Mol Breeding
DOI 10.1007/s11032-013-0008-9

Genetic variation underlying pod size and color traits of common bean depends on quantitative trait loci with epistatic effects

Fernando J. Yuste-Lisbona · Ana M. González · Carmen Capel · Manuel García-Alcázar · Juan Capel · Antonio M. De Ron · Marta Santalla · Rafael Lozano

Received: 9 August 2013 / Accepted: 19 December 2013

Abstract Common bean is an important vegetable legume in many regions of the world. Size and color of fresh pods are the key factors for deciding the commercial acceptance of bean as a fresh vegetable. The genetic basis of important horticultural traits of common bean is still poorly understood, which hinders DNA marker-assisted breeding in this crop. Here we report the identification of single-locus and epistatic quantitative trait loci (QTLs), as well as their environment interaction effects for six pod traits, namely width, thickness, length, size index, beak length and color, using an Andean intra-gene pool recombinant inbred line population from a cross between a cultivated common bean and an exotic nuña bean. The QTL analyses performed detected a total of 23 QTLs (single-locus QTLs and epistatic QTLs): five with only individual additive effects and six with only epistatic effects, while the remaining twelve showed both effects. These QTLs were distributed across linkage groups (LGs) 1, 2, 4, 6, 7, 8, 9, 10 and 11; particularly noteworthy are the QTLs for pod size co-located on LGs 1 and 4, indicative of tight linkage or genes with pleiotropic effects governing these traits. Overall, the results obtained showed that additive and epistatic effects are the major genetic basis of pod size and color traits. The mapping of QTLs including epistatic loci for the six pod traits evaluated provides support for implementing marker-assisted selection toward genetic improvement of common bean.

Keywords Snap bean · Horticultural traits · QTL analysis · Epistasis · Breeding · *Phaseolus vulgaris*

Fernando J. Yuste-Lisbona and Ana M. González have contributed equally to this work.

Electronic supplementary material The online version of this article (doi:10.1007/s11032-013-0008-9) contains supplementary material, which is available to authorized users.

F. J. Yuste-Lisbona · C. Capel · M. García-Alcázar · J. Capel · R. Lozano (✉)
Departamento de Biología y Geología (Genética), Edificio CITE II-B, Centro de Investigación en Biotecnología Agroalimentaria (BITAL), Universidad de Almería, Carretera de Sacramento s/n, 04120 Almería, Spain
e-mail: rlozano@ual.es

A. M. González · A. M. De Ron · M. Santalla
Departamento de Recursos Fitogenéticos, Grupo de Biología de Agrosistemas, Misión Biológica de Galicia, CSIC, P.O. Box 28, 36080 Pontevedra, Spain

Introduction

Common bean (*Phaseolus vulgaris* L., $2n = 2x = 22$) is an important legume crop grown on all continents. The principal products derived from this crop are dry beans (seeds harvested at complete maturity), shell beans (seeds harvested at physiological maturity, i.e. before the desiccation associated with complete maturity sets in) and green or snap beans (pods

Published online: 12 January 2014

harvested before the seed development phase). Much of the adaptive radiation in snap bean diversity appears to have occurred in Europe after the Colombian exchange, mainly focused on Mediterranean countries. From Europe, snap beans were dispersed to the rest of the world (Gepts 1988), where they have acquired particular importance both as fresh and processed foods. Due to selection during domestication, common bean shifted from small to large pods, and from types that shatter due to highly fibrous and parchmented pod walls to forms with less fiber that are less subject to shattering, which favored the development of cultivars for vegetable use (Gepts 1988; Gepts and Debouck 1991). Breeding efforts have focused on pod fruit qualities, such as sensory quality, sugar content, size, maturity and color (see review of Myers and Bagget 1999). However, the limited diversity of commercial snap bean varieties suggests that an important goal of bean breeding should be to broaden the genetic diversity of specific commercial genotypes. Common bean genetic resources exist as a complex array of major and minor gene pools, races and intermediate types, with occasional introgressions between wild and domesticated types. Hence, one of the most important challenges facing snap bean breeders is the identification and transfer of traits from other backgrounds into snap beans. The essence of the problem is how to incorporate useful economic traits without breaking apart the snap bean complex of traits. The demand for new bean varieties with improved and novel horticultural traits means that the breeder must look for methods and strategies to improve efficiency and to reduce the time required to develop new varieties (De Ron et al. 2004). In this framework, the use of molecular markers may help to facilitate the transfer of traits from a non-adapted background into snap beans.

Knowledge of bean genetics, together with very few examples of possible snap bean landraces from Meso- and South-America (Singh 1989), suggest that snap beans were derived from dry beans, which would mean that genes encoding fleshy and succulent pods may be a consequence of recent selection and breeding efforts. However, little is known about the genetic control and the molecular variation underlying important pod traits such as length, shape, color, straightness, smoothness, rate of seed development, fiber content, internal color and texture, presence of interlocular cavitations, and point of detachment (Silbernagel 1986). Pod cross-sectional shape is a function of wall thickness and timing of development. At least four genes (*Ea*, *Eb*, *Ia* and *Ib*) are known to control this trait, although its inheritance pattern is uncertain (Leakey 1988). The color of immature pods, which varies from green to red and purple, is caused by a differential accumulation of anthocyanin. *P* and *V* genes control solid purple coloring or purple stripes depending on the allele at the [*C Prp*] locus (Bassett 1996). Bassett (2005) identified a gene [$c^{u}Prp^{i}$] for intensified anthocyanin expression in several plant organs (flower, pod, stem and leaf) in common bean. Different authors (see Leakey 1988 for a review; Prakken 1934; Drijfhout 1978) described a single dominant gene *Stringless* (*St*) preventing string formation, and a temperature-sensitive dominant gene (*Ts*) that may influence its expression. Some of the pod traits are quantitatively inherited based on their field behaviors, and, as such, dissecting their genetic basis calls for adequate statistical methods such as quantitative trait locus (QTL) mapping.

The goal of QTL mapping is to identify the genes responsible for generating differences between individuals within a polymorphic population. However, the presence of epistasis can greatly affect the mapping between genotype and phenotype. The effects of QTLs may be masked by interactions with other loci, which can make mapping difficult (Phillips 2008). Therefore, not only can epistasis be considered the major barrier to inferring the genetic architecture of complex traits, it also hampers the efficiency of breeding programs. A direct implication of epistasis is that the lower fitness of individual alleles could be increased when they are found together in a given genotype (Holland 2007). Thus any attempt to use QTLs for improved plant performance and adaptation to different environmental conditions should take into account such epistatic effects, involving activities which tend to accumulate favorable allele combinations in the same genotype. Hence, the identification of QTLs and the elucidation of their genetic control (main and epistatic effects) are essential for the development of efficient marker-assisted selection (MAS) aimed at improving breeding efficiency (Govindaraj et al. 2009).

Recent progress in common bean genomics has provided an opportunity to unravel the genetic basis of important horticultural traits. Tanksley and McCouch (1997) suggested that exotic or non-adapted lines may

possess desirable alleles for quantitative traits that may not be present in elite lines. The identification of these alleles by plant breeders can be made more efficient by combining the information from genetic linkage maps and QTL studies. A relatively large number of linkage maps have been developed in common bean, mainly from inter-gene pool crosses, which have been used to identify single-locus QTLs for yield, vegetative and seed traits (Koinange et al. 1996; Tsai et al. 1998; Park et al. 2000; Tar'an et al. 2002; Johnson and Gepts 2002; Beattie et al. 2003; Guzman-Maldonado et al. 2003; Blair et al. 2006; Pérez-Vega et al. 2010; Yuste-Lisbona et al. 2012). The recently developed common bean consensus map offers the opportunity to increase the number of markers in selected genomic regions and provide greater genome coverage (Galeano et al. 2011). QTLs with genetic main and epistatic effects related to eating quality traits, such as size and fiber traits, have been reported in a few legume crops (asparagus bean: Xu et al. 2013; azuki bean: Isemura et al. 2007; Kaga et al. 2008; cowpea: Andargie et al. 2011; soybean: Kang et al. 2009; and yardlong bean: Kongjaimun et al. 2012a, b). In the case of common bean, several QTLs have been reported for pod fiber, sugar content, color, cross section, width and length traits (Koinange et al. 1996; Kelly et al. 2003; Myers et al. 2004; Davis et al. 2006; VandenLangenberg et al. 2012), but epistatic effects were not analyzed. As epistasis is considered an integral part of the genetic architecture of quantitative traits (Parvez et al. 2007), in the current work we report the identification of single-locus and epistatic QTLs, as well as their environment interaction effects, for six horticultural traits using an Andean intra-gene pool recombinant inbred line (RIL) population. Our results revealed the importance of epistatic QTLs in the genetic control of pod size and color traits, as well as the co-location of some pod QTLs, and hence their usefulness as breeding tools in common bean.

Materials and methods

Population development

A RIL population consisting of 185 F7 lines was developed by single-seed descent from an F2 population. The parents, PMB0225 (white-seeded and green pod common bean line, resistant to the bean common mosaic virus, and indeterminate erect growth habit type II, abbreviated as P1) and PHA1037 (photoperiod-sensitive red-seeded and purple pod nuña bean line, and indeterminate climbing growth habit type IV, abbreviated as P2), were both accessions belonging to the Andean gene pool (Fig. 1).

Experimental design

Given the sensitivity to photoperiod conditions of PHA1037, fifteen plants from each of the 185 RILs and their parents were grown in four greenhouse environments over two consecutive years (2009 and 2010), under long-day (LD) and short-day (SD) natural photoperiod conditions with average day and night temperatures of 25 and 20 °C, respectively. Sowing dates of LD experiments were February 20, 2009 (LD09 code) and March 15, 2010 (LD10 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.

Measurement of pod traits

The quantitative pod traits included (1) width (PWI), the distance at right angles to the sutures at the level of the second seed from the apex, (2) thickness (PT), the distance between sides at the level of the second and third seed from the apex, (3) length (PL), the exterior distance from the peduncle connection point to the apex excluding the beak, (4) the size index (PSI), calculated as the length divided by the width, (5) the length of beak (PBL), and (6) color (PC), recorded as 0 = absence, 1 = presence of red color and 2 = presence of purple color. Measurements were carried out in individual fully expanded immature pods from ten random normal plants.

Statistical data analysis

Variation in the expression of pod traits over all the environments was analysed using ANOVA (PROC GLM, SAS software, SAS Institute Inc v.9.02, 2010,

Fig. 1 Fresh and mature pods of the parental genotypes PMB0225 (**a**) and PHA1037 (**b**). *Scale bar* 1 cm

Cary, NC, USA). The following random factors were included in each model: lines, environments, replication within environments, and the line-by-environment interaction. 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. Significant differences ($P \leq 0.05$) between two means were determined by *t* tests. Descriptive statistical parameters were obtained for each trait and environment (mean value, standard deviation and range of variation), and variances and normality (Kolmogorov–Smirnov test) of the phenotypic traits. Broad-sense heritabilities of additive effects for pod traits and phenotypic correlations were implemented using the statistical SAS software.

QTL analysis

The genetic linkage map described by Yuste-Lisbona et al. (2012) was used for QTL analysis. The *P* locus was added to this map, which consisted of 194 loci (85 amplified fragment length polymorphism, 95 simple sequence repeat, 13 single nucleotide polymorphism, and one morphological marker) distributed over 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-QTLs) 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 scanning to detect putative single-locus QTLs (defined as those showing significant main additive effects) and their environment interactions. In addition, a two-dimensional genome scan was carried out to identify epistatic interaction effects. An experiment-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 a 1,000-permutation test at the confidence level of 95 %. 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, while QTLs with environment interaction effects suggested that their expressions were environmentally dependent. The QTLs detected were designated as recommended by Miklas and Porch (2010). The genetic map and the QTLs detected were drawn using MapChart 2.2 software (Voorrips 2002).

Results

Phenotypic variation of pod horticultural traits in the RIL population

Table 1 shows the mean values and standard errors of the parental genotypes and the RIL population, as well as the ranges of variation of the RIL population for the pod traits for each environment. Analyses of variance showed that environmental effects, genotypic differences and genotype × environment interaction were significant for all traits, while environment effects did not influence PSI (data not shown). All pod traits, with the exception of color, were normally distributed in all environments, as assessed by Kolmogorov–Smirnov tests (data not shown), suggesting that multiple factors interact to affect pod size, perhaps in an additive fashion, and that the presence of major genetic factors controls pod color. Pods of PHA1037 (exotic nuña bean) were larger and pigmented but with smaller beak than those of PMB0225 (cultivated common bean) (Fig. 1). Some pod size components such as PWI and PT were significantly different among RILs but not between parents, likely due to transgressive segregation promoted by new allele combinations appearing in the RIL population. In fact, transgressive segregation in both directions was apparent for all size traits, with a substantial number of lines exhibiting larger pod size and beak length than PHA1037 and PMB0225, indicating that both parents carry genes that contribute to pod quality variation.

The estimated broad-sense heritabilities for pod size traits were above 50 % in both LD09 and SD10 environments (Table S1). The heritability estimates for PBL were high (≥70 %) in all experiments except SD09 (59 %), and PC presented high heritability estimates (≥65 %) in all of the environments studied. A report of the correlation analysis is provided in Table S2. The highest positive correlations were found between PWI/PL and PSI ($r > 0.65$). Low positive and negative correlations were found between PWI/PT and PBL ($r = 0.15$ and -0.19, respectively), PBL and PSI ($r = 0.12$), and PWI and PT ($r = 0.11$).

Main-effect QTLs detected by single-locus analysis

The evaluation of the 185 RILs developed from the cross PMB0225 × PHA1037 under LD and SD natural photoperiod conditions has allowed the identification of 17 single-locus QTLs for pod traits, which were distributed throughout seven LGs (Fig. 2). Eleven of the QTLs only exhibited significant genetic main effects, while six showed both significant genetic main effects and QE interaction effects. A complete report of the single-locus QTLs detected for pod traits is given in Table 2. The additive effects of all putative QTLs explained from 2.2 to 5.9 % of the total phenotypic variation for pod size traits (PWI, PT, PL and PSI), 12.2 % for PBL, and 20.6 % for PC. For PWI, PT and PSI traits, all the QTLs detected had negative values, which indicates that the increase in these traits is due to the presence of the alleles from PMB0225. For PL, PBL and PC 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 contribute to increase these traits. The QTLs with only genetic main effects were located on six LGs: three on LG 1, four on LG 4, and one on LGs 2, 6, 8 and 11. Each QTL explained only a small proportion of the phenotypic variance, ranging from 0.2 to 4.7 %. The four QTLs located on LG 4 ($PWI4^{PP}$, $PT4.1^{PP}$, $PSI4^{PP}$ and $PBL4^{PP}$) were mapped between 55.5 and 58.3 cM. The fact that they were mapped relatively close together and also the significant correlations found between PWI, PT, PSI and PBL seem to indicate that related or pleiotropic genetic factors govern these traits.

In addition, six single-locus QTLs were involved in significant QE interactions in different environments: one QTL for PWI and PSI (SD09 and LD10), PBL (SD09) and PC (SD10), and two QTLs for PL (SD09 and LD10, and SD10). These QTLs were located on three LGs: four on LG 1, and one on each of LGs 4 and 7. The percentage of phenotypic variation explained by these QTLs ranged from 0.2 to 3.2 % for pod size (PWI, PL and PSI), and PBL traits. For PC, QTL $PC7.1^{PP}$ had the highest additive effect, accounting for 13.8 % of the

phenotypic variance, and was located at the position of *P* locus on LG 7, between BM185 and *P* markers. The QE interactions explained from 3.2 to 4.7 % of the phenotypic variance for pod size traits (PWI, PL and PSI), 1.1 % for PBL, and 1.2 % for PC. $PL4^{PP}$ and $PC7.1^{PP}$ showed a significant QE interaction effect only in a SD environment (SD10), explaining 1.1 and 1.2 % of the phenotypic variance, respectively. QTLs ($PWI1^{PP}$, $PL1^{PP}$ and $PSI1.1^{PP}$) affecting pod size traits and located on LG 1 shared the same marker interval, again

Fig. 2 Location of single-locus QTLs and E-QTLs associated with pod size and color traits on a genetic linkage map of common bean based on the RIL population developed from the cross PMB0225 × PHA1037. Distances between 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 2 and 3. Single-locus QTLs are indicated in *white*, E-QTLs are shown in *gray*, and QTLs with both individual additive and epistatic effects are represented in *black*. Epistatic interactions between QTLs are indicated with *numbered stars* and linked by *dashed lines*

Table 1 Phenotypic evaluation (means, standard errors, range of variation and variance analysis results) for pod traits of two common bean parents, PMB0225 and PHA1037, and the RIL population under long-day (LD) and short-day (SD) environments (Env)

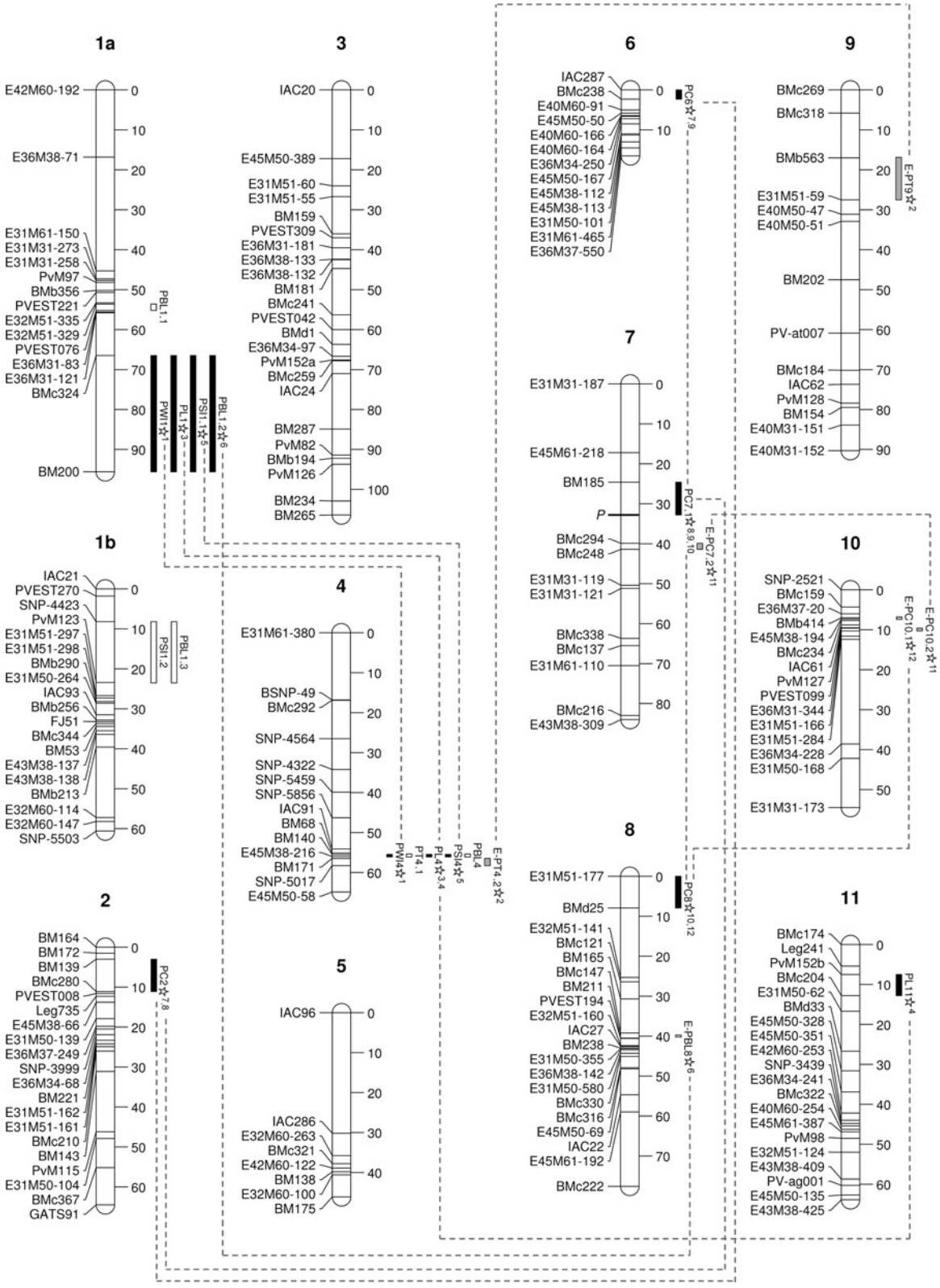
Trait	Env	Block effect	Parents			RILs		
			PMB0225	PHA1037	P^{a}_{PAR}	Mean	Range	P^{a}_{RIL}
Width (PWI)[a]	LD09	ns	12.13 ± 0.33	ND		13.76 ± 0.10	9.18–18.95	**
	SD09	**	13.72 ± 0.46	14.51 ± 0.46	ns	13.18 ± 0.10	9.99–18.45	**
	LD10	ns	13.58 ± 0.33	ND		13.33 ± 01.3	8.66–18.22	ns
	SD10	ns	15.45 ± 0.45	14.62 ± 0.33	ns	15.30 ± 0.10	9.31–22.22	**
Thickness (PT)[a]	LD09	ns	5.99 ± 0.09	ND		6.43 ± 0.06	4.21–9.79	**
	SD09	ns	6.93 ± 0.31	6.48 ± 0.25	ns	6.30 ± 0.04	4.83–10.21	**
	LD10	ns	6.57 ± 0.21	ND		7.14 ± 0.08	4.68–10.77	ns
	SD10	ns	7.02 ± 0.22	6.53 ± 0.23	ns	6.97 ± 0.05	3.66–12.22	**
Length (PL)[a]	LD09	**	94.96 ± 1.70	ND		105.31 ± 0.96	45.00–165.00	**
	SD09	**	97.41 ± 2.38	104.71 ± 2.03	*	107.20 ± 1.14	67.00–166.75	ns
	LD10	ns	96.92 ± 2.45	ND		104.83 ± 1.19	65.00–162.50	*
	SD10	ns	96.18 ± 2.92	102.18 ± 1.09	*	94.73 ± 0.68	47.50–130.00	**
Size index (PSI)[a]	LD09	*	1,152.9 ± 38.8	ND		1,455.8 ± 18.9	556.5–2,722.5	**
	SD09	**	1,328.4 ± 36.9	1,515.8 ± 50.2	**	1,426.5 ± 22.7	692.7–2,926.9	ns
	LD10	ns	1,323.4 ± 61.5	ND		1,402.2 ± 23.6	715.3–2,352.6	*
	SD10	ns	1,480.8 ± 49.6	1,494.6 ± 41.4	ns	1,454.7 ± 14.6	504.1–2,832.4	**
Beak length (PBL)[a]	LD09	ns	10.43 ± 0.46	ND		11.39 ± 0.18	4.30–23.16	**
	SD09	ns	12.24 ± 0.33	9.78 ± 0.30	**	12.54 ± 0.54	6.16–20.28	**
	LD10	ns	12.19 ± 0.34	ND		10.71 ± 0.23	3.75–20.34	ns
	SD10	ns	11.99 ± 0.60	11.00 ± 0.35	ns	12.91 ± 0.12	5.70–19.47	**
Color (PC)[b]	LD09	ns	0.00 ± 0.00	ND		0.27 ± 0.05	0.00–2.00	**
	SD09	ns	0.00 ± 0.00	2.00 ± 0.00	**	0.36 ± 0.05	0.00–2.00	**
	LD10	ns	0.00 ± 0.00	ND		0.37 ± 0.04	0.00–2.00	**
	SD10	ns	0.00 ± 0.00	2.00 ± 0.00	**	0.44 ± 0.03	0.00–2.00	**

ns Non-significant differences between parents or RILs, *ND* no data taken for pod traits in the parent PHA1037 under LD conditions

*, ** Significant at the 0.05 and 0.01 probability levels, respectively, for difference among parents (P_{PAR}) or RILs (P_{RIL})

[a] Size dimensions are given in mm

[b] 0 = all plants showing absence of pod color, 1 = all plants with red pod color trait, and 2 = all plants with purple pod color trait


1a
E42M60-192
E36M38-71
E31M61-150
E31M31-273
E31M31-258
PvM97
BMb356
PVEST221
E32M51-335
E32M51-329
PVEST076
E36M31-83
E36M31-121
BMc324
BM200
PBL1.1
PW1☆1
PL1☆3
PSI1.1☆5
PBL1.2☆6
3
IAC20
E45M50-389
E31M51-60
E31M51-55
BM159
PVEST309
E36M31-181
E36M38-133
E36M38-132
BM181
BMc241
PVEST042
BMd1
E36M34-97
PvM152a
BMc259
IAC24
BM287
PvM82
BMb194
PvM126
BM234
BM265
6
IAC287
BMc238
E40M60-91
E45M50-50
E40M60-166
E40M60-164
E36M34-250
E45M50-167
E45M38-112
E45M38-113
E31M50-101
E31M61-465
E36M37-550
PC6☆7,9
9
BMc269
BMc318
BMb563
E31M51-59
E40M50-47
E40M50-51
BM202
PV-at007
BMc184
IAC62
PvM128
BM154
E40M31-151
E40M31-152
E-PT9☆2
7
E31M31-187
E45M61-218
BM185
P
BMc294
BMc248
E31M31-119
E31M31-121
BMc338
BMc137
E31M61-110
BMc216
E43M38-309
PC7.1☆8,9,10
E-PC7.2☆11
1b
IAC21
PVEST270
SNP-4423
PvM123
E31M51-297
E31M51-298
BMb290
E31M50-264
IAC93
BMb256
FJ51
BMc344
BM53
E43M38-137
E43M38-138
BMb213
E32M60-114
E32M60-147
SNP-5503
PSI1.2
PBL1.3
4
E31M61-380
BSNP-49
BMc292
SNP-4564
SNP-4322
SNP-5459
SNP-5856
IAC91
BM68
BM140
E45M38-216
BM171
SNP-5017
E45M50-58
PW4☆1
PT4.1
PL4☆3,4
PSI4☆5
PBL4
E-PT4.2☆2
10
SNP-2521
BMc159
E36M37-20
BMb414
E45M38-194
BMc234
IAC61
PvM127
PVEST099
E36M31-344
E31M51-166
E31M51-284
E36M34-228
E31M50-168
E31M31-173
E-PC10.1☆12
E-PC10.2☆11
8
E31M51-177
BMd25
E32M51-141
BMc121
BM165
BMc147
BM211
PVEST194
E32M51-160
IAC27
BM238
E31M50-355
E36M38-142
E31M50-580
BMc330
BMc316
E45M50-69
IAC22
E45M61-192
BMc222
PC8☆10,12
E-PBL8☆6
2
BM164
BM172
BM139
BMc280
PVEST008
Leg735
E45M38-66
E31M50-139
E36M37-249
SNP-3999
E36M34-68
BM221
E31M51-162
E31M51-161
BMc210
BM143
PvM115
E31M50-104
BMc367
GATS91
PC2☆7,8
5
IAC96
IAC286
E32M60-263
BMc321
E42M60-122
BM138
E32M60-100
BM175
11
BMc174
Leg241
PvM152b
BMc204
E31M50-62
BMd33
E45M50-328
E45M50-351
E42M60-253
SNP-3439
E36M34-241
BMc322
E40M60-254
E45M61-387
PvM98
E32M51-124
E43M38-409
PV-ag001
E45M50-135
E43M38-425
PL11☆4

suggesting the possibility of the existence of pleiotropic genetic factors on LG 1. PWI1^{PP}, PL1^{PP} and PSI1.1^{PP} showed the largest variation between environments, with negative and positive QE interaction effects in SD (SD09) and LD (LD10) environments, respectively.

Epistatic QTLs identified by two-locus analysis

A total of 18 E-QTLs (two each for PWI, PT, PSI and PBL, three for PL and seven for PC) involved in 12 epistatic interactions (one each for PWI, PT, PSI and PBL, two for PL and SP and six for PC) were detected for the six pod traits evaluated by the combined analysis of the multi-environment phenotypic values. A complete description of digenic epistatic interaction analysis for pod traits is shown in Table 3. Interestingly, 12 of the 18 E-QTLs identified were previously detected as single-locus QTLs. Hence, with the exception of E-PT4.2^{PP} and E-PT9^{PP} for PT, E-PBL8 ^{PP} for PBL, and E-PC7.2^{PP}, E-PC10.1^{PP} and E-PC10.2^{PP} for PC, the remaining E-QTLs not only participated in epistatic interactions, but they also had an individual genetic effect. The analysis revealed novel loci on LGs 4, 7, 8, 9, and 10 interacting to influence PT, PBL, and PC traits. The percentage of phenotypic variance explained by the interaction of the E-QTLs ranged from 1.1 to 4.2 % for pod size traits (PWI, PT, PL, and PSI), 3.1 % for PBL and 13.3 % for PC. Among the 12 digenic interactions identified in this study, only two had both significant genetic and E-QE interaction effects. For PL, the percentage of phenotypic variance explained by the epistatic interaction between E-PL4^{PP} and E-PL11^{PP} loci was 1.2 % in LD10, while for PBL the percentage of phenotypic variance explained by the epistatic interaction between PBL1.2^{PP} and PBL8^{PP} loci was 1.1 and 0.8 % in LD10 and SD10, respectively. The positive and negative E-QE effect values obtained for this epistatic interaction indicate that both parent alleles could contribute to increasing the trait, depending on the environmental conditions.

Discussion

The main goal of the current study was to unravel the genetic variation underlying pod horticultural traits in common bean. The QTL analyses performed detected a total of 23 QTLs (single-locus QTLs and E-QTLs) for six pod traits: five of them had only individual additive effects and six showed only epistatic effects, while twelve had both effects. Hence, the genetic analysis carried out indicated that pod horticultural traits show a polygenic inheritance, where epistasis clearly plays a significant role, making this the first work to report a comprehensive QTL analysis of these traits in common bean.

Single-locus QTLs identified for pod horticultural traits

The total phenotypic variation explained by all putative single-locus QTLs was 2.2–5.9 % for pod size traits (PWI, PT, PL and PSI), 12.2 % for PBL and 20.6 % for PC. The single-locus QTL analysis results showed that the genetic basis of pod size traits and PBL seems to be controlled by a few minor QTLs. In addition, one major QTL (PC7.1^{PP}) plus several minor ones were detected for PC. These results are in accordance with previous reports for pod traits in common bean (Koinange et al. 1996) and other legumes (azuki bean: Isemura et al. 2007; Kaga et al. 2008; rice bean: Isemura et al. 2010; and soybean: Liu et al. 2007), where each trait was controlled by a few minor QTLs or by a major QTL and several minor ones. Most of the main genetic QTLs detected were consistent over the four environments, although six single-locus QTLs were subject to environmental modification. Interestingly, QTLs PWI1^{PP}, PL1^{PP} and PSI1.1^{PP} showed a differential expression between LD and SD environmental conditions, with negative and positive QE interaction effects in SD (SD09) and LD (LD10) environments, respectively. These results suggest that pod traits seem to be affected by genetic make-up as well as environmental factors, particularly those related to changes in temperature and rainfall.

There are few studies on the genetics of pod size traits in common bean. Single-locus QTLs for pod length have been reported in a Midas × G12873 (Andean cultivar × Mesoamerican wild genotype) RIL population by Koinange et al. (1996) on LGs 1, 2 and 7. In this study, using an Andean RIL population, three single-locus QTLs for PL were detected on LGs 1, 4 and 11. Despite the fact that comparative analysis of QTLs for different parent populations are especially complex, our results suggest that the genomic region of LG 1 seems to be involved in the genetic control of

Table 2 Single-locus QTLs and QTLs × environment (QE) interaction effects for pod traits identified in the RIL population PMB0225 × PHA1037 based on long-day (LD) and short-day (SD) environments

QTL	Marker interval	LG (pos.)[a]	*F* value[b]	*A*[c]	h^2 (a)[d]	QE AE[e]	h^2 (ae)[f]
Width (PWI)							
PWI1^{PP}	BMc324–BM200	1a (66.5–95.6)	6.3	−0.56*	0.2	–22.25** AE2	1.9
						18.06* AE3	1.3
PWI4^{PP}	BM140–E45M38-216	4 (55.5–55.9)	7.4	−18.72***	2.9	ns	
Thickness (PT)							
PT4.1^{PP}	BM140–E45M38-216	4 (55.5–55.9)	5.9	−0.84***	2.2	ns	
Length (PL)							
PL1^{PP}	BMc324–BM200	1a (66.5–95.6)	8.3	−161.6**	0.6	–369.52*** AE2	2.4
						280.14** AE3	1.2
PL4^{PP}	BM140–E45M38-216	4 (55.5–55.9)	8.5	−161.2***	3.1	114.58* AE4	1.1
PL11^{PP}	PvM152b–BMc204	11 (7.5–12.8)	7.1	66.13***	2.2	ns	
Size index (PSI)							
PSI1.1^{PP}	BMc324–BM200	1a (66.5–95.6)	6.6	−1,033.4*	0.3	–4,172.7*** AE2	2.2
						3,550.9** AE3	1.6
PSI1.2^{PP}	SNP-4423–PvM123	1b (8.2–23.5)	5.7	−970.9***	2.1	ns	
PSI4^{PP}	BM171–SNP-5017	4 (56.5–58.3)	5.8	−2,229.3***	2.5	ns	
Beak length (PBL)							
PBL1.1^{PP}	E32M51-329–PVEST76	1a (53.6–55.2)	8.9	12.1***	4.1	ns	
PBL1.2^{PP}	BMc324–BM200	1a (66.5–95.6)	6.3	−21.69***	0.2	ns	
PBL1.3^{PP}	SNP-4423–PvM123	1b (8.2–23.5)	8.8	−0.85***	3.2	–23.83* AE2	1.1
PBL4^{PP}	BM140–E45M38-216	4 (55.5–55.9)	10.7	−24.62***	4.7	ns	
Color (PC)							
PC2^{PP}	BM139–BMc280	2 (3.0–11.1)	5.8	−0.11***	1.7	ns	
PC6^{PP}	IAC287–BMc238	6 (0.0–2.3)	9.5	−0.16***	3.5	ns	
PC7.1^{PP}	BM185-*P*	7 (24.6–32.8)	34.2	0.29***	13.8	0.11*** AE4	1.2
PC8^{PP}	E31M51–177–BMd25	8 (0.0–7.9)	5.9	−0.08***	1.6	ns	

ns No significant effects in the four environments evaluated

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$. Only significant effects are listed

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

[b] *F* values of significance of each QTL. Threshold *F* values were 5.3, 5.3, 5.2, 5.2, 5.3 and 5.2 for PWI, PT, PL, PSI, PBL and PC, respectively

[c] Estimated additive effect. Positive values indicate that alleles from PHA1037 increase the trait value, and negative values indicate that the increase in the trait 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. AE1, AE2, AE3 and AE4 additive-by-environment interaction effects are associated with environments LD09, SD09, LD10 and SD10, respectively. The meaning of sign values is described in footnote [c]

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

pod length in both Andean and Mesoamerican gene pools. On the other hand, the QTLs identified on LGs 4 and 11 might be specific to the Andean background, though additional studies would be necessary to draw definitive conclusions.

The *Prp* locus regulates anthocyanin in pods and *V* is an intensifier for other color genes, with *Prp V* and *Prp v* expressing purple and red pods, respectively (Okonkwo and Clayberg 1984; Bassett 1996, 2005). Kelly and Vallejo (2004) showed the existence of *Prp* located on

Table 3 Epistatic QTLs (E-QTLs) and E-QTL × environment (E-QE) interaction effects for pod traits detected in the RIL population PMB0225 × PHA1037

E-QTLi[a]	Marker interval	LG (pos.)[b]	E-QTLj[a]	Marker interval	LG (pos.)	*F* value[c]	AA[d]	h^2 (aa)[e]	E-QE AAE[f]	h^2 (aae)[g]
Width (PWI)										
E-PWI1^{PP}	BMc324–BM200	1a (66.5–95.6)	E-PWI4^{PP}	BM140–E45M38–216	4 (55.5–55.9)	5.6	−29.71***	1.5	ns	
Thickness (PT)										
E-PT4.2^{PP}	BM171–SNP-5017	4 (56.5–58.3)	E-PT9^{PP}	BMb563–E31M51–59	9 (16.9–27.5)	6.4	−11.75***	4.2	ns	
Length (PL)										
E-PL1^{PP}	BMc324–BM200	1a (66.5–95.6)	E-PL4^{PP}	BM140–E45M38–216	4 (55.5–55.9)	6.1	−333.83**	0.8	ns	
E-PL4^{PP}	BM140–E45M38–216	4 (55.5–55.9)	E-PL11^{PP}	PvM152b–BMc204	11 (7.5–12.8)	5.9	61.16*	0.3	111.96* AAE3	1.2
Size index (PSI)										
E-PSI1.1^{PP}	BMc324–BM200	1a (66.5–95.6)	E-PSI4^{PP}	BM171–SNP-5017	4 (56.5–58.3)	6.2	−4,501.1**	1.1	ns	
Beak length (PBL)										
E-PBL1.2^{PP}	BMc324–BM200	1a (66.5–95.6)	E-PBL8^{PP}	BM211–PVEST194	8 (40.5–40.6)	8.5	0.96***	3.1	0.64* AAE3	1.1
									−0.61* AAE4	0.8
Color (PC)										
E-PC2^{PP}	BM139–BMc280	2 (3.0–11.1)	E-PC6^{PP}	IAC287–BMc238	6 (0.0–2.3)	16.8	0.13***	3.1	ns	
E-PC2^{PP}	BM139–BMc280	2 (3.0–11.1)	E-PC7.1^{PP}	BM185-*P*	7 (24.6–32.8)	9.1	−0.08***	1.7	ns	
E-PC6^{PP}	IAC287–BMc238	6 (0.0–2.3)	E-PC7.1^{PP}	BM185-*P*	7 (24.6–32.8)	9.8	−0.12***	2.1	ns	
E-PC7.1^{PP}	BM185–*P*	7 (24.6–32.8)	E-PC8^{PP}	E31M51–177–BMd25	8 (0.0–7.9)	9.6	−0.07***	2.1	ns	
E-PC7.2^{PP}	BMc294–BMc248	7 (39.9–41.4)	E-PC10.2^{PP}	PVEST99–E36M31-344	10 (9.6–10.3)	15.6	0.14***	3.2	ns	
E-PC8^{PP}	E31M51–177–BMd25	8 (0.0–7.9)	E-PC10.1^{PP}	BMb414–E45M38-194	10 (7.0–7.3)	7.3	−0.11***	1.1	ns	

ns No significant effects on the four environments evaluated

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$. Only significant effects are listed

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

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

[c] *F* values of significance of each epistatic interaction. Threshold *F* values were 4.9, 4.8, 5.3, 5.4, 5.3 and 5.9 for PWI, PT, PL, PSI, PBL and PC, respectively

[d] Estimated additive-by-additive epistatic effect. Positive values indicate that alleles from PHA1037 increase the trait value, and negative values indicate that the increase in the trait is due to the presence of the alleles from PMB0225

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

[f] Predicted additive-by-additive epistatic effect by environment interaction effect. AAE1, AAE2, AAE3, and AAE4: epistasis associated with environments LD09, SD09, LD10 SD10, respectively. The meaning of sign values is described in footnote d

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

LG 8, while the *V* gene was previously located on LG6 (McClean et al. 2002). The QTLs detected in this study for PC seem to be dispersed across the genome (LGs 2, 6, 7 and 8); of them, two QTLs were mapped on LGs 8 (PC8) and 6 (PC6), which could correspond to the *Prp* and *V* genes. The major QTL PC7.1^{PP} was mapped on LG 7, where the locus *P*, known as the ground factor for all color organs (McClean et al. 2002), was previously identified (Vallejos et al. 1992; Koinange et al. 1996; Erdmann et al. 2002). In this population, the exotic nuña genotype (PHA1037) possessed the *PP* dominant alleles (pink flower, red seed and purple pods) while the cultivated genotype (PMB0225) had the *pp* recessive ones (white flower and seed, and green pods). Moreover, the negative additive values of QTLs for PC on LGs 2, 6 and 8 suggest that alleles from PMB0225 parent also contributed to the pod color segregation observed in the RIL population.

Epistasis is an important genetic basis of pod horticultural traits

Despite the fact that epistasis is to be expected in traits that are controlled by several genes/QTLs in autogamous plants (Holland 2001), previous QTL reports on pod-related traits (Koinange et al. 1996; Kelly et al. 2003; Myers et al. 2004; Davis et al. 2006; Vanden-Langenberg et al. 2012) have not taken into account the identification of epistatic effects. In the current study, epistasis was detected for the six pod traits evaluated and 12 epistatic interactions were identified. A common feature of the epistatic interactions detected for pod-related traits is that most of them occur between QTLs with main additive effects, but QTLs that showed only epistatic effects were also detected. These epistatic QTLs might be considered as modifying genes, which have no significant effects alone but might affect the trait's expression by epistatic interactions with other loci. Overall, the results suggest that, if epistatic effects are ignored in QTL mapping, the individual additive effects might be confused by epistatic effects. Hence, breeders must take into account not only the effects of individual alleles, but also the epistatic effects due to the interaction between alleles at different loci.

Among the epistatic interactions detected, we should highlight the E-QTLs involved in six epistatic interactions identified for PC, whose interactions explained 13.3 % of the phenotypic variance observed, indicating the significant role of epistasis in the genetic control of this trait. This complex genetic inheritance 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, interactions that define the many colors observed within the species. In addition, the percentage of phenotypic variance explained by the remaining epistatic interactions was 1.1–4.2 % for pod size traits (PWI, PT, PL and PSI) and 3.1 % for PBL. Therefore, the results showed that not only individual additive effects but also digenic epistatic interactions clearly play an important role in the genetic control of size and pod color traits, suggesting that some loci have been co-adapted during domestication. In addition, the findings indicate the presence of favorable allele combinations (involved in epistatic interactions) within the Andean gene pool. Nevertheless, it should be noted that, although this study revealed a large number of epistatic interactions through statistical genetic analysis, many further studies are needed before we can fully understand the biological meaning of this phenomena.

Co-location of QTLs governing size horticultural traits

The QTL analyses showed that the regions of LGs 1a (66.5–95.6 cM), 1b (8.2–23.5 cM), and 4 (55.5–58.3 cM) bear single-locus QTLs and E-QTLs for PWI, PT, PL, PSI and PBL traits. In addition, significant correlations were found between pod size (PWI, PL, PT and PSI) and beak length (PBL) traits. Therefore, QTLs controlling pod size are generally not randomly distributed across the common bean genome, which also agrees with the results reported by Gepts (2004). Most of the QTLs affecting pod morphology clustered on LGs 1 and 4, which indicates that these genomic regions may contain linked genes or a gene with pleiotropic effects governing these traits (Smartt 1976). Further studies on fine mapping of the target genomic regions should help to elucidate the issue of pleiotropy versus tight linkage of QTLs. Previous studies have also described the co-location of QTLs for different agronomic traits in common bean (Tsai et al. 1998; Tar'an et al. 2002; Beattie et al. 2003; Blair et al. 2006; Pérez-Vega et al. 2010; Yuste-Lisbona et al. 2012). Likewise, QTL clusters for pod size traits (length and width) have been observed in other legume species, such as *Vigna unguiculata* (Kongjaimun et al. 2012b) and *Vigna angularis* (Isemura et al. 2007).

Future perspectives and challenges in marker-assisted common bean breeding programs for pod horticultural traits

The mapping of QTLs associated with key pod traits in common bean could open up various opportunities to improve the efficiency of plant breeding and selection for lines with improved pod appearance and, hence, quality and market value. The results provide a foundation for marker-assisted selection of horticultural QTLs in common bean because most of these QTLs showed stability across significantly correlated traits, while also sharing QTLs for more than one trait, and they could be manipulated simultaneously in breeding programs. Therefore, dissecting the genetics of important horticultural traits in mapping populations is not only theoretically useful, it can also facilitate the choice of appropriate DNA markers to aid selection. The mapping of QTLs including epistatic loci for six important pod traits in the current study has strengthened the case for implementing marker-assisted breeding toward genetic improvement of common bean. In addition, the results of this work may contribute not only to better understanding of pod-related traits, but also to initiating a map-based cloning approach to the genes related to pod quality. Initiatives on sequencing and functional genomics of the common bean genome are currently in progress (McClean et al. 2009) and they will provide an excellent means of achieving this objective.

Acknowledgments This work was financed by the Ministerio de Economía y Competitividad and UE-FEDER Program (AGL2011-25562). We thank Junta de Andalucía (Grant Number P10-AGR-06931) and Campus de Excelencia Internacional Agroalimentario-CeiA3 for partially supporting this work.

References

Andargie M, Pasquet RS, Gowda BS, Muluvi GM, Timko MP (2011) Construction of a SSR-based genetic map and identification of QTL for domestication traits using recombinant inbred lines from a cross between wild and cultivated cowpea (*V. unguiculata* (L.) Walp.). Mol Breed 28:413–420. doi:10.1007/s11032-011-9598-2

Bassett MJ (1996) List of genes—*Phaseolus vulgaris* L. Annu Rep Bean Improv Coop 39:1–19

Bassett MJ (2005) A new gene (*Prpi-2*) for intensified anthocyanin expression (IAE) syndrome in common bean and a reconciliation of gene symbols used by early investigators of gene symbols for purple pod and IAE syndrome. J Am Soc Hortic Sci 130:550–554

Beattie AD, Larsen J, Michaels TE, Pauls KP (2003) Mapping quantitative trait loci for a common bean (*Phaseolus vulgaris* L.) ideotype. Genome 46:411–422. doi:10.1139/g03-015

Blair MW, Iriarte G, Beebe S (2006) QTL analysis of yield traits in an advanced backcross population derived from a cultivated Andean wild common bean (*Phaseolus vulgaris* L.) cross. Theor Appl Genet 112:1149–1163. doi:10.1007/s00122-006-0217-2

Davis JW, Kean D, Yorgey B, Fourie D, Miklas PN, Myers JR (2006) A molecular marker linkage map of snap bean (*Phaseolus vulgaris*). Annu Rep Bean Improv Coop 49:73–74

De Ron AM, Casquero PA, González AM, Santalla M (2004) Environmental and genotypic effects on pod characteristics related to common bean quality. J Agron Crop Sci 190:248–255

Drijfhout E (1978) Inheritance of temperature-dependent string formation in common bean (*Phaseolus vulgaris* L.). Neth J Agric Sci 26:99–105

Erdmann PM, Lee RK, Bassett MJ, McClean PE (2002) A molecular marker tightly linked to *P*, a gene required for flower and seed coat color in common bean (*Phaseolus vulgaris* L.), contains the Ty3-*gypsy* retrotransposon *Tpv3g*. Genome 45:728–736. doi:10.1139/g02-037

Galeano CH, Fernandez AC, Franco-Herrera N, Cichy KA, McClean PE (2011) Saturation of an intra-gene pool linkage map: towards a unified consensus linkage map for fine mapping and synteny analysis in common bean. PLoS One 6:12. doi:10.1371/journal.pone.0028135

Gepts P (1988) A Middle American and an Andean common bean gene pool. Curr Plant Sci Biotechnol Agric 6:375–390

Gepts P (2004) Crop domestication as a long time selection experiment. Plant Breed Rev 24:1–44. doi:10.1002/9780470650288.ch1

Gepts P, Debouck D (1991) Origin, domestication, and evolution of the common bean. In: Voysest O, Van Schoonhoven A (eds) Common beans: research for crop improvement. CAB, Oxon, pp 7–53

Govindaraj P, Vinod KK, Arumugachamy S, Maheswaran M (2009) Analysing genetic control of cooked grain traits and gelatinization temperature in a double haploid population of rice by quantitative trait loci mapping. Euphytica 166:165–176. doi:10.1007/s10681-008-9808-0

Guzman-Maldonado SH, Martínez O, Acosta-Gallegos JA, Guevara-Lara F, Paredes-López O (2003) Putative quantitative trait loci for physical and chemical components of common bean. Crop Sci 43:1029–1035. doi:10.2135/cropsci 2003.1029

Holland JB (2001) Epistasis and plant breeding. Plant Breed Rev 21:27–82. doi:10.1002/9780470650196.ch2

Holland JB (2007) Genetic architecture of complex traits in plants. Curr Opin Plant Biol 10:156–161. doi:10.1016/j.pbi.2007.01.003

Isemura T, Kaga A, Konishi S, Ando T, Tomooka N, Han OK, Vaughan DA (2007) Genome dissection of traits related to domestication in azuki bean (*Vigna angularis*) and their comparison with other warm season legumes. Ann Bot 100:1053–1071. doi:10.1093/aob/mcm155

Isemura T, Kaga A, Tomooka N, Shimizu T, Vaughan DA (2010) Construction of a genetic linkage map and genetic analysis of the domestication related traits in rice bean (*Vigna umbellata*). Ann Bot 106:927–944. doi:10.1093/aob/mcq188

Johnson WC, Gepts P (2002) The role of epistasis in controlling seed yield and other agronomic traits in an Andean × Mesoamerican cross of common bean (*Phaseolus vulgaris* L.). Euphytica 125:69–79

Kaga A, Isemura T, Tomooka N, Vaughan DA (2008) The genetics of domestication of azuki bean (*Vigna angularis*). Genetics 178:1013–1036. doi:10.1534/genetics.107.078451

Kang ST, Kwak M, Kim HK, Choung MG, Han WY, Baek IY, Kim MY, Van K, Lee SH (2009) Population-specific QTLs and their different epistatic interactions for pod dehiscence in soybean [*Glycine max* (L.) Merr.]. Euphytica 166:15–24. doi:10.1007/s10681-008-9810-6

Kelly JD, Vallejo VA (2004) A comprehensive review of the major genes conditioning resistance to anthracnose in common bean. HortScience 39:1196–1207

Kelly JD, Gepts P, Miklas PN, Coyne DP (2003) Tagging and mapping of genes and QTL and molecular-marker assisted selection for traits of economic importance in bean and cowpea. Field Crop Res 82:135–154. doi:10.1016/S0378-4290(03)00034-0

Koinange EMK, Singh SP, Gepts P (1996) Genetic control of the domestication syndrome in common bean. Crop Sci 36:1037–1045

Kongjaimun A, Kaga A, Tomooka N, Somta P, Shimizu T, Shu Y, Isemura T, Vaughan DA, Srinives P (2012a) An SSR-based linkage map of yardlong bean (*Vigna unguiculata* (L.) Walp. subsp. *unguiculata* Sesquipedalis Group) and QTL analysis of pod length. Genome 55:81–92. doi:10.1139/g11-078

Kongjaimun A, Kaga A, Tomooka N, Somta P, Vaughan DA, Srinives P (2012b) The genetics of domestication of yardlong bean, *Vigna unguiculata* (L.) Walp. ssp. *unguiculata* cv.-gr. *sesquipedalis*. Ann Bot 109:1185–1200. doi:10.1093/aob/mcs048

Kosambi DD (1944) The estimation of map distances from recombination values. Ann Eugen 12:172–175

Leakey CLA (1988) Genotypic and phenotypic markers in common bean. In: Gepts P (ed) Genetic resources of Phaseolus beans. Kluwer, Dordrecht, pp 245–347

Liu B, Fujita T, Yan ZH, Sakamoto S, Xu D, Abe J (2007) QTL mapping of domestication-related traits in soybean (*Glycine max*). Ann Bot 100:1027–1038. doi:10.1093/aob/mcm149

McClean PE, Lee RK, Otto C, Gepts P, Bassett MJ (2002) Molecular and phenotypic mapping of genes controlling seed coat pattern and color in common bean (*Phaseolus vulgaris* L.). J Hered 93:148–152. doi:10.1093/jhered/93.2.148

McClean PE, Cannon S, Gepts P, Hudson M, Jackson S, Rokhsar D, Schmutz J, Vance C (2009) Towards a whole genome sequence of common bean (*Phaseolus vulgaris*): background, approaches, applications. http://www.csrees.usda.gov/business/reporting/stakeholder/pdfs/pl_common_bean.pdf. Accessed 26 Dec 2013

Miklas PN, Porch T (2010) Guidelines for common bean QTL nomenclature. Annu Rep Bean Improv Coop 53:202–204

Myers JR, Bagget JR (1999) Improvement of snap beans. In: Singh SP (ed) Common bean improvement in the twenty-first century. Kluwer, Dordrecht, pp 289–329

Myers JR, Davis J, Yorgey B, Kean D (2004) Mapping quantitative trait loci for green bean traits of horticultural importance. Annu Rep Bean Improv Coop 47:75–76

Okonkwo CA, Clayberg CD (1984) Genetics of flower and pod color in *Phaseolus vulgaris*. J Hered 75:440–444

Park SO, Coyne DP, Jung G, Skroch PW, Arnaud-Santana E, Steadman JR, Ariyarathne HM, Nienhuis J (2000) Mapping of QTL for seed size and shape traits in common bean. J Am Soc Hort Sci 125:466–475

Parvez AS, Rather AG, Warsi MZK (2007) Implications of epistasis in maize breeding. Int J Plant Breed Genet 1:1–11. doi:10.3923/ijpbg.2007.1.11

Pedrosa-Harand A, Porch T, Gepts T (2008) Standard nomenclature for common bean chromosomes and linkage groups. Annu Rep Bean Improv Coop 51:106–107

Pérez-Vega E, Pañeda A, Rodríguez-Suárez C, Campa A, Giraldez R, Ferreira JJ (2010) Mapping of QTLs for morpho-agronomic and seed quality traits in a RIL population of common bean (*Phaseolus vulgaris* L.). Theor Appl Genet 120:1367–1380. doi:10.1007/s00122-010-1261-5

Phillips PC (2008) Epistasis—the essential role of gene interactions in the structure and evolution of genetic systems. Nat Rev Genet 9:855–867. doi:10.1038/nrg2452

Prakken R (1934) Inheritance of colours and pod characters in *Phaseolus vulgaris* L. Genetica 16:177–294

Silbernagel MJ (1986) Snap bean breeding. In: Bassett M (ed) Breeding vegetable crops. AVI, Westport, CT, pp 243–282

Singh SP (1989) Patterns of variation in cultivated common bean (*Phaseolus vulgaris*, Fabaceae). Econ Bot 43:39–57

Smartt J (1976) Tropical pulses. Longman, London, p 348

Tanksley SD, McCouch SR (1997) Seed banks and molecular maps: unlocking genetic potential from the wild. Science 277:1063–1066. doi:10.1126/science.277 5329.1063

Tar'an B, Michaels TE, Pauls KP (2002) Genetic mapping of agronomic traits in common bean. Crop Sci 42:544–556. doi:10.2135/cropsci 2002.5440

Tsai SM, Nodari RO, Moon DH, Camargo LEA, Vencovsky R, Geps P (1998) QTL mapping for nodule number and common bacterial blight in *Phaseolus vulgaris* L. Plant Soil 204:135–145

Vallejos CE, Sakiyama NS, Chase CD (1992) A molecular-marker-based linkage map of *Phaseolus vulgaris* L. Genetics 131:733–740

van Ooijen JH (2006) JoinMap®4, software for the calculation of genetic linkage maps in experimental populations. Kyazma BV, Wageningen

VandenLangenberg KM, Bethke PC, Nienhuis J (2012) Identification of quantitative trait loci associated with fructose, glucose, and sucrose concentration in snap bean (*Phaseolus vulgaris* L.) pods. Crop Sci 52:1593–1599. doi:10.2135/cropsci2011.07.0396

Voorrips RE (2002) MapChart: software for the graphical presentation of linkage maps and QTLs. J Hered 93:77–78. doi:10.1093/jhered/93.1.77

Wang CS, Rutledge JJ, Gianola D (1994) Bayesian analysis of mixed linear models via Gibbs sampling with an application to litter size in Iberian pigs. Genet Sel Evol 26:91–115. doi:10.1186/1297-9686-26-2-91

Xu P, Wu X, Wang B, Hu T, Lu Z, Liu Y, Qin D, Wang S, Li G (2013) QTL mapping and epistatic interaction analysis in asparagus bean for several characterized and novel

horticulturally important traits. BMC Genet 14:4. doi:10.1186/1471-2156-14-4

Yang J, Hu CC, Hu H, Yu RD, Xia Z, Ye XZ, Zhu J (2008) QTLNetwork: mapping and visualizing genetic architecture of complex traits in experimental populations. Bioinformatics 24:721–723. doi:10.1093/bioinformatics/btm494

Yuste-Lisbona FJ, Santalla M, Capel C, García-Alcázar M, De La Fuente M, Capel J, De Ron AM, Lozano R (2012) Marker-based linkage map of Andean common bean (*Phaseolus vulgaris* L.) and mapping of QTLs underlying popping ability traits. BMC Plant Biol 12:136. doi:10.1186/1471-2229-12-136