

Novel Genetic Variation in Common Bean from the Iberian Peninsula

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ABSTRACT

The common bean (*Phaseolus vulgaris* L.) was introduced from the Americas into the Iberian Peninsula approximately 500 years ago. Considerable genetic variation for morphological traits, allozymes, phaseolin protein, and reaction to bacterial, fungal, and viral diseases exist in the germplasm. Our objective was to identify novel genetic variation in an collection from the Iberian Peninsula. Three hundred forty-seven accessions were characterized for seven morphological traits, phaseolin protein, and eight allozymes at the Misión Biológica de Galicia, Pontevedra, Spain, between 1998 and 2005. All 347 accessions were cultivated common bean of which 102 were typical Andean and 52 were Middle American, corresponding to the two major gene pools. Nine groups could be identified among the remaining 193 accessions. Twenty-eight accessions with the Middle American phaseolin formed four groups: 13 large (41 to 55 g 100 seed weight⁻¹), five very large (56 to 70 g 100 seed weight⁻¹), two extra-large (>70 g 100 seed weight⁻¹), and eight inter-gene pool recombinants. The latter had one or more morphological and allozyme traits of the Andean gene pool. Similarly, 165 accessions with the Andean phaseolin formed five groups: 19 extra-large, 30 very large, 80 medium (25 to 40 g 100 seed weight⁻¹), 10 small (<25 g 100 seed weight⁻¹), and 26 inter-gene pool recombinants. Seed yield potential and physiological, breeding, genetics, and evolutionary significance of these novel forms and recombinants need to be determined.

The common bean was domesticated in Mexico, Central America, and South America (Gepts and Debouck, 1991; Gepts et al., 1986). The non-centric origin (Harlan and de Wet, 1971), large variation in wild bean populations (i.e., the immediate ancestor of cultivars) along the distribution range (Gepts et al., 1986; Koenig and Gepts, 1989; Koenig et al., 1990; Tohme et al., 1996), edaphic and climatic factors, and the Native Americans that have inhabited the American continents over thousands of years contributed to a large genetic diversity among the domesticated common bean. Approximately 30,000 accessions of common bean are available in the germplasm bank at the Centro Internacional de Agricultura Tropical (CIAT), Cali, Colombia (Debouck, 1999) and elsewhere. Two distinct gene pools, namely Andean and Middle American are recognized in the wild (Koenig and Gepts, 1989; Koinange and Gepts, 1992) and cultivated bean (Evans, 1973). In addition to phaseolin seed protein, an evolutionary marker (Gepts, 1993; Gepts et al., 1986), morphological and agronomic traits (Singh et al., 1991c), allozymes (Singh et al., 1991b), molecular markers (Becerra-Velásquez and Gepts, 1994; Haley et al., 1994), and partial reproductive barriers (Gepts and Bliss, 1985; Singh and Gutiérrez, 1984) have been used to describe the two gene pools. In addition to these major gene pools, Debouck et al. (1993) reported some unique germplasm collected between Northern Peru and Colombia that did not conform to the two major gene pools.

Common bean was first introduced into the Iberian Peninsula (Spain and Portugal) around 1500 (Zeven, 1997), mainly from Mexico (small- and medium-seeded types often weighing $<40 \text{ g } 100 \text{ seed}^{-1}$), due to extensive commerce among Mexico, the Caribbean islands, and Spain. However, germplasm introductions from the Southern Andes, mainly Peru (often weighing $> 40 \text{ g } 100 \text{ seed}^{-1}$) that probably occurred after 1530 could have enhanced the genetic diversity in the Iberian Peninsula and Europe at large (Debouck and Smartt, 1995). Gepts and Bliss (1988) while tracing the dissemination pathways of common bean from the

Americas to Europe and Africa evidenced that germplasm of the Iberian Peninsula originated in a different region in Latin America than the rest of the European germplasm.

There is considerable diversity in common bean germplasm from the Iberian Peninsula. Puerta-Romero (1961) described the Spanish common bean landraces. In addition, Gil and De Ron (1992), Escribano et al. (1998), Rodiño et al. (2001, 2003), and Santalla et al. (2002) described the range and patterns of variation in germplasm accessions from the Iberian Peninsula. They used morphological and agronomic traits, phaseolin protein, and allozymes, and grouped accessions in different market classes (Santalla et al., 2001) according to Voyses and Dessert (1991), the Andean and Middle American gene pools, and their affiliations with the races described by Singh et al. (1991a) in the Americas. Furthermore, Rodiño et al. (2003) formed a core collection to facilitate germplasm evaluation and utilization. The objective of this research was to identify novel variation in the common bean germplasm from the Iberian Peninsula, using highly heritable and ancestral morphological traits, allozymes, and phaseolin protein.

MATERIALS AND METHODS

Three hundred forty-seven of 729 common bean accessions from the Iberian Peninsula maintained at the Misión Biológica de Galicia-CSIC, Pontevedra and forming the integral part of the national collection maintained in Madrid, Spain were characterized for morphological traits, allozymes, and phaseolin seed protein. Accessions were divided in three sets, one set grown at a time in the field at Pontevedra (42 °N 8 °W latitude, 40 m elevation, 14 °C average temperature, and 1,600 mm annual rainfall) in 1998, 1999, and 2003. ‘ICA Pijao’ (Middle American) and Dark Red Kidney (Andean) were used as common checks. The experimental design was a hill-plot, with 8 plants plot⁻¹, spaced 1 m between plots, thus a density of 80,000 plants ha⁻¹. Growth habit (determinate Type I and indeterminate Types II, III, and IV) was recorded during flowering and verified at pod maturity according to Singh (1982). The shape of the central leaflet of the fully-developed trifoliolate leaf (cordate, lanceolate, or ovate), leaf hairiness (sparse or dense), shape of flower bracteole (cordate, lanceolate, or ovate), presence or absence of the stripes on the outer base of flower standard (stripped or smooth), and seed weight (g 100 seed weight⁻¹) were recorded as described by Singh et al. (1991a). The seed coat color and market classes were recorded according to Santalla et al. (2001) and Voysest and Dessert (1991).

A small sample from cotyledons of five seeds for each accession was taken for phaseolin determination using one-dimensional sodium dodecyl sulphate polyacrylamide gel electrophoresis (SDS-PAGE), according to Brown et al. (1981) and Gepts et al. (1986). Leaf or root tissues (depending on the allozyme assayed) from 12 plants were used at the primary leaf stage for allozyme analysis according to Wendel and Weeden (1989) and Santalla et al. (2002). The enzyme systems assayed were: malic enzyme (*Me*), shikimate dehydrogenase (*Skdh*), ribulose biphosphate carboxylase (*Rbcs*), peroxidase (*Prx*), malate dehydrogenase (*Mdh*), and diaphorase (*Diap*) (Koenig and Gepts, 1989; Vallejos, 1983). In each gel, the

controls were ICA-Pijao and Dark Red Kidney which had the following allozyme alleles: *Rbcs*¹⁰⁰, *Skdh*¹⁰³, *Prx*⁹⁸, *Me*¹⁰⁰, *Mdh-1*¹⁰⁰, *Mdh-2*¹⁰⁰, *Diap-1*⁹⁵, and *Diap-2*¹⁰⁵ and *Rbcs*⁹⁸, *Skdh*¹⁰⁰, *Prx*⁹⁸, *Me*⁹⁸, *Mdh-1*¹⁰³, *Mdh-2*¹⁰², *Diap-1*¹⁰⁰, and *Diap-2*¹⁰⁰, respectively. Accessions were classified into Andean and Middle American gene pools primarily based on their phaseolin type. Morphological and allozyme data were used in conjunction with phaseolin for multivariate analysis (Santalla et al., 2002) and to form a core collection (Rodiño et al., 2003).

RESULTS AND DISCUSSION

Large variation for each of the seven morphological traits and phaseolin were observed among 347 accessions of common bean from the Iberian Peninsula (Table 1; Rodiño et al., 2003). Of eight allozyme systems, alleles *Diap-2*¹⁰⁰ and *Prx*⁹⁸ were monomorphic (Singh et al., 1991b). Indeterminate aggressive climbing growth habit Type IV was the most common (54.1 %) followed by determinate Type I (23.5%). Farmers in the northern Iberian Peninsula, characterized by semi-humid and humid, and relatively long frost-free growing season, often intercrop bean and maize (*Zea mays* L). The maize stalk serves as an inexpensive support for the climbing bean and feed for animal. The bean-maize intercropping system is typical of traditional production regions of Latin America such as humid and semi-humid highlands and southern Mexico, Central America, and Andean highlands. In contrast, in Central Spain (e.g., Castilla & Leon), the largest bean production region, Type I cultivars grown in monoculture predominate.

Frequency of accessions with ovate leaflet shape, sparse short leaf hair, lanceolate bracteole, smooth (i.e., absence of stripes at the outer base of flower standard), and large (41 to 55 g 100 seed weight⁻¹), very large (56 to 70 g 100 seed weight⁻¹), and extra large (>70 g 100 seed weight⁻¹) white seed were high. Similarly, accessions with Andean phaseolin protein (i.e., T, C, H) and allozyme alleles *Skdh*¹⁰⁰, *Me*¹⁰⁰, *Rbc*¹⁰⁰, *Mdh-1*¹⁰⁰, and *Mdh-2*¹⁰⁰ were in higher frequency than their counterparts. Thus, 77% accessions possessed principal characteristics of the Andean and 23% of the Middle American gene pool (Gepts et al, 1986; Singh et al., 1991a, b, c). Gepts and Bliss (1988), Gil and De Ron (1992), and Ocampo et al. (2005) also reported similar results for bean germplasm from the Iberian Peninsula. Nonetheless, upon close examination the following sub-groups or novel types within the Middle American and the Andean gene pool were identified.

Middle American Extreme Types. Of 20 novel accessions with S or B phaseolin, 13 had large (41 to 55 g 100 seed weight⁻¹), five very large (56 to 70 g 100 seed weight⁻¹), and two extra large (>70 g 100 seed weight⁻¹) seed (Tables 2 and 3). The three groups had leaflet, bracteole, flower, and allozyme characteristics typical of the Middle American gene pool. Furthermore, all were white seeded similar to the flattened great northern market class in the U.S.A. (which often are of growth habit Type III and weigh 25 to 40 g 100 seed⁻¹) with predominance of strong climbing growth habit Type IV.

Andean Extreme Types. While this group comprising 123 accessions possessed the typical Andean phaseolin protein (i.e., T, C, H), allozymes, leaf, bracteole, and flower characters, on the basis of seed weight, they formed three sub-groups: 10 small-seeded, 80 medium-seeded, 30 very large, and 19 extra large-seeded. There was considerable variation for growth habit and seed coat color and shape within the small- and medium-seeded groups. But all very large and extra large-seeded accessions had white seed and growth habit Type IV.

Recombinants between the Andean and Middle American Gene Pools. Accessions that possessed phaseolin typical of one gene pool and one or more morphological and allozyme traits of the other gene pool were classified as inter-gene pool recombinants. Thus, there were eight accessions that had Middle American phaseolin protein (i.e., S, B) but also had some allozyme alleles and morphological traits that were more typical of the Andean gene pool. Similarly, 26 accessions possessed the Andean phaseolin (i.e., T, C, H) and one or more allozyme alleles and morphological traits common in the Middle American gene pool. Both groups were variable for seed weight, seed color and shape, and growth habit. But, in these recombinants also, all very large and extra large-seeded accessions had white seed and growth habit Type IV.

It is worth noting that some accessions in the novel groups were variable for one or more characters (Table 3). Similarly, few accessions in the typical Andean and Middle

American gene pool were also variable (Rodiño et al., 2003). Furthermore, from the above observations and results summarized in Tables 1, 2, and 3 and Figure 1, it should be evident that considerable variation exists in common bean from the Iberian Peninsula despite the fact that the zone is relatively small and was represented by only 347 of 729 accessions in the national collection.

Introduction from the American continents into the Iberian Peninsula of common bean and other field crops, fruits, flowers, and vegetables very likely was not systematic. Also, although no specific records were kept as to the region of origin and types of bean, both Andean and Middle American germplasm were introduced. However, either a much larger proportion of large-seeded Andean germplasm was introduced and/or they were preferred by the farmers and consumers in the region and possessed selective advantage over the Middle American bean. Prior to the discovery of the Americas large-seeded faba bean (*Vicia faba* L.) was cultivated in the Iberian Peninsula. In fact, the names "faba" for the dry and "haba" for green or snap bean are commonly used in northern Spain. Because consumers were accustomed to eating large faba bean selection for large, very large, and extra large common bean might have been practiced from the early on. In addition, long frost-free humid and semi-humid growing environment would have favored full-season climbing genotypes that took advantage of maize stalks and required longer flowering and seed-filling periods. Furthermore, consumer preference for a milder flavor and clear broth would have worked against the adoption of richly colored bean such as black, dark red, brown, etc. Thus, the combined effects of favorable environments and strong consumer preference for nearly 500 years resulted in very large and extra large white seeded bean of especially flattened "Planchada" or "Ganxet" (PHA-0414), kidney or "Riñón" (PHA-0400), and cylindrical or "Faba" (PHA-0926) and "Alubia" (PHA-0574) shapes. These market classes are highly sought-after for special cuisines (e.g., fabada) and often fetch the highest price (ranging from

\$5 to >20 U.S. dollar kg⁻¹) among edible grains, legumes, fruits, and vegetables in the Iberian Peninsula and surroundings. In contrast, in the centers of origin and domestication in Mexico, Central America, and the Andean South America, white bean is not very popular. Small-seeded bush Type I navy bean (introduced from the U.S.A.) is grown in monoculture in few countries (e.g., Panama, Chile, and coastal Ecuador and Peru) and large and very large round seeded climbing “Caballeros” landraces are grown in the Peruvian highlands (above 2000 m elevation). Only Argentina has large (60,000 to 80,000 ha) monoculture production of Alubia (or cultivars of similar cylindrical shape), a bush growth habit Type I landrace introduced by the Spanish settlers. The majority of Argentine production is exported to Spain and other countries. Thus, in contrast to the Iberian Peninsula, genetic variation for large, very large, and extra large seeded white bean in Latin America may be limited.

Of 34 accessions that were classified as the recombinants, eight had the Middle American and 26 Andean phaseolin that was approximately proportional to the overall representation of the two gene pools in an germplasm collection of Iberian Peninsula. The recombinant accessions with the Middle American S or B phaseolin, allozyme alleles *Diap-I*⁹⁵ and *Skdh*¹⁰³, cordate leaflet with sparse and short hairs, and stripped standard combined the Andean allozyme alleles *Skdh*¹⁰⁰ and *Diap-I*¹⁰⁰ and lanceolate flower bracteole. These had mainly Type II or Type IV growth habit. Accessions PHA-0047, PHA-0065, PHA-0107, PHA-0414, PHA-0430, and PHA-0598 were small or medium-seeded, and PHA-0589 and PHA-0593 were large-seeded. Twenty-six recombinant accessions (e.g., PHA-0122, PHA-0157, PHA-0213, PHA-0481, PHA-0493, PHA-0497, PHA-0501, PHA-0554, PHA-0917, PHA-0923) with the Andean phaseolin (C, H, or T), lanceolate flower bracteole, and dense and long leaf hairs had the Middle American cordate leaflet, stripped base of flower standard, and allozyme alleles *Skdh*¹⁰³ and/or *Diap-I*⁹⁵. These had predominantly Type I or IV growth habit and large, very large, or extra large seed of favada, marrow, white kidney, cranberry,

bolon bayo, and red pinto market classes. However, some were also small (e.g., PHA-0122, chicho) or medium-seeded (PHA-0481, alavesa). Some wild and cultivated common bean from the northern Peru, Ecuador, and Colombia are known to possess characteristics of the two gene pools (Debouck et al., 1993; Islam et al., 2002; Koenig and Gepts, 1989). Johns et al. (1997) thought these to be as an unusual group of germplasm. Furthermore, Paredes and Gepts (1995) reported evidence of introgression between the Middle American and Andean (Chilean) germplasm, using phaseolin protein and allozyme markers. As noted earlier, the fact that some accessions (including a few in Table 3) were mixtures of two or more variants for one or more traits (Rodiño et al., 2001, 2003) the role of out-crossing, albeit often small (0.74%) in adapted common bean in the Iberian Peninsula (Ferreira et al., 2000), cannot be ruled out. It is very unlikely that a wide range of germplasm introduced from the Americas was equally adapted in its new habitat in the Iberian Peninsula. In fact, a great majority of tropical and sub-tropical germplasm is highly sensitive to long (>14 hr) summer days at higher latitudes in Europe, Canada, and U.S.A., hence poorly adapted (Singh, 2001). It is common that some accessions do not flower, where as in other accessions flower may remain open for a longer period due to infertile pollen thus stay prone to out-crossing by visiting insects. Cultivation of a mixture of Andean and Middle American beans in close proximity in home gardens combined with occasional out-crossing may have further facilitated introgression between the two gene pools. Ibarra-Pérez et al. (1997) reported exceptionally high rates of out-crossing in some common bean cultivars in California.

While occurrence of a relatively higher frequency of large, very large, and extra large white Andean, Middle American, and the recombinants between the two gene pools could be explained, why were the small- and medium-seeded Andean extreme types and recombinant accessions still maintained in the Iberian Peninsula is not well understood. In common bean, seed weight is negatively correlated with seed yield (White et al., 1992). Furthermore, Park et

al. (2000) found an association between quantitative trait loci (QTL) for seed weight and the phaseolin (*Phs*) locus on the linkage group B7. As noted earlier, the small- and medium-seeded Middle American germplasm possess B or S phaseolin and the large-seeded Andean bean T, C, or H phaseolin (Gepts et al., 1986; Koenig et al., 1990; Singh et al., 1991a). Because some small- and medium-seeded germplasm from the Iberian Peninsula possessed Andean phaseolin, would these be as high yielding as their Middle American counterparts is not known. Similarly, would the negative association between seed yield and seed weight also hold in large, very large, and extra large accessions that possessed the Middle American phaseolin, is not known. Therefore, breeding, genetics, and evolutionary significance of the novel and recombinant accessions would be worthwhile to determine.

The genetic divergence and partial reproductive barriers (Gepts and Bliss, 1985; Mumba and Galway, 1999; Singh and Gutiérrez, 1984; Singh and Molina, 1996) between the Andean and Middle American gene pools for millennia have led to development and accumulation of favorable alleles, QTL, and their epistatic interactions imparting harmonious morpho-physiological development, growth, and higher seed yield within each gene pool (Johnson and Gepts, 1999, 2002). Hybridization between the gene pools breaks these linkages and interactions, resulting in poor agronomic performance such that often it is not possible to recover even the Andean and Middle American parental genotypes from single-crosses (Welsh et al., 1995). Could these novel extreme forms and recombinants serve as a bridging-parent to facilitate inter-gene pool transfer of favorable alleles and QTL is also not known. Promising inter-gene pool crosses will facilitate a strategic deployment and pyramiding of favorable alleles and QTL from both gene pools for higher levels and more stable resistance to a much broader range of highly variable pathogens such as *Colletotrichum lindemuthianum* (Sacc. & Magn.) Bri. & Cav. (the cause of anthracnose) and *Uromyces appendiculatus* (Pers.) Ung. (causing rust) that coevolved with the common bean (Balardin and Kelly, 1998; Pastor-

Corrales et al., 1995; Stavely et al., 1997). Such inter-gene pool and interracial crosses will also facilitate broadening the genetic base of cultivars and maximizing gains from selection for plant type, adaptation, yield, and resistance to high and low temperature, drought, and low soil fertility (Singh, 2001).

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Figure 1. Seed characteristics of some common bean accessions of the typical Andean and Middle American and novel extreme types and recombinants between the two gene pools from the Iberian Peninsula evaluated at Pontevedra, Spain between 1998 and 2005. (The left and right scales represent 6x5 mm).



Table 1. Variation for growth habit, leaflet shape and hair, bracteole shape, presence or absence of stripes at the outer base of flower standard, seed weight and color, phaseolin, and alleles at allozyme loci *Skdh*, *Me*, *Rbc*, *Diap-1*, *Diap-2*, *Prx*, *Mdh-1*, *Mdh-2* in 347 common bean accessions from the Iberian Peninsula evaluated at Pontevedra, Spain between 1998 and 2005.

Trait	Proportion (%)	Trait	Proportion (%)
Growth habit†		Phaseolin	
I	23.5	T	30.3
II	18.8	C	11.1
III	3.6	H	26.9
IV	54.1	S	22.3
		B	9.4
Shape of terminal leaflet		Allozymes‡	
Cordate	16.4	<i>Skdh</i> ¹⁰³	26.6
Ovate	66.1	<i>Skdh</i> ¹⁰⁰	73.4
Lanceolate	17.5		
Straight leaf hairs		<i>Me</i> ¹⁰²	7.2
Short, sparse	63.0	<i>Me</i> ¹⁰⁰	71.8
Long, dense	37.0	<i>Me</i> ⁹⁸	21.0
Shape of bracteole		<i>Rbc</i> ¹⁰²	6.6
Cordate	29.3	<i>Rbc</i> ¹⁰⁰	65.3
Ovate	17.7	<i>Rbc</i> ⁹⁸	28.1
Lanceolate	53.0		
Outer base of flower standard		<i>Diap-1</i> ¹⁰⁰	55.6
Striped	11.0	<i>Diap-1</i> ⁹⁵	44.4
Smooth	89.0		
Seed weight		<i>Mdh-1</i> ¹⁰³	5.6
Small (<25 g 100 seed weight ⁻¹)	8.2	<i>Mdh-1</i> ¹⁰⁰	89.9
Medium (25-40 g 100 seed weight ⁻¹)	36.9	<i>Mdh-1</i> ⁹⁸	4.5
Large (41-55 g 100 seed weight ⁻¹)	37.2		
Very large (56-70 g 100 seed weight ⁻¹)	10.9	<i>Mdh-2</i> ¹⁰²	1.7
Extra large (>70 g 100 seed weight ⁻¹)	6.8	<i>Mdh-2</i> ¹⁰⁰	98.3
Seed color			
White	43.8		
Bicolor	4.8		
Cream	16.4		
Yellow	6.1		
Brown	6.1		
Red	15.1		
Black	7.7		

† Growth habit Type I= determinate erect, II=indeterminate erect, III=indeterminate semi-climber, and IV=indeterminate strong climber.

‡ Allozyme loci *Diap-2* and *Prx* were monomorphic in all 347 common bean accessions.

Table 2. Classification of 347 common bean accessions from the Iberian Peninsula based on morphological traits, phaseolin, and allozymes evaluated at Pontevedra, Spain between 1998 and 2005.

Class	Number of accessions
Middle American (phaseolin S or B)	80
Typical (≤ 40 g 100 seed weight ⁻¹)	52
Large (41 to 55 g 100 seed weight ⁻¹)	13
Very large (56 to 70 g 100 seed weight ⁻¹)	5
Extra large (> 70 g 100 seed weight ⁻¹)	2
Recombinant	8
Andean (phaseolin T, C or H)	267
Typical (41 to 55 g 100 seed weight ⁻¹)	102
Small (< 25 g 100 seed weight ⁻¹)	10
Medium (25 to 40 g 100 seed weight ⁻¹)	80
Very large (56 to 70 g 100 seed weight ⁻¹)	30
Extra large (> 70 g 100 seed weight ⁻¹)	19
Recombinant	26
Total	347

Table 3. Phaseolin, allozymes, seed weight and color, leaflet shape and hair, bracteole shape, presence or absence of stripes at the outer base of flower standard, growth habit, and market class of representative Middle American, Andean, and novel types of common bean accessions from the Iberian Peninsula evaluated at Pontevedra, Spain between 1998 and 2005.

Accession†	Phaseolin	Allozyme		Seed weight (g 100 seeds ¹⁾		Seed color	Leaflet shape		Leaf hair		Bracteole shape		Flower standard		Growth habit‡	Market class
		M	A	M	A		M	A	M	A	M	A				
PHA-0151 M typical	S	<i>Skdh</i> ¹⁰³ , <i>Diap-1</i> ⁹⁵		36.6		White	Cordate		Short		Ovate		Striped		IV	Planchada
PHA-0071 M large	S	<i>Skdh</i> ¹⁰³ , <i>Diap-1</i> ⁹⁵			49.8	White	Cordate		Short		Cordate		Striped		IV	Planchada
PHA-0419 M extra large	S	<i>Skdh</i> ¹⁰³ , <i>Diap-1</i> ⁹⁵			75.0	White	Cordate		Short		Cordate		Striped		IV	Planchada
PHA-0414 M recombinant	S		<i>Skdh</i> ¹⁰⁰ , <i>Diap-1</i> ¹⁰⁰	35.1		Yellow	Cordate		Short		Lanceolate		Smooth		I	Chicho amarillo
PHA-0430§ M recombinant	S	<i>Diap-1</i> ⁹⁵ , <i>Me</i> ⁹⁸	<i>Skdh</i> ¹⁰⁰	28.6		White	Ovate		Short		Lanceolate		Smooth		IV	Pocha
PHA-0589§ M recombinant	B	<i>Diap-1</i> ⁹⁵	<i>Skdh</i> ¹⁰⁰	43.9		White	Cordate		Short		Cordate		Smooth		I	Arrocina
PHA-0593§ M recombinant	S	<i>Skdh</i> ¹⁰³	<i>Diap-1</i> ¹⁰⁰	44.7		White	Ovate		Short		Lanceolate		Striped		IV	Ganxet
PHA-0400 A typical	C		<i>Skdh</i> ¹⁰⁰ , <i>Diap-1</i> ¹⁰⁰	47.4		White	Ovate		Long		Lanceolate		Smooth		IV	Blanca riñon
PHA-0475 A small	H		<i>Skdh</i> ¹⁰⁰ , <i>Diap-1</i> ¹⁰⁰	21.2		Yellow	Ovate		Long		Lanceolate		Smooth		IV	Roxina
PHA-0574 A medium	T		<i>Skdh</i> ¹⁰⁰ , <i>Diap-1</i> ¹⁰⁰	36.8		White	Ovate		Long		Lanceolate		Smooth		I	Alubia
PHA-0926 A extra large	T		<i>Skdh</i> ¹⁰⁰ , <i>Diap-1</i> ¹⁰⁰	108.0		White	Ovate		Long		Lanceolate		Smooth		IV	Faba
PHA-0122 A recombinant	C	<i>Skdh</i> ¹⁰³ , <i>Diap-1</i> ⁹⁵		23.2		Cream	Ovate		Short		Cordate		Smooth		I	Chicho

Table 3. Continued.

Accession	Phaseolin	Allozyme†		Seed weight (g 100 seeds ⁻¹)		Seed color	Leaflet shape		Leaf hair		Bracteole shape		Flower standard		Growth habit‡	Market class
		M	A	M	A		M	A	M	A	M	A				
PHA-0481 A recombinant	H	<i>Diap-I</i> ⁹⁵ , <i>Me</i> ⁹⁸	<i>Skdh</i> ¹⁰⁰	33.3		Red	Ovate	Short		Ovate		Striped		II	Alavesa	
PHA-0497 A recombinant	C	<i>Skdh</i> ¹⁰³ , <i>M</i> ₁₀₂	<i>Skdh</i> ¹⁰⁰ , <i>Diap-I</i> ¹⁰⁰ , <i>Me</i> ¹⁰⁰	44.5		White	Cordate	Short		Cordate		Smooth		II	Blanca redonda	
PHA-0501§ A recombinant	H	<i>Skdh</i> ¹⁰³	<i>Skdh</i> ¹⁰⁰ , <i>Diap-I</i> ¹⁰⁰	45.7		Black	Ovate	Long		Lanceolate		Striped		IV	Tolosana	
PHA-0554§ A recombinant	T	<i>Skdh</i> ¹⁰³	<i>Diap-I</i> ¹⁰⁰	50.4		White	Cordate	Short		Cordate		Smooth		I	Alubia	
PHA-0923 A recombinant	T	<i>Diap-I</i> ⁹⁵	<i>Skdh</i> ¹⁰⁰	98.0		White	Cordate	Long		Lanceolate		Smooth		IV	Faba	

† M= Middle American, and A=Andean.

‡ Growth habit Type I= determinate erect, II=indeterminate erect, III=indeterminate semi-climber, and IV=indeterminate strong climber.

§ Variable for leaflet and/or bracteole shape.