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ORIGINAL PAPER

Genetic analysis of single-locus and epistatic QTLs for seed traits in an adapted × nuña RIL population of common bean (*Phaseolus vulgaris* L.)

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Abstract
Key message **The QTLs analyses here reported demonstrate the significant role of both individual additive and epistatic effects in the genetic control of seed quality traits in the Andean common bean.**
Abstract Common bean shows considerable variability in seed size and coat color, which are important agronomic traits determining farmer and consumer acceptability. Therefore, strategies must be devised to improve the genetic base of cultivated germplasm with new alleles that would contribute positively to breeding programs. For that purpose, a population of 185 recombinant inbred lines derived from an Andean intra-gene pool cross, involving an adapted common bean (PMB0225 parent) and an exotic nuña bean (PHA1037 parent), was evaluated under six different—short and long-day—environmental conditions for seed dimension, weight, color, and brightness traits, as well as the number of seed per pod. A multi-environment Quantitative Trait Loci (QTL) analysis was carried out and 59 QTLs were mapped on all linkage groups, 18 of which had only individual additive effects, while 27 showed only epistatic effects and 14 had both individual additive and epistatic effects. Multivariate models that included significant QTL explained from 8 to 68 % and 2 to 15 % of the additive and epistatic effects, respectively. Most of these QTLs were consistent over environment, though interactions between QTLs and environments were also detected. Despite this, QTLs with differential effect on long-day and short-day environments were not found. QTLs identified were positioned in cluster, suggesting that either pleiotropic QTLs control several traits or tightly linked QTLs for different traits map together in the same genomic regions. Overall, our results show that digenic epistatic interactions clearly play an important role in the genetic control of seed quality traits in the Andean common bean.

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Introduction

Common bean (*Phaseolus vulgaris* L., $2n = 22$), a member of the Fabaceae family, is one of the most important grain legume crops for direct human worldwide consumption due to its high seed protein content and quality (Broughton et al. 2003), which occupies 85 % of the production area dedicated to the *Phaseolus* species (Singh 2001). Seed size and coat color are important agronomic traits in common bean, the former also being an important component of yield (Al-Mukhtar and Coyne 1981; Conti 1982, 1985). Common bean presents a great variety of phenotypes regarding seed size and coat color, and consumers have developed specific preferences for different combinations of seed size,

shape, and color (Beninger and Hosfield 2003). In fact, a wide phenotypic variability has been reported as a result of the domestication process, although only <5 % of the available genetic diversity has been used globally, and in consequence the genetic base of the modern new world common bean varieties is narrow (Broughton et al. 2003; Acosta-Gallegos et al. 2007). Therefore, strategies must be carried out to enrich the genetic base of the cultivated common bean with new alleles which enhance consumer acceptability.

Domestication of wild types from diverging taxa is known to have occurred in two distinct centers of origin in South America and Central America, giving rise to the Andean and Mesoamerican gene pools, respectively (Gepts 1998; Chacón et al. 2005). In both gene pools, most common bean improvements have been made using crosses among elite germplasm rather than crosses with exotic germplasm or wild relatives. However, exotic germplasm could be an important source of genes especially for disease and pest resistance and food industry-related characters (Acosta-Gallegos et al. 2007). Popbean or nuña bean cultivars seem to originate in the Andes, where they are sympatric with wild populations in Peru and Bolivia, and they may have been present in the early stages of Andean agriculture (Voysest 1983; Gepts et al. 1986; Zimmerer 1986). Nuña bean is consumed as a snack after grains explode in response to heating, its texture and flavor often described as being similar to roasted peanuts, and it is becoming increasingly relevant as a new food product in the agro-food industry due to its nutritional and health properties. However, since seed quality-related traits are key factors determining its commercial acceptance, there is a need to identify and transfer novel alleles from unadapted to cultivated germplasm. Molecular tools provide a way to tap successfully the genetic diversity available in exotic germplasm and allow the isolation of beneficial genes that are often tied up in unfavorable linkages, to transfer them into elite commercial germplasm (Tanksley and McCouch 1997).

Significant attention has long been paid to the inheritance of common bean seed size and coat color. Seed size in cultivated beans has been described as a polygenic trait (Sax 1923), and complex quantitative inheritance patterns of some determinants of bean seed size and shape such as seed length, width, and height have been reported (Vallejos and Chase 1991). In addition, the genetic association between seed weight and seed pigmentation (*P* gene) was found by Sax (1923). Seed coat color shows a complex genetic inheritance, where many of these genes display epistatic interactions that define the many colors observed within the species (McClean et al. 2002). According to the currently accepted model (Prakken 1970, 1972), *C*, *D*, and *J* are genes for seed color and are expressed only in the presence of gene *P*, which is hyperstatic to all seed color and pattern genes and determines color expression in both seed coats and flowers (Emerson 1909). The *P* locus, particularly important as the basic color gene, has multiple alleles for seed coat and flower pattern and is known as the ground factor for all seed coat color genotypes (Bassett 2007). In addition, there are modifier genes (*G*, *B*, *V*, and *Rk*) that intensify colors or influence their hue (McClean et al. 2002).

Genetic segregation analysis over multi-generations and mapping of Quantitative Trait Loci (QTL) are the main approaches taken to clarify the genetic basis of quantitative traits, which also include their mode of action and how their function is modulated by the environment (Xiao et al. 1996). A relatively large number of linkage maps have been developed in common bean, most of them created from inter-gene pool crosses, which have been used to identify single-locus QTLs for plant architecture (Koinange et al. 1996; Tar'an et al. 2002; Blair et al. 2006), flowering and maturity time (Koinange et al. 1996; Johnson and Gepts 2002; Tar'an et al. 2002; Beattie et al. 2003; Blair et al. 2006; Pérez-Vega et al. 2010), yield (Koinange et al. 1996; Johnson and Gepts 2002; Tar'an et al. 2002; Beattie et al. 2003; Blair et al. 2006), pod fiber (Koinange et al. 1996), seed size (Koinange et al. 1996; Tsai et al. 1998; Park et al. 2000; Tar'an et al. 2002; Guzman-Maldonado et al. 2003; Blair et al. 2006; Pérez-Vega et al. 2010), seed coat color (Caldas and Blair 2009), and popping (Yuste-Lisbona et al. 2012). Holland (2001) pointed out that, in autogamous plants, epistasis is to be expected in traits that are controlled by several genes/QTLs. Strong interactions between QTLs have been detected in common bean for seed yield (Johnson and Gepts 2002). If alleles involved in positive epistatic interactions are not transferred together to the cultivar that is being developed, improvement will be unsuccessful due to the presence of epistatic effects (Lark et al. 1995). To date, there are no reports on the combined identification of single-locus and epistatic QTLs and their environment interaction effects on seed size and coat color in common bean. Therefore, the aim of this study was to identify the genomic region associated with seed size and coat color, and estimate the genetic parameters affecting these traits, including main effects, digenic epistasis, and genotype by environment interactions. For that purpose, nine seed size and color traits have been evaluated in a recombinant inbred line (RIL) population derived from a cross between two Andean common bean genotypes under six different environmental conditions. Single-locus and two-loci QTL analyses indicated that both individual additive and epistatic effects were important in the genetic basis of seed size and color traits, and were also subject to environmental modification. These results could be used for enhancing the efficiency of common bean breeding programs through

the implementation of optimal strategies of marker-assisted selection (MAS).

Materials and methods

Population development

A RIL population consisting of 185 F_7 lines was developed by single-seed descent from an F_2 population generated from the cross of two lines belonging to the Andean gene pool, PMB0225 and PHA1037. Both parents are large seeded (>45 g 100 seed $wt^{-1)}$ and differ in several agronomic traits: PMB0225 (abbreviated as P1) is a white-seeded dry bean line, resistant to the bean common mosaic virus, and shows indeterminate erect growth habit type II; while PHA1037 (abbreviated as P2) is a photoperiod-sensitive red-seeded nuña bean line and shows an indeterminate climbing growth habit type IV.

Experimental design

Fifteen plants from each of the 185 RILs and their parents were grown in six greenhouse environments of Pontevedra (Northwest Spain, 42º 24′ N, 8º 38′ W, 40 masl) over three consecutive years (2009, 2010 and 2011). With the aim to assess if seed traits were affected by photoperiod conditions, greenhouse assays were developed under long-day (LD, more than 12 h of light) and short-day (SD, <12 h) natural photoperiod conditions and an average day/night temperature of 25/20 °C. Sowing dates of LD experiments were February 20, 2009 (LD09 code), March 15, 2010 (LD10 code), March 1, 2011 (LD11a code), and April 27, 2011 (LD11b code); while sowing dates of SD experiments were August 15, 2009 (SD09 code) and September 21, 2010 (SD10 code). For all environments, the experiments were conducted in a randomized complete block design with two or three replicates of single row plots (3.0 × 0.8 m). Each plot was sown with two seeds per hill and adjusted to a crop density of about 30,000 plants/ha. Pods were harvested when they were completely dried. Seeds were removed and cleaned using a mechanical thresher followed by hand cleaning and winnowing.

Phenotypic evaluation

Five plants from each RIL family were selected randomly and their seeds were used to represent the phenotype. As seeds matured, the weight of 100 seeds was determined for each line, and two seeds from the middle of one pod per plant were collected for the rest of phenotypic evaluation. Seed size data were determined after drying for 72 h at 80 °C (Escribano et al. 1997). The quantitative seed size and color traits included (1) width (SWI), the longest distance across the hilum; (2) thickness (ST), measured from hilum to opposite side; (3) length (SL), measured parallel to the hilum; (4) the size index (SSI), as the length by width; (5) weight (SW), determined on 100 dry seeds per plot; (6) primary or darker coat color (PSC), scored as 0 = white, 1 = lilac, 2 = purple, 3 = black, and 4 = red; (7) secondary or lighter coat color (SSC), measured as 0 = absence of pigmentation, and 1 = presence of pigmentation; (8) brightness (SB), recorded as 0 = matt seed, 1 = medium brightness seed, and 2 = shiny seed; and (9) the number of seeds per pod (SP). Unlike other traits, the number of seeds per pod was evaluated in only four environmental conditions (SD09, LD09, SD10, and LD10).

Statistical data analysis

Variation in the expression of seed size and color traits across all the environments was analyzed using PROC MIXED (SAS Institute Inc. v. 9.02, 2010, Cary, NC, USA), and considering the following random factors: lines, environments, replication within environments, and the line by environment interaction. The main effects of random factors were tested with likelihood-ratio tests (Littell et al. 1996). Each location by year combination was considered a separate environment in the analysis. Each trait was first analyzed by one-way ANOVA for each environment individually, and then for the combined environments. A one-way ANOVA (PROC MIXED, SAS) was carried out to compare means between photoperiod treatments (SD vs LD) and parents (PHA1037 vs PMB225). Descriptive statistical parameters (mean value, standard deviation, and range of variation), variances, and normality (Kolmogorov–Smirnov test) were obtained for each phenotypic trait and environment. PSC, SSC, and SB traits failed to meet normality assumptions, and the Box–Cox transformation was used prior to analysis to identify transformations that improved normality. Variance components and broad-sense heritabilities with their standard errors were estimated by restricted maximum likelihood (REML) option of the PROC MIXED and IML (SAS Institute Inc. v. 9.02, 2010, Cary, NC, USA) for the phenotypic traits (Holland et al. 2003; Holland 2006). Phenotypic Pearson correlation coefficients among traits were implemented using PROC CORR across the environments (SAS Institute Inc. v. 9.02, 2010, Cary, NC, USA).

QTL detection

The genetic linkage map described by Yuste-Lisbona et al. (2012) was used for QTL analysis. The morphological marker *P* locus was added to this map, which finally consisted of 194 loci (85 AFLP, 95 SSR, 13 SNP, and *P* locus)

distributed on 12 linkage groups (LGs). The map spanned 824.95 cM, with an average distance of 4.3 cM between adjacent markers. Marker data were analyzed by JoinMap® 4.0 software (van Ooijen 2006). A minimum logarithm of odds ratio (LOD) score of 6.0 and a recombination frequency value of 0.3 were set as the linkage threshold for grouping markers. The Kosambi map function (Kosambi 1944) was used to calculate the genetic distance between markers. The LGs were designated according to Pedrosa-Harand et al. (2008).

QTLNetwork 2.0 software (Yang et al. 2008) was used to identify single-locus QTLs, epistatic QTLs (E-QTL) and their environment interaction effects (QTLs × Environment, QE; and E-QTLs × Environment, E-QE). The mixed-model-based composite interval mapping method (MCIM) was carried out for one-dimensional genome scan to detect putative QTLs and their environment interactions, and for two-dimensional genome scan to identify epistatic interaction effects. The average trait values for each RIL assessed in each environment were used for MCIM. An experimental-wise significance level of 0.05 was designated for candidate interval selection, putative QTL detection, and QTL effect. Both testing and filtration window size were set at 10 cM, with a walk speed of 1 cM. The critical F value to declare putative QTLs was determined by the 1,000 permutation test. The effects of QTLs and environment interactions were estimated by the Markov Chain Monte Carlo method (Wang et al. 1994). QTLs with only genetic effects indicated that these were expressed in the same way across environments. In addition, QTLs with environment interaction effects suggested that their expressions were environmentally dependent. The detected QTLs were designated as recommended by Miklas and Porch (2010). The genetic map and the QTLs detected were drawn using the MapChart 2.2 software (Voorrips 2002). Markers linked to the significant single-locus and epistatic QTLs identified by MCIM were assembled into a multiple regression model, to determine the total proportion of the phenotypic variation explained by individual additive and epistatic effects. For this purpose, a PROC REG (SAS Institute Inc. v. 9.02, 2010, Cary, NC, USA) was used.

Results

Seed size and coat color phenotype in different environments

PMB0225 and PHA1037 were significantly different for seed size and coat color in the SD environments ($P < 0.05$) except for SL and SP in SD09 environment, and for SSC in SD environments (Table 1). PHA1037 is a short-day line and consequently it develops flowers only when day photoperiod length is <12 h, while PMB225 flowers independently to the photoperiod conditions. For this reason, no seed data were taken from PHA1037 under LD conditions. The predicted means of the seed size and color traits in the testing environments fitted a normaldistribution, with the exception of PSC, SSC, and SB traits (data not shown). This type of distribution is typicalof polygenic traits showing a phenotypic segregation suitable for QTL mapping, while the PSC, SSC, and SB deviated from normality. Transgressive segregation in both directions was observed for seed shape and weight (SWI, ST, SL, SSI and SW), SB and SP traits under the different environments, indicating that both parents carry genes that contribute to seed variation. Variance analysis was conducted for each environment and difference between blocks was not significant for most of the environments and traits. Combined analyses of variance showed significant differences among lines and environments, and a significant interaction of line by environment for most of the traits except for PSC and SSC, which only showed differences among lines (data not shown). Broad-sense heritability was calculated considering all the different environments (Table 2). Overall, the highest broad-sense heritability estimates (≥90 %) were obtained for PSC, SSC, and SB. Seed dimension traits (SWI, ST, SL, SSI) showed moderate to high average heritability estimates (≥60 %). Relatively moderate heritability estimates for SW have also been reported in common bean, ranging from 56 to 81 % (Singh 1991). Conti (1985) reported moderated h^2 values for ST (47 %) and SWI (65 %). Estimated single-site heritability for SW was low to moderate (39–69 %) in the different environmental conditions, while a low heritability estimate (<40 %) was observed for SP in SD09 and LD09 conditions. Overall, RIL populations in all environments demonstrated quite high heritability estimates, suggesting that selective breeding can improve the seed size and coat color traits. The phenotypic correlation analysis (Table 3) showed that seed shape traits (SWI, ST, SL, and SSI) were correlated positively with SW trait ($r = 0.84^{**}$, 0.79^{**}, 0.60^{**}, and 0.84^{**}, respectively), and negatively with SP trait ($r = -0.31^{**}$, -0.18^{**}, -0.16^{**}, and -0.28^{**}, respectively). A positive association between PSC and SSC ($r = 0.59^{**}$) was observed.

Single-locus QTLs

Five plants of each 185 RILs from the PMB0225 × PHA1037 population were characterized under LD and SD natural photoperiod conditions, which allowed the identification of 32 significant single-locus QTLs across environments (three for SWI, two for ST, six for SL, four for SSI, four for SW, five for PSC, four for SSC, two for SB, and two for SP). Twenty of these QTLs only showed significant genetic main effects, while the remaining 12

Table 1 Phenotypic evaluation (means, standard errors, range of variation and variance analysis results) for seed traits of the two common bean parents, PMB0225 and PHA1037, and the RIL population grown in six different environments (Env), including long-day (LD) and short-day (SD) photoperiod conditions

Trait	Env	Block effect	Parents				RILs			
			PMB0225	PHA1037	P^a_{PAR}	N^b	Mean	Range	P^a_{RIL}	P^a_{LD-SD}
Width (mm)	LD09	*	8.91 ± 0.10	ND		137	8.64 ± 0.04	7.05–10.26	**	
	SD09	ns	9.57 ± 0.16	8.60 ± 0.18	**	151	8.59 ± 0.04	5.78–14.97	**	
	LD10	ns	9.14 ± 0.52	ND		139	8.47 ± 0.06	6.61–16.61	**	
	SD10	ns	10.94 ± 0.04	8.68 ± 0.20	**	179	9.71 ± 0.04	6.36–11.94	**	
	LD11a	ns	9.31 ± 0.11	ND		79	8.44 ± 0.06	6.73–10.00	**	
	LD11b	**	9.10 ± 0.26	ND		136	7.82 ± 0.04	6.01–9.68	**	
	LD		9.29 ± 0.25	ND		164	8.26 ± 0.04	7.19–9.67		**
	SD		10.15 ± 0.06	8.63 ± 0.17		183	9.20 ± 0.04	7.33–10.56		
Thickness (mm)	LD09	**	7.55 ± 0.12	ND		137	6.97 ± 0.04	4.99–8.70	**	
	SD09	ns	8.17 ± 0.14	7.38 ± 0.18	*	151	7.00 ± 0.05	4.53–8.84	**	
	LD10	ns	8.12 ± 0.33	ND		139	6.82 ± 0.05	3.94–9.06	**	
	SD10	ns	8.53 ± 0.10	7.46 ± 0.20	**	179	7.81 ± 0.03	5.28–9.69	**	
	LD11a	ns	8.50 ± 0.03	ND		79	6.86 ± 0.06	4.97–8.72	**	
	LD11b	ns	8.16 ± 0.33	ND		136	6.44 ± 0.04	4.64–13.62	**	
	LD		8.08 ± 0.20	ND		164	6.74 ± 0.04	4.87–8.28		**
	SD		8.35 ± 0.12	7.42 ± 0.20		183	7.46 ± 0.04	5.78–9.28		
Length (mm)	LD09	**	12.03 ± 0.12	ND		137	12.40 ± 0.09	8.53–15.29	**	
	SD09	ns	12.08 ± 0.14	11.65 ± 0.15	ns	151	11.93 ± 0.08	8.53–15.21	**	
	LD10	ns	12.38 ± 0.22	ND		139	12.57 ± 0.09	8.16–15.79	**	
	SD10	ns	13.86 ± 0.29	11.91 ± 0.10	**	179	13.28 ± 0.06	9.94–17.58	**	
	LD11a	ns	12.29 ± 0.17	ND		79	12.16 ± 0.09	9.06–14.52	**	
	LD11b	**	12.09 ± 0.20	ND		136	11.61 ± 0.07	8.53–14.90	**	
	LD		12.19 ± 0.12	ND		164	12.09 ± 0.09	8.66–14.70		**
	SD		12.96 ± 0.15	11.80 ± 0.12		183	12.65 ± 0.08	9.66–15.80		
Size index	LD09	**	106.10 ± 2.11	ND		137	107.43 ± 1.01	64.58–144.62	**	
	SD09	ns	115.62 ± 3.22	100.33 ± 3.16	*	151	102.73 ± 0.93	51.15–178.42	**	
	LD10	ns	113.21 ± 8.46	ND		139	106.97 ± 1.20	59.11–236.11	**	
	SD10	ns	141.59 ± 3.50	103.40 ± 3.19	**	179	129.29 ± 0.89	84.55–198.27	**	
	LD11a	ns	114.34 ± 2.85	ND		79	102.70 ± 1.16	69.44–131.63	**	
	LD11b	**	110.07 ± 3.74	ND		136	91.11 ± 0.76	54.59–126.31	**	
	LD		110.93 ± 4.25	ND		164	100.37 ± 1.08	70.10–136.22		**
	SD		123.60 ± 3.36	101.86 ± 3.17		183	116.98 ± 1.02	83.12–158.96		
Weight (g/100 seeds)	LD09	ns	46.07 ± 2.86	ND		137	48.69 ± 0.87	23.28–83.00	**	
	SD09	ns	71.05 ± 3.25	52.60 ± 2.68	**	151	50.67 ± 0.69	11.00–98.96	**	
	LD10	ns	63.30 ± 8.04	ND		139	47.93 ± 0.71	15.50–73.52	**	
	SD10	ns	77.71 ± 0.00	54.16 ± 0.00	*	179	57.81 ± 0.86	41.80–116.00	**	
	LD11a	ns	66.70 ± 1.00	ND		79	48.58 ± 0.83	27.66–74.90	**	
	LD11b	**	62.73 ± 3.24	ND		136	41.30 ± 0.48	13.30–65.90	**	
	LD		59.70 ± 3.77	ND		164	45.76 ± 0.66	26.50–83.00		**
	SD		74.38 ± 1.60	53.38 ± 1.32		183	59.69 ± 0.62	34.25–88.35		
Primary coat color[c]	LD09	ns	0.00 ± 0.00	ND		137	1.41 ± 0.13	0.00–4.00	**	
	SD09	ns	0.00 ± 0.00	4.00 ± 0.00	**	153	1.46 ± 0.12	0.00–4.00	**	
	LD10	ns	0.00 ± 0.00	ND		139	1.34 ± 0.10	0.00–4.00	**	
	SD10	ns	0.00 ± 0.00	4.00 ± 0.00	**	180	1.47 ± 0.11	0.00–4.00	**	
	LD11a	ns	0.00 ± 0.00	ND		79	1.56 ± 0.15	0.00–4.00	**	
	LD11b	ns	0.00 ± 0.00	ND		136	1.39 ± 0.08	0.00–4.00	**	

Table 1 continued

Trait	Env	Block effect	Parents				RILs			
			PMB0225	PHA1037	P^{a}_{PAR}	N^{b}	Mean	Range	P^{a}_{RIL}	$P^{a}_{LD–SD}$
	LD		0.00 ± 0.00	ND		163	1.42 ± 0.11	0.00–4.00		ns
	SD_		0.00 ± 0.00	4.00 ± 0.00		183	1.47 ± 0.11	0.00–4.00		
Secondary coat color[d]	LD09	ns	0.00 ± 0.00	ND		137	0.34 ± 0.04	0.00–1.00	**	
	SD09	ns	0.00 ± 0.00	0.00 ± 0.00	ns	153	0.32 ± 0.04	0.00–1.00	**	
	LD10	ns	0.00 ± 0.00	ND		139	0.39 ± 0.03	0.00–1.00	**	
	SD10	ns	0.00 ± 0.00	0.00 ± 0.00	ns	180	0.33 ± 0.03	0.00–1.00	**	
	LD11a	ns	0.00 ± 0.00	ND		79	0.45 ± 0.05	0.00–1.00	**	
	LD11b	ns	0.00 ± 0.00	ND		136	0.40 ± 0.03	0.00–1.00	**	
	LD		0.00 ± 0.00	ND		163	0.35 ± 0.04	0.00–1.00		ns
	SD		0.00 ± 0.00	0.00 ± 0.00		183	0.33 ± 0.03	0.00–1.00		
Brightness[e]	LD09	ns	1.00 ± 0.00	ND		137	0.61 ± 0.06	0.00–2.00	**	
	SD09	ns	1.00 ± 0.00	0.00 ± 0.00	**	153	0.57 ± 0.06	0.00–2.00	**	
	LD10	ns	1.00 ± 0.00	ND		139	0.67 ± 0.05	0.00–2.00	**	
	SD10	ns	1.00 ± 0.00	0.00 ± 0.00	**	180	0.48 ± 0.05	0.00–2.00	**	
	LD11a	ns	1.00 ± 0.00	ND		79	0.76 ± 0.07	0.00–2.00	**	
	LD11b	ns	1.00 ± 0.00	ND		136	0.73 ± 0.04	0.00–2.00	**	
	LD		1.00 ± 0.00	ND		163	0.61 ± 0.06	0.00–2.00		ns
	SD		1.00 ± 0.00	0.00 ± 0.00		183	0.51 ± 0.05	0.00–2.00		
Seeds per pod	LD09	ns	4.15 ± 0.25	ND		151	4.42 ± 0.08	1.00–8.00	**	
	SD09	ns	4.00 ± 0.28	4.17 ± 0.27	ns	153	4.71 ± 0.07	2.00–7.50	**	
	LD10	ns	4.00 ± 0.37	ND		142	4.06 ± 0.07	1.50–7.50	**	
	SD10	ns	3.67 ± 0.22	4.47 ± 0.24	*	185	3.44 ± 0.05	1.00–7.00	**	
	LD11a		NE	NE			NE	NE		
	LD11b		NE	NE			NE	NE		
	LD		4.07 ± 0.26	ND		168	4.25 ± 0.07	1.00–6.75		**
	SD		3.83 ± 0.24	4.32 ± 0.23		183	3.94 ± 0.06	1.00–5.83		

ns no significant differences, *NE* not evaluated, *ND* no data taken for seed traits in the parent PHA1037 under LD conditions

[a] *, ** Significant at the 0.05 and 0.01 probability levels, respectively, for difference among parents (P_{PAR}), RILs (P_{RIL}), and LD vs SD ($P_{LD–SD}$)

[b] *N* number of lines recorded

[c] *0* all plants white, *1* lilac, *2* purple, *3* black, and *4* red seed

[d] *0* all plants absence of seed pigmentation, and *1* presence of seed pigmentation

[e] *0* all plants matt seed, *1* medium brightness seed, and *2* shiny seed

also exhibited significant QE interaction effects (Table 4). Except for SB and SP traits, QTLs with positive (alleles from PHA1037) and negative (alleles from PMB0225) additive values were identified for the same trait, indicating that alleles from both parents have a positive agronomical effect on the trait. For seed shape traits (SWI, ST, SL, SSI), 15 single-locus QTLs were detected on six LGs: three on Pv1a, Pv2, and Pv7, and two on Pv6, Pv9 and Pv10 (Fig. 1), explaining a phenotypic variance from 0.3 to 12.4 %. Regarding the SW trait, four single-locus QTLs were identified on Pv1a, Pv6 and Pv9, explaining from 0.5 to 3.9 % of the phenotypic variance. For PSC, SSC, and SB traits, 11 single-locus QTLs were detected on eight LGs: one on Pv3, Pv5, Pv6, Pv8, Pv9, Pv10, two on Pv4, and three on Pv7 (Fig. 1). These QTLs explained from 0.1 to 42.5 % of the phenotypic variance, among them $PSC7.1^{PP}$ and $SSC7^{PP}$ were particularly noteworthy as they were responsible of 42.5 and 26.9 % of the phenotypic variance, respectively. Both QTLs were located at the position of *P* locus on Pv7, between markers BM185-*P* and *P*-BMc294, respectively. For the SP trait, two single-locus QTLs were identified on Pv1a and Pv4 (Fig. 1), explaining from 0.4 to 6.6 % of the phenotypic variance. When the significant single-locus QTLs detected by MCIM were placed into a multivariate model, the total variance explained for each trait ranged from 8 to 68 % for ST and PSC, respectively (Table 2). In addition, 12 of the 32 single-locus QTLs showed QE interaction effects:

Table 2 Broad-sense heritability estimates and proportion of phenotypic variance explained by single-locus and epistatic QTLs for seed traits detected in the RIL population PMB0225 × PHA1037 grown in six different environments, including long-day and short-day (LD and SD) photoperiod conditions

Trait	Heritability estimates									R^2 of single-locus QTLs[d]	R^2 of epistatic QTLs[e]
	LD09	SD09	LD10	SD10	LD11a	LD11b	LD[a]	SD[b]	E[c]		
Width (SWI)	0.71 ± 0.06	0.37 ± 0.09	0.44 ± 0.10	0.68 ± 0.05	0.53 ± 0.12	0.48 ± 0.09	0.80 ± 0.03	0.67 ± 0.07	0.73 ± 0.03	32	–
Thickness (ST)	0.57 ± 0.08	0.43 ± 0.09	0.51 ± 0.11	0.64 ± 0.06	0.59 ± 0.11	0.31 ± 0.09	0.75 ± 0.03	0.75 ± 0.05	0.79 ± 0.06	8	–
Length (SL)	0.79 ± 0.04	0.67 ± 0.07	0.76 ± 0.06	0.78 ± 0.04	0.60 ± 0.11	0.67 ± 0.07	0.92 ± 0.01	0.88 ± 0.02	0.83 ± 0.01	35	12
Size index (SSI)	0.73 ± 0.05	0.53 ± 0.08	0.51 ± 0.09	0.73 ± 0.05	0.42 ± 0.16	0.53 ± 0.09	0.84 ± 0.02	0.75 ± 0.06	0.87 ± 0.02	35	2
Weight (SW)	0.57 ± 0.09	0.69 ± 0.10	0.51 ± 0.11	0.52 ± 0.10	0.42 ± 0.17	0.39 ± 0.09	0.65 ± 0.06	0.79 ± 0.04	0.68 ± 0.03	15	–
Primary color (PSC)	0.76 ± 0.06	0.73 ± 0.06	0.72 ± 0.05	0.77 ± 0.05	0.78 ± 0.06	0.82 ± 0.04	0.99 ± 0.02	0.98 ± 0.03	0.98 ± 0.01	68	9
Secondary color (SSC)	0.78 ± 0.05	0.75 ± 0.06	0.73 ± 0.06	0.77 ± 0.05	0.79 ± 0.06	0.81 ± 0.04	0.99 ± 0.14	0.99 ± 0.09	0.95 ± 0.07	54	9
Brightness (SB)	0.64 ± 0.09	0.56 ± 0.09	0.70 ± 0.06	0.65 ± 0.08	0.84 ± 0.04	0.79 ± 0.04	0.96 ± 0.07	0.98 ± 0.08	0.91 ± 0.03	19	15
Seeds per pod (SP)	0.33 ± 0.10	0.31 ± 0.09	0.53 ± 0.10	0.47 ± 0.08	NE	NE	0.56 ± 0.08	0.36 ± 0.12	0.60 ± 0.06	9	8

NE not evaluated

[a] Broad-sense heritability estimates considering together the LD09, LD10, LD11a, and LD11b environments

[b] Broad-sense heritability estimates considering together the SD09 and SD10 environments

[c] Broad-sense heritability estimates considering together all the environments

[d] Proportion of phenotypic variation explained by significant epistatic QTLs detected by MCIM across environments

[e] Proportion of phenotypic variation explained by significant single-locus QTLs identified by MCIM across environments

Table 3 Pearson correlation coefficients for seed traits from the RIL population PMB0225 × PHA1037 based on combined data from six different environments

Trait	SWI	ST	SL	SSI	SW	PSC	SSC	SB
Width (SWI)								
Thickness (ST)	0.76**							
Length (SL)	0.45**	0.19**						
Size index (SSI)	0.84**	0.53**	0.86**					
Weight (SW)	0.84**	0.79**	0.60**	0.84**				
Primary color (PSC)	0.18**	−0.09*	0.17**	0.20**	0.05			
Secondary color (SSC)	0.09**	−0.16**	0.12**	0.12**	−0.04	0.59**		
Brightness (SB)	0.12**	0.02	0.10**	0.13**	0.06	0.03	−0.08*	
Seeds per pod (SP)	−0.31**	−0.18**	−0.16**	−0.28**	−0.26**	−0.01	−0.04	0.07

*, ** Significant at the 0.05 and 0.01 probability levels, respectively

5 QTLs and 7 QE interaction effects for seed shape (SWI, SL, SSI), 1 QTL and 1 QE interaction effects for SW, 4 QTLs and 9 QE interaction effects for seed coat color (PSC, SSC, SSC), and 2 QTLs and 2 QE interaction effects for SP (Table 4). For ST and SB traits, single-locus QTLs with QE interaction effects were not detected. The percentage of phenotypic variance explained by QE interaction effects ranged from 0.3 % (for PSC) to 2.9 % (for SW and SP). A complete report of the one-dimensional genome scan analysis for seed traits is provided in Table 4.

Epistatic QTLs

A total of 41 significant E-QTLs across environments were identified for six of the nine seed traits here evaluated (nine for SL, four for SSI, eight for PSC, seven for SSC, nine for SB, and four for SP), and these were involved in 26 epistatic interactions (six for SL, two for SSI, five for PSC, six for SSC, five for SB, and two for SP) (Table 5). Interestingly, 14 of these 41 E-QTLs had previously been detected as single-locus QTLs, which indicated that these QTLs not only participated in epistatic interactions, but also had

Table 4 Single-locus QTLs and QTLs × Environment (QE) interaction effects for seed traits identified in the RIL population PMB0225 × PHA1037 grown in six different environments, including long-day (LD) and short-day (SD) photoperiod conditions

QTL	Marker interval	LG (pos.)[a]	*F* value[b]	A[c]	R^2(a)[d]	QE AE[e]	R^2 (ae)[f]
Seed width (SWI)							
SWI2^{PP}	BM164–BM172	2 (0.0–1.5)	13.3	-0.22^{***}	10.6	ns	
SWI7^{PP}	*P*-BMc294	7 (32.8–39.9)	7.9	0.21^{***}	6.2	ns	
SWI9^{PP}	BMc184–IAC62	9 (70.2–73.7)	6.1	0.26^{***}	6.6	0.19^{**} SD10	1.3
Seed thickness (ST)							
ST2^{PP}	BM164–BM172	2 (0.0–1.5)	10.2	-0.18^{***}	5.9	ns	
ST9^{PP}	PV-at007–BMc184	9 (60.9–70.2)	4.7	0.23^{***}	2.5	ns	
Seed length (SL)							
SL1.1^{PP}	E31M31-258–PvM97	1a (47.7–48.2)	4.8	0.19^{***}	1.8	ns	
SL1.2^{PP}	BMc324–BM200	1a (66.5−95.6)	4.5	-0.07^{*}	0.3	0.14^{*} LD09	0.6
SL2.1^{PP}	BM139–BMc280	2 (3.0–11.1)	16.3	0.52^{***}	12.1	ns	
SL6^{PP}	E40M60-91–E45M50-50	6 (5.0–5.8)	30.2	-0.56^{***}	12.4	-0.25^{***} SD10	1.3
						0.14^{*} LD11b	0.4
SL7^{PP}	BM185-*P*	7 (24.6–32.8)	14.5	0.38^{***}	6.5	ns	
SL10^{PP}	E36M37-20–BMb414	10 (6.0–7.0)	7.5	-0.26^{***}	9.1	-0.18^{**} LD09	0.8
Seed size index (SSI)							
SSI1^{PP}	E31M31-258–PvM97	1a (47.7–48.2)	5.2	2.35^{***}	2.5	ns	
SSI6^{PP}	E40M60-166–E40M60-164	6 (6.4–6.6)	24.5	-6.46^{***}	7.9	2.64^{*} LD10	0.9
						-4.70^{***} SD10	2.2
SSI7^{PP}	BM185-*P*	7 (24.6–32.8)	21.9	6.03^{***}	9.3	ns	
SSI10^{PP}	SNP-2521–BMc159	10 (0.0–4.3)	9.7	-3.57^{***}	7.8	ns	
Seed weight (SW)							
SW1^{PP}	E31M31-258–PvM97	1a (47.7–48.2)	4.7	1.64^{***}	1.5	ns	
SW6^{PP}	IAC287–BMc238	6 (0.0–2.3)	7.0	-2.37^{***}	3.9	ns	
SW9.1^{PP}	BMb563–E31M51-59	9 (17.0–27.5)	4.9	-1.51^{***}	0.5	2.83^{***} LD09	2.9
SW9.2^{PP}	IAC62–PvM128	9 (73.7–78.4)	5.1	4.68^{***}	3.5	ns	
Primary seed color (PSC)							
PSC3^{PP}	BMb194–PvM126	3 (92.2–93.7)	9.1	-0.47^{***}	2.6	ns	
PSC4^{PP}	BM140–E45M38-216	4 (55.5–55.9)	13.2	-0.53^{***}	1.7	-0.32^{*} LD10	0.5
						-0.42^{**} SD10	0.8
PSC7.1^{PP}	BM185-*P*	7 (24.6–32.8)	105.6	1.06^{***}	42.5	0.17^{**} SD09	0.3
						0.31^{***} SD10	1.1
						-0.34^{***} LD11b	1.5
PSC7.2^{PP}	BMc137–E31M61-110	7 (65.5–70.5)	5.9	-0.15^{***}	0.7	ns	
PSC9^{PP}	E40M50-51–BM202	9 (32.9–47.5)	6.1	-0.17^{***}	0.1	0.19^{**} LD10	0.4
						-0.18^{**} LD11b	0.5
						0.16^{*} LD11a	0.3
Secondary seed color (SSC)							
SSC4^{PP}	BM140–E45M38-216	4 (55.5–55.9)	12.9	-0.14^{***}	5.9	ns	
SSC7^{PP}	*P*-BMc294	7 (32.8–39.9)	34.2	0.24^{***}	26.9	-0.06^{**} LD11b	0.7
SSC8.2^{PP}	BMc121–BM165	8 (26.4–30.7)	9.2	-0.08^{***}	4.9	ns	
SSC9^{PP}	PV-at007–BMc184	9 (60.9–70.2)	7.8	-0.05^{***}	5.3	ns	
Seed brightness (SB)							
SB5^{PP}	IAC96–IAC286	5 (0.0–30.2)	4.8	-0.11^{***}	6.8	ns	
SB6^{PP}	E40M60-91–E45M50-50	6 (5.0–5.8)	5.3	-0.13^{***}	10.9	ns	

Table 4 continued

QTL	Marker interval	LG (pos.)[a]	*F* value[b]	A[c]	R^2(a)[d]	QE AE[e]	R^2 (ae)[f]
Seeds per pod (SP)							
$SP1^{PP}$	BMc324–BM200	1a (66.5–95.6)	8.6	-0.55^{*}	0.4	-1.74^{***} SD09	1.9
$SP4^{PP}$	BM140–E45M38-216	4 (55.5–55.9)	15.2	-1.03^{***}	6.6	1.25^{***} SD10	2.9

ns not significant effects on the six environments evaluated

* $P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$. Experiment-wide *P* value. Only significant effects are listed

[a] Linkage group and the estimated confidence interval of QTL position in brackets (in Kosambi cM)

[b] *F* values of significance of each QTL. Threshold *F* values were 4.2, 4.2, 4.3, 4.3, 4.2, 4.1, 4.3, 4.2, and 4.7 for SWI, ST, SL, SSI, SW, PSC, SSC, SB, and SP, respectively

[c] Estimated additive effect. Positive values indicate that alleles from PHA1037 have a positive effect on the traits, and negative values indicate that positive effect on the traits is due to the presence of the alleles from PMB0225

[d] Percentage of the phenotypic variation explained by additive effects

[e] Predicted additive by environment interaction effect. The meaning of sign values is described in the second footnote ([c])

[f] Percentage of the phenotypic variation explained by additive by environment interaction effect

an individual genetic effect. For seed shape traits (SL and SSI), 13 single-locus QTLs involved in 8 epistatic interactions were detected on Pv1a, Pv2, Pv4, Pv5, Pv7, Pv10, and Pv11 (Fig. 1), explaining a phenotypic variance ranging from 0.5 to 2.5 %. In the multiple regression model, these E-QTLs explained 2 and 12 % of the total trait variation for SSI and SL, respectively (Table 2). Regarding PSC, SSC and SB traits, 24 single-locus QTLs involved in 16 epistatic interactions were detected on Pv1a, Pv1b, Pv2, Pv3, Pv4, Pv5, Pv7, Pv8, Pv9, and Pv11 (Fig. 1), explaining a phenotypic variance from 0.8 to 4.7 %. The proportion of total phenotypic variation explained by E-QTLs for seed color (PSC and SSC) and SB was 9 and 15 %, respectively (Table 2). For SP trait, four single-locus QTLs involved in two epistatic interactions were detected on Pv1a, Pv3, Pv4, and Pv9 (Fig. 1), explaining a phenotypic variance from 0.1 to 2.5 %. The proportion of the phenotypic variation explained by these E-QTLs for SP was 8 % (Table 2). For SP trait, four single-locus QTLs involved in two epistatic interactions were detected on Pv1a, Pv3, Pv4, and Pv9 (Fig. 1), explaining a phenotypic variance from 0.1 to 2.5 %. Among the epistatic interactions identified, only six pairs of E-QTLs showed E-QE interaction effects (two for SSI, two for PSC, and two for SP), the remaining E-QTLs only had significant genetic effects. The percentage of phenotypic variance explained by the E-QE interactions ranged from 0.2 % (for PSC) to 0.9 % (for SSI and SP). A comprehensive description of the digenic epistatic interaction analysis for seed traits is provided in Table 5.

Discussion

Seed size and coat color in common bean are important agronomic traits as they are associated with consumer acceptability and markets. Moreover, these traits are known to influence biochemical functions involved in antioxidant activity and disease resistance (Takeoka et al. 1997; Beninger and Hosfield 1999). The genetic basis of seed size and coat color has not been well understood. Although genetic studies have been conducted to identify single-locus QTLs associated with seed characteristics (Koinange et al. 1996; Park et al. 2000; Tar'an et al. 2002; Guzman-Maldonado et al. 2003; Blair et al. 2006; Caldas and Blair 2009; Pérez-Vega et al. 2010), epistatic QTLs and QTL × environment interaction effects have not been studied in depth in common bean. Therefore, an examination of QTL architecture underlying seed size and coat color, including genetic main effects, epistatic interactions among QTLs and QTLs by environment interactions, would be a step towards understanding the genetic basis of these traits. Although co-adapted gene complexes and/or epistatic relationships are expected within each gene pool, most previous studies have analyzed seed traits from inter-gene pool crosses (Koinange et al. 1996; Tsai et al. 1998; Park et al. 2000; Tar'an et al. 2002; Guzman-Maldonado et al. 2003; Caldas and Blair 2009; Pérez-Vega et al. 2010), or from a cultivated Andean × wild common bean cross (Blair et al. 2006). In the present study, we have evaluated nine seed size and coat color traits in six different photoperiod environments (long-day and short-day) using a RIL population derived from a dry bean × exotic nuña bean cross from the Andean gene pool. This population showed a continuous distribution, a wide range of variability and high heritability, indicating a quantitative nature of inheritance for seed size and coat color and a valuable resource for improvement of common bean cultivars. Information about the correlations among traits is important for defining bean ideotypes for selection. Positive correlations among the components of bean yield, such as SP and SW would be desirable. However, a negative relationship between these traits was found; this is known as yield component compensation, whereby a gain

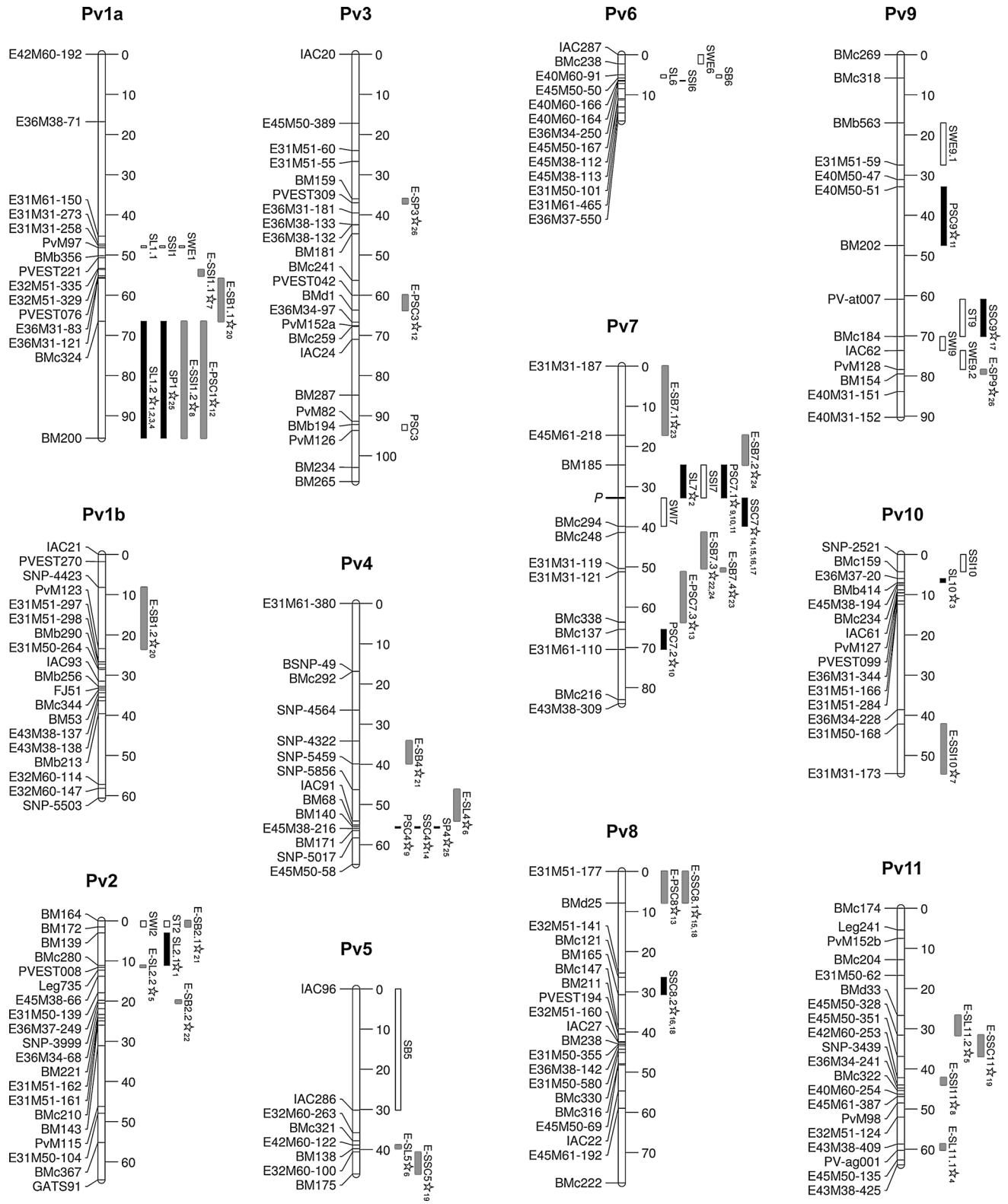

Fig. 1 Location of single-locus QTLs and E-QTLs associated with seed size and coat color traits on a genetic linkage map of common bean based on the RIL population developed from the cross PMB0225 × PHA1037. Distances among markers are indicated in cM to the *right* of the linkage groups; names of markers are shown on the *left*. QTLs are depicted as *vertical bars* to the right of the linkage groups. Names of QTLs are listed in Tables 4 and 5. Single-locus QTLs are indicated in *white*, E-QTLs are shown in *grey*, and QTLs with both individual additive and epistatic effects are represented in *black*. Epistatic interactions between QTLs are indicated with *numbered stars*

Table 5 Epistatic QTLs (E-QTLs) and E-QTL × Environment (E-QE) interaction effects for seed traits detected in the RIL population PMB0225 × PHA1037 grown in six different environments, including long-day (LD) and short-day (SD) photoperiod conditions

E-QTLi[a]	Marker interval	LG (pos.)[b]	E-QTLj[a]	Marker interval	LG (pos.)	*F* value[c]	AA[d]	R^2 (aa)[e]	E-QE AAE[f]	R^2 (aae)[g]
Seed length (SL)										
E-SL1.2^{PP}	BMc324–BM200	1a (66.5–95.6)	E-SL2.1^{PP}	BM139–BMc280	2 (3.0–11.1)	5.3	-0.11^{**}	0.5	ns	
E-SL1.2^{PP}	BMc324–BM200	1a (66.5–95.6)	E-SL7^{PP}	BM185-*P*	7 (24.6–32.8)	5.1	0.14^{**}	0.5	ns	
E-SL1.2^{PP}	BMc324–BM200	1a (66.5–95.6)	E-SL10^{PP}	E36M37-20–BMb414	10 (6.0–7.0)	5.4	-0.16^{***}	1.5	ns	
E-SL1.2^{PP}	BMc324–BM200	1a (66.5–95.6)	E-SL11.1^{PP}	E43M38-409–PV-ag001	11 (58.7–60.3)	5.2	-0.14^{***}	1.1	ns	
E-SL2.2^{PP}	BMc280–PVEST008	2 (11.1-11.6)	E-SL11.2^{PP}	BMd33–E45M50-328	11 (26.7-31.6)	5.9	0.23^{***}	2.3	ns	
E-SL4^{PP}	SNP-5856–IAC91	4 (46.3–54.1)	E-SL5^{PP}	E42M60-122–BM138	5 (38.9–39.8)	5.3	0.41^{***}	2.5	ns	
Seed size index (SSI)										
E-SSI1.1^{PP}	E32M51-329–PVEST76	1a (53.6–55.2)	E-SSI10^{PP}	E31M50-168–E31M31-173	10 (42.2–54.5)	7.8	-35.93^{***}	1.4	-32.38^{*} LD10	0.9
E-SSI1.2^{PP}	BMc324–BM200	1a (66.5–95.6)	E-SSI11^{PP}	E42M60-253–SNP-3439	11 (42.2–44.0)	6.2	-21.49^{**}	0.9	26.05^{*} SD10	0.5
Primary seed color (PSC)										
E-PSC4^{PP}	BM140–E45M38-216	4 (55.5–55.9)	E-PSC7.1^{PP}	BM185-*P*	7 (24.6–32.8)	5.6	-0.35^{***}	2.2	-0.31^{*} LD10	0.3
									-0.28^{*} LD11a	0.2
E-PSC7.1^{PP}	BM185-*P*	7 (24.6–32.8)	E-PSC7.2^{PP}	BMc137–E31M61-110	7 (65.5–70.5)	5.2	-0.25^{***}	2.1	ns	
E-PSC7.1^{PP}	BM185-*P*	7 (24.6–32.8)	E-PSC9^{PP}	E40M50-51–BM202	9 (32.9–47.5)	5.5	-0.17^{***}	0.8	0.18^{**} LD10	0.3
									-0.18^{*} LD11b	0.3
									0.13^{*} LD11a	0.2
E-PSC1^{PP}	BMc324–BM200	1a (66.5–95.6)	E-PSC3^{PP}	PVEST042–BMd1	3 (59.9–63.7)	8.2	0.61^{***}	1.5	ns	
E-PSC7.3^{PP}	E31M31-121–BMc338	7 (51.2–63.7)	E-PSC8^{PP}	E31M51-177–BMd25	8 (0.0–7.9)	8.3	-0.35^{***}	1.5	ns	
Secondary seed color (SSC)										
E-SSC4^{PP}	BM140–E45M38-216	4 (55.5–55.9)	E-SSC7^{PP}	*P*-BMc294	7 (32.8–39.9)	6.3	-0.16^{***}	3.6	ns	
E-SSC7^{PP}	*P*-BMc294	7 (32.8–39.9)	E-SSC8.1^{PP}	E31M51-177–BMd25	8 (0.0-7.9)	5.9	-0.04^{***}	2.4	ns	
E-SSC7^{PP}	*P*-BMc294	7 (32.8–39.9)	E-SSC8.2^{PP}	BMc121–BM165	8 (26.4–30.7)	5.9	-0.06^{***}	3.8	ns	
E-SSC7^{PP}	*P*-BMc294	7 (32.8–39.9)	E-SSC9^{PP}	PV-at007–BMc184	9 (60.9–70.2)	6.4	-0.04^{***}	0.9	ns	
E-SSC8.1^{PP}	E31M51-177–BMd25	8 (0.0–7.9)	E-SSC8.2^{PP}	BMc121–BM165	8 (26.4–30.7)	7.5	-0.03^{***}	1.5	ns	
E-SSC5^{PP}	E32M60-100–BM175	5 (40.6–46.1)	E-SSC11^{PP}	E45M50-328–E45M50-351	11 (31.6–36.9)	13.8	-0.09^{***}	3.1	ns	
Seed brightness (SB)										
E-SB1.1^{PP}	E36M31-121–BMc324	1a (55.8–66.5)	E-SB1.2^{PP}	SNP-4423–PvM123	1b (8.2–23.5)	6.8	0.12^{***}	1.1	ns	
E-SB2.1^{PP}	BM164–BM172	2 (0.0–1.5)	E-SB4^{PP}	SNP-4322–SNP-5459	4 (34.2–39.9)	9.2	-0.22^{***}	3.9	ns	
E-SB2.2^{PP}	E36M37-249–SNP-3999	2 (19.8–20.5)	E-SB7.3^{PP}	BMc248–E31M31-119	7 (41.4–50.4)	6.4	0.19^{***}	1.5	ns	
E-SB7.1^{PP}	E31M31-187–E45M61-218	7 (0.0–17.2)	E-SB7.4^{PP}	E31M31-119–E31M31-121	7 (50.4–51.2)	7.1	-0.17^{***}	4.1	ns	

Table 5 continued

E-QTLi[a]	Marker interval	LG (pos.)[b]	E-QTLj[a]	Marker interval	LG (pos.)	*F* value[c]	AA[d]	R^2 (aa)[e]	E-QE AAE[f]	R^2 (aae)[g]
E-SB7.2^{PP}	E45M61-218–BM185	7 (17.2–24.6)	E-SB7.3^{PP}	BMc248–E31M31-119	7 (41.4–50.4)	6.9	−0.27***	4.7	ns	
Seeds per pod (SP)										
E-SP1^{PP}	BMc324–BM200	1a (66.5–95.6)	E-SP4^{PP}	BM140–E45M38-216	4 (55.5–55.9)	6.2	−0.98*	0.1	−20.13* LD09	0.9
E-SP3^{PP}	BM159–PVEST309	3 (35.9–37.1)	E-SP9^{PP}	PvM128–BM154	9 (78.4–79.5)	9.8	12.41***	2.5	−0.91* SD10	0.6

ns not significant effects on the six environments evaluated

* $P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$. Experiment-wide *P* value. Only significant effects are listed

[a] E-QTLi and E-QTLj are the two QTLs involved in epistatic interaction

[b] *F* values of significance of each QTL. Threshold *F* values were 4.4, 4.3, 4.5, 4.5, 4.5, and 4.3 for SL, SSI, PSC, SSC, SB, and SP, respectively

[c] Linkage group and the estimated confidence interval of QTL position in brackets (in Kosambi cM)

[d] Estimated additive by additive epistatic effect. Positive values indicate that alleles from PHA1037 have a positive effect on the traits, and negative values indicate that positive effect on the traits is due to the presence of the alleles from PMB0225

[e] Percentage of the phenotypic variation explained by additive epistatic effects

[f] Predicted additive by additive epistatic effect by environment interaction effect. The meaning of sign values is described in the third footnote ([d])

[g] Percentage of the phenotypic variation explained by additive by additive epistatic effect by environment interaction effect

in one yield component is generally reflected by a loss in another component. This is the result of competition among yield components for limited resources which prevents all components from simultaneously achieving their genetic potential (Adams 1967; Tar'an et al. 2002). The current study revealed transgressive segregation and positive and significant correlations between shape (SWI, ST, SL, and SSI) and weight (SW) of seeds, indicating that extreme phenotypes can be maintained through artificial selection, since transgressive segregation relies on additive genetic variation. Thus, our results show that alleles from the exotic nuña parent could potentially improve agronomic seed traits in common bean, offering the potential for breeding of this crop.

A total of 59 significant QTLs across environments (single-locus QTLs and E-QTLs) were identified for seed size and coat color traits, distributed throughout all LGs (Fig 1). Eighteen of them had only individual additive effects, while 27 showed epistatic effects and 14 had both individual additive and epistatic effects. The results show that not only individual additive effects but also epistasis clearly play a significant role in the genetic basis of the seed traits. Most of these QTLs were consistent over environment, although some of them were subject to environmental modification (Tables 4, 5). However, QTLs with differential effect on LD and SD environmental conditions were not found for seed traits, even though interactions were detected between QTLs and environment (QE and E-QE). With regards to seed dimension traits, single-locus QTLs have been previously reported for seed length, thickness, and width on most LGs, with the exception of Pv1, Pv5, and Pv9 (Park et al. 2000; Pérez-Vega et al. 2010). Comparative analysis of QTLs affecting seed size traits is difficult due to the lack of anchor markers among populations. However, several QTLs detected in the current study are consistent with those identified previously. Pérez-Vega et al. (2010) detected a QTL for seed length on the top of Pv2 close to the SSR marker BM172, which corresponds to the same genomic region where the single-locus QTLs SWI2^{PP}, ST2^{PP}, and SL2^{PP} were detected. The single-locus QTLs SSI7^{PP} and SL7^{PP}, and SWI7^{PP} were mapped on Pv7, between markers BM185-*P* and *P*-BMc294, respectively. The *P* locus was the closest marker to the QTL identified by Pérez-Vega et al. (2010) on Pv7 for seed width, indicating that the genomic region where the *P* locus is located seems to be involved not only in seed color, but also in seed size. Besides, other single-locus QTLs for seed size were mapped by Park et al. (2000) and Pérez-Vega et al. (2010) on the top of Pv6 and Pv8, close to the center of Pv4, Pv6, Pv8, and Pv11, and close to the bottom of Pv3 and Pv10. In this report, we also identified single-locus QTLs for seed dimension traits on Pv1a and Pv9, making this the first report of the involvement of these LGs in the genetic control of seed dimension traits. In addition, 13 E-QTLs and 8 epistatic interactions were detected for SL and SSI, showing the complex pattern of inheritance of these seed traits. Nine of these E-QTLs were identified for SL and their interactions explained 12 % of the total phenotypic variance observed for this trait. Regarding the SW trait, single-locus QTLs were mapped on Pv1a, Pv6, and Pv9, but no epistatic interactions were detected. Previous work reported in the literature detected single-locus QTLs for seed weight

on Pv1, Pv2, Pv3, Pv4, Pv6, Pv7, Pv8, Pv9, Pv10 and Pv11 (Koinange et al. 1996; Tsai et al. 1998; Park et al. 2000; Tar'an et al. 2002; Guzman-Maldonado et al. 2003; Blair et al. 2006; Pérez-Vega et al. 2010). Among them, the single-locus QTL detected on Pv9 has only been described once by Blair et al. (2006) in a cultivated Andean × wild common bean population. Herein, two single-locus QTLs, SWE9.1^{PP} and SW9.2^{PP} were mapped on Pv9, close to the top and close to the bottom of this LG, respectively. Interestingly, the QTL identified by Blair et al. (2006) on Pv9 was mapped between markers Pv-at007 and BM154, which is the same genomic region where the single-locus QTL SW9.2^{PP} was identified, indicating that both QTLs might be the same. Overall, even though comparative analysis of QTLs for different parent populations is especially complex, our results suggest that the single-locus QTLs located on Pv9, not only for seed weight, but also for seed shape (SWI and ST) traits might be specific to the Andean background, although additional studies would be necessary to draw definitive conclusions.

Color of seed coat tissue is determined by the dominant *P* gene, which was mapped on Pv7 in previous reports (Vallejos et al. 1992; Koinange et al. 1996; Erdmann et al. 2002). The homozygous recessive *pp* genotype (as PMB0225 parent) expresses white seed coat regardless of the genotype at any other gene in the complex genetic system controlling seed coat color (Bassett 2007). The QTL analysis results in the present work showed that both PSC and SSC traits are mainly controlled by the major single-locus QTLs PSC7.1^{PP} and SSC7 ^{PP}, which were both located at the *P* locus and explained 42.5 and 26.9 % of the phenotypic variation, respectively. The additive effect of these major QTLs had positive values, indicating that alleles from PHA1037 (colored seed parent) have a positive effect on the traits (i.e. presence of color). Interestingly, the additive effects of the remaining single-locus QTLs identified for PSC (PSC3^{PP}, PSC4^{PP}, PSC7.2^{PP}, and PSC9^{PP}) had negative values, which indicate that the alleles present in these QTLs from PMB0225 (uncolored seed parent) could modify the seed coat color, but do not determine the presence of it. The existence of a continuous distribution of primary coat color in the RIL population could be explained by the presence of other color genes, which are expressed only in the presence of *P* gene. The *C* gene has multiple alleles and exists in a complex locus with the *R* gene for red seed coat, hence the genes are represented as *[C-R]* (Bassett 2007). The *[C-R]* locus was previously mapped on the center of Pv8, close to the marker BM165 (Caldas and Blair 2009). In this report, the single-locus QTL SSC8.2^{PP} was located between markers BMc121 and BM165 and its additive effect had negative value, showing that alleles from PHA1037 (red-seeded parent) have a positive effect on the seed color. Therefore, the single-locus QTL SSC8.2^{PP} seems to carry the *[C-R]* gene. The color genes *D* and *G* have been previously located on the center of Pv3 and Pv4, respectively (McClean et al. 2002; Caldas and Blair 2009). The *D* gene was located by Caldas and Blair (2009) close to the BMd1 marker, which corresponds to the same genomic region where the epistatic QTL E-PSC3^{PP} was detected. However, the location of the single-locus QTL PSC4^{PP} and the *G* gene could not be compared because of the absence of common markers among genetic maps. Partly colored seed coat patterns require the homozygous recessive *tt* genotype at *T* locus (Emerson 1909) and epistatic interactions among three other genes, i.e. *D*, *L* and *Bip* (Bassett and McClean 2000). In this study, the parental genotypes showed no significant differences in SSC trait, suggesting that one or two parents bear the *T*-genotype (seeds that are totally colored). In addition, the high number of epistatic interactions identified not only for PSC but also for SSC traits (across the two traits, a total of 15 E-QTLs involved in 11 epistatic interactions were identified that explained 9 % of the phenotypic variation for each trait), indicates that the different seed coat colors observed in the RIL population could be explained by the presence of epistasis. Overall, this complex genetic inheritance of seed coat color is in accordance with the results obtained by McClean et al. (2002), who reported the existence of many genes that exhibit epistatic interactions with other genes and these interactions define the many colors observed within the species.

The only gene described to date that affects the shine of the seed coat is the *Asp* gene (Lamprecht 1940; Beninger et al. 2000), which has been previously mapped on the upper portion of Pv7 (Miklas et al. 2000). In this report, two single-locus QTLs not previously described, SB5^{PP} and SB6^{PP}, were located on Pv5 and Pv6 and explained 6.8 and 10.9 % of the phenotypic variation for seed brightness, respectively. The negative additive values of these QTLs indicate that alleles from PMB0225 (parent with the brightest seed) provide glossiness to the seeds. Interestingly, five epistatic interactions were detected, which explained 15 % of the phenotypic variation beyond the effects of single-locus QTLs for seed brightness, showing that epistasis has a significant role in the genetic control of this trait. Although single-locus QTLs were not mapped on Pv7, where *Asp* locus is located, four E-QTLs involved in three epistatic interactions were detected on this LG, suggesting that one of them could harbor the *Asp* gene.

In a broader context, it is possible to distinguish a location on each of LGs Pv1a, Pv2, Pv4, Pv6, Pv7, and Pv9 where most QTLs identified for seed-related traits are positioned in a cluster. Hence, the QTL analyses suggest that either pleiotropic QTLs control several seed traits, or tightly linked QTLs for different traits are present together in the same genomic regions. The clustering organization

of common bean QTLs has been reported previously, and other studies have also described the co-locations of QTLs for different traits (Tsai et al. 1998; Tar'an et al. 2002; Beattie et al. 2003; Blair et al. 2006; Pérez-Vega et al. 2010). Nevertheless, further studies on fine mapping of the target genomic regions should help to elucidate the issue of pleiotropy versus tight linkage of QTLs.

Due to the difficulty of making comparative analysis of QTLs for different populations, we have not been able to provide deeper insights into the identification of specific QTLs of the Andean intra-gene pool. Nonetheless, digenic epistatic interactions clearly play an important role in the genetic control of seed morpho-agronomic traits in the Andean background. These results are in agreement with the co-adaptation hypothesis, which proposes the presence of favorable gene complexes (involved in epistatic interactions) within each gene pool. In common bean, due to outbreeding depression (Templeton 1981), the low fitness of the progenies obtained from Andean × Mesoamerican inter-gene pool crosses (Welsh et al. 1995; Johnson and Gepts 2002; Santalla et al. 2005; Moreto et al. 2012) also supports the co-adaptation hypothesis. Hence, in an inter-gene pool cross, the alleles from the different gene loci segregate independently and recombine randomly causing the breakage of co-adapted gene complexes and/or epistatic relationships.

Based on the results of this study, we conclude that epistasis is an important component of the genetic variance of seed size and coat color traits in the Andean background, and it will play a significant role in enhancing MAS efficiency. The QTLs here reported are not only of great importance to understand the genetic architecture underlying seed quality traits, but they may also prove useful to define the location of genes that govern the target traits in this study, which represents the first step towards the artificial selection of new alleles of interest in elite common bean lines. The common bean is a species of emerging social and economic interest worldwide, and it will undoubtedly assume a position of importance alongside agricultural species whose complete genetic sequences will soon be available, such as the chickpea (Varshney et al. 2013). Integrating whole genome sequencing data with QTL information will reveal novel genes and new alleles of known genes that have been identified in specific genetic backgrounds under predetermined environmental conditions (Mace and Jordan 2011). Therefore, the novel QTLs identified represent a valuable genetic tool for a detailed genomic analysis of seed size and coat color. They will also permit the efficient application of MAS to create elite common bean lines with better seed quality, which will prove more acceptable to both farmers and consumers.

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical standards Experiments conducted for this study comply with the current laws of Spain.

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