Genetic Diversity in Cultivated Common Bean: II. Marker-Based Analysis of Morphological and Agronomic Traits

Shree P. Singh, J. A. Gutiérrez, A. Molina, C. Urrea, and P. Gepts*

ABSTRACT

Knowledge of patterns of genetic diversity enhances the efficiency of germplasm conservation and improvement. This study examined the organization of diversity for morphological and agronomic characteristics in 306 landraces of cultivated common bean (*Phaseolus vulgaris* L.) from Latin America and its relationship with phaseolin seed protein and allozyme diversity of the landraces. Data on pigmentation, growth habit, and leaflet, pod, seed, and phenology traits, as well as reaction to four important diseases and an insect pest, obtained from field evaluations at three locations in Colombia during the 1987–1988 cropping season, were analyzed by multivariate statistical analyses. In addition, these same 306 landraces were characterized by electrophoresis for phaseolin seed protein and nine allozymes. Results permitted separation of these landraces into Mesoamerican and Andean groups, confirming prior phaseolin and allozyme data. A marker-based multivariate analysis, using phaseolin or allozymes as an initial classification criterion, followed by a corroborating analysis of morpho-agronomic traits, suggested the existence of subgroups within each of the major Andean and Mesoamerican groups, with distinctive morphology, adaptation, and disease resistances. Molecular analyses in conjunction with morphological and agronomic evaluations of gene bank accessions are recommended, because these provide complementary information and increase the resolving power of genetic diversity analyses.

CULTIVATED COMMON BEAN is a morphologically diverse crop (Hedrick, 1931). Strikingly large variations are found for growth habit, pigmentation, pod, seed, phenology, and other characters (Leakey, 1988; Singh, 1989; Vanderborght, 1986). This diversity reflects the wide range of ecological and human environments under which the crop has evolved over millennia. In spite of the importance of these traits, the organization of their genetic diversity is poorly understood.

Study of patterns of variation for phaseolin seed protein (Gepts and Bliss, 1985; Gepts et al., 1986) and allozymes (Koenig and Gepts, 1989; Singh et al., 1991) has revealed the existence of two major groups, a Mesoamerican and an Andean, within common bean germplasm. Attempts have been made to suggest subdivisions within the Mesoamerican and Andean germplasm. Evans (1976) and Vanderborght (1986) proposed classifications relying primarily on growth habit. Singh et al. (1989) identified three races within each of the Mesoamerican and Andean groups, and Singh (1988, 1989) proposed the existence of 12 gene pools in dry bean on the basis of growth habit and seed, morphological, and adaptational traits.

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Multivariate statistical methods have been used previously to analyze patterns of genetic diversity. For example, Polignano and Spagnoletti-Zeuli (1985) examined variation of 10 morphological and agronomic traits in Mediterranean populations of *Vicia faba* L. with canonical discriminant and factor analyses. They were able to distinguish populations of different geographic origins within the Mediterranean basin, and they identified the specific traits responsible for the differences among them. In common bean, Vanderborght (1986) analyzed the morphological diversity of Mesoamerican and Andean germplasm using cluster analysis and principal component analysis.

Our objectives were to study patterns of diversity for morphological and agronomic traits in cultivated common bean and their relationship with patterns of diversity for phaseolin seed protein and allozymes.

MATERIALS AND METHODS

Plant Materials

Our sample consisted of 306 cultivated accessions from Latin America obtained from the International Center for Tropical Agriculture (CIAT), Cali, Colombia. To the best of our knowledge, all accessions were landraces as defined by Gepts et al. (1986). Seventy-two accessions originated in Mexico, 10 in Guatemala, 2 in Nicaragua, 5 in El Salvador, 1 in Honduras, 2 in Costa Rica, 2 in the Dominican Republic, 97 in Colombia, 44 in Ecuador, 31 in Peru, 17 in Chile, 1 each in Bolivia and Argentina, and 21 from Brazil. Seeds of all accessions used in this study originated from CIAT.

Morphological and Agronomic Traits

All 306 landraces were grown at two CIAT farms, Palmira (1000 m above sea level; mean growing temperature, 24 °C) and Popayán (1750 m above sea level; mean growing temperature, 18 °C), Colombia, in the 1987–1988 cropping season. Plots consisted of single 3-m rows spaced 60 cm apart. Within-row spacing was about 10 cm between plants. Plots were kept free from weeds, diseases, and insects throughout the growing season. Soil fertility and moisture conditions were adequate for normal crop growth at both locations. Five plants, surrounded by other plants in the row, under full competition were used for observations in each plot. Data were recorded on hypocotyl and flower color, days to flower and maturity, growth habit, length of fifth internode (cm), number of nodes to first flower, length and width of the central leaflet of the fifth trifoliolate leaf (cm), dry seed length and height (mm), seed shininess, 100-seed weight (g), and seed yield (g/plant).

Separate complementary nurseries were grown at Popayán for observation of the reaction to anthracnose (*Colletotrichum lindemuthianum* [Sacc. & Magn.] Scrib.), and at Santander de Quilichao (990 m above sea level; mean temperature, 24 °C) for reaction to common bacterial blight (*Xanthomonas campestris* pv. *phaseoli* [Smith] Dye) and angular leaf spot (*Phaeoisariopsis griseola* [Sacc.] Ferraris). Nurseries were inoculated with a mixture of local strains 35, 45, and 55 d after planting. Reaction to leafhoppers (*Empoasca kraemeri* Ross & Moore) was observed in a nursery established during the dry season in Palmira. The presence of the dominant *I* gene for resistance to bean common mosaic virus (BCMV) was verified in glasshouse inoculations of 7 to 10-d-old seedlings with the NL3 strain. Data on all these diseases and the insect damage were taken on a 1 to 9 scale (1 = immune and 9 = very susceptible) according to Van Schoonhoven and Pastor Corrales (1987).

Phaseolin Seed Protein

A small sample from cotyledons of a single seed of each landrace was taken for phaseolin determination using one-dimensional sodium dodecylsulfate–polyacrylamide gel electrophoresis (SDS–PAGE) as described by Brown et al. (1981). Details of these results have been reported elsewhere (Koenig et al., 1990).

Allozymes

Five individuals per accession were analyzed. The primary leaf or root apex tissue (depending on the enzymes assayed) of 10-d-old seedlings was utilized for preparation of crude homogenate. Paper wicks, dipped in homogenate, were then used for starch gel electrophoresis following the procedures of Weeden (1984). Nine polymorphic enzyme systems were assayed. The most common allele was designated as 100 and all other allozymes were measured in millimeters from the standard. Details of these allozyme diversity analyses are reported elsewhere (Singh et al., 1991).

Statistical Analysis

The SAS UNIVARIATE procedure (PLOT option) from SAS Institute (1985) was performed to test for normality. All variables approximate normality with the exception of hypocotyl and flower color, growth habit, seed shininess, number of nodes to first flower, and reaction to bean common mosaic virus, leafhoppers, common bacterial blight, anthracnose, and angular leaf spot. The first four represent categorical data, whereas the last five had highly skewed distributions. Analyses performed with the non-normal variables led, however, to results and conclusions similar to those of analyses performed without those variables. Results presented here come from analyses including all variables. In order to avoid effects due to scaling differences, variables were standardized to zero mean and unit variance using the SAS procedure STANDARD (SAS Institute, 1985).

Three types of multivariate analyses were performed, using SAS Institute (1985) programs. A principal component analysis was performed on the standardized variables listed in Table 1 using PROC PRINCOMP. Subsequently, a discriminant analysis was carried out with PROC DISCRIM. The initial classification criterion used was either the phaseolin type (Gepts and Bliss, 1985; Gepts et al., 1986; Koenig et al., 1990) or allozyme cluster membership (Singh et al., 1991). Posterior probabilities of membership were calculated using the same procedure. The contribution of each variable to the classification was estimated by calculating standardized discriminant coefficients (Afifi and Clark, 1984). Finally, a canonical discriminant analysis was performed using PROC CANDISC with phaseolin type or allozyme cluster membership as an initial classification criterion.

Univariate analyses of variance with PROC GLM (SAS Institute, 1985) were performed in order to identify those variables that distinguish the allozyme cluster groups within the Andean cultigens. Duncan's multiple range test was used to identify differences between means.

RESULTS

Morphological Differences between Mesoamerican and Andean Cultivated Genotypes

Principal component analysis showed that Mesoamerican and Andean cultigens (i.e., cultivated genotypes) had a distinct morphology and that the Mesoamerican group was morphologically more diverse than its Andean counterpart (Fig. 1). The first three principal components accounted for 24, 10, and 9%, respectively, of total variation. The traits respon-

sible for separation along the first principal component included (with loadings in parentheses) the fifth internode length (0.23), seed length (0.23), seed height (0.22), 100-seed weight (0.24), and number of seeds (−0.21). Traits affecting separation along the second principal component included growth habit (−0.23), days to flower (0.21), nodes to first flower (0.21), leaflet length (0.32), leaflet width (0.33), and number of pods per plant (−0.20). Along the third principal component, accessions were separated according to days to maturity (0.28) and number of nodes to first flower (0.33). In order to further examine the differences between Mesoamerican and Andean cultigens, a discriminant analysis was conducted using phaseolin type as a classification criterion. Landraces with Type S, Sd, Sb, and B phaseolin were classified as Mesoamerican, while landraces with Type T, C, and H phaseolin were classified as Andean (Gepts and Bliss, 1986; Gepts et al., 1986; Koenig et al., 1990; Koenig and Gepts, 1989). The variables that had the strongest effect on the discriminant function included length of fifth internode, node to first flower, leaflet length, leaflet width, seed length, seed height, and seed yield. Posterior probabilities of membership indicated that classification of landraces into the Mesoamerican or the Andean group corresponded in >96% of the cases with the classification into these same groups based on morpho-agronomic traits.

Landraces whose phaseolin and morphological classifications did not match included 'de Celaya' (Mexico), 'Mantequilla' (Mexico), Boyacá 17A (Colombia), and Cundinamarca 137 (Colombia) all of which had a Mesoamerican phaseolin but an Andean morphology. Conversely, landraces 'Burrito de Enrame' (PI 152313 from Ecuador), Antioquia 6 (Colombia), and Cauca 11 (Colombia) exhibited an Andean phaseolin and a Mesoamerican morphology. Most of these landraces originated from the Colombia–Ecuador area, which was hypothesized earlier to be a meeting place of the Mesoamerican and Andean germplasms (Gepts and Bliss, 1986).

A canonical discriminant analysis using phaseolin type as a classification criterion further confirmed the separation of the two groups of cultigens. The traits responsible for the separation of the two groups were similar to those identified by principal component analysis.

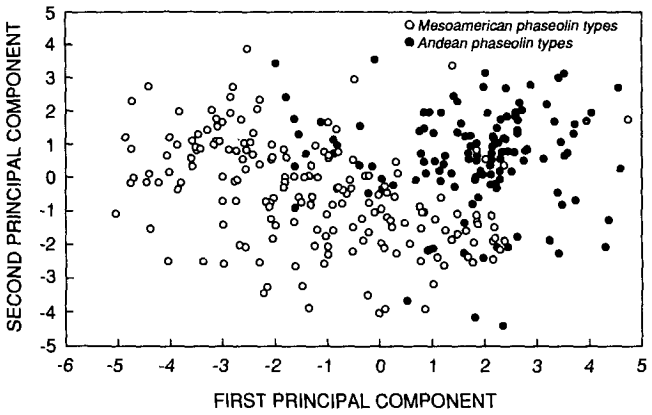

Fig. 1. Principal component analysis of diversity for morphological and agronomic traits in cultivated common bean.

Identification of Subgroups within Mesoamerican and Andean Cultivated Genotypes

In a next stage, we examined whether the large Andean and Mesoamerican groups could be further divided into subgroups consisting of related landraces. Using principal component analysis, which attempts to identify distinct groups independently of any prior classification criterion, it was not possible to identify distinct subgroups within the Mesoamerican or Andean cultigens. The situation was improved when discriminant analysis or canonical discriminant analysis were used, both of which rely on prior classification criteria. However, we will focus only on the results obtained by canonical discriminant analysis, because this method provides a graphic output illustrating the existence of morphological groups. We used both phaseolin and allozymes as initial classification criteria.

Phaseolin

Using phaseolin as a classification criterion, canonical discriminant analysis allowed us to distinguish groups of cultigens with a common phaseolin type on the basis of their morphology. Because Andean cultivars were better adapted to the Popayán conditions, results from the Popayán nursery included fewer missing data compared to the Palmira nursery. Data from the former nursery will, therefore, be presented here. Among Mesoamerican cultigens, landraces with phaseolin Type B or an Sd could be distinguished from those with Type S or Sb phaseolin (Fig. 2). The canonical correlations corresponding to the first two axes ($r = 0.58$ and $r = 0.54$, respectively) were significantly different from zero ($P < 0.01$). Traits that separated groups along the first canonical variable included days to flowering and maturity, number of nodes to first flower, leaflet size, and seed yield (Table 1). Along the second canonical variable, groups were separated ac-

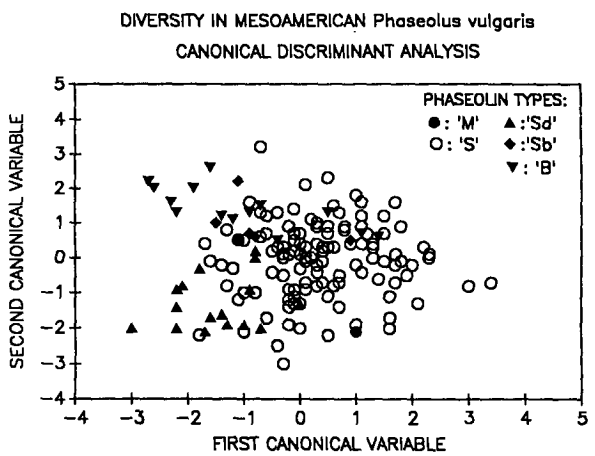

Fig. 2. Canonical discriminant analysis of diversity for morphological and agronomic traits of Mesoamerican cultivated genotypes of common bean using phaseolin type as an initial classification criterion.

Table 1. Correlation coefficients between original and canonical variables in a canonical discriminant analysis of cultivated common beans from Latin America using phaseolin as a classification criterion.

Trait	Mesoamerican landraces		Andean landraces	
	FCV†	SCV	FCV	SCV
	r			
Hypocotyl color	−0.62	0.52	0.78	0.63
Flower color	−0.08	0.83	−1.00	0.10
Days to flowering	0.87	0.39	1.00	0.06
Days to maturity	0.95	−0.05	0.89	−0.45
Fifth internode length	−0.51	−0.86	0.92	0.39
Number of nodes to first flower	0.90	−0.04	−0.91	−0.42
Leaflet length	0.85	0.44	1.00	0.07
Leaflet width	0.75	0.52	0.98	0.21
Seed length	0.03	−0.94	−0.70	0.71
Seed height	0.02	−0.98	0.58	0.05
Seed shininess	0.30	0.55	−0.15	0.99
100-seed weight	0.06	−0.96	0.93	0.38
Yield/plant	0.96	−0.20	0.60	0.80

† FCV and SCV = first and second canonical variables, respectively.

cording to flower color, fifth internode length, and seed size (Table 1).

Among Andean cultivars, landraces with 'T' phaseolin were morphologically distinct from those with 'C' or 'H' phaseolin type (Fig. 3). The canonical correlations of the first and second canonical variables ($r = 0.60$ and $r = 0.47$, respectively) were significantly at the $P < 0.01$ and $P < 0.05$ levels, respectively. The group of Type T phaseolin cultivars is characterized by a predominance of the *Mdh-1*^{100} allele (Table 2 and Singh et al., 1991). Compared to the next two groups, it has less strongly pigmented hypocotyls but more strongly pigmented flowers, it flowers and matures earlier, exhibits a more bushy growth habit (often Type I, as described by Singh, 1982), exhibits relatively smaller and more elongated leaflets, and has elongated seeds (Table 1). This group includes a high proportion of landraces from the northern Andes (Colombia and Ecuador), such as 'Algarrobo', 'Estrada Rosado', 'Sangretoro', 'Mortiñito', and 'Canario Alargado'. There are some notable exceptions to this general pattern, in particular with regard to growth habit. This group includes a proportion of cultigens with

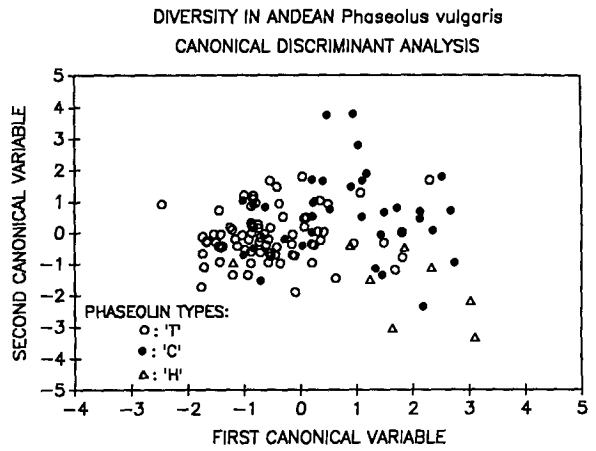

Fig. 3. Canonical discriminant analysis of diversity for morphological and agronomic traits of Andean cultivated genotypes of common bean using phaseolin type as an initial classification criterion.

Table 2. Distribution of phaseolin types among allozyme groups of cultivated common bean from Latin America.

Phaseolin type†	Allozyme groups‡								
	A	B	C	D	E	F	G	H	I
M	1	0	0	0	0	0	0	0	0
S	42	13	4	10	3	0	1	0	1
Sd	4	9	1	0	0	0	0	0	0
Sb	0	0	2	0	1	0	0	0	0
B	3	1	0	0	0	0	0	0	0
T	0	0	0	0	0	4	40	3	14
C	1	0	0	0	0	3	9	3	16
H	1	0	0	0	0	0	1	0	5

† After Koenig et al., 1990.
‡ After Singh et al., 1991.

either Growth Habit IV (e.g., 'Cargamanto', 'Calabozo', 'Radical'), often originating in the high altitude regions of the Andes, or Growth Habit III, originating mostly in the southern Andes (e.g., 'Coscorrón', 'Burrito', 'Frutilla Corriente', and 'Jalo'). The Growth Habit I cultivars of this group may correspond to the race 'Nueva Granada' of Singh et al. (1989). The Growth Habit III cultivars may fall within the race 'Chile' proposed by the same authors.

The Type C and H phaseolin cultivars are characterized by a high frequency of the *Mdh-1*^{103} allele (Table 2 and Singh et al., 1991). Morphologically, these cultivars exhibit many alternate traits from the preceding group, i.e., weaker pigmentation, late maturity, a stronger climbing tendency, larger and more obovate leaflets, and larger and more rounded seeds. Furthermore, landraces possessing Type C phaseolin can be distinguished from those with Type H phaseolin by their higher levels of seed shininess, their less elongated leaflets, longer seeds, and higher yield (Table 1). This group of Type C and H cultivars appears to correspond to the race 'Peru' of Singh et al. (1989).

Allozymes

Canonical correlation analysis was conducted using observations of the Popayán and Palmira nurseries. Because results of the two nurseries were similar, only the correlation coefficients between the original Popayán variables and the canonical variables are pre-

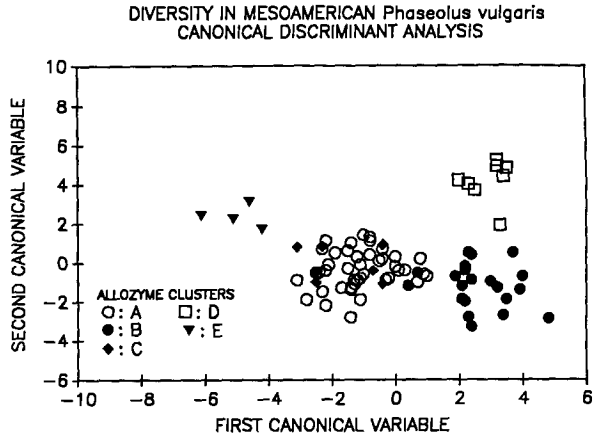

Fig. 4. Canonical discriminant analysis of diversity for morphological and agronomic traits of Mesoamerican accessions of cultivated common bean using allozyme groups as an initial classification criterion.

Table 3. Correlation coefficients between original and canonical variables in a canonical discriminant analysis of cultivated common bean from Mesoamerica using allozyme cluster membership as a classification criterion.

Trait	FCV†	SCV
	r	
Hypocotyl color	−0.97	0.00
Flower color	−0.93	−0.05
Days to flowering	−0.75	0.55
Days to maturity	0.13	0.95
Fifth internode length	0.79	0.10
Number of nodes to first flower	−0.77	0.24
Leaflet length	−0.27	0.91
Leaflet width	−0.24	0.89
Seed length	0.80	−0.08
Seed height	0.89	0.03
Seed shininess	0.65	0.32
100 seed weight	0.92	0.15
Yield/plant	0.33	0.86
Leafhoppers	0.48	−0.07
Bean common mosaic virus	0.84	−0.19
Common bacterial blight	0.40	0.70
Anthracnose	−0.79	−0.30
Angular leaf spot	−0.86	0.50

† FCV and SCV = first and second canonical variables, respectively.

sented. When canonical discriminant analysis was applied using individual isozyme loci as a classification criterion such as *Me* and *Mdh-1* that differentiate genotypes within the Mesoamerican and Andean gene pools, respectively (Singh et al., 1991), it was not possible to distinguish morphologically distinct groups. However, when the entire array of nine isozyme loci were used (Singh et al., 1991), a different picture emerged. The clusters of Mesoamerican cultigens with similar allozymes exhibited similar morphology, phenology, adaptation, and disease resistance (Fig. 4 and Table 3). The canonical correlation of the first axis ($r = 0.91$) was significantly different from zero ($P < 0.01$) and the canonical correlation of the second axis ($r = 0.85$) was nearly so ($P = 0.07$). Together, these two axes account for 73% of the total variation. The original variables that contributed most to the separation along the first canonical variable included hypocotyl and flower color, days to flowering, growth habit, fifth internode length, number of nodes to first flower, seed size, and reaction to BCMV, anthracnose, and angular leaf spot (Table 3). Along the second canonical variable, groups were separated according to days to maturity, leaflet length and width, and seed yield (Table 3).

The first canonical variable separated principally the E, C, A, and B clusters (in increasing order of their mean along this axis). A first major group, exhibiting the Me^{98} allele (Allozyme Group C) or allele $Diap\text{-}2^{105}$ (Allozyme Group E) and a high frequency of 'Sb' phaseolin (Table 2), contrasted with Allozyme Group B for many traits. It exhibited darker hypocotyl and flower pigmentation, later flowering, generally Growth Habit II, a shorter fifth internode, flowering at higher nodes, larger leaflets but smaller seeds, and increased incidence of resistance to BCMV and susceptibility to anthracnose. This group originates in the humid lowlands of Mexico, Central America, and Brazil and comprises tropical blacks and the mulatinhos, including landraces such as 'Rio Tibagi', 'Negro Argel', 'Pata de Zope', 'Rabia de Gato', and 'Porrillo Sintético'. These landraces correspond to race Mesoamerica of Singh et al. (1989). Compared to Cluster E, members of Cluster C flower earlier, have longer pods and seeds, have fewer seeds per plant, and exhibit a lower frequency of BCMV resistance.

A second major group is characterized by allele Me^{102} (Allozyme Group B) and a high frequency of Type Sd phaseolin (Table 3). It exhibits (compared to other Mesoamerican groups) reduced hypocotyl and flower pigmentation, Growth Habits III or IV, a longer fifth internode, flowering starting on lower nodes, earlier flowering, smaller leaflets, larger seeds,and a higher incidence of susceptibility to BCMV and resistance to anthracnose. Members of this group originate in the arid highlands of central and northern Mexico and include landraces such as 'Pinto', 'Bayo Río Grande', 'Durango 222', 'G 2618', 'Garbancillo Zarco', and 'Garrapato' (all from Mexico). This group corresponds to the race 'Durango' suggested by Singh et al. (1989).

The third group, characterized by the Me^{100} allele (Allozyme Groups A and D) and a high frequency of the Type S phaseolin (Table 2, with exceptions noted below), is a more heterogeneous group. Its core appears to consist of landraces with either Type III or Type IV growth habits and small- to medium-sized seeds. Most members originate in the humid highlands of Mexico, Central America, and the northern Andes. Landraces represented in this group include 'Flor de Mayo', 'Azufrado', 'Canario', 'Apetito', 'Conejo', and 'Cacahuate Criollo'. This group may correspond to the race Jalisco proposed by Singh et al. (1989) It could be further subdivided on the basis of additional markers such as Type B phaseolin (humid highlands of Central America and Colombia; Koenig et al., 1990) or $Mdh\text{-}2^{102}$ (Allozyme Group D; see below). Possible hybridizations with other groups is suggested by the presence of some landraces such as 'Pinto Texano' and 'Bayo' (Group B) and 'Carioca', 'Rim de Porco', and 'Mulatinho de Irece' (Groups C or E).

Allozyme Group D is separated from other groups along the second canonical variable. It consists of small- to medium-seeded landraces of growth habit IV originating in the humid highlands of Mexico, such as 'Charrito', 'Rosa de Castilla', 'Colorado de Teopisca', and 'Naranja Coral'. Compared to cultivars of other allozyme groups, cultivars in this group are later, have larger leaflets and a higher seed yield per plant. This group is characterized by the presence of the $Mdh\text{-}2^{102}$ allele (Singh et al., 1991). This allele was observed only in some wild *P. vulgaris* populations from Mexico (Koenig and Gepts, 1989), suggesting that Group D represents cases of introgression from wild common beans.

Canonical discriminant analysis of morphological and agronomic traits distinguishing Andean allozyme groups did not reveal a canonical correlation that was significantly different from zero. However, analyses of variance revealed some significant differences among the various groups. A comparison between Groups G and I, which contain a large number of landraces, reveals that those of Group G tend to have a bush (as opposed to climbing) growth habit, tend to have rel-

atively smaller and more elongated leaflets, and have more elongated seeds, when compared to landraces of Group I.

DISCUSSION

Results from the three methods of multivariate analyses consistently identified fifth internode length, number of nodes to first flower, leaflet size, and seed weight as major traits separating cultigens of Andean and Mesoamerican origin. The Andean germplasm possessed a higher number of nodes to first flower, and larger leaflets and seeds than Mesoamerican germplasm. Our results confirm those obtained previously by Gepts et al. (1986), Gepts and Bliss (1986), and Sprecher and Isleib (1989). In addition, further subdivisions within the Mesoamerican and Andean groups were possible. The identification of these groups of cultivars is made possible by the existence of strong associations between the traits considered in this study. Such associations can arise through multilocus genetic associations or developmental correlations. The former are favored by the predominantly autogamous reproductive system of common bean and by geographical (e.g., Mesoamerican vs. Andean) and ecological (e.g., arid highlands vs. humid lowlands in Mesoamerica) isolations. The latter are exemplified by the relationships between yield and its components.

The approach we have followed to identify subgroups or races within Mesoamerican and Andean germplasm marks a departure from the traditional way of analyzing genetic diversity in cultivated common bean, which relied exclusively on morphological traits (Evans, 1976; Hidalgo, 1988; Vanderborght, 1986). Our approach relied on a prior classification of cultigens using molecular markers (phaseolin and isozymes), followed by a corroborating analysis of morphological and agronomic traits. This strategy was first used to determine that common bean cultivars of Andean origin, on the average, had larger seeds than Mesoamerican common bean cultivars (Gepts et al., 1986). More recently, a preliminary report outlines morphological differences, as detected by principal component analysis, in Malawian common bean cultivars of Mesoamerican and Andean origin, as determined by allozyme analysis (Sprecher and Isleib, 1989). The importance of the prior (molecular classification is twofold. First, molecular markers are more useful than morpho-agronomic traits in determining the genetic relationships among accessions. Because morpho-agronomic traits are phenotypic traits, accessions may be similar morphologically, yet be distant genetically. For example, molecular markers show that Growth Habit I cultivars had two independent origins, one in Mesoamerica and the other in the Andes. Second, the complex genetic control of many of the morpho-agronomic traits often precludes the determination of the precise genotype underlying each phenotype. The complexity is caused by the number of genes involved, the presence of pleiotropy and epistasis, and environmental influence. Because molecular markers are mostly devoid of these disadvantages, several authors (e.g., Tanksley, 1983) have argued in favor of marker-based selection in breeding programs. By analogy, we show here that a marker-based classification of genetic diversity is an informative approach towards our understanding of the genetic structure of a species.

The amount of information provided by this marker-based approach will depend on the type and number of markers, and their linkage relationships. Phaseolin type may be more useful in this respect than any individual allozyme because of its molecular complexity (Gepts, 1990). Two accessions may show the same allozyme because of common ancestry, independent mutation, or recombination. On the other hand, the molecular complexity of phaseolin makes it unlikely that the same phaseolin type would have appeared repeatedly through independent mutation. With either type of marker, the availability of several markers, preferably unlinked, may increase the power of the analysis because it would detect recombination. In common bean grown in Latin America, the importance or recombination especially between the Mesoamerican and Andean gene pool is probably minor because of the self-pollinating nature of the species, the geographic isolation of the two gene pools, and their reproductive isolation (Gepts and Bliss, 1985).

Finally, our analysis also reveals that within the allozyme groups, considerable morphological variation can exist with respect to growth habit and seed type, in spite of the uniformity at the allozyme level. Crosses may be attempted between two genotypes which, based on morphological arguments, may appear to be very diverse in order to maximize the potential gain from selection in the progeny. Our phaseolin and allozyme data indicate that in some cases these crosses may involve materials that are actually genetically closely related. Conversely, genotypes with similar morphological traits may be evolutionarily distant (within the primary gene pool) as exemplified by the existence of Growth Habit I cultivars in both the Mesoamerican and Andean gene pools. The benefit of molecular markers is that they characterize accessions at the genotypic level and allow us to evaluate evolutionary relationships and levels of genetic divergence more accurately than morphological markers. It is suggested here that gene banks should integrate morphological, agronomical, and biochemical and molecular evaluations of their genetic resources because the different types of traits provide complementary information.

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REFERENCES

Afifi, A.A., and V. Clark. 1984. Computer-aided multivariate analysis. Van Nostrand Reinhold, New York.

Brown, J.W.S., and Y. Ma, F.A. Bliss, and T.C. Hall. 1981. Genetic variation in the subunits of globulin-1 storage protein of French bean. Theor. Appl. Genet. 59:83–88.

Evans, A. 1976. Beans. p. 168–172. *In* N.W. Simmonds (ed.) Evolution of crop plants. Longman, London.

Gepts, P. 1990. Biochemical evidence bearing on the domestication

of *Phaseolus* (Fabaceae) beans. Econ. Bot. 44 (3 Suppl.):28–38.
Gepts, P., and F.A. Bliss. 1985. F_1 hybrid weakness in the common bean: Differential geographic origin suggests two gene pools in cultivated bean germplasm. J. Hered. 76:447–450.
Gepts, P., and F.A. Bliss. 1986. Phaseolin variability among wild and cultivated common beans from Colombia. Econ. Bot. 40:469–478.
Gepts, P., T.C. Osborn, K. Rashka, and F.A. Bliss. 1986. Electrophoretic analysis of phaseolin protein variability in wild forms and landraces of the common bean, *Phaseolus vulgaris*: Evidence for multiple centers of domestication. Econ. Bot. 40:451–468.
Hedrick, U.P. 1931. The vegetables of New York: The beans of New York. New York (Geneva) Agric. Exp. Stn. Rep. 1(2):1–110.
Hidalgo, R. 1988. The *Phaseolus* world collection. p. 67–90. *In* P. Gepts (ed.) Genetic resources of *Phaseolus* beans. Kluwer, Dordrecht, the Netherlands.
Koenig, R., and P. Gepts. 1989 Allozyme diversity in wild *Phaseolus vulgaris*: Further evidence for two major centers of genetic diversity. Theor. Appl. Genet. 44:809–817.
Koenig, R., S.P. Singh, and P. Gepts. 1990. Novel phaseolin types in wild and cultivated common bean (*Phaseolus vulgaris*, Fabaceae). Econ. Bot. 44:50–60.
Leakey, C.L.A. 1988. Genotypic and phenotypic markers in common bean. p. 245–327. *In* P. Gepts (ed.) Genetic resources of *Phaseolus* beans. Kluwer, Dordrecht, the Netherlands.
Polignano, G.B., and P.L. Spagnoletti-Zeuli. 1985. Variation and covariation in *Vicia faba* L. populations of Mediterranean origins. Euphytica 34:659–668.
SAS Institute. 1985. SAS user's guide: Statistics. 5th ed. SAS Institute, Cary, NC.
Singh, S.P. 1982. A key for identification of different growth habits of *Phaseolus vulgaris* L. Annu. Rep. Bean Improv. Coop. 25:92–95.
Singh, S.P. 1988. Gene pools in cultivated dry bean. Annu. Rep. Bean Improv. Coop. 31:180–182.
Singh, S.P. 1989. Patterns of variation in cultivated common bean (*Phaseolus vulgaris*, Fabaceae). Econ. Bot. 43:39–57.
Singh, S.P., D.G. Debouck, and P. Gepts. 1989. Races of common bean, *Phaseolus vulgaris* L. p. 75–89. *In* S. Beebe (ed.) Current topics in breeding of common bean. Working document 47. Bean Program, CIAT, Cali, Colombia.
Singh, S.P., R. Nodari, and P. Gepts. 1991. Genetic diversity in cultivated common bean: I. Allozymes. Crop Sci. 31:19–23 (this issue).
Sprecher, S.L., and T.G. Isleib. 1989. Morphological and phenological diversity between bean gene pools. Annu. Rep. Bean Improv. Coop. 32:54–55.
Tanksley, S.D. 1983. Molecular markers in plant breeding. Plant Mol. Biol. Rep. 1:3–8.
Vanderborght, T. 1986. L'étude de la variabilité chez le haricot commun (*Phaseolus vulgaris* L.) par l'utilisation de méthodes statistiques multivariées appliquées à une banque de données. Ph.D. diss. Fac. des Sci. Agron., Gembloux, Belgium (Diss. Abstr. 47:3190B–3191B).
Van Schoonhoven, A., and M.A. Pastor Corrales. 1987. Standard system for the evaluation of bean germplasm. CIAT, Cali, Colombia.
Weeden, N.F. 1984. Linkage between the gene coding the small subunit of ribulose bisphosphate carboxylase and the gene coding malic enzyme in *Phaseolus vulgaris*. Annu. Rep. Bean Improv. Coop. 27:123–124.