



Genetic variation and environmental effects on agronomical and commercial quality traits in the main European market classes of dry bean

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Abstract

Repeated testing of diverse commercial classes of beans over time and space and selection for a minimal degree of genotype \times environment interaction (GEI) is a common feature of all plant breeding programs. The GEI effect limits the accuracy of yield estimates and complicates the identification of specific genotypes suited for specific environments. The purpose of this work was to study GEI on yield of the main European dry bean market classes by the site regression (SREG) and multiple trait data by genotype–trait (GT) methods, which graphically displayed the interrelationships among traits and facilitated visual comparison of genotypes. Sixty-seven genotypes of common bean, grown in three different sites in northwestern Spain during the 2001 and 2002 growing seasons, were evaluated for yield, two phenological and four commercial seed traits. Interactions between GEI and yield were established using a SREG analysis model to generate a genotype–GEI (GGEI) biplot. The GGEI biplot revealed GEI as a major source of bean yield variation and the different growing sites served to discriminate among the genotypes. This method provided information on the three growing sites: Lugo was identified as the location that best represents the target environment for seed yield; Pontevedra was the location showing the greatest yield stability and León separated the genotypes clearly although as this was not consistent over other sites, León was not representative of an average environment. Each site was represented by a group of genotypes, which showed a superior performance. Large-seed genotypes of the favada market class were best suited to the Lugo site. Commercial seed traits (seed coat fraction, water absorption, crude protein content and seed weight) and days to maturity showed wide variation, as indicated by the relative length of their vectors in the GT plot. Genotypes with the highest yield showed the highest protein content and the poorest seed coat quality and were the latest to flower, while the genotypes that exhibited a high seed coat fraction had the poorest water absorption capacity. The results presented in this work permitted the identification of optimal adapted dry bean genotypes for each bean producing area. These high-yielding genotypes with a

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good commercial seed quality merit special attention as they could have potential applications for the development of breeding strategies.

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1. Introduction

The common bean (*Phaseolus vulgaris* L.) accounts for over 90% of the *Phaseolus* production areas in the world. It is the third most important food legume crop worldwide, surpassed only by the soybean (*Glycine max* (L.) Merr.) and peanut (*Arachis hypogea* L.). Among the main food crops, the common bean shows the greatest variation in growth habit, seed characteristics (size, shape and colour) and maturation time. This variability enables its production in a wide range of cropping systems and environments as diverse as the Americas, Africa, the Middle East, China and Europe. Despite being cultivated for its green pods, fresh shelled and dry seeds, the dry bean is produced and consumed in largest quantities (accounting for 76.2% of its production worldwide), followed by fresh shelled seeds (17.4%) and snap bean (6.4%) (FAO, 2002). Dry bean production is declining in the majority of European countries due to relatively low yields and insufficient income for growers, although an increased demand occurred over the past years.

Among some 600 bean varieties grown in the world, 62 dry bean market classes are recognized (FAO, 2002) according to consumer preferences, production and market price. High yielding bean genotypes with improved commercial quality traits, along with other agricultural features is an ongoing concern. Thus, the knowledge of the genetic variation in phenological, yield and seed traits and their interrelationships should make possible to increase the yield potential of the common bean while maintaining seed commercial quality. Several studies have focused on establishing interrelations among breeding objectives (Kelly and Bliss, 1975; Yan and Wallace, 1995; Elia et al., 1997) in an effort to select the most appropriate cultivars for a given environment.

The main purpose of multi-environment trials (METs) is the identification of superior genotypes and the locations that best represent the target environment for production. Genotype \times environment interactions (GEIs) have been defined as the failure of genotypes to achieve the same relative performance in different environments (Baker, 1998). Thus, the best genotype for one environment should not be the best for another. The development of improved statistical tools to analyse and understand GEIs offers the possibility of creating improved genotypes for target environments by selecting the adaptive values of the best genotypes (Kang, 1988; Boerma and Mian, 1998). Several methods can be used to study GEIs (Crossa, 1990; Brancourt-Hulmel et al., 1997). The most suitable methods for understanding the response of a genotype to different environments are based on multiplicative and factorial regression models. Among the multiplicative models, the SREG method (Crossa and Cornelius, 1997) is appropriate for analysing the results of METs when environments explain most of the total variation. However, although the measured yield is the combined effect of genotype (G), environment (E) and GEI, only G and GEI are relevant to cultivar evaluation and must be simultaneously considered for cultivar selection. These two factors are combined in the model to give genotype–GEI (GGEI). The GGEI (Yan et al., 2000, 2001) allows visual examination of the GEI pattern in data from METs. Thus, the method also allows to the environments to be evaluated just as genotypes. The GGEI biplot will graphically summarize the effects of G and GEI, and address the question of ‘which one where’ for a METs dataset. Cultivar evaluation based on multiple traits is another issue in plant breeding. Yan and Rajcan (2002) used a GT biplot, which is an application of the GGEI biplot technique, to analyse genotype \times trait data in soybean.

Table 1
Identification of 67 common bean genotypes grouped in the main European dry bean market classes used in the GGEI and GT study

Accession code	Market class	Synonyms
112	azufrado	
61	bayo gordo	feijão sete semanas, tabacchino
397	black turtle	negrita
475	canario	
118, 910, 26158	canela	yellow flageolet
201, 253, 3499, 3569, 11072	canellini	alubia, haricot blanc, fasolia, fagioli
4	carioca	
632	chumbihno	garbanzo marrón
242, 4000	cranberry	pinta de león, vermont cranberry
455	dark garbanzo	garbanzo oscuro
3746	dark red kidney	morada larga, red flageolet
222, 3190, 3284, 25580, 26216, 27958	favada	fava, granja
413	favada pinto	speckled brown cow bean, tourihna
19, 273, 3384, 22814, 26195	great northern	garbanzo, gallega de Carballo, planchada
631	guernikesa	
17	hen eye	ollo de pita, nasieddu
593	hook	ganxet
1409	kidney caparron	caparrón de riñón
104, 4004, 4451, 9980	large cranberry	avinado
419, 3714, 4488	large great northern	plancheta
261	light red kidney	
1026, 3701, 3966	marrow	blanca redonda, riso bianco, fagioli de controne
678	mulatihno	
65	navy	chichos blancos
502	negro brillante	tolosana
434, 3990	ojo de cabra	borlotto, lingua di fuoco, ciuoto
57	pinto	pinta
404	red caparron	red calypso, caparrón rojo
319, 621, 9979, 27961	red pinto	palmeña
331, 2016, 4437	rounded caparron	caparrón redondo, tuvagliedda
568, 1404, 22359	sangretoro	morada redonda, del vino
9, 395, 30452	small white	garbancillo, arrocina
598	small yellow	de aceite
187, 3276, 3505	white kidney	flageolet, blanca de riñón

Herein, we assessed GEI effects on yield of the main European dry bean market classes in north-western Spain, and evaluated genotypes on the basis of two phenological and four commercial seed traits. The objectives were: (i) to identify the best performing genotypes in each dry bean production area; (ii) to identify locations that best represent the target environment for high yield; (iii) to rank the genotypes according to yield performance and stability; (iv) to establish interrelationships among the traits examined; and (v) to compare the genotypes on the basis of multiple traits with the aim of recommending possible high-yielding genotypes with an acceptable commercial seed quality.

2. Materials and methods

2.1. Plant material and experimental design

The study was conducted on 67 common bean genotypes from northwestern Spain, representing the main European dry bean market classes (Table 1). Genetic material was obtained from the germplasm collections of the MBG-CSIC (Misión Biológica de Galicia, Spanish Council for Scientific Research, Pontevedra, Spain) (from 4 to 1409 accessions) and CRF-INIA (Centro de Recursos Fitogenéticos, Alcalá de Henares, Spain) (from 2016 to 30452 accessions).

The dry bean genotypes were evaluated in a randomized complete block design with two replica-

tions per trial. Field experiments were performed over the years 2001 and 2002 in three main production areas in northwestern Spain: Pontevedra (42°26'N, 8°38'W, 40 masl), Lugo (43°26'N, 7°16'W, 130 masl) and León (42°21'N, 2°03'W, 810 masl). For each environment, soil properties, mean temperature and rainfall (Table 2) were recorded to provide a biological explanation for the environmental effects and interactions observed. Each experimental plot comprised of a single 3.5 m row, with 0.80 m between rows and 0.25 m between plants. Seeds were hand-sown and thinned to 15 plants per plot after emergence. Weeds were controlled by manual methods. Diseases and pests were controlled as far as possible in all trials by conventional pesticides.

2.2. Data collection

For each plot, the agronomical data recorded were: days to first flower (from the time of planting until one plant had at least one open flower), days to maturity (from planting until one plant had at least one dry pod) and seed yield (expressed in kilograms per hectare and determined at a moisture content of 140 g kg⁻¹). Commercial seed quality data recorded were: 100-seed weight, seed coat fraction (as the ratio of seed coat weight versus cotyledon plus seed coat weight, determined by removing the seed coat from the cotyledon and storing for 24 h at 105 °C), water absorption (reflecting the amount of water absorbed by 100 dry seeds after soaking for 18 h at room temperature and dividing the difference in weight before and after soaking by the dry weight) and crude protein determined by the near infrared transmittance method.

2.3. Statistical analysis

Analyses were performed using a SAS (SAS Institute, 2000) program designed to generate GGEI biplots (Burgueño et al., 2001). The GGEI biplot was constructed by plotting the first two principal components (PC1 and PC2) derived from subjecting the GGEI matrix to singular value decomposition (SVD) (Yan, 1999; Yan et al., 2000) of the environment-centred data. Multilocation data were analysed by a two-way model of the form:

$$Y_{ij} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \varepsilon_{ij}$$

Table 2
Agro-climatic characteristics of the three locations in northwestern Spain in the GGEI and GT study

Location	Soil properties ^a		Average temperature monthly ^b (°C)												Total rainfall monthly ^b (mm)															
	Type	pH	Texture	Organic matter (%)	2001				2002				2001				2002													
					M	J	JL	A	S	O	M	J	JL	A	S	O	M	J	JL	A	S	O	M	J	JL	A	S	O	T	
Pontevedra	District Cambisol	5.8	Sandy loam	6.5	16	19	19	20	18	16	14	17	19	19	18	15	139	21	85	67	47	390	2164	161	59	19	10	78	343	1938
Lugo	District Cambisol	6.0	Sandy loam	5.3	12	15	15	17	14	13	12	13	15	15	14	13	49	50	100	49	170	175	1675	120	115	5	30	70	245	1660
León	District Cambisol	5.9	Sandy loam	2.5	14	19	19	19	15	13	12	18	19	18	15	12	32	2	14	13	18	43	1025	46	23	9	12	95	44	531

^a FAO-UNESCO system (1974).

^b M: May, J: June, JL: July, A: August, S: September, O: October, T: 12 months.

where Y_{ij} is the mean yield of genotype i in environment j ; μ is the overall mean; α_i and β_j are the main genotype and environmental effects; $(\alpha\beta)_{ij}$ is the GEI effect; and ε_{ij} is the residual associated with genotype i in environment j . Deletion of α_i and/or β_j allows variation explainable by the deleted term(s) to be absorbed into the $(\alpha\beta)_{ij}$ term. The matrix of $(\alpha\beta)_{ij}$ values is then subjected to SVD. SVD is a complex mathematical operation that decomposes a matrix into two component matrices using the least-squares method, such that each element in the GGEI matrix is recovered through:

$$Y_{ij} - \mu - \beta_j = \lambda_1 \xi_{i1} \eta_{j1} + \lambda_2 \xi_{i2} \eta_{j2} + \varepsilon_{ij}$$

where λ_1 and λ_2 are the singular values for the first and second principal components, PC1 and PC2, respectively, the square of which is the sum of squares explained by PC $_n$; ξ_{i1} and ξ_{i2} are the PC1 and PC2 scores respectively, for genotype i ; and η_{j1} and η_{j2} are the PC1 and PC2 scores, respectively, for environment j . Cornelius (1993) introduced some statistics such as the F_{GH2} , which can be applied to test for significance of individual PCs in SVD analysis.

To achieve symmetric scaling between the genotype and environment scores, the equation is rewritten as:

$$Y_{ij} = \xi_{i1}^* \eta_{j1}^* + \xi_{i2}^* \eta_{j2}^* + \varepsilon_{ij}$$

where $\xi_{in}^* = \lambda_n^{0.5} \xi_{in}$ and $\eta_{jn}^* = \lambda_n^{0.5} \eta_{jn}$, and $n = 1, 2$.

The values ξ_{in}^* and η_{jn}^* are simultaneously obtained by subjecting the environment-centred yield (i.e., $Y_{ij} - \beta_j$) to SVD such that genotype and environment scores have the same units (square root of original unit kg ha⁻¹ in terms of yield) for both PC1 and PC2. In the SREG method, PC analysis is performed on the residuals of an additive model with the environment as the only main effect. Therefore, the term $\xi_{in}^* + \eta_{jn}^*$ contains the variation due to G and GEI.

In the GGEI biplot, corner genotypes are joined by straight lines such that markers of all other genotypes fall inside the polygon. The performance of different genotypes in each location can be established by drawing lines perpendicular to the sides of the polygon, starting from the biplot origin, to divide the biplot into sectors, each with a corner genotype. The corner genotype for each sector is the one giving the highest yield for the location that falls within that

sector. Ideal cultivars should have large PC1 scores (high yielding ability) and near zero PC2 scores (high stability). Similarly, ideal test environments should have large PC1 scores (more discriminating of the cultivars) and near zero PC2 scores (more representative of an average environment).

The GT biplot method (Yan and Rajcan, 2002) was used to display genotypes by two-way trait data in a biplot. It is based on the following formula:

$$\frac{(T_{ij} - \check{T}_{ij})}{S_j} = \lambda_1 \xi_{i1} \eta_{j1} + \lambda_2 \xi_{i2} \eta_{j2} + \varepsilon_{ij}$$

where T_{ij} is the average value of genotype i for trait j ; \check{T}_{ij} is the average value of all genotypes for trait j , and S_j is the standard deviation of trait j among the genotype averages; ξ_{in} and η_{jn} are scores for genotype i and trait j on PC $_n$ ($n = 2$), respectively, and ε_{ij} is the residual associated with genotype i for trait j . Because different traits use different units, standardization is needed to remove the units such that we assume an equal ability of all traits to discriminate among genotypes. In the GT biplot, a vector is drawn from the biplot origin to each trait marker in order to visualize the relationships among traits. The correlation coefficient between any two traits is approximated by the cosine of the angle between their vectors.

3. Results

3.1. Analyses of variance and agronomic performance

Analysis of variance of seed yield of the 67 genotypes tested for the three locations and each of the two years (Table 3) showed that 33.1% of the total sum of squares was attributable to location effects, 24.6% to genotypic effects and 22.7% to GL interaction, whereas the year effect accounted only for 1.9%, and the GY interaction was not significant. This indicates there were no substantial differences in the genotypic response across years.

The Table 4 displays the means for each location. Significant differences among locations were found for seed yield and dry weight. Location significant differences observed for yield may be attributed to environmental variables. The average yield by sites

Table 3
Combined analysis of variance for seed yield (kg ha⁻¹) in 67 common bean genotypes grown at three locations in northwestern Spain in 2001 and 2002

Source of variation	d.f. ^a	Sum of squares	Mean squares	Variation (%)
Year (Y)	1	21.13	21.13**	1.92
Location (L)	2	363.37	181.69**	33.12
Y × L	2	28.75	14.37**	2.62
Replications/Y × L	6	12.20	2.03	1.11
Genotypes (G)	66	269.76	4.09**	24.59
G × Y	66	55.89	0.86	5.09
G × L	132	249.04	1.89**	22.70
G × Y × L	132	96.86	0.87	8.82
Error	471	630.69	1.34	

^a Degrees of freedom.

** Significant at $p \leq 0.01$.

was 2570, 1544 and 860 kg ha⁻¹ for Lugo, León and Pontevedra, respectively. Mean yield for 87% of the genotypes (data not shown) was higher in Lugo than in the other locations. Dry bean genotypes showed larger seed weight and longer maturity period in Lugo than the other sites, although it was not significant.

3.2. GGEI biplot

The GGEI biplot (Fig. 1) method enables the visual comparison of the locations and genotypes studied and their interrelationships, demonstrating that selection for yield in different environments could serve to enhance yield average across environments, and to preserve yield within each environment. The components PC1 and PC2 obtained, explained 91.67% of the overall G + GL variation that makes up the GGEI biplot, although only PC1 was significant (Table 5) as indicated by the FGH2 statistic ($p \leq 0.01$). The corner genotypes (65, 1401, 22359, 568, 17, 3569, 475, 593, 253 and 57) of the biplot are the most responsive to the environment, they were either the best or the poorest performers at some or all locations, since they appear furthest away from the origin. The genotypes in the biplot that clustered close to the perpendicular lines that separate the locations and those towards the right hand side of the polygon are the superior genotypes (568, 22359, 331, 419, 434, 502, 2016, 3990 and 1401) since they showed a large PC1 value.

Contrary to the PC1, the PC2 has both positive and negative values. Therefore, if a genotype shows a large positive interaction with some of the locations studied,

Table 4
Mean, standard error (S.E.), range and coefficient of variation (C.V.) for phenological, yield and seed commercial traits in 67 common bean genotypes grown at three locations in northwestern Spain in 2001 and 2002

	Pontevedra			Lugo			León						
	Mean ± S.E.	Range of variation	C.V.	LSD ^a	Mean ± S.E.	Range of variation	C.V. ^a	LSD ^a	Mean ± S.E.	Range of variation	C.V. ^a	LSD ^a	LSD ^b
Days to flower	55.7 ± 3.45	44.7–76.5	12.4	9.9	57.7 ± 3.54	41.2–67.5	12.2	9.9	52.0 ± 3.75	44.2–62.7	14.2	10.3	n.s. ^c
Days to maturity	104.8 ± 4.90	85.5–135.1	9.3	15.1	108.2 ± 4.65	86.2–120	8.4	12.9	104.4 ± 3.22	88–129	6.2	9.1	n.s. ^c
Yield (kg ha ⁻¹)	860 ± 446.3	94–2417	105	1558	2569 ± 843.1	860–5785	66	1456	1544 ± 642.1	190–3292	76	1306	1006
Dry weight (g 100 seeds ⁻¹)	53.1 ± 7.52	22.3–82.4	28.1	26.4	66.2 ± 11.23	38.9–96.3	33.8	25.7	54.7 ± 7.7	27.0–73.7	28.0	22.7	11.1
Water absorption (%)	101.7 ± 10.03	70.8–123.8	19.7	35.7	94.3 ± 8.92	66.1–108.7	18.9	20.5	103.6 ± 9.12	80.59–125.8	17.5	27.0	n.s. ^c
Seed coat fraction (%)	7.86 ± 0.432	5.0–10.1	10.9	1.5	7.52 ± 0.813	6.4–10.5	21.4	1.8	7.50 ± 0.441	6.16–8.43	11.1	1.3	n.s. ^c
Crude protein (%)	26.8 ± 0.62	25.0–30.3	4.6	2.2	26.1 ± 0.62	24.4–28.9	4.73	1.4	26.5 ± 0.92	24.35–30.57	7.0	2.7	n.s. ^c

^a For comparison of mean values of 67 genotypes.

^b For comparison among locations.

^c n.s.: not significant.

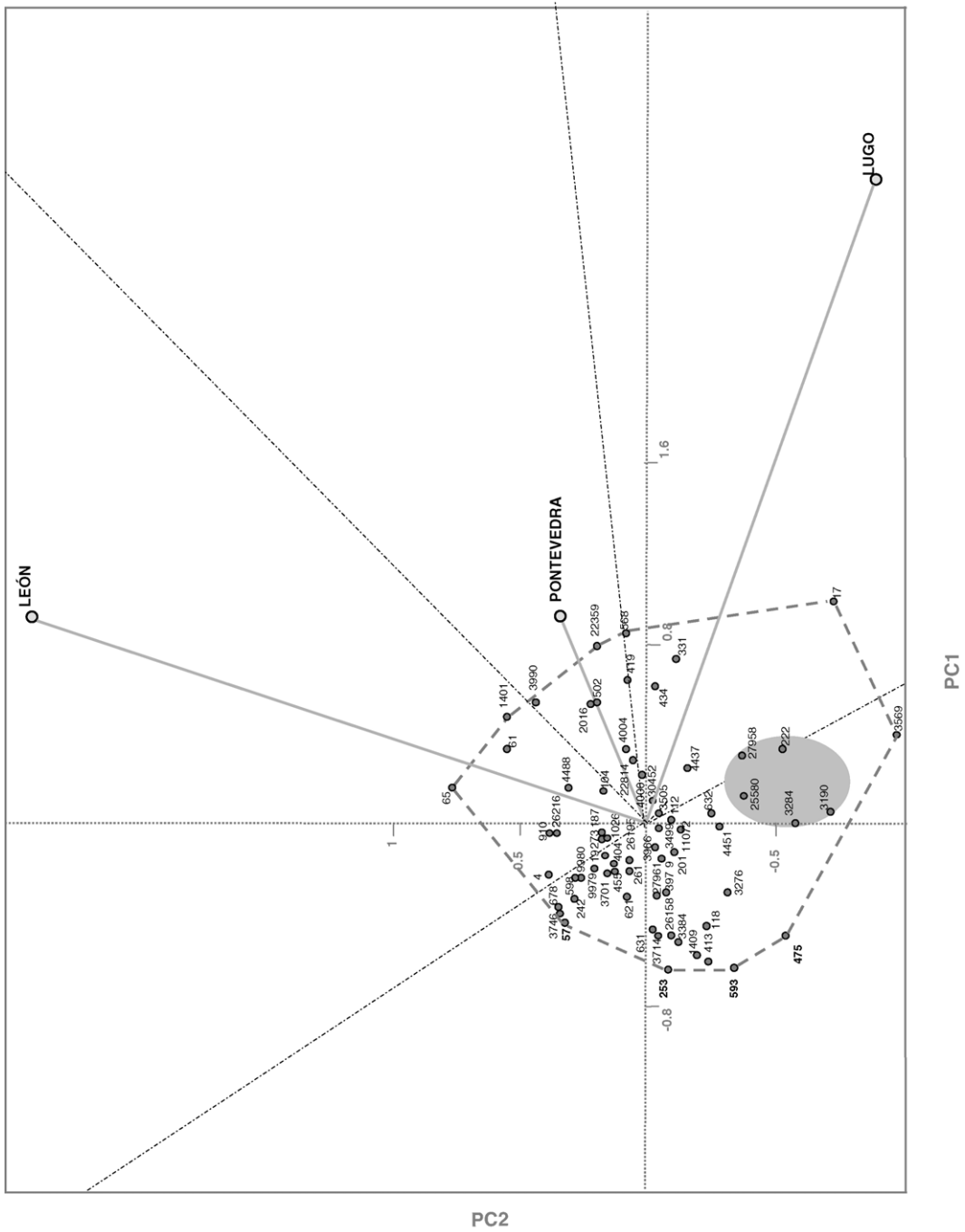


Fig. 1. GGEI biplot based on the yield data of 67 common bean genotypes grown at three locations in northwestern Spain, in 2001 and 2002. The genotype markers located away from the plot origin were connected with straight lines to form a polygon. Lines perpendicular to the side of the polygon are drawn. PC, principal component. The grey circle represents the group of the favada genotypes clustered and associated with the Lugo site.

Table 5

Computation of F_{GH2} statistics of the first (PC1), second (PC2) and third (PC3) principal components of seed yield in the GGEI study of 67 common bean genotypes grown at three locations in northwestern of Spain in 2001 and 2002

PC	λ^{2a}	% of G + GL	u^b	MS ^c	F_{GH2}^d	$P > F$
PC1	192.43	70.46	67	2.87	2.11	0.0000
PC2	57.94	21.21	65	0.89	0.65	0.9828
PC3	22.72	8.32	63	0.36	0.26	1.0000

^a λ^2 is the sum of squares owing to the PC tested.

^b u is the numerator of degrees of freedom for computing the mean square [$MS = (\lambda^2)/u$].

^c Mean square.

^d $F_{GH2} = (\lambda^2)/us^2$, where s^2 is the pooled error mean square.

it must simultaneously have a large negative interaction with some of the other locations. Since only PC1 was significant, the information presented by PC2 should be considered complementary to, or reinforced, those suggested by PC1. Pontevedra negatively interacted with genotypes 475, 413, 1409, 253 and 118, given the PC2 scores for these genotypes and this location had opposite signs. Lugo showed negative interactions with genotypes 57, 3746, 678, 242 and 4 (all these are colour seeded genotypes); while León negatively interacted with genotypes 3190, 475, 3284, 593 and 25580. Three of these genotypes (3190, 3284 and 25580) belong to the favada seeded type, so this market class did not seem to adjust well to León, where the best performers were great northern, white kidney, navy, bayo and cranberry market classes.

The performance of the best genotypes in each location is indicated by their position in each sector. The line perpendicular to the polygon side that connects genotypes 1401 and 22359 allows the comparison between León and Pontevedra sites. Genotypes such as 65, 61, 910, 26216 and 4488 fall in the León sector, and genotypes 22359, 502, 2016, 4004 and 22814 fall in the Pontevedra sector, whereas genotypes 1401, 3990 and 104 appear close to the line, indicating that these three genotypes produced similar yields in Pontevedra and León. In the Lugo sector, the genotypes giving rise to the highest yields were 17, 3569 and 331, those belonging to the favada market class (222, 3190, 27958, 3284 and 25580) and 4437, whereas 568, 419 and 434 performed well in Pontevedra and Lugo. The favada genotypes clustered and were associated with the location of Lugo, as revealed by the acute angles formed among their vectors.

3.3. GT biplot

The GT biplot (Fig. 2) was used to compare genotypes on the basis of multiple traits and to identify genotypes that are particularly desirable in terms of several traits. Provided that the biplot explained 95% of the total GT variation of the standardized data, so the main patterns among the traits seem to be captured by the biplot. The largest amount of genotype variation was explained by five traits such as seed coat fraction, water absorption, days to maturity, seed weight and crude protein, as indicated by the relative lengths of their vectors. The most outstanding relationships revealed by the biplot were: a low positive correlation between seed yield and days to first flower, a negative association between seed yield and days to maturity, and a lack of correlation between seed yield and seed weight. Seed yield, crude protein and coat fraction were positively related, and a strong negative association between seed yield and water absorption was found.

Similar to the analysis of the GGEI biplot, a polygon was drawn on the GT biplot. Selection on the basis of seed yield alone is the simplest and most efficient strategy of selection, but commercial seed traits should be also considered. Although the GT analysis was performed independently of the market groupings, the genotypes from the same market class plotted together. The following genotypes appeared as the best for commercial seed quality: 61 (bayo), 222 and 27958 (favada), 22359, 1401 and 568 (sangretoro), 419 and 4488 (large great northern), 331 and 434 (rounded caparron), 22814 (great northern), 4004 and 104 (large cranberry), 3499 (canellini), and 3505 and 187 (white kidney). Most of these genotypes were also identified as high-yielding in the GGEI biplot.

4. Discussion

The variation in yield was due mainly to the location effect, a common observation in multiple environment trials for most field crops (Van Eeuwijk et al., 1995; Kaya et al., 2002; Yan et al., 2002). This observation justifies the selection of SREG as the appropriate model for analysing METs data, and reveals that the sites were diverse, with large differences among location means causing most of the variation in seed yield. Therefore, three distinct dry

bean-producing areas were identified. Lugo was the best location for seed yield, as indicated by the relative length of its vector, whereas Pontevedra was the most representative of an average environment, due to the acute angle formed with the axis. León separated the genotypes clearly, because of the longest distance between its marker and the plot origin.

Different genotypes should be evaluated in the three environments to identify optimal adaptation of individual genotypes. Genotypes with a long duration of seed filling period have been favoured in Lugo site. Lugo is located on a fertile river valley, which helps to preserve moderate summer temperatures. The relatively mild climate at this location maintained adequate soil moisture and delayed the maturity, which caused a slower vegetative growth. Genotypes use a major water amount during the period after anthesis (Terán and Singh, 2002). Thus, the latest maturity genotypes, as those belonging to the favada market class, could be recommended in environments with mild summers. However, León favoured to the earliest to flowering genotypes corresponding to the great northern, sangretoro, navy, azufrado and bayo market classes. This region has a warm summer climate with a low rainfall during the whole growth cycle. Pontevedra showed the lowest seed yield average that could be attributed to plant yield losses at harvest due to a great amount of rainfall at that time (ranged from 47 to 390 mm) compared to Lugo (ranged from 70 to 245 mm) and León (ranged from 18 to 95 mm). Genotypes representing the sangretoro, large cranberry, and great northern market classes exhibited a good performance in this location.

The GGEI biplot may also be useful for selection according to yield stability. Genotypes corresponding to sangretoro, rounded caparron, negro brillante, and great northern market classes showed high and stable yield across all locations. However, genotypes denoted as hook (593), a heirloom variety traditionally grown in northeastern Spain, had a low average yield at each location, particularly when compared to the yield obtained by farmers in its area of origin (3800 kg ha^{-1}) (Bosch et al., 1998) where this market class has acquired a high market value due to its tenderness and buttery texture (Casañas et al., 1999). This low yield may be the result of the lack of adaptation of this market class to the environmental conditions of northwestern Spain.

Numerous external factors can affect productivity. Therefore, many traits may also have a potential advantage to yield. The GT biplot identified some traits favouring a high yield. The differences in productivity from one genotype to another could arise mainly during plant development because of a low positive correlation between days to first flower and seed yield and a negative association between days to maturity and seed yield. The latest to flowering genotypes will develop more branches, leading to a high seed yield as observed Rubio et al. (2004) in a study of white lupin.

Selection on the basis of seed yield alone is the simplest and most efficient strategy of selection, but commercial seed characteristics should be also considered. Positive relationship between a good commercial quality and high seed yield was noted in some genotypes, although the GT biplot also revealed that the genotypes showing the highest seed coat fraction were those with the highest yield and protein content. Thus, high-yielding genotypes belonging to the bayo, favada, sangretoro, great northern, rounded caparron, large cranberry, canellini and white kidney market classes exhibited the best commercial seed characteristics too (high seed weight and crude protein and low seed coat fraction). This finding is inconsistent with the results of other authors (Leleji et al., 1972; Kelly and Bliss, 1975; Polignano, 1982), who described a small negative correlation or non-association between yield and protein content (Avila et al., 1987). The seed coat contains the highest protein proportion of the whole seed (Singh et al., 1968), which explains the positive relationship between seed coat fraction and protein content observed. Moreover, seed coat fraction was negatively correlated with water absorption, because the highest thick seed coat genotypes were the slowest to take up water (Agbo et al., 1987; Elia et al., 1997). Despite several reports of a negative association between seed yield and weight (Redden et al., 1985; Singh, 1989; White and González, 1990), it has also been shown that the environment affects both traits, so the lack of correlation between seed yield and weight showed in these results is possible, and agrees with Avila et al. (1987).

The results showed that the GGE biplot provided an overall picture of the behaviour of the genotypes, the locations and GEIs, separating the three locations studied as different dry bean-producing areas. Each site has a set of optimally adapted genotypes. Interrelation-

ships among plant performance, seed quality and yield components were evidenced and those permitted to identify optimal genotypes for several traits. The high-yielding genotypes with a good commercial seed quality merit special attention, since they could have potential applications toward variety selection and to broaden the range of the diversity of cultivars for human consumption.

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References

- Agbo, G.N., Hosfield, G.L., Uebersax, M.A., Klomparens, K., 1987. Seed microstructure and its relationship to water uptake in isogenic lines and cultivar of dry beans (*Phaseolus vulgaris* L.) Food Microstruct. 6, 91–102.
- Avila, A., Zamora, A., Angulo, B., 1987. Correlación entre el contenido de proteína, el rendimiento y el volumen del grano en frijoles (*Phaseolus vulgaris* L.) del valle de Cochabamba. In: Instituto Italo-Americano, Investigación sobre el mejoramiento genético y cultural de trigo duro, girasol, maíz, frijol, lupino y haba en Bolivia. Roma, Fundación pro-Bolivia, Centro de Investigaciones Fitogenéticas de Pairumani, pp. 191–197.
- Baker, R.J., 1998. Tests for crossover genotype \times environment interactions. Can. J. Plant Sci. 68, 405–410.
- Boerma, H.R., Mian, M., 1998. Application of DNA markers for selection of intractable soybean traits. Korean Soybean Digest 15 (2), 106–121.
- Bosch, L., Casañas, F., Sanchez, E., Pujolá, M., Nuez, F., 1998. Selection L67, a pure line with true seed type of the Ganxet common bean (*Phaseolus vulgaris* L.) Hort. Sci. 33 (5), 905–906.
- Brancourt-Hulmel, M., Biarnes-Dumoulin, V., Denis, J.B., 1997. Points de repère dans l'analyse de la stabilité et de l'interaction génotype-milieu en amélioration des plantes. Agronomie 17, 219–246.
- Burgueño, J., Crossa, J., Vargas, M., 2001. SAS programs for graphing GE and GGE biplots. Biometrics and Statistics Unit, CIMMYT, Int. México.
- Casañas, F., Bosch, L., Pujola, M., Sánchez, E., Sorribas, X., Baldi, M., Nuez, F., 1999. Characteristics of a common bean landrace (*Phaseolus vulgaris* L.) of a great culinary value and selection of a commercial inbred line. J. Sci. Food Agric. 79, 693–698.
- Crossa, J., Cornelius, P.L., 1997. Sites regression and shifted multiplicative model clustering of cultivar trial sites under heterogeneity of error variances. Crop Sci. 37, 406–415.
- Cornelius, P.L., 1993. Statistical tests and retention of terms in the additive main effects and multiplicative interaction model for cultivar trials. Crop Sci. 33, 1186–1193.
- Crossa, J., 1990. Statistical analyses of multilocation trials. Adv. Agron. 44, 55–85.
- Elia, F.M., Hosfield, G.L., Kelly, J.D., Uebersax, M.A., 1997. Genetic analysis and interrelationships between traits for cooking time, water absorption and protein and tannin content of Andean dry beans. J. Am. Hort. Sci. 122, 512–518.
- Food and Agriculture Organization of the United Nations, 2002. FAO, vol. 56. Production Yearbook. Rome, Italy.
- Food and Agriculture Organization of the United Nations, 1974. Soil map of the world, scale 1:5,000,000, vols. I–X. United Nations Educational, Scientific, and Cultural Organization, Paris.
- Kang, M.S., 1988. Interactive BASIC program for calculating stability-variance parameters. Agron. J. 80, 153.
- Kaya, Y., Palta, Ç., Taner, S., 2002. Additive main effects and multiplicative interactions analysis of yield performance in bread wheat genotypes across environments. Turk. J. Agric. For. 26, 275–279.
- Kelly, J.D., Bliss, F.A., 1975. Quality affecting the nutritive value of bean seed proteins. Crop Sci. 15, 757–760.
- Leleji, O.I., Dickson, M.H., Crowder, L.V., Bourke, J.B., 1972. Inheritance of crude protein percentage and its correlation with seed yield in beans, *Phaseolus vulgaris* L. Crop Sci. 12, 168–171.
- Polignano, G.B., 1982. Breeding for protein percentage and seed weight in *Phaseolus vulgaris* L. J. Agric. 99, 191–197.
- Redden, R.J., Rose, J.L., Gallagher, E.C., 1985. The breeding of navy and culinary beans in Queensland. Aust. J. Exp. Agric. 25, 470–479.
- Rubio, J., Cubero, J.I., Martín, L.M., Suso, M.J., Flores, F., 2004. Biplot analysis of trait relations of white lupin in Spain. Euphytica 135 (2), 217–224.
- SAS Institute, 2000. The SAS System. SAS online Doc. HTML Format. Version eight. SAS Institute, Cary, NC, USA.
- Singh, S.P., 1989. Patterns of variation in cultivated common bean (*Phaseolus vulgaris*, Fabaceae). Econ. Bot. 43, 39–57.
- Singh, S.P., Singh, H.D., Sikka, K.C., 1968. Distribution of nutrients in the anatomical parts of common bean Indian pulse. Cereal Chem. 45, 13–18.
- Terán, H., Singh, S.P., 2002. Comparison of sources and lines selected for drought resistance in common bean. Crop Sci. 42 (1), 64–70.
- Van Eeuwijk, F.A., Keizer, L.C.P., Baker, J.J., 1995. Linear and bilinear models for the analysis of multi-environment trials: II. An application to data from the Dutch maize variety trials. Euphytica 84, 9–22.
- White, J.W., González, A., 1990. Characterization of the negative association between seed yield and seed size among genotypes of common bean. Field Crops Res. 23, 159–175.

- Yan, W., 1999. Methodology of cultivar evaluation based on yield trial data-with special reference to winter wheat in Ontario. Ph.D. diss. Univ of Guelph, ON, Canada.
- Yan, W., Wallace, D.H., 1995. Breeding for negatively associated traits. *Plant Breed. Rev.* 13, 141–177.
- Yan, W., Hunt, L.A., Sheng, Q., Slavnic, Z., 2000. Cultivar evaluation and mega-environment investigation based on the GGE biplot. *Crop Sci.* 40, 597–605.
- Yan, W., Cornelius, P.L., Crossa, J., Hunt, L.A., 2001. Two types of GGE biplots for analyzing multi-environment trial data. *Crop Sci.* 41, 656–663.
- Yan, W., Rajcan, I., 2002. Biplot evaluation of test sites and trait relations of soybean in Ontario. *Crop Sci.* 42, 11–20.
- Yan, W., Hunt, L.A., Johnson, P., Stewart, G., Lu, X., 2002. On farm strip trials vs. replicated performance trials for cultivar evaluation. *Crop Sci.* 42, 385–392.