several environments to assess genetic control and select lines.

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