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# Seed curvature as a useful marker to transfer morphologic, agronomic, chemical and sensory traits from Ganxet common bean (*Phaseolus vulgaris* L.)

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## ABSTRACT

The Ganxet bean is a highly appreciated landrace characterized by markedly curved seeds, high protein content, low seed-coat perceptibility, and low mealiness. To analyze the genetic control of seed curvature and of morphological, agronomical, chemical, and sensory traits related to high quality in these beans, we used an Additive, Dominance, and Additive  $\times$  Additive model applied to Ganxet and Faba Asturiana varieties, their  $F_1$ ,  $F_2$ ,  $BC_1P_1$ , and  $BC_1P_2$  progenies.

The narrow-sense heritability ( $h^2$ ) of seed curvature was 0.72. The  $h^2$  of the number of seeds per pod was 0.75. The  $h^2$  of area and length of the seed were 0.55 and 0.60, respectively. The  $h^2$  for seed width, 100-seed weight, pod length, Mg content, and sensory traits mealiness, seed-coat roughness and seed-coat perceptibility, ranged from 0.3 to 0.4. Seed curvature behaved like a continuously variable trait that is probably controlled by 3 loci. The expression of this trait depends partly on the environment, and its expression is greatest in environments that favor larger seeds. Seed curvature also had strong additive genetic correlations with protein content (positive) and with mealiness (negative).

Given the ease of determining seed curvature and its apparently simple control, this trait could be used as an easy-to-select morphological marker to transfer high protein content and low mealiness to other varieties by backcross procedures, regardless of whether the correlation between traits is due to pleiotropic or linkage effects.

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## 1. Introduction

Beans are the most important legume in the human diet (Broughton et al., 2003). They are consumed throughout the world, but especially in developing countries (Shimelis and Rakshit, 2005). Beans are nutritious, having 2 or 3 times as much protein as cereals (Siddiq and Uebersax, 2013), and are easily adapted to many environments. In developed countries, there is a growing interest in beans due to their nutraceutical properties (Hayat et al., 2014) and importance in crop rotation. However, if beans are to regain a predominant role in developed countries' diets, their nutritional and environmental strengths must be accompanied by improvements in culinary and sensory characteristics (cooking time, seed-coat

perception, aroma, flavor, mealiness, breakage during cooking) to appeal to increasingly demanding consumers (Casañas et al., 2006; Ghasemlou et al., 2013; Mkanda et al., 2007). Thus, the challenge is to obtain varieties that meet nutritional needs while fulfilling consumers' sensory demands. To meet this challenge, landraces can provide excellent starting material for breeding programs because some of them retain great sensory and nutritional potential.

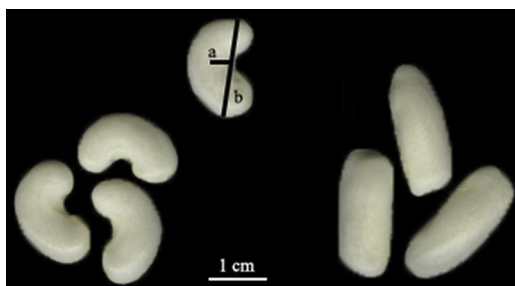
The Ganxet landrace derives from the Mesoamerican gene pool (Sánchez et al., 2007) and is cultivated in Catalonia (northeastern Spain). Ganxet seeds are white, slightly shiny, flat, and very hook-shaped ("ganxet" means little hook in Catalan) (Fig. 1). Ganxet seeds have a high content of protein (24–29%, Bosch et al., 1998; Casañas et al., 2006). This landrace enjoys great culinary prestige thanks to its sensory traits (creaminess, low seed-coat perceptibility, and mild flavor) (Casañas et al., 2006, 2002; Romero del Castillo et al., 2008), and it has an important role in some emblematic dishes of Catalan cuisine, such as pork sausage with beans, beans with clams, beans with salt cod, bean omelets, etc. The Ganxet bean has

Abbreviation: ADAA, additive dominance and additive  $\times$  additive.

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**Fig. 1.** Gaxnet seeds (left) are curved, Xana seeds (right) are not. Curvature trait defined as  $a/b$ , (a) is a perpendicular distance from the center of the object at the point of maximum straight width to the straight length and (b) is the straight length.

Protected Designation of Origin status from the European Union according to EC Regulation 1376/11. In Catalonia, the historical home of Gaxnet cultivation, 257 entries with different agricultural and morphological characteristics have been collected (Rull et al., 2012) and are conserved in the FMA-BarcelonaTech germplasm bank.

Seed shape, size, and seed-coat color are important in consumers' preferences and market acceptance (Costa et al., 2011; Mkanda et al., 2007). The study of these traits goes back to the beginning of the twentieth century, with Johannsen's landmark study on size (Johannsen, 1903). Some authors have reported quantitative inheritance for seed length, width, and thickness, and for 100-seed weight (Coyné, 1968; Dalla Corte et al., 2010; Motto et al., 1978; Nienhuis and Singh, 1988; Vallejos and Chase, 1991), and in recent years quantitative trait loci (QTLs) have been identified for these traits (Blair et al., 2006; Park and Coyne, 2000; Pérez-Vega et al., 2010; Tar'an et al., 2002; Yuste-Lisbona et al., 2014). Marker-assisted selection using these QTLs has been useful in breeding programs. These studies have used the length/width index to analyze the shape of the seed, but none of them took into account the curvature of the seed, although genetic variability in this trait occurs in collections such as those of the Spanish National Plant Genetic Resource Center (<http://wwwx.inia.es/inventarionacional>) and the International Center for Tropical Agriculture (<http://isa.ciat.cgiar.org/urg/beancollection.do>).

Seed shape and size have also been associated with yield. White and González (1990) found that seed weight correlates negatively with yield. Dalla Corte et al. (2010) found that both seed length and thickness correlated negatively with yield, suggesting larger yields from plants with smaller seeds. Blair et al. (2006), in a study using advanced backcrossing between a commercial variety and a wild variety, reported QTLs associated with larger yield and lower seed weight. However, we have no information about possible correlations between shape and chemical and/or sensory traits.

Thus, we studied the Gaxnet bean, a landrace characterized by a highly curved seed that is appreciated for its nutritional and sensory traits to: (i) analyze the genetic determinants of seed curvature and other traits related to the shape and size of the seeds; (ii) estimate and analyze possible correlations between seed curvature and agronomic, morphological, chemical, and sensory traits; and (iii) evaluate the possibilities of using this extremely easy-to-measure trait in breeding programs aimed at increasing the nutritional and sensory value of beans.

## 2. Material and methods

### 2.1. Plant material

This study was carried out using two varieties of beans that represent the two extremes of seed curvature: Montcau ( $P_1$ ), an inbred developed by our group within the Gaxnet landrace for its high

degree of curvature and reasonable agronomic behavior (Bosch et al., 1998), and Xana ( $P_2$ ), an inbred developed by the Servicio Regional de Investigación y Desarrollo Agroalimentario (SERIDA) in Asturias from crosses between two varieties of Andean origin, Andecha and V203. Montcau has type IV indeterminate growth habit (Singh, 1982) and mid-sized white seeds belonging to the Hook market class (Santalla et al., 2001) (Fig. 1). Xana has type I determinate growth habit (Singh, 1982) and very large, not hooked, white seeds belonging to the Fabada market class (Santalla et al., 2001) (Fig. 1). We studied the parents ( $P_1$  and  $P_2$ ), their descendants ( $F_1$  and  $F_2$ ), and backcrosses with both parents ( $BC_1P_1$  and  $BC_1P_2$ ). Multiple controlled  $P_1 \times P_2$  crosses were performed in the greenhouse to obtain enough  $F_1$  seeds. Some  $F_1$  plants were used to obtain  $F_2$  by self-pollination and some were used to obtain the backcrosses  $BC_1P_1$  ( $F_1 \times P_1$ ) and  $BC_1P_2$  ( $F_1 \times P_2$ ).

### 2.2. Field trials

The trial comparing the different generations was carried out in 3 locations in northeast Spain: Sabadell ( $41^\circ 32' 41'' N$ ,  $2^\circ 4' 26'' E$ ), Rubí ( $41^\circ 30' 08.2'' N$ ,  $2^\circ 01' 02.2'' E$ ), and Viladecans ( $41^\circ 17' 22'' N$ ,  $2^\circ 02' 41'' E$ ). In Sabadell and Rubí, plants were cultivated in open fields with mild Mediterranean climate. Both locations have moderately alkaline soils with high levels of calcium and medium or low levels of other soil parameters. In general, the soil in Sabadell is poorer in nutrients than the soil in Rubí. In the third location, Viladecans, plants were cultivated in greenhouses, where the temperature and humidity are higher than in open fields, favoring more turgid plant development and larger seeds (Hanan, 1998). Plants in the greenhouse were cultivated in pots with acid substrate with high concentrations of all soil parameters studied except calcium carbonate equivalent, which was very low.

In each location, we used a randomized 4 block design with 10 plants per elementary furrow (40 plants for genotype and location). Seeds were sown at a low density (18519 plants/ha) to facilitate individualized management of plants. Plants with indeterminate growth habit were trellised onto a vertical plastic mesh in the open fields and onto poles in the greenhouse. Plants were cultivated using the traditional methods in the area, including drip irrigation.

### 2.3. Determination of agronomic and morphological traits

The trait days-to-flowering (IBPGR, 1982) was recorded for each plant. All the plants were harvested individually, and the following traits were measured and recorded in the laboratory for each plant: pod length, number of pods, and number of seeds per pod (IBPGR, 1982). A sample of 100 seeds per plant was scanned and then processed using WinSeedle Pro v2005b (Regent 156 Instruments, Inc. Quebec, Canada) to estimate seed length (line connecting the two farthest points on the projected image perimeter) and seed width (the maximum width perpendicular to length), projected area, and curvature (defined as  $a/b$ , where (a) is a perpendicular distance from the center of the object at the point of maximum straight width to the straight length and (b) is the straight length (Fig. 1). We also recorded the dry weight of 100 seeds, gross yield (total yield including seeds affected by disease or pest), and net yield (commercial seeds) from each plant.

### 2.4. Determination of chemical and sensory traits

Seeds from plants grown in the same furrow and location were mixed to obtain homogeneous groups. The seed coat of common beans accounts for only 8–15% of the mass of the seed and has different chemical and sensory traits, so it must be separated from the embryo prior to analysis to enable its composition to be accurately determined and related if possible with the sensory properties of

each fraction. To this end, 40 g of seeds from each sample were soaked in deionized water for 24 h at 15 °C, and the seed coat was manually separated from the embryo. The two fractions were immediately dehydrated and ground to a particle size less than 0.4 mm; thus, flour from the raw seed coat was obtained separately from flour from the raw embryo. Additionally, 150 g of seeds from each sample were cooked using the protocol described by Romero del Castillo et al. (2012). Cooking time was recorded as the time elapsed from breaking a boil to the end of cooking process. Approximately 100 g of the cooked beans were used to estimate the percentage of whole beans remaining after cooking (Romero del Castillo et al., 2012). Afterward, the sample was dehydrated and ground to a particle size less than 0.4 mm to obtain flour from cooked seeds.

To estimate chemical and sensorial attributes, we recorded near-infrared spectroscopy (NIRS) data from the three types of milled samples (raw bean seed coats, raw embryos, and cooked beans) using a model 5000 spectrophotometer (Foss NIRSystems, Silver Spring, MD, USA) equipped with a rapid content analyzer (RCA) module. Spectra were recorded every 2 nm between 1100 nm and 2500 nm and averaged from 32 scans. Three spectra were registered for each sample and the average spectrum was used for computations. We calculated the absorbance at each wavelength as  $(\log(1/R))$ ; this variable correlates with chemical constituents better than reflectance does. We used Vision software, version 2.51, (Foss NIRSystems, Silver Spring, MD, USA) to control the recorder, collect the spectra, and import the data.

We used the robust regression models developed by Plans et al. (2012) and Plans et al. (2013) on the NIRS data to estimate the dietary fiber, uronic acids, ash, calcium, magnesium, and phosphorus in the raw seed coats and the protein, starch, and apparent amylose in the raw embryo. We used the regression models developed by Plans et al. (2014), applied to the NIR registers made on cooked beans flour, to estimate the mealiness, seed-coat roughness, seed-coat perceptibility, seed-coat brightness, flavor, and aroma (Romero del Castillo et al., 2008).

### 2.5. Genetic models and data analysis methodology

As a first approach to describing the variation, we used the linear model  $X_{ijkl} = \mu + G_i + E_j + GE_{ij} + B_{k(j)} + \epsilon_{ijk}$ , where  $\mu$  is the mean,  $G_i$  is the effect of the different genotypes,  $E_j$  is the environment effect,  $GE_{ij}$  is the interaction effect,  $B_{k(j)}$  is the block effect within the environment, and  $\epsilon_{ijk}$  is the residual. In variables with significant differences between generations in the ANOVA, we used the least significant difference (LSD) test for separation of means ( $P \leq 0.05$ ). We used the Agricolae package (Mendiburu, 2010) of R software (R Development Core Team, 2007) for all analyses.

To gain deeper insight into to the genetic components of the variation and their interactions, the genetic terms in the above model were partitioned using an Additive, Dominance, and Additive  $\times$  Additive (ADAA) model (Zun, 1992; Yan et al., 1998). The ADAA model assumes normal diploid segregation, inbred parents in diallel mating, and linkage equilibrium. Additive  $\times$  Dominance and Dominance  $\times$  Dominance epistases were considered negligible because in comparison with other genetic components, these epistatic components are very complicated and will decline quickly with progressive generations (Xu and Zhu, 1999). The ADAA model included  $G \times E$  interactions.

The linear model for the phenotypic value  $Y_{ijkl}$  of the  $k$ th mating type ( $k=0$  for parent,  $k=1$  for  $F_1$ ,  $k=2$  for  $F_2$ ,  $k=3$  for  $BC_1P_1$ , and  $k=4$  for  $BC_1P_2$ ) from lines  $i$  and  $j$  in the  $l$ th block within the  $h$ th environment was:

$$Y_{ijkl} = \mu + G_{ijk} + E_h + GE_{hijk} + B_{l(k)} + \epsilon_{hijkl}$$

where  $Y_{ijkl} \sim (\mu, \sigma_p^2)$ ;  $G_{ijk}$  is the total genetic main effect, where  $G_{ijk} \sim (0, \sigma_G^2)$ ;  $E_h$  is the environment effect, where  $E_h \sim (0, \sigma_E^2)$ ;  $GE_{hijk}$  is the total  $G \times E$  interaction effect, where  $GE_{hijk} \sim (0, \sigma_{GE}^2)$ ;  $B_{l(k)}$  is the randomized complete block effect, defined as  $B_{l(k)} \sim (0, \sigma_B^2)$ ;  $\epsilon_{hijkl}$  is the residual effect, where  $\epsilon_{hijkl} \sim (0, \sigma_\epsilon^2)$ .

For the family generations used (parents and their  $F_1$ ,  $F_2$ ,  $BC_1P_1$ , and  $BC_1P_2$ ), the  $G_{ijk}$  and  $GE_{hijk}$  components were partitioned into genetic subcomponents for each generation (Yan et al., 1998; Zhu, 1992).

As a result, the phenotypic variance ( $V_p$ ) was partitioned as:

$$V_p = V_G + V_{G \times E} + V_e = V_A + V_D + V_{AA} + V_{AE} + V_{DE} + V_{AAE} + V_e$$

where  $V_G$  is the genotypic main variance, which was partitioned into additive ( $V_A$ ), dominance ( $V_D$ ), and epistatic ( $V_{AA}$ ) variances;  $V_{GE}$  is the  $G \times E$  interaction variance, partitioned into additive  $\times$  environment ( $V_{AE}$ ), dominance  $\times$  environment ( $V_{DE}$ ), and epistatic  $\times$  environment ( $V_{AAE}$ ) interaction variances; finally,  $V_e$  is the residual variance.

Analogously, the equivalent expression for covariance components is:

$$C_p = C_G + C_{G \times E} + C_e = C_A + C_D + C_{AA} + C_{AE} + C_{DE} + C_{AAE} + C_e$$

Variances and covariance components were estimated by the minimum norm quadratic unbiased estimation method 1 (MINQUE 1) (Zhu and Weir, 1996). Standard errors of the statistics were obtained by the jackknife technique (Miller, 1974). These computations were performed with QGA Station software ver. 1.0 (provided by Prof. Jun Zhu, Bioinformatics Institute, Zhejiang University, China).

Narrow-sense heritability ( $h^2$ ) was calculated as  $V_A/V_p$  (Falconer, 1970).

The effective number of loci ( $\hat{n}_e$ ) in which the accessions studied differ for the control of the recorded trait was estimated using the Castle–Wright estimator (Lynch and Walsh, 1998):

$$\hat{n}_e = \frac{(\bar{P}_1 - \bar{P}_2)^2 - V_{P_1} - V_{P_2}}{8V_S}$$

where  $\bar{P}_1$  and  $\bar{P}_2$  are the phenotypic means of parents 1 and 2, respectively;  $V_{P_1}$  and  $V_{P_2}$  are the phenotypic variances of parents 1 and 2, respectively;  $V_S$  is the estimated segregation variance. The  $V_S = 2V_{F_2} - V_{BC_1P_1} - V_{BC_1P_2}$  expression was used to consider possible dominance effects (Wright, 1968), where  $V_{BC_1P_1}$  and  $V_{BC_1P_2}$  are phenotypic variances of the two backcross generations. The standard error of ( $\hat{n}_e$ ) from Castle–Wright estimator was calculated using the methods described in (Lynch and Walsh, 1998).

### 3. Results

The ANOVA on data from the parents and from the four generations studied found significant differences between the parents for the traits curvature, projected area, seed length, seed width, 100-seed weight, pod length, seed/pod, ashes, Ca, Mg, protein, starch, mealiness, seed-coat roughness, and seed-coat perceptibility (Table 1). Only these traits were included in the genetic study.

There were significant differences between locations for all traits except the number of seeds per pod, the magnesium content of the seed coat, and seed-coat roughness (Table 1). In the plants cultivated in the greenhouse, seeds were larger and more curved, and they had higher protein content and were less mealy. They also had a lower content of calcium and ash in the seed coat. The interaction genotype  $\times$  location was significant for all agronomic and morphologic traits except degree of curvature. The block effect was not significant.



**Table 1**  
Q5 Mean ( $\pm$ standard error) values of the traits submitted to the ADAA analysis, in each of the generations and locations studied.

	P <sub>1</sub> (Montcau)	P <sub>2</sub> (Xana)	F <sub>1</sub>	F <sub>2</sub>	BC <sub>1</sub> P <sub>1</sub>	BC <sub>2</sub> P <sub>2</sub>	LSD	Open field (Sabadell)	Open field (Rubí)	Greenhouse	LSD
Curvature <sup>a</sup>	0.15 $\pm$ 0	0.04 $\pm$ 0 <sup>e</sup>	0.07 $\pm$ 0	0.09 $\pm$ 0.01	0.12 $\pm$ 0	0.06 $\pm$ 0	0.01	0.08 $\pm$ 0.01	0.08 $\pm$ 0.01	0.1 $\pm$ 0.01	0.01
Projected area(mm <sup>2</sup> )	95.1 $\pm$ 1.8	129.7 $\pm$ 5.7 <sup>e</sup>	117.7 $\pm$ 6.2	111.3 $\pm$ 5.7	110.4 $\pm$ 4.6	119.1 $\pm$ 6.8	4.0	102.7 $\pm$ 1.7	102.3 $\pm$ 2.4	136.3 $\pm$ 3.6	2.8
Seed length (mm)	15.5 $\pm$ 0.1	20.8 $\pm$ 0.4 <sup>e</sup>	18.8 $\pm$ 0.4	17.9 $\pm$ 0.4	17.3 $\pm$ 0.3	19.2 $\pm$ 0.4	0.4	17.5 $\pm$ 0.3	17.5 $\pm$ 0.3	19.7 $\pm$ 0.4	0.3
Seed width (mm)	8 $\pm$ 0.1	7.8 $\pm$ 0.2 <sup>e</sup>	7.7 $\pm$ 0.3	7.8 $\pm$ 0.2	8.1 $\pm$ 0.2	7.7 $\pm$ 0.3	0.2	7.4 $\pm$ 0.1	7.3 $\pm$ 0.1	8.8 $\pm$ 0.1	0.1
100-seed weight (g)	45.2 $\pm$ 1.3	91.6 $\pm$ 7.5 <sup>e</sup>	76.2 $\pm$ 4.3	64.6 $\pm$ 2.9	61.7 $\pm$ 3.4	79.9 $\pm$ 5.8	5.1	57.2 $\pm$ 1.9	64.6 $\pm$ 3.1	86.3 $\pm$ 4.9	3.6
Pod length (cm)	17.1 $\pm$ 0.2 <sup>e</sup>	15.4 $\pm$ 0.3	16.6 $\pm$ 0.2	16.7 $\pm$ 0.2	17.9 $\pm$ 0.4	15.7 $\pm$ 0.4	0.7	16.3 $\pm$ 0.3	16.5 $\pm$ 0.3	16.9 $\pm$ 0.2	0.5
Seed/pod	4.2 $\pm$ 0.2 <sup>e</sup>	2.2 $\pm$ 0.1	3.6 $\pm$ 0.1	3.5 $\pm$ 0.1	4.1 $\pm$ 0.2	3 $\pm$ 0.1	0.3	3.4 $\pm$ 0.2	3.6 $\pm$ 0.2	3.4 $\pm$ 0.1	–
Ashes (mg/kg)	51.3 $\pm$ 2.8 <sup>e</sup>	41.3 $\pm$ 3	63.9 $\pm$ 2.9	54.1 $\pm$ 2.2	54.1 $\pm$ 2.4	53.6 $\pm$ 2.8	5.4	60.1 $\pm$ 1.3	61 $\pm$ 1.6	44.5 $\pm$ 1.6	3.7
Calcium (mg/kg)	13.5 $\pm$ 0.9 <sup>e</sup>	9.7 $\pm$ 1	18.2 $\pm$ 1.1	14.4 $\pm$ 0.9	14.5 $\pm$ 0.9	13.8 $\pm$ 1.1	1.7	16.9 $\pm$ 0.5	17.1 $\pm$ 0.6	10.6 $\pm$ 0.5	1.2
Magnesium (mg/kg)	3.7 $\pm$ 0.1	2.8 $\pm$ 0.1 <sup>e</sup>	3.2 $\pm$ 0.1	3.4 $\pm$ 0.1	3.4 $\pm$ 0.1	3.2 $\pm$ 0.1	0.5	3.3 $\pm$ 0.1	3.2 $\pm$ 0.1	3.4 $\pm$ 0.1	–
Protein (g/kg)	268.8 $\pm$ 3.5	236 $\pm$ 2.4 <sup>e</sup>	229.8 $\pm$ 5.4	244.8 $\pm$ 6.2	252.1 $\pm$ 4.6	237.5 $\pm$ 6	14.2	243.9 $\pm$ 3.4	232.5 $\pm$ 4.7	255.6 $\pm$ 3.4	10.0
Starch (g/kg)	358.9 $\pm$ 6.1	390.7 $\pm$ 6.3 <sup>e</sup>	403.6 $\pm$ 6.7	388.4 $\pm$ 7	380 $\pm$ 5.9	398.7 $\pm$ 8.2	17.8	391.9 $\pm$ 4.2	403.8 $\pm$ 5.2	370 $\pm$ 4.4	12.5
Mealiness <sup>b</sup>	3.8 $\pm$ 0.2	4.8 $\pm$ 0.1 <sup>e</sup>	4.5 $\pm$ 0.2	4.3 $\pm$ 0.1	4.3 $\pm$ 0.2	4.6 $\pm$ 0.2	0.3	4.9 $\pm$ 0.1	4.4 $\pm$ 0.1	3.9 $\pm$ 0.1	0.2
Seed-coat Roughness <sup>c</sup>	7 $\pm$ 0.1 <sup>e</sup>	5.3 $\pm$ 0.1	6.7 $\pm$ 0.1	6.9 $\pm$ 0.1	6.9 $\pm$ 0.2	6.2 $\pm$ 0.2	0.5	6.6 $\pm$ 0.1	6.9 $\pm$ 0.1	6.5 $\pm$ 0.2	–
Seed-coatPerceptibility <sup>d</sup>	3.2 $\pm$ 0.2	6.4 $\pm$ 0.4 <sup>e</sup>	5.6 $\pm$ 0.2	4.9 $\pm$ 0.2	4.7 $\pm$ 0.2	5.2 $\pm$ 0.4	0.8	4.6 $\pm$ 0.2	5.2 $\pm$ 0.3	5.2 $\pm$ 0.3	0.6

<sup>a</sup> Measured in a scale from 0 to 0.17, (0 correspond to uncurved seed and 0.17 correspond to the most curved possible seed).

<sup>b</sup> 0 represents Ganxet Montcau reference intensity and 10 represents Tolosa reference.

<sup>c</sup> 0 represents Ganxet Montcau (cooked with distilled water) reference intensity and 10 represents Ganxet Montcau (cooked with 200 ppm of Ca) reference intensity.

<sup>d</sup> 0 represents Tolosa reference intensity and 10 represents Ganxet Montcau reference intensity.

<sup>e</sup> Corresponding to the dominant parent for each trait.

**Table 2**  
Results from the ADAA analysis, together with heritability estimated for all traits and followed by their standard error.

	V <sub>A</sub>	V <sub>D</sub>	V <sub>AA</sub>	V <sub>AE</sub>	V <sub>DE</sub>	V <sub>AAE</sub>	V <sub>e</sub>	V <sub>P</sub>	h <sup>2</sup>
Curvature <sup>a</sup>	32.7 $\pm$ 3.86**	10.16 $\pm$ 1.78**	0	0	1.17 $\pm$ 0.32**	0.02 $\pm$ 0**	1.28 $\pm$ 0.28**	45.33 $\pm$ 5.95**	0.72 $\pm$ 0.04**
Projected area	187.5 $\pm$ 32.99**	76 $\pm$ 16.46**	0	1.47 $\pm$ 0.28**	21.51 $\pm$ 4.36**	27.42 $\pm$ 6.33**	29.59 $\pm$ 5.47**	343.49 $\pm$ 94.04**	0.55 $\pm$ 0.04**
Seed length	4.49 $\pm$ 0.59**	1.91 $\pm$ 0.35**	0.26 $\pm$ 0.04**	0	0.46 $\pm$ 0.09**	0.13 $\pm$ 0.02**	0.26 $\pm$ 0.04**	7.52 $\pm$ 1.10**	0.60 $\pm$ 0.04**
Seed width	0.11 $\pm$ 0.03**	0.03 $\pm$ 0.01**	0	0	0	0.10 $\pm$ 0.02**	0.06 $\pm$ 0.02**	0.30 $\pm$ 0.16*	0.35 $\pm$ 0.02**
100-seed weight	219.32 $\pm$ 43.02**	268.17 $\pm$ 52.51**	24.27 $\pm$ 4.66**	83.19 $\pm$ 15.43**	55.09 $\pm$ 13.99**	16.61 $\pm$ 3.42**	27.93 $\pm$ 6.73**	694.60 $\pm$ 176.84**	0.32 $\pm$ 0.03**
Pod length	1.07 $\pm$ 0.26**	0	0.01 $\pm$ 0**	1.01 $\pm$ 0.22**	0	0.03 $\pm$ 0.01**	0.92 $\pm$ 0.21**	3.03 $\pm$ 1.06**	0.35 $\pm$ 0.04**
Seed/pod	0.98 $\pm$ 0.13**	0	0.02 $\pm$ 0**	0.18 $\pm$ 0.04**	0	0	0.14 $\pm$ 0.03**	1.32 $\pm$ 0.25**	0.75 $\pm$ 0.04**
Ashes	0	263.77 $\pm$ 40.55**	0	0 $\pm$ 0	7.88 $\pm$ 1.47**	3.03 $\pm$ 0.66**	25.62 $\pm$ 7.19**	300.30 $\pm$ 85.90**	0
Calcium	0	39.68 $\pm$ 5.64**	0	1.05 $\pm$ 0.27**	2.49 $\pm$ 0.53**	0	2.59 $\pm$ 0.66**	45.81 $\pm$ 11.45**	0
Magnesium	0.13 $\pm$ 0.03**	0.08 $\pm$ 0.02**	0	0	0	0.04 $\pm$ 0.01**	0.12 $\pm$ 0.04**	0.36 $\pm$ 0.32	0.35 $\pm$ 0.04**
Protein	68.94 $\pm$ 16.36**	531.48 $\pm$ 141.51**	0	0	0	117.23 $\pm$ 30.27**	134.08 $\pm$ 30.22**	851.72 $\pm$ 521.45	0.08 $\pm$ 0.03**
Starch	41.42 $\pm$ 10.02**	454.79 $\pm$ 114.44**	0	154.31 $\pm$ 37.72**	0	0	241.52 $\pm$ 56.38**	892.04 $\pm$ 613.84	0.05 $\pm$ 0.02**
Mealiness	0.19 $\pm$ 0.03**	0.01 $\pm$ 0**	0.01 $\pm$ 0**	0.13 $\pm$ 0.04**	0.07 $\pm$ 0.02**	0	0.07 $\pm$ 0.02**	0.47 $\pm$ 0.19**	0.4 $\pm$ 0.03**
Seed-coat roughness	0.15 $\pm$ 0.03**	0	0.1 $\pm$ 0.04**	0.05 $\pm$ 0.02**	0	0.02 $\pm$ 0**	0.19 $\pm$ 0.04**	0.55 $\pm$ 0.48	0.27 $\pm$ 0.04**
Seed-coat perceptibility	1.44 $\pm$ 0.34**	1.10 $\pm$ 0.25**	0	0.48 $\pm$ 0.11**	0	0	0.74 $\pm$ 0.17**	3.77 $\pm$ 1.36**	0.38 $\pm$ 0.03**

V<sub>A</sub>, additive variance; V<sub>D</sub>, dominance variance; V<sub>AA</sub>, additive epistatic variance; V<sub>AE</sub>, variance of the interaction between the additive and environmental effects; V<sub>DE</sub>, variance of the interaction between the dominance and environmental effects; V<sub>AAE</sub>, variance of the interaction between the additive epistatic and environmental effects; V<sub>e</sub>, Variance of the error term in the model; V<sub>P</sub>: phenotypic variance; h<sup>2</sup>, narrow-sense heritability.

\* Significant at P < 0.05.

\*\* Significant at P < 0.01.

<sup>a</sup> The same units than Table 1.

The ADAA analysis found significant genetic variance for all traits (Table 2). The total genetic variance (V<sub>A</sub> + V<sub>D</sub> + V<sub>AA</sub>) was very high for all agronomic and morphologic traits studied, accounting for more than 73% of the phenotypic variance except in the traits seed width and pod length. In the remaining traits, the proportion of genetic variance was lowest for mealiness, where it accounted for 44.14% of the phenotypic variance. In the trait curvature, the total genetic variance accounted for 94.6% of the phenotypic variance, mainly due to additive effects; the environmental variance was very low for this trait. Other traits where the environmental variance was low include the projected area, seed length, 100-seed weight, ash, and calcium. Although variance due to the interaction G  $\times$  E was present in all the traits, the only cases where it accounted for more than 17% of the total phenotypic variance were seed width, 100-seed weight, pod length, and mealiness.

The narrow-sense heritability was significant for all traits except ash and calcium in the seed coat (Table 2), because these two traits do not have an additive component. The traits with the highest narrow sense heritability (about 0.75) were curvature and the number

of seeds per pod. The traits with the lowest heritability (<0.01) were protein and starch content; heritability for the remaining traits ranged from 0.27 to 0.60 (Table 2).

The estimates of dominance variance were significantly greater than zero for all traits except pod length, number of seeds per pod, and seed-coat roughness, whereas the epistatic component was significant only for seed length, 100-seed weight, pod length, number of seeds per pod, mealiness, and seed-coat roughness, all of which, however, had very low values, accounting for less than 3.5% of the phenotypic variance (except for the trait seed-coat roughness, where the epistatic variance was the main component, with a value very similar to the additive variance). As epistatic variance was generally low, dominance variance in the traits where it was found must be attributed to partial or total dominance within loci (Table 2).

The effective number of loci is an estimate of the number of genes for which parental lines differ and that are involved in the control of a trait. We started with lines that were on the opposite extremes for the curvature of the seed (Fig. 1). Thus, we consid-

**Table 3**

Significant genetic additive and phenotypic correlations between seed curvature and the other traits studied, followed by their standard error.

	Additive	Phenotypic
Projected area (mm <sup>2</sup> )	-1 ± 0.22**	-0.87 ± 0.10**
Seed length (mm)	-0.98 ± 0.12**	-0.98 ± 0.07**
Seed width (mm)	0.97 ± 0.14**	0.7 ± 0.18**
100-seed weight (g)	-1 ± 0.13**	90.93 ± 0.08**
Pod length (cm)	1 ± 0.22**	0.7 ± 0.20**
Seed/pod	1 ± 0.11**	0.83 ± 0.15**
Magnesium (mg/Kg)	0.79 ± 0.12**	0.73 ± 0.20**
Protein (g/Kg)	1 ± 0.40*	0.74 ± 0.13**
Starch (g/Kg)		-0.87 ± 0.20**
Mealiness		-0.97 ± 0.12**
Seed-coat roughness	1 ± 0.36*	1 ± 0.19**
Seed-coat perceptibility		-0.58 ± 0.19**

\* Significant at  $P < 0.05$ .

\*\* Significant at  $P < 0.01$ .

ered that only the estimates for this trait were reliable. By location, the estimates of the effective number of loci for the trait degree of curvature were  $2.06 \pm 0.1$  loci in Sabadell,  $2.93 \pm 0.17$  in Rubí, and  $2.77 \pm 0.14$  in Viladecans' greenhouse. Thus, we consider it reasonable that the extreme curvature of the Ganxet derives from alleles at three loci.

The ADA model makes it possible to determine the additive and dominance components of the genetic covariances to calculate the different types of correlations and evaluate the possibilities of carrying out indirect selection. Table 3 shows the significant additive and phenotypic correlations between the traits studied and the curvature of the seed.

The majority of the additive correlations were very high. Seed curvature correlated positively with seed width, pod length, number of seeds per pod, magnesium content, protein content, and seed-coat roughness, and negatively with projected seed area, seed length, 100-seed weight, and mealiness (Table 3). All the phenotypic correlations were significant and of the same sign as the genetic additive ones.

#### 4. Discussion

Two of the experimental environments (Sabadell and Rubí) were selected because they are representative of the area and soil specified for Ganxet bean cultivation in the definition of the Protected Designation of Origin. The third environment was a greenhouse with controlled, optimal conditions for the development of all the genotypes. The high cation exchange capacity of the substrate used in the greenhouse environment is especially important, given that this characteristic is associated with higher protein content and less mealiness in beans (Flórez et al., 2009).

In our experiment, materials cultivated in the greenhouse had not only higher protein content and less mealiness, but also greater curvature and size of the seed (greater projected area, length, width, and 100-seed weight). The increase in the size of the seeds along all dimensions seems reasonable given the greater abundance of nutrients and especially moisture. However, the explanation for why favorable environmental conditions should lead to greater seed curvature does not seem so simple. One plausible hypothesis is that the degree of curvature in Ganxet beans might be the consequence of the inhibition of seed growth in the area of the hilum; in this case, factors that favor the growth of the rest of the seed would tend to increase the curvature. To test this hypothesis, we analyzed the environmental correlations in F<sub>1</sub>, because this generation had no genetic variance, so the differences observed must be due to environmental effects. We found significant positive environmental correlations ( $p < 0.001$ ) between seed curvature and the traits related to the size of the seed (100-seed weight

( $r = 0.67$ ), projected area ( $r = 0.75$ ), seed length ( $r = 0.65$ ), and seed width ( $r = 0.83$ )), which would support our hypothesis.

The distribution of the population according to the curvature in the different generations studied suggests that the uncurved shape is dominant; the mean for the individuals in F<sub>1</sub> is closer to that for the uncurved parents than to that for the curved parents (Table 1). The deviations from the mean observed both in the parents and in F<sub>1</sub> must be attributed to environmental effects because these are non-segregating generations. The environmental effects probably convert any model based on the control of a trait by two or more loci into a continuous model (Table 1). Thus, based on the means and distributions, it seems that curvature fits a quantitative model with partial dominance toward uncurved seed shape within the locus.

The ADA model confirmed the mode of inheritance of the curvature trait in which the additive component of variance predominates over the dominance component (Table 2). Both the environmental variance (contained within the residual variance) and the genotype  $\times$  environment variance, although significant, were small. This results in a narrow-sense heritability of 0.72, which indicates that the response to selection in heterogeneous populations will be high. Of particular importance for breeding, the low effect of the environment on this trait indicates that the phenotype is a good reference for the genetic constitution of each plant (Table 2).

The estimated effective number of loci involved in the control of the curvature using the Castle–Wright method was about three. So if we assume that the wild-type bean is uncurved, the parent P<sub>1</sub> (Montcau) would be a partially recessive triple homozygote with complete additivity among loci, given that the epistatic variance is null. This is not true for the interactions  $V_{AE}$  and  $V_{DE}$ , which is also reflected in the different estimates of the number of loci involved according to the location.

The rest of the agronomic and morphologic traits except the number of pods per plant and the length of the seed were normally distributed in F<sub>2</sub>; this finding, together with the breakdown of the phenotypic variance (Table 2), suggests control by multiple genes, with two or more loci involved. This supposed quantitative control coincides with the results reported by Pérez-Vega et al. (2010), who identified QTLs for some of these traits in a Xana  $\times$  Cornell family of recombinant inbred lines, as well as with the data reported by Akande and Balogun (2007), Dalla Corte et al. (2010), Motto et al. (1978), Vallejos and Chase (1991), and Yuste-Lisbona et al. (2014).

Casañas et al. (2013) found polygenic control for the chemical traits in both the seed coat and embryo and mapped the QTLs involved in the genetic control of the chemical traits in the Xana  $\times$  Cornell family of recombinant inbred lines mentioned above. The normal distribution of these traits in our F<sub>2</sub> generation is in concordance with these previous results.

The only trait that had a heritability of the same order of magnitude as degree of curvature was the number of seeds per pod ( $h^2 = 0.75$ ) (Table 2). Nearly all the genetic variance for this trait was additive, and there was no dominance variance, although there was also very small epistatic variance. Nienhuis and Singh (1988) reported a somewhat lower heritability for the trait number of seeds per pod ( $h^2 = 0.57$ ). The heritabilities of the remaining traits varied widely and can be divided into three groups. The first group includes the area and length of the seed, which had heritabilities of 0.55 and 0.60, respectively. In both cases, the additive variances were much higher than the dominance variances, with a significant  $V_{GE}$  (Table 2). The second group, with heritabilities ranging between 0.27 and 0.4, includes seed width, 100-seed weight, pod length, magnesium content, and the sensory traits mealiness, seed-coat roughness, and seed-coat perceptibility. In this group, the heritabilities resulted from different combinations of variances. In 100-seed weight, the dominance genetic variance was greater than the additive, whereas in the rest of the traits the variance

of the interactions and the environmental variance were what led to medium and low heritabilities. Finally, a third group includes ash content, calcium content, protein content, and starch content. In these traits, the dominance genetic variance was much greater than the additive. This, together with the large interaction and environmental variances, led to heritabilities near zero (Table 2). Nevertheless, even the traits with low narrow-sense heritabilities had high broad-sense heritabilities (100-seed weight = 0.74, ash = 0.88, Ca = 0.87, protein = 0.7, and starch = 0.56). As the main aim of this investigation is to apply the results in backcross procedures, we can also transfer the dominant variability to our recurrent lines because this process results in homozygous individuals. The transfer of recessive genes is slow in the absence of linked molecular markers, but even without these markers this practice is widely used.

In a study starting from a cross between a domesticated variety and a wild variety, Motto et al. (1978) reported much higher narrow-sense heritabilities for seed length and seed width than those found in the present study. On the other hand, our results fall within the wide range of heritabilities for these two traits calculated by Dalla Corte et al. (2010) from crosses among three varieties. Since heritability is a population-dependent parameter, the differences in the values reported is not surprising.

We found numerous significant additive genetic and phenotypic correlations between the curvature of the seed and the other traits (Table 3). In general, high additive genetic correlations suggest pleiotropic effects rather than linkage (Table 3). It seems that a high curvature is related to small seeds with high protein content, low mealiness, and high seed-coat roughness, together with long pods and many seeds per pod. Other authors have reported similar genotypic correlations. Casañas et al. (1998) found a positive genotypic correlation between curvature and protein content ( $r = 0.68$ ,  $p \leq 0.05$ ). Pujolà et al. (2004) found a negative genotypic correlation between mealiness and protein content ( $r = -0.59$ ,  $p \leq 0.1$ ). Given the Ganxet parent was characterized by highly curved seeds with high protein content and low mealiness, these traits could also be caused by linkage and would therefore be unaffected by recombination in the generations studied.

In view of the additive correlations found, the trait curvature can be a simple morphologic marker for introducing Ganxet's high protein content and low mealiness into other varieties, improving nutritional and sensory value (low mealiness is a preferential trait in beans, Casañas et al., 2006). Large increases in protein and decreases in mealiness would not be expected through backcrossing with Xana, because Xana has medium protein content and mealiness. Ganxet would be most useful in backcrosses with other varieties with lower protein content and higher mealiness.

Earlier studies found evidence of negative genotypic correlation between the degree of curvature and yield ( $-0.68$ ,  $p \leq 0.05$ , Casañas et al., 1998). In our general study of correlations, curvature had no significant genetic correlation with yield. Nevertheless, this could be partly due to the lower than usual yields for the Xana parent in all three locations than in their usual place of cultivation or to the lower yield of plants with type I growth habit compared to those with type IV habit. An analysis of the genotypic correlations done solely from the data collected in the greenhouse (where both parents had equally optimal conditions for their development) showed negative correlations between curvature and yield ( $r = -0.42$ ,  $p < 0.05$ ), and environmental correlations done only on the data from the Ganxet variety in the three locations were similar ( $r = -0.62$ ,  $p < 0.001$ ).

Decreased protein content has been associated with domestication because wild beans have a greater proportion of protein than cultivated beans (Guzman-Maldonado et al., 2000; Sotelo et al., 1995). A negative correlation between protein content and yield has also been reported (Shellie-Dessert and Bliss, 1991). It remains

to be determined to what extent increases in protein from introgression from Ganxet into other materials would compensate for accompanying losses in yield.

Our data (Tables 2 and 3) indicate that, in general, all the traits studied have a quantitative basis with a high additivity effect between loci and a variable dominance effect within loci. The Montcau parent (Ganxet) would have a predominance of recessive genes for curvature, 100-seed weight, and mealiness and a predominance of dominant genes for high protein content (Table 1). Pleiotropy/linkage between the degree of curvature and some traits makes it difficult to establish separate models for the genetic structure that controls the traits studied.

We do not know the position of the loci involved within the genome or whether they are located in areas with high or low recombination. We are now undertaking two approaches to resolve this problem. On the one hand, in a practical way, we are using a classical approach to try to introduce the trait into diverse inbred lines through backcrossing and checking the results (ease of recovery of the genetic background of the recurrent, confirmation of the pleiotropic/linking effects of the genes involved in the degree of curvature of the seed in Ganxet). On the other hand, we are developing a family of recombinant inbred lines from Montcau x Xana and trying to map the loci involved as accurately as possible. The complete sequencing of the bean genome (Schmutz et al., 2014) and comparison of the syntenies with model species studied in greater detail offers hope for the identification of the genes and the development of internal markers that will facilitate the definitive evaluation of the potential of Ganxet as a donor of genes in bean breeding programs.

## 5. Conclusions

The genetic control of the curvature of the seed in the Ganxet variety comes mainly from an additive component and to a lesser extent from a dominance component, which is reflected in high narrow-sense heritability. The trait seed curvature correlates with other traits of interest such as protein content and mealiness, probably due to pleiotropy. Moreover, seed curvature is controlled by only three loci and is not very sensitive to environmental effects, so it will be relatively easy and fast to create new inbred lines that incorporate this trait in homozygosis. The Ganxet variety, the only variety reported to date with a large incidence of this trait, can become an important resource for breeding programs to improve the nutritional and sensory quality of beans. Apparently the use of backcrossing methods could increase protein content and creaminess in most varieties.

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