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Dissecting the genetic basis of popping ability in nuña bean, an ancient cultivar of common bean

Ana M. González · Fernando J. Yuste-Lisbona · María Lores · Antonio M. De Ron · Rafael Lozano · Marta Santalla

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Abstract Nuña beans (*Phaseolus vulgaris* L.), an ancient and pre-ceramic landrace native to Andean region, possess the property of popping and a high content of proteins and carbohydrates, which makes it an alternative nutritious snack. Knowledge on the genetic bases of popping ability is relevant for common bean improvement. Progenies derived from two nuña bean crosses were used in a generation mean based mating design to determine the inheritance and gene action for five popping related traits: length of popped seeds (PSL), popping dimension index (PDI), percentage of un-popped seeds (PUS), popping percentage average (PPA) and expansion coefficient (EC). Significant additive gene effects were found for all traits, and was the only source of the observed variation for PSL, while dominance and higher-order interactions among loci contributed to the genetic divergence for the other traits. The dominance of the cultivated over nuña alleles for PDI, PPA, EC and PUS, was confirmed by high mid-parent heterosis values and generation mean comparisons. The [d] and [dd] gene effects were in opposite direction for PPA and EC, indicating duplicate epistasis. Therefore, epistasis is likely to be an important explanation for the heterosis in both traits. For PDI and PUS, the opposite signs for [aa] and [dd] gene effects indicated that the genes for increasing popping are dispersed between the parents. Generation means and variances of BC_1P_2 indicated advantages of the backcross breeding procedure to improve the adaptation of the exotic germplasm and at the same time, transfer part of the desired donor genes to cultivated common bean. The backcross to the nuña parent could be an alternative to maintain/recover the favorable epistatic gene combinations found for PDI, PPA, EC and PUS traits.

Keywords *Phaseolus vulgaris* · Popping · Breeding programs · Generation mean analysis · Quantitative inheritance

Ana M González, Fernando J Yuste-Lisbona should be regarded as joint First Authors.

A. M. González · M. Lores · A. M. De Ron · M. Santalla (✉)
Grupo de Biología de Agrosistemas, Departamento de Recursos Fitogenéticos, Misión Biológica de Galicia-CSIC, P.O. Box 28, 36080 Pontevedra, Spain
e-mail: msantalla@mbg.csic.es

F. J. Yuste-Lisbona · R. Lozano
Departamento de Biología Aplicada (Genética), Centro de Investigación en Biotecnología Agroalimentaria (BITAL), Universidad de Almería, Campus de Excelencia Internacional Agroalimentario, CeiA3, 04120 Almería, Spain

Introduction

Popbean or nuña bean (*Phaseolus vulgaris* L., Fabaceae) is considered an early-domesticated common bean, traditionally grown in the Andean highlands of

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South America. Linguistic, ethnobotanical, and archaeological data suggest that they were grown in highlands of Peru and Bolivia during pre-Hispanic times (Tohme et al. 1995). Observations of ancient beans at the Guitarrero Cave in Ancash, Peru, indicate that nuña beans may have been available 11,000 years ago (Kaplan and Kaplan 1988), they may have been the first bean consumed by man since they can easily be prepared for eating by toasting them on a heated stone. The first selection pressures leading to domestication of common bean could have resulted in the development of popping beans, and it appears that toasting grains was a well-established tradition in the Andes and possibly in Mesoamerica, where early maize races have also been used for popping (Mangelsdorf and Smith 1949). However, no evidence of nuña beans has been found in Mesoamerica, most likely due to genetic differences in photoperiod response between the Mesoamerican and Andean gene pools (Kornegay et al. 1993; Tohme et al. 1995). Nuña bean could be considered as the bean counterpart of popcorn, both are old forms of their respective crops and their grains explode with heat, but the popping expansion mechanism is different (Hoseney et al. 1983; Spaeth et al. 1989; da Silva et al. 1993; Vorwald and Nienhuis 2009a). The lack of day-length-insensitive nuña bean germplasm is likely one of the biological factors that has restricted its production and commercialization in temperate regions (Kmiecik and Nienhuis 1998; Ogg et al. 1998).

Common bean breeding programs aimed at rapid cultivar improvement have generally relied on the use of established cultivars and elite lines in the development of breeding material. The result has been a narrowing of the germplasm base of the cultivated common bean. To broaden the germplasm base and maintain genetic diversity in the crop, breeders have considered incorporating exotic germplasm into their cultivar development programs (Blair et al. 2006; Acosta et al. 2007). While many of the available common bean germplasm lines have been screened for yield, pest and abiotic tolerance and nutritional quality, fewer efforts have been directed toward the identification of lines with potential for improving the seed characters considered important for application in the industry as snack food or candy (Kmiecik and Nienhuis 1997; Ogg et al. 1998, 2008; Vorwald and Nienhuis 2009a, b; Pearson et al. 2012). Taking advantage of useful quantitative genes from an exotic line or related wild species requires a different approach than the introgression of specific traits into the adapted population. An independent germplasm enhancement program allows for the retention of progenies with favorable alleles for quantitative traits that would otherwise be discarded in a breeding program as being unproductive or undesirable. Genetic studies to determine combining abilities, heritability, and relative importance of additive, dominance, and epistatic gene effects in controlling traits of interest can be valuable in deciding the most appropriate breeding approach.

Important traits in nuña bean, including ability for popping and adaptability, are considered to be quantitatively inherited, and the exploitation of genetic variability of these quantitative traits through hybridization, inbreeding, and selection must be an important focus of the improvement programs in bean such as in other crops as maize, peanut and rice (Clary 1954; Ashman 1983; Dofing et al. 1990, 1991; Murugesan and Bhattacharya 1991; Isleib et al. 1998; Zeigler 2001; Pattee et al. 2001; Lu et al. 2003; Babu et al. 2006; Miranda et al. 2008). Although methods for characterizing genetic variability in self-fertilizing species are available, and information on the types of gene action and their relative importance in some traits of common bean has slowly started to accumulate during the last three decades (Zimmermann et al. 1985; Kornegay and Temple 1986; Sauter et al. 1990; Chung et al. 1991; Hanson et al. 1993; Park et al. 1994; Rainey and Griffiths 2005a; Checa et al. 2006), there have been few studies of the genetic basis for popping in nuña bean (Vorwald and Nienhuis 2009b; Yuste-Lisbona et al. 2012). Heterosis has been observed in common bean for agronomic traits in crosses between genetically diverse varieties and is related to genetic diversity (Ghaderi et al. 1984; Nienhuis and Singh 1986; Franco et al. 2001). Similar results have been obtained in other crop species, both self-pollinated (Parker et al. 1970; Layrisse et al. 1980; Isleib and Wynne 1983; Melchinger et al. 1994; Riday et al. 2003) and cross-pollinated (Moll et al. 1962; Sriwatanapongse and Wilsie 1968; Ajmone Marsan et al. 1998; Badu-Apraku et al. 2013).

Additive and non-additive genetic effects were found to play a significant role in the inheritance of a number of traits in common bean—yield (Gonçalves-Vidiga et al. 2008), components of partial resistance (Hernández-Delgado et al. 2009; Nkalubo et al. 2009),

and various nitrogen-fixing traits (Franco et al. 2001; Provorov and Tikhonovich 2003)—and popping in other crops (Dofing et al. 1991; Lu et al. 2003; Babu et al. 2006; Li et al. 2007). Additive genetic variance seems of primary importance in crosses made between parents from a single botanical variety, but additive and non-additive genetic variance may be significant in crosses made between parents from different botanical varieties (Wynne and Gregory 1981). Dominance and additive × additive epistasis contributed to the significant estimates of specific combining ability (SCA) in various studies (Araújo et al. 2005; Rainey and Griffiths 2005b). While variation due to dominance cannot effectively be exploited in a self-pollinating species, additive × additive epistatic variation is potentially useful to breeders because it can be fixed in the homozygous state.

The objectives of this study were to estimate the relative importance of additive and non-additive genetic effects in controlling the inheritance of popping characters in two crosses between an exotic nuña bean germplasm line and two adapted cultivars, and to relate the results obtained to the appropriate breeding method for transferring desirable alleles from exotic germplasm into adapted cultivars. This has permitted to confirm that popping ability is the result of a complex interaction between multiple genetic factors, being additive and non-additive interactions ubiquitous component of the genetic architecture of popping traits.

Materials and methods

Development of the population

Three bean genotypes were chosen for a genetic study on the inheritance of popping characters, and two populations were derived from crosses between an exotic and two adapted common bean cultivars. The adapted cultivars (PMB225 [type II] and PMB200 [type I]), with resistance to the bean common mosaic necrosis virus (BCMNV, gene *I*), and white large-sized seed and flower, were used as the female parents in the two crosses. A germplasm nuña line (PHA1037 [type IV]), with red large-sized seed and purple flower, was used as the male parent in the present study. P_2 always refers to the nuña line and P_1 to either PMB225 or PMB200 lines. F_1 plants were confirmed to be hybrids based on growth habit, flower and seed color, and presence of the SW13 scar for BCMNV resistance (Melotto et al. 1996), and were self-fertilized to produce the F_2 generation. BC_1P_1 and BC_1P_2 refer to the backcrosses of the F_1 to the P_1 and P_2, respectively. Reciprocal crosses were made and kept separate within each generation for data collection. However, the maternal effect was not significant, and reciprocal crosses were considered together in the analysis in order to increase the sample size. A total of 6 treatments per cross were obtained, corresponding to the 2 parents and the F_1, F_2, BC_1P_1, and BC_1P_2 generations.

Experimental design and data collection

The six treatments (P_1, P_2, F_1, F_2, BC_1P_1, and BC_1P_2) of each cross were grown under short-days—less than 12 h of light (September 2010 to March 2011) in a controlled temperature greenhouse site in the north of Spain (42°24′N, 8°38′W, 40 masl, 14 °C mean temperature, average annual rainfall 1,600 mm). Field plots each with five plants and spaced at 0.80 m were arranged in a randomized complete design with two blocks. A total of 56 field plots per block were included in the experiment according to the following structure: 5 plots for each P_1 and P_2, one plot for F_1, 25 plots for F_2, and 10 plots for each BC_1P_1 and BC_2P_2. Agronomic management following technical recommendations for bean crop with preventive treatments for diseases and insect pests, as well as manual hilling and harvesting, were applied.

In the present study, five popping seed traits such as PSL, PDI, PUS, PPA, and EC have been considered. A sample of 50 dry seeds of each plant was popped with a Palson Denver popcorn maker (1,200 W, 230 V, 50 Hz) for 150 s. Seed was considered fully popped when the cotyledons had expanded sufficiently to shed the seed coat, and un-popped or partially popped if the seed coat failed to crack or no expansion of the cotyledons was observed (Fig. 1). PSL was determined in a random 10-seed sample of each plant, and PDI was recorded as $[(\sum \text{popped seed dimensions} - \sum \text{un-popped seed dimensions})/\sum \text{un-popped seed dimensions} \times 100]$ according to Yuste-Lisbona et al. 2012. PUS was calculated as the percentage of 50 seeds that were un-popped (Yuste-Lisbona et al. 2012). PPA is the weighted average of popped and un-popped seed

proportions. Each 50-seed sample was placed into a graduated cylinder and distilled water was added until the total volume of water and seeds equaled 100 mL. The total volume of water added was subtracted from the total volume to give the un-popped seed volume (unPV). The seeds were drained and patted dry with paper toweling and immediately popped to minimize absorption of water by the seeds. The volume of seed after popping (PV) was obtained using a procedure similar to that used for un-popped seed. EC was defined as $[(PV - unPV)/unPV] \times 100$ according to Vorwald and Nienhuis (2009b).

Generation mean and genetic parameter analysis

Analyses of variance of the phenotypic data of the six treatments or generations for each cross were performed using PROC GLM (SAS v. 9.02, SAS Institute Inc. 2010). Blocks and generations were considered random and fixed effects, respectively. F_2 population was tested for normality by using the Shapiro–Wilk's test (Shapiro and Wilk 1965). A standard deviation transformation was applied to PDI, PUS, PPA and EC traits in order to conform an additive model that is necessary for the generation mean analysis (Mather and Jinks 1977). In those traits for which the analysis of variance showed significant differences among generations, separation of means was carried out with Tukey's procedure for multiple comparisons ($P \leq 0.05$).

Fig. 1 Seed was considered un-popped or partially popped (*left*) when no expansion of the cotyledons was observed, and was considered fully popped (*right*) when the cotyledons had expanded sufficiently to shed the seed coat

The following heterosis parameters were estimated for each cross and trait: Mid-parent heterosis or $MPH = (F_1 - MP)/MP$, in percent, High-parent heterosis or $HPH = (F_1 - \text{high P})/\text{high P}$, in percent, Average heterosis of the F_2 population or $HF_2 = (2F_2 - P_i - P_j)/(P_i + P_j)$, in percent,where F_1 is the mean of the F_1 population, MP is the average of the values of the two parents, high P is the average of the parental with the high value, HF_2 is the average heterosis of the F_2 population obtained from the cross of i and j parents, F_2 is the mean of the F_2 population, and, P_i and P_j are the corresponding means of parents i and j, respectively (Falconer and Mackay 1996). The *t* test was used to check whether F_2 means were significantly different from mid and better parental values (Wynne et al. 1970).

Correlations between popping traits were investigated at the phenotypic and genotypic levels. Phenotypic correlations of Pearson were conducted by using PROC CORR (SAS Institute Inc. 2010). The genotypic correlation of two traits was calculated as $r_A = cov_{Axy}/[\sigma^2_{Ax}\,\sigma^2_{Ay}]^{1/2}$, where cov_{Axy} is the genetic covariance and σ^2 subscripts are additive genetic variances for traits X and Y (Falconer and Mackay 1996). The genetic covariances were obtained by using mean cross products from the MANOVA option of SAS PROC GLM (SAS Institute Inc. 2010). Environmental (V_E), genotypic (V_G), and additive (V_A) F_2 generation variance estimates were calculated using SASQuant (Gusmini et al. 2007). Estimates of narrow-sense heritability or h^2 were calculated as $\delta^2_A/\delta^2_{(F_2)}$, where δ^2_A is the additive variance. Negative variance components were assumed to be zero (Robinson et al. 1955), but are reported herein as recommended by Dudley and Moll (1969) and Hallauer and Miranda (1988).

The genetic effects were estimated using the models suggested by Mather and Jinks (1982) and Jinks and Jones (1958). An additive-dominance (three-parameter) model and a model including epistatic interaction (six-parameter) were applied to the data and tested for goodness-of-fit. Gamble's (1962) notation was used in defining the parameters of the

model: [m] (midparent value), [a] (pooled additive gene effects), [d] (pooled dominance gene effects), [aa] (pooled additive × additive epistatic effects), [ad] (pooled additive × dominance epistatic effects), and [dd] (pooled dominance × dominance epistatic effects). The model parameters (m, a, d, aa, ad, dd) were estimated by SASQuant (Gusmini et al. 2007). The mean values, standard errors and variances of the different generations were subjected to weighed least-squares analysis using the scaling test (Mather 1949). The significance of the scales and gene effects were tested by using the Student's t test (Singh and Chaudhary 1985). Genetic components with $t \leq 0.05$ were considered different from zero and significant to the model. The significance scaling tests indicate presence of non-allelic interactions. The A and B scaling tests provide the evidence for the presence of [aa] and [ad] gene interactions types. The C scaling test provides a test for [dd] epistasis type. The type of epistasis was determined only when dominance [d] and dominance x dominance [dd] effects were significant. The effects were complementary when these effects had the same sign, while different signs indicated duplicate epistasis (Kearsey and Pooni 1996).

Minimum number of effective genes contributing to the variance of the quantitative characters was estimated using the following methods (Gusmini et al. 2007):

Wright's (1968):

$$(\mu_{P1} - \mu_{P2})^2 \times \{1.5 - [2 \times (\mu_{F1} - \mu_{P1}/\mu_{P2} - \mu_{P1}) \times (1 - (\mu_{F1} - \mu_{P1}/\mu_{P2} - \mu_{P1}))]\} / ([8 \times [\delta^2_{F2} - \{\delta^2_{P1} + \delta^2_{P2} + (2\,\delta^2_{F1})\}/4]$$

Mather's method (Mather and Jinks 1982):

$$\left[(\mu_{P1} - \mu_{P2})^2/2\right]/2 \times \delta^2_{F2}) - (\delta^2_{BCP1} + \delta^2_{BCP2})$$

Lande's method I (Lande 1981):

$$(\mu_{P1} - \mu_{P2})^2/8 \times [\delta^2_{F2-}\{\delta^2_{P1} + \delta^2_{P2} + (2\,\delta^2_{F1})\}/4]$$

Lande's method II:

$$(\mu_{P1} - \mu_{P2})^2/8 \times [(2 \times \delta^2_{F2}) - (\delta^2_{BCP1} + \delta^2_{BCP2})]$$

where μ_{P1}, μ_{P2} and μ_{F1} refers to the mean of parent 1, 2, and F_1 generation, respectively. δ^2_{BCP1}, δ^2_{BCP2}, δ^2_{F2}, δ^2_{P1}, and δ^2_{P2} refer to the variance of the BCP_1, BCP_2, F_2, P_1, and P_2 and generations respectively.

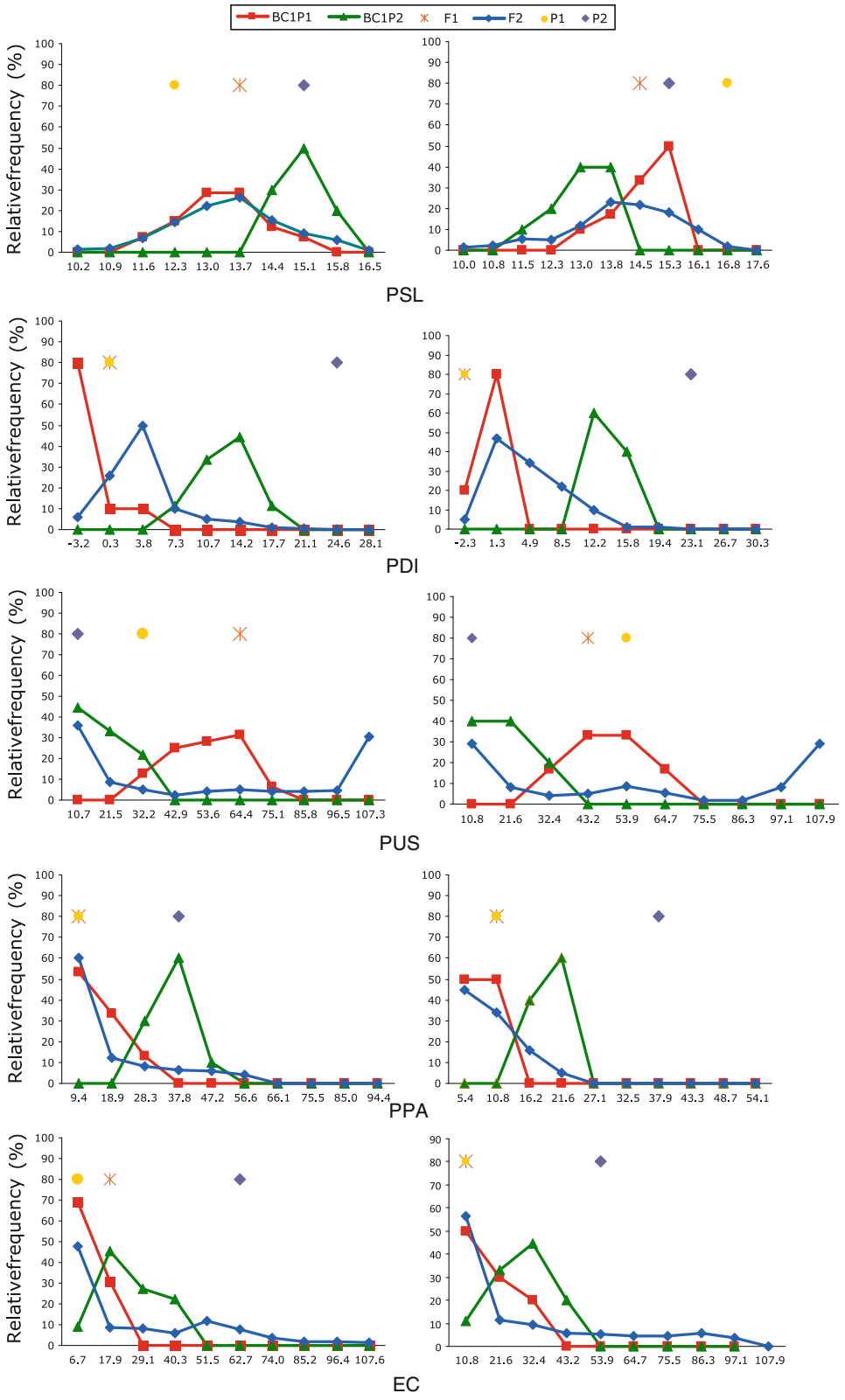
Results

Phenotypic variation of popping traits

Distribution of means among generations for each cross is presented in Fig. 2. The distribution of PDI, PPA and EC traits in the F_1 and F_2 generations was skewed toward the un-popped or adapted P_1 parent. PUS evidenced two separated groups with few individuals having intermediate or partial popping ability phenotype, and suggesting that a major gene could be interacting with other minor segregating genes. The backcross generations were similar to those of their respective recurrent parents, and were located at the opposite extremes of the continuum variation observed in the distribution histograms of both crosses. Transgressed values were observed in F_2, BC_1P_1 and BC_1P_2 generations for PSL, PPA and EC, which suggested that combinations of alleles from both parents had effects in the same direction.

Highly significant differences were detected among generations for all popping traits measured in both crosses. No significant differences were observed among blocks for any trait. Tukey's multiple comparison of generation means showed that both parents were contrasting for popping and un-popping traits in both crosses (Table 1). Hybrids showed decreased popping performance compared to the P_2 nuña parent. In general, mean values of popping traits for the F_1, F_2 and BC_1P_1 generations were lower than the corresponding ones for the BC_1P_2 generations. In most of the situations, the backcrosses increased the frequency of alleles of the recurrent parent. A significant difference in mean values was observed between BC_1P_1 and BC_2P_2 in both crosses. This was due to the positive and negative effects associated with each respective parent (Mather and Jinks 1982). The results from comparison of the generation means, as well as observations from the population distributions (Fig. 2), suggest that dominance is important in controlling popping traits in both crosses.

Non-additive inheritance was found for most of the traits, except for PSL, resulting in a positive or negative MPH (Table 1). Significant and negative MPH and HPH were found for PDI, PPA and EC, while significant and positive MPH and HPH were detected for PUS. Significant and negative HPH was only found for PSL in PMB200 × P_2 cross. On average in both crosses, PDI showed the highest


BC1P1
BC1P2
F1
F2
P1
P2
Relativefrequency (%)
PSL
PDI
PUS
PPA
EC

◀**Fig. 2** Distribution of popping traits for the six generations in the PMB225 × PHA-1037 and PMB200 × PHA-1037 crosses. In all histograms the y-axis depicts relative frequency in percentage, whereas the x-axis corresponds to the distributions of the means. In each case, the means for each parent (P_1 and P_2) and F_1 as well as the distributions for the BC_1P_1, BC_1P_2 and F_2 generations are indicated

significant and negative MPH and HPH. The average heterosis was significant for all traits in the F_2, except for PSL in PMB225 × P_2 cross.

Significant and positive phenotypic and genotypic correlations between popping traits were found (Table 2). The strong and positive genotypic association (>0.67) between PDI, EC and PPA, and negative genotypic correlation (>−0.43) with PUS, suggest that could be possible to improve popping ability through selection for those popping associated traits. PDI and EC showed no significant genotypic correlations with PSL in PMB200 × P_2 cross, and in this case PSL could not be a good predictor of popping ability.

Variance components and gene factor number estimates

The estimates of additive, dominance, and environmental components of variance for the popping traits are presented in Table 3. It appears that although estimates differ in magnitude, the results are similar in terms of interpretation. For all traits, the variance due to genotypes was greater than the environmental variance. Signs associated with the variances indicate the influence of each parent. A negative estimate of dominance genetic variance was found for all traits, and it was assumed to be zero (Robinson et al. 1955). Negative variances are not uncommon and are often found for dominance variance components (Hallauer and Miranda 1988). Negative dominance variances suggest the presence of epistatic interactions in the traits measured, which could be due to a dominance bidirectional effect resulting in the cancellation between positive and negative effects of the alleles

Table 1 Tukey's multiple generation means comparison for PSL, PDI, PUS, PPA and EC derived from PMB225 × P_2 and PMB200 × P_2 crosses

Generation	PSL	PDI	PUS	PPA	EC
PMB225 × P_2					
P_1 (PMB225)	12.07 B	−0.95 D	31.02 B	11.58 C	5.03 C
BC_1P_1	12.31 B	−1.39 D	55.21 A	8.09 D	4.31 C
F_1	13.15 B	−1.48 D	56.61 A	8.81 D	14.61 B
F_2	12.56 B	1.18 C	42.14 B	7.47 D	11.08 B
BC_1P_2	13.84 B	11.02 B	15.25 C	29.23 B	10.86 B
P_2 (Nuña)	14.63 A	23.41 A	4.12 D	33.37 A	56.33 A
MPH (%)	−1.50	−113.18**	222.20**	−60.79**	−52.38**
HPH (%)	−10.12	−93.68**	82.49**	−73.60**	−74.06**
HF_2 (%)	5.92	−89.49**	139.84**	−66.76**	63.60**
PMB200 × P_2					
P_1 (PMB200)	16.30 A	−0.50 D	52.70 A	8.59 C	4.31 C
BC_1P_1	14.05 B	0.61 C	51.37 A	4.92 C	6.05 C
F_1	14.44 B	−0.59 D	39.95 A	8.13 C	7.93 C
F_2	13.73 C	0.93 C	54.05 A	6.59 C	11.64 B
BC_1P_2	13.57 C	12.38 B	13.61 AB	21.63 B	10.85 B
P_2 (Nuña)	14.93 B	24.33 A	4.04 B	37.87 A	65.86 A
MPH (%)	−7.49	−95.05**	40.82**	−65.00**	−77.39**
HPH (%)	−11.41*	−102.42**	−24.19*	−78.53**	−87.96**
HF_2 (%)	−11.01*	−92.19**	90.41**	−71.63**	−66.82**

Within each column, means followed by the same letter did not significantly differ at $P < 0.05$

MPH mid-parent heterosis, *HPH* high-parent heterosis, HF_2 the average heterosis of the F_2 population

* Significant at $P \leq 0.05$; ** significant at $P \leq 0.01$

Table 2 Phenotypic and genotypic correlations between PSL, PDI, PUS, PPA and EC derived from PMB225 × P_2 and PMB200 × P_2 crosses

Trait	PSL	PDI	PUS	EC	PPA
PMB225 × P_2					
PSL		0.75**	−0.78**	0.70**	0.85**
PDI	0.95**		−0.47*	0.72**	0.82**
PUS	−0.79**	−0.57**		−0.45*	−0.74**
EC	0.70**	0.98**	−0.96**		0.68**
PPA	0.85**	0.92**	−0.93**	0.67**	
PMB200 × P_2					
PSL		0.46*	−0.74**	0.55*	0.66**
PDI	0.21		−0.48*	0.65**	0.82**
PUS	−0.43*	−0.75**		−0.52*	−0.79**
EC	0.22	0.98**	−0.95**		0.76**
PPA	0.38*	0.99**	−0.91**	0.96**	

Upper and lower diagonal denoted phenotypic and genotypic correlations, respectively

* Significant at $P \leq 0.05$; ** Significant at $P \leq 0.01$

Table 3 Genotypic (V_G), additive (V_A), dominance (V_D) and environmental variances (V_E), and narrow sense heritabilities (h^2) for PSL, PDI, PUS, PPA and EC derived from PMB225 × P_2 and PMB200 × P_2 crosses

Trait	V_G	V_A	V_D^a	V_E	h^2
PMB225 × P_2					
PSL	0.43	1.37	−0.94	0.59	0.69
PDI	8.44	15.96	−7.51	3.10	0.83
PUS	1920.52	3,905.70	−1,985.52	247.24	0.94
PPA	31.70	66.19	−34.48	15.25	0.81
EC	540.47	1,051.35	−510.81	20.21	0.98
PMB200 × P_2					
PSL	1.29	1.92	−0.63	0.61	0.66
PDI	4.78	7.22	−2.45	2.54	0.74
PUS	2182.43	4,409.92	−2,227.87	127.19	0.97
PPA	37.92	95.54	−57.61	16.44	0.85
EC	633.40	1,248.33	−614.92	26.20	0.98

[a] Negative V_D estimates were assumed to be zero (Robinson et al. 1955)

that controlling the trait (Fatokun et al. 1992; Lark et al. 1995; Maughan et al. 1996). Therefore, epistasis effects would seriously bias any attempt to partition the genetic variances of the segregating generations into additive or dominance components. The values of negative dominance are in accordance with negative MPH and HPH values observed, indicating that heterozygosity was not always favorable for the good expression of the trait. The additive variance estimates were high and consistent between crosses. Narrow-sense heritability estimates ranged from 66 to 98 % for all traits. These high heritability estimates are consistent with the additive variance component estimates observed, and other studies of common bean popping traits (Kmiecik and Nienhuis 1997; Ogg et al. 1998; Vorwald and Nienhuis 2009b). However, direct estimation of variance components and narrow heritability estimates in multiple environments may be needed for a correct quantification of these values.

In our study, two methods (those of Wright and Mather) provided similar estimates of the minimum number of effective factors determining the traits, while Lande's methods provided lower estimates and were disregarded (Table 4). The number of effective factors was 2 for PUS and EC, ranged from 1 to 2, and, 3 to 4 for PSL and PPA, respectively. A high and different number of effective factors (average = 16.1 and 28.3 for the PMB225 × P_2 and PMB200× P_2 crosses, respectively) were found to influence PDI. These results indicate that the genotypes may possess different number of genes responsible for the expression of PSL, PDI, and PPA traits, while PUS and EC

had the same number of genes in both crosses, although these estimates should be considered with caution.

Goodness of fit to the genetic models

The scaling tests A, B and C of Mather and Jinks (1982) were applied in the present study to test the presence of non-allelic gene interactions (Table 5). A simple additive-dominance model was adequate for PSL in both crosses, as inferred from the non-significance in all the scales. For PDI, PUS, PPA and EC, the significant scaling tests (one or more scales in A, B and C) indicated the presence of digenic epistasis. Departures from a simple additive-dominance are most pronounced in PMB225 × P_2 cross, in which all scaling tests depart significantly from expectation for PUS, PPA and EC, while PDI showed only significant values in both B and C tests. For PMB200 × P_2 cross, all the scaling tests depart from expectation for PUS, while for PDI and PPA only C test departs from expectation, and EC showed significant values in both B and C tests. The C scaling test is sensitive to disturbances caused by [aa] and [dd] interactions, while A and B scaling tests are affected by [ad] interactions.

The variation among generation means for most popping traits could be explained by an additive-dominance and epistasis model (Table 6). The model described as [m], [a], [d], [aa], [ad], [dd] showed the best goodness of fit for most of the traits except for PSL, which had only significant [a] effects. Significant and negative [a] effects were found for most popping traits, except for PUS in both crosses, and for PSL in PMB200 × P_2 cross, which indicated that [a] genetic effect is also present in those popping traits. It should be noted that the sign of parameters [a] and [ad] depends upon the parents being considered as P_1 or P_2. The most [a] estimates were of a negative nature because the best parent for popping (nuña parent) was

Table 4 Minimum number of effective factors for PSL, PDI, PUS, PPA and EC derived from PMB225 × P_2 and PMB200 × P_2 crosses

Effective factors	Wright's	Mather's	Lande's I	Lande's II
PMB225 × P_2				
PSL	1.9	2.3	1.8	0.6
PDI	13.5	18.7	8.8	4.7
PUS	2.3	2.1	1.0	1.0
PPA	3.4	3.3	1.9	0.8
EC	2.0	2.2	0.6	0.3
PMB200 × P_2				
PSL	0.5	0.5	0.2	0.1
PDI	24.2	32.5	16.1	10.6
PUS	2.2	2.3	1.1	1.1
PPA	4.3	4.5	2.8	1.1
EC	2.0	2.5	0.8	0.4

Table 5 Estimation of gene effects based on scaling test for PSL, PDI, PUS, PPA and EC derived from PMB225 × P_2 and PMB200 × P_2 crosses

Trait	A	B	C
PMB225 × P_2			
PSL	−0.6 ± 0.25	−0.09 ± 0.24	2.76 ± 0.58
PDI	−0.35 ± 0.96	11.11 ± 1.64**	−14.78 ± 1.43**
PUS	22.79 ± 1.47**	−30.23 ± 2.20**	20.2 ± 5.82**
PPA	−4.21 ± 2.59**	16.28 ± 3.35**	−32.69 ± 2.96**
EC	−11.02 ± 3.47**	−49.22 ± 5.16**	−46.26 ± 6.54**
PMB200 × P_2			
PSL	−2.64 ± 0.73	−2.23 ± 0.68	−5.19 ± 0.73
PDI	2.31 ± 1.50	1.02 ± 1.29	−18.93 ± 1.34**
PUS	10.09 ± 8.90**	−16.77 ± 7.23**	79.56 ± 4.48**
PPA	−1.8 ± 1.67	−2.74 ± 3.00	−36.36 ± 3.25**
EC	−0.14 ± 2.84	−52.09 ± 5.53**	−39.47 ± 7.32**

** Significant at $P \leq 0.01$

Table 6 Estimates of main and epistatic gene effects, their corresponding standard errors, and Student's *t* significance level for PSL, PDI, PUS, PPA and EC derived from PMB225 × P_2 and PMB200 × P_2 crosses

Six-parameter model[a]	PSL	PDI	PUS	PPA	EC
PMB225 x P_2					
[m]	12.56 ± 0.06***	1.18 ± 0.21***	42.13 ± 2.90***	7.46 ± 0.43***	11.08 ± 1.47***
[a]	−1.18 ± 0.41*	−12.29 ± 1.28***	40.17 ± 6.17***	−21.27 ± 1.79***	−6.63 ± 2.24*
[d]	2.48 ± 1.49	2.01 ± 4.30	12.70 ± 11.51	30.90 ± 7.39***	−41.61 ± 12.63**
[aa]	2.03 ± 1.62	14.64 ± 3.41***	−27.82 ± 3.92**	44.61 ± 5.29***	−13.54 ± 10.37
[ad]	−0.24 ± 0.87	−0.09 ± 1.77	28.19 ± 9.00**	−10.34 ± 3.11**	19.03 ± 3.57***
[dd]	−1.33 ± 3.82	−14.44 ± 5.86*	32.54 ± 21.42	−56.39 ± 13.07***	49.53 ± 19.36*
Epistasis[b]	–	–	–	D	D
PMB200 x P_2					
[m]	13.73 ± 0.08***	0.94 ± 0.17***	54.06 ± 2.95***	6.58 ± 0.45***	11.64 ± 1.58***
[a]	0.96 ± 0.29*	−11.79 ± 1.61**	37.73 ± 8.69**	−16.76 ± 2.20**	−4.82 ± 2.89*
[d]	−1.13 ± 2.44	9.67 ± 5.75	14.45 ± 15.69	11.60 ± 3.17*	−39.77 ± 19.09*
[aa]	−0.14 ± 0.98	22.14 ± 3.89***	−86.00 ± 29.19**	26.67 ± 6.21***	−12.63 ± 16.08
[ad]	1.10 ± 2.54	−0.61 ± 2.04	13.36 ± 11.15	−2.09 ± 1.55	26.01 ± 6.59*
[dd]	4.75 ± 4.54	−25.48 ± 8.84**	92.66 ± 59.56	−16.99 ± 4.53**	65.12 ± 31.88*
Epistasis[b]	–	–	–	D	D

[a] *[m]* Midparent, *[a]* additive, *[d]* dominance, *[aa]* additive × additive, *[ad]* additive × dominance, *[dd]* dominance × dominance effects

[b] *D duplicate epistasis* the epistasis was not determined because [d] and/or [dd] were not significant

* Significant at $P \leq 0.05$; ** significant at $P \leq 0.01$; *** significant at $P < 0.001$

designated as P_2 during the generation mean data analysis. The [d] genetic estimates were significant for PPA and EC in both crosses. The [d] effects were positive for PPA and negative for EC, which demonstrated that the dominance was towards the adapted and the nuña parent, respectively.

Both crosses exhibited significant epistatic gene estimates, including one or more of the three types of epistasis, for all traits except for PSL. The [aa] epistatic component was significant and positive for PDI and PPA, and negative for PUS in both crosses. The negative [aa] estimates of PUS showed that the gene pairs responsible for popping are in dispersive form (Mather and Jinks 1977), suggesting the gene contributing of both parents. The [dd] component was significant and negative for PDI and PPA, and positive for EC, whereas the [ad] component was significant and positive for EC in both crosses, and positive and negative for PUS and PPA, respectively, in PMB225 × P_2 cross. The [aa] interactions were greater than their corresponding [a] for PDI and PPA in both crosses, and for PUS in PMB225 × P_2 cross, while [dd] interactions were greater than their corresponding [d] components for PDI, PPA and EC in both crosses, indicating that epistasis contributed significantly to their genetic variances. Epistatic QTLs were also found for PDI, PUS and EC in other study (Yuste-Lisbona et al. 2012).The significant and opposite sign values for [d] and [dd] effects for PPA and EC traits indicated a duplicate type of epistasis and demonstrate predominantly dispersed alleles at the interacting loci (Jinks and Jones 1958; Kearsey and Pooni 1996). In addition, [a] and [aa] effects had significant and opposite sign for PDI, PUS and PPA. The presence of duplicate epistasis for PPA and EC traits could complicate the selection of high-popping genotypes because diminishes the effect of dominant genes and therefore decreases the expression of the considered traits, which is unfavorable for breeding for popping increase. There is a probability that crossing different parental lines would lead to complementary epistasis that would increase popping for these traits. The [dd] interaction was larger than the [aa] and [ad] effects put together for EC in both crosses, and PPA in PMB225 × P2 cross. The [aa] interaction was more pronounced for PPA and PUS in

PMB200 × P2 cross, while [ad] was larger than the other interactions for PUS in PMB225 × P2. Finally, PDI showed similar contribution of [aa] and [dd] interactions.

Discussion

In common bean, as in any other crop, the effectiveness of selection for a given quantitative trait as popping is primarily determined by the nature of the genetic effects determining its inheritance mode. Once the relative importance of the contributions from various genetic effects (additive, dominance, epistasis) are estimated for a particular trait, the breeding objectives will dictate how the various effects will be exploited for the development of breeding lines or improved cultivars (Baenziger et al. 2006). Here, we demonstrated that the differences for the popping traits between the parents of each cross-used in this work were indeed real and significant. The distribution of means of the F_2 generations for all traits in both crosses confirmed their quantitative genetic basis. Some of the traits (PSL, PPA and EC) exhibited transgressive segregation suggesting that the nuña parent did not contain all favorable alleles for these traits. As expected, mean values of the backcrosses BC_1P_1 and BC_1P_2 tended to be located close to those of their respective recurrent parents. These results confirmed the choice of parents for this study as contrasting, which is a prerequisite for generation mean analysis (Mather and Jinks 1977). The same methodology has been used in common bean to study the inheritance of other complex traits such as leafhopper insect resistance (Kornegay and Temple 1986), rate of ethylene production (Sauter et al. 1990), pod morphology (Chung et al. 1991), ascochyta leaf blight tolerance (Hanson et al. 1993), leaf trichome density (Park et al. 1994), heat tolerance (Rainey and Griffiths 2005a, b), and climbing ability (Checa et al. 2006).

A complete dominance of the cultivated parent was observed for PDI, PUS, PPA and EC in PMB200 × P_2, because there were no significant differences between P_1, BC_1P_1, and F_1 generations, despite significant differences between the two parents. Meanwhile over-dominance was evidenced for PUS and PPA, and partial dominance for EC in PMB225 × P_2 cross. In addition, the comparison of means for the different generations in each of the two crosses, together with the analysis of frequency distributions, showed that mid-parent heterosis was high and negative for PDI, PPA and EC, and positive for PUS, which confirmed the predominance of dominance of the cultivated over nuña genotype. Heterosis in common bean was significant for yield components (Nienhuis and Singh 1986), nodulation (Franco et al. 2001) and maturity (Johnson and Gepts 2002). In popcorn and for the popping expansion trait, Zanette (1989) showed the existence of intermediate heterosis in a diallel program including seven populations, while other diallel studies indicated a negative specific heterosis (Scapim et al. 2006; Rangel et al. 2008). Dispersion of alleles in parents and unidirectional dominance are thought to be responsible for heterosis (Pooni and Treharne 1994; Becker and Link 2000). Thus, the result found it is likely due to the great genetic distance presumed to exist for popping ability between an exotic cultivar as nuña and an adapted cultivar. Both crosses have in common the nuña parent, which suggests that the lack of dominance observed may be a characteristic of this exotic material. The presence of significant [d] effects for PPA and EC support the importance of dominance in these traits and indicate that selection for these popping traits should be delayed after inbreeding is obtained and the frequency of heterozygous loci within families decreased. However, the relationships among over-dominance and complete or partial dominance, and patterns of heterosis, as well as the existence of transgressive segregation, for PDI and PUS could not be explained simply by the dominance parameters in the model.

The significant and positive magnitude of the phenotypic and genotypic correlations observed between PDI, EC and PPA traits in both crosses suggest that can be increased simultaneously by selection for either trait in these temperate-adapted nuña bean crosses. We also observed substantial amounts of additive genetic variation, and consequently, high narrow-sense heritabilities. However, different factors such as shared environment, dominance effects and epistasis (i.e. non-additive interactions) could upwardly bias our additive variance estimates and therefore heritabilities values in these populations (Falconer and Mackay 1996). Therefore, to further study of these traits, we needed to implement a more complex model with epistatic interactions. The

sign of [a] gene effects was negative for PSL in PMB225 × Nuña, and PDI, PPA and EC in both crosses, which suggest a large influence of the cultivated parent. However, although [a] effects were significant for all traits, [a] effects were of moderate importance compared with dominance and/or epistatic interactions for PDI, PUS, PPA and EC.

A simplistic additive-dominance model did not adequately explain the observed variation for the traits studied herein, except for PSL, indicating that digenic or higher-order epistatic interactions contributed to their variation. The magnitude and significance of the [aa], [ad], and [dd] estimates for PDI, PUS, PPA and EC indicate that epistatic gene effects are present and are important in the genetic mechanisms of popping inheritance in the temperated-nuña crosses studied. This result agree with Yuste-Lisbona et al. (2012) that observed a total of ten epistatic QTLs for PDI, PUS and EC traits, which were involved in six epistatic interactions. Although the epistatic interactions observed for PDI, PPA, EC and PUS are not incompatible with the existence of additive genetic variance reported for these traits; the heritabilities could have an additional bias, proportional to the variance due to these interactions (Zuk et al. 2012).

The [aa] and [dd] effects contributed more to the performance for PDI and PPA than [ad] effects in both crosses. The presence of significant [aa] effect for PDI, PUS and PPA could be the result of a complex gene pathway that involves several genes of small effect (Mathews et al. 2008). The signs associated with [aa] and [ad] epistatic gene effects were in opposite direction for PUS, PPA and EC in both crosses, which indicate the direction in which gene effects influence the population means. The negative [aa] estimates for PUS in both crosses suggest the presence of gametic disequilibrium due to accumulation of favorable epistatic gene combinations in the parent lines (Melchinger 1988). These gene combinations are at least partly disrupted by recombination in the F_2 generation, but to a lesser degree in the BC generations, which explains the greater popping values of the BCP_2. The [d] and [dd] gene effects were in opposite direction for PPA and EC, indicating duplicate rather than complementary epistasis. Heterosis was negative in both traits because the [d] and [dd] effects cancelled each other. Therefore, epistasis is likely to be an important explanation for the heterosis in popping ability.

The results presented in this work suggest that all popping traits are quantitatively inherited and confirm that all the three types of gene action i.e., additive, dominance and interaction component played an important role in the inheritance of PDI, PUS, PPA and EC traits. Duplicate epistasis seems to be the major component for PPA and EC traits, and crossing different parental lines could be a probability in order to lead to complementary epistasis that would increase these popping traits. While the magnitude of the [aa] and [dd] effects was similar for PDI and PUS traits, indicating that the genes for increasing popping are dispersed between the parents.

Due to additive effects have only moderate importance in the total variation of popping performance of these four traits, more rapid advance will be made in a breeding program focus on improvement that emphasizes the dominance and epistatic gene effects. In this study, the BC_1P_2 showed a mean value that tended towards their respective recurrent parent, which supports the idea that at least one backcross generation may be useful in incorporating popping ability into adapted populations (Lambert and Leng 1965; Lawrence and Frey 1975; Kenworthy and Brim 1979). This backcross to the nuña parent could be an alternative to maintain/recover the favorable epistatic gene combinations for popping traits. These results agree with Dudley's theory (Dudley 1982) according to if one parent has more loci containing favorable alleles than the other, at least one generation of backcrossing prior to initiation of selection will enhance the probability of recovering a population. In a previous study (Ogg et al. 1998), a single cross between nuña bean and adapted cultivar did not recover lines with high popping ability, while Kmiecik and Nienhuis (1997) evidenced that a backcross with the nuña as the recurrent parent enhanced popping ability among progeny. Thus, a generation of backcrossing to the exotic germplasm will help to make possible the integration of favorable alleles into the adapted genotypes, and it would allow the exploitation of unadapted germplasm recipient of unique characteristics as is nuña bean in breeding programs.

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