

PLANT GENETIC RESOURCES

Diversity and Origin of Andean Landraces of Common Bean

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ABSTRACT

Landraces of common bean (*Phaseolus vulgaris* L.) pertaining to the Andean gene pool are remarkably diverse in plant and grain morphology and agroecological adaptation. The objectives of this study were to determine the genetic structure of a large sample of Andean landraces, and to establish a correspondence between Andean landraces and wild bean populations that might have served as the source of domesticated bean. A total of 182 landraces representing the three recognized races of Andean bean and including many popping bean types were analyzed using amplified fragment length polymorphism (AFLP) technology with multiple correspondence analysis (MCA) and unweighted pair group method with arithmetic mean (UPGMA). Twenty-nine wild bean accessions representing the diversity of wild bean in South America and Middle America were also included. Two sets of primers were used to generate 189 polymorphic AFLP. The graph of the results of MCA indicated that most landrace accessions formed a single undifferentiated group, and analysis by UPGMA combined with bootstrapping confirmed this. A small number of outliers presented bands that suggested introgression from Mesoamerican beans. Among wild bean populations from South America, those from Bolivia graphed in closest proximity to the cultivated bean, suggesting that Bolivia might have been an important primary domestication site. The narrow genetic base of Andean beans emphasizes the need to broaden the genetic base of the Andean gene pool.

THE COMMON BEAN is the most important grain legume for direct human consumption in the world (CIAT, 1993). The wild ancestor of the cultivated bean is an annual climbing vine that prospers at mid-altitudes (1500–2000 m above sea level) in forest clearings or disturbed environments from northern Mexico to northern Argentina (Toro et al., 1990). The genetic resources of wild bean consist of two major gene pools, one Mesoamerican and one Andean, and one or two minor gene pools in the northern Andes (Koenig and Gepts, 1989). AFLP analysis revealed that wild bean populations in the Andean zone have probably been isolated from each other, resulting in rather discrete populations in Ecuador and northern Peru, in southern Peru, in Bolivia, and in northern Argentina (Tohme et al., 1996). Another population in Colombia probably presents ample introgression from several sources.

The genetic structure of common bean landraces reflects the structure of the wild bean. Two major gene pools exist (Gepts, 1988a) that are distinguished by phaseolin seed protein (Gepts, 1988b), plant morphology (Singh et al., 1991b), isozymes (Singh et al., 1991c)

and DNA markers (Nodari et al., 1992). Phaseolin and isozymes of the cultivated beans correspond to the same morphotypes as found in the wild beans from the same area (Gepts, 1988b; Koenig et al., 1990). These facts suggest that two or more domestication events in distinct wild populations contributed to the formation of gene pools of cultivated bean.

It has been suggested that major cultivated gene pools can be subdivided into races. Mesoamerican beans were classified into three races on the basis of morphology and ecological adaptation (Singh et al., 1991a). DNA analysis with random amplified polymorphic DNA (RAPD) markers confirmed the existence of these three races, demonstrated the existence of sub-races, and indicated the existence of still another race among the climbing beans of Guatemala and neighboring countries (Beebe et al., 2000). The Andean gene pool was likewise subdivided into three races on the basis of morphological and ecological criteria (Singh et al., 1991a). Race Nueva Granada (N) represents the medium-to-large seeded accessions of bush growth habits, and includes the majority of the commercial large seeded cultivars in use today. Its name indicates a possible origin in the northern Andes. Race N is the most widely cultivated Andean race, and is grown at both mid-altitudes of the Andes and Africa; in warm lowland environments of Brazil, Mexico and the Caribbean; and in temperate climates of North America and Europe. Race Peru (P) consists of Andean climbing beans, most of which are adapted to highland environments above 2,000 m above sea level. Race Chile (C) is typical of landraces of Chile and is characterized by prostrate type 3 growth habit, medium-sized, rounded to oval seed, and usually pale colors. Race C is often found at higher latitudes in Turkey, Iran, and China as well.

Although Andean cultivated bean has been classified into three races on the basis of growth habit and adaptation regime, by other criteria Andean landraces appear to be even more diverse. For example, Andean beans present diverse phaseolin seed proteins, and include the popping beans (or ñuñas), which are thought to be ancient, pre-ceramic landraces (Tohme et al., 1995). Therefore, the elucidation of the genetic structure and origin of Andean landraces deserves additional study. The objectives of this study were (i) to determine genetic structure of Andean landrace germplasm using AFLP markers, and (ii) to establish correspondence between

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Abbreviations: AFLP: amplified fragment length polymorphism; CIAT: Centro Internacional de Agricultura Tropical; MCA: multiple correspondence analysis; RAPD: random amplified polymorphic DNA; UPGMA: unweighted pair group method with arithmetic mean.

Andean landraces and wild populations that might have served as the source of the domesticated bean.

MATERIALS AND METHODS

One hundred eighty-two landraces originating in the Andean countries and secondary centers of diversity were selected from the CIAT (Centro Internacional de Agricultura Tropical) bean core collection (Tohme et al., 1994). Briefly, the core was selected on the basis of an agroecological classification of sites of origin (on the basis of estimated rainfall, temperature, day length at flowering, and soil type) to capture the broadest possible range in genetic adaptation to these environmental variables. Within agroecological classes, a stratified sample was practiced to maximize variability in seed color and size within the four bean growth habits. A study of molecular markers in the core and reserve accessions of Mexican origin indicated that the core was a faithful representation of the reserve collection (Skroch et al., 1998). In this study, a subsample was made to represent the range of variability in the core with respect to seed types, growth habits, and country of origin (Table 1). Representation by country was as follows: Argentina, 10; Bolivia, 12; Burundi, 1; Brazil, 5; Chile, 10; Colombia, 21; Cuba, 1; Dominican Republic, 1; Ecuador, 19; Haiti, 1; Mexico, 2; Malawi, 1; Peru, 91; Portugal, 1; Spain, 2; former Soviet Union, 1; Turkey, 1; and United States, 2. The vast majority of accessions originated from Colombia, Ecuador, Peru, Bolivia, and Argentina. The geographic origins of these accessions are plotted on a map of the Andean countries (Fig. 1). Growth habits 1, 2, 3 (all bush types), and climbing types habit 4 (Schoonhoven and Pastor-Corrales, 1987) were represented by 25, 5, 33, and 119 accessions, respectively. Race Peru was especially well represented, including at least 44 *fiuña* beans from Peru, to permit studying these unusual types in greater detail. Race Chile was represented by six growth habit 3 landraces from Chile and another similar accession from Turkey. Most of the remaining accessions would be classed as race Nueva Granada on the basis of morphological criteria. One Mesoamerican check cultivar, ICA Pijao, was included for comparison. Six of the Andean landraces (G8706, G7317, G19842, G23703, G23874, and G23773C) were duplicated in the laboratory analysis to verify the degree of repeatability of the AFLP technique.

A previous study with AFLP analysis of a wild bean core collection with 114 accessions had identified one gene pool in Middle America and three gene pools in South America; one in Colombia, a second in Ecuador and northern Peru, and a third in the central and southern Andes (Tohme et al., 1996). This latter pool in turn could be sub-divided into three groups, centered in south-central Peru, in Bolivia, and in Argentina. Twenty-seven wild bean accessions were chosen to represent gene pools and groups on the basis of previous results: Mexico (3) and Guatemala (1), Colombia (3), Ecuador (2) and northern Peru (2), south-central Peru (9), Bolivia (6), and Argentina (1) (Table 1). Twenty-two of these accessions had been included in the previous study and thus gave us confidence that they represented the broad variability of wild common bean. Additional wild beans were included to strengthen the representation of Bolivia. Wild beans were analyzed with landraces to determine wild accessions with the greatest similarity to cultivated bean.

DNA was extracted and AFLP analysis was performed as per Tohme et al. (1996), using primer combinations that had proven to reveal ample polymorphism. AFLP were read as present or absent, and the resulting data matrix including both wild and landrace accessions was analyzed by MCA (SAS, 1989). MCA is a multivariate technique similar to principal components analysis, but in which the distance between indi-



Fig. 1. Geographic distribution of wild and cultivated accessions drawn from the Andean countries of Colombia, Ecuador, Peru, Bolivia and Argentina, and included in an analysis by amplified fragment length polymorphism. Squares represent wild accessions and triangles represent landraces.

viduals is calculated from a chi-squared metric involving a weighting factor that considers the quantity of information of each individual and each band (Hair et al., 1992). Data of the cultivated landraces were also used to calculate genetic similarity according to Nei and Li (1979)

$$S_{ij} = [2a/(2a + b + c)]$$

where S_{ij} is the similarity between two individuals i and j , a is the number of bands present in both i and j , b is the number of bands present in i and absent in j , and c is the number of bands present in j and absent in i . The similarity matrix was analyzed by the UPGMA procedure of the NTSYS software to create a dendrogram representing the diversity among the landraces. Differences among nodes in the dendrogram were verified using a bootstrap program (J.A. García, M.C. Duque, J. Tohme, S. Xu, and M. Levy, 1995, personal communication). Gene diversity (H), or the average probability that two randomly chosen alleles at a locus are different (Nei, 1973), was calculated for the entire set, as well as for the two subgroups identified by the UPGMA analysis and illustrated by the dendrogram, one consisting of the majority of Andean landraces and a second composed of outliers:

$$H = 1 - J, \quad \text{and} \quad J = \sum_k x_k^2$$

where x_k is the frequency of the k th allele in the population.

RESULTS AND DISCUSSION

An average of 56 bands per accession were obtained with one combination of primers, while the second com-

Table 1. continued.

Germplasm number†	Germplasm				Germplasm				Germplasm			
	Country‡	Province	PC§ SC§ W¶ H#	Hab# Group††	Country‡	Province	PC§ SC§ W¶ H#	Hab# Group††	Country‡	Province	PC§ SC§ W¶ H#	Hab# Group††
G23605	PER	Apurimac	6 0 40	4	PER	Cuzco	7 0 40	1	PER	La Libertad	1 7 43	4
G23773C	PER	Apurimac	8 0 32	4	PER	Cuzco	3 0 37	1	PER	La Libertad	1 0 51	4
G23727	PER	La Libertad	1 5 48	4	PER	Cuzco	2 7 67	4	COL	Cundinamarca	2 9 9	4
G23746	PER	La Libertad	8 0 49	4	PER	Cuzco	9 0 43	4	ECU	Chimborazo	2 9 13	4
G 6590	PER	Loreto	2 0 23	4	PER	Azuay	2 7 32	4	GTM	Sacatepequez	2 0 8	4
G1575	PER	Loreto	3 0 28	4	PER	Apurimac	9 8 24	4	MEX	Mexico	9 8 4	4
G 7446	PER	Piura	1 0 16	4	PER	Cuzco	4 0 16	4	MEX	Michoacan	9 0 10	4
G12169	PER	Piura	6 2 40	4	PER	Tucuman	2 9 6	4	MEX	Puebla	9 2 7	4
G11525	PER	Puno	2 7 34	1/3	ARG	Tucuman	2 9 10	4	PER	Apurimac	9 4 13	4
G 4724	PER	San Martin	6 2 42	3	BOL	Chuquisaca	2 9 9	4	PER	Apurimac	2 9 11	4
G10298	PRT	San Martin	5 6 56	1	BOL	Chuquisaca	2 9 10	4	PER	Apurimac	2 9 8	4
G 1414	SSU	San Martin	9 0 35	1	BOL	Cochabamba	2 9 10	4	PER	Apurimac	2 9 12	4
G 433	TKY	Urfia	2 6 49	3	BOL	Cochabamba	2 9 10	4	PER	Cajamarca	2 9 17	4
G 4801	USA	Urfia	5 0 45	1	BOL	Tarija	2 9 12	4	PER	Cuzco	2 4 9	4
G17668	USA	Urfia	2 6 44	1	BOL	Tarija	2 9 11	4	PER	Huanuco	2 4 9	4
G23567B	PER	Cuzco	3 6 53	4	COL	Cundinamarca	2 9 16	4	PER	Junin	2 4 9	4
					COL	Cundinamarca	2 9 16	4	PER	Piura	2 9 8	4

† Germplasm number of CIAT's Genetic Resources Unit.

‡ Country of origin: ARG = Argentina; BND = Burundi; BOL = Bolivia; BRA = Brazil; CBA = Cuba; CHL = Chile; COL = Colombia; DOM = Dominican Republic; ECU = Ecuador; HTI = Haiti; MEX = Mexico; MWI = Malawi; PER = Peru; PRT = Portugal; SPN = Spain; SSU = Former Soviet Union; TKY = Turkey; USA = United States of America; GTM = Guatemala.

§ PC and SC: Principal color and secondary color, respectively. 1 = white; 2 = cream; 3 = yellow; 4 = brown; 5 = pink; 6 = red; 7 = purple; 8 = black; 9 = other.

¶ W = Weight (g) of 100 seed.

Hab = Growth habit. 1 = determinate bush; 2 = indeterminate upright bush; 3 = indeterminate prostrate bush; 4 = indeterminate climbing; 5 = determinate climbing.

†† Group = Numbers 1, 2, and 3 refer to clusters of cultivated bean in the UPGMA analysis (Fig. 3) and "W" identifies wild beans.

combination produced an average of 38 per accession. A total of 189 bands were analyzed across the wild and cultivated accessions. The six accessions that were duplicated were 97.5% similar on the average across the two replications, thus validating the repeatability of the AFLP technique.

The Mesoamerican check separated widely from Andean types in the MCA, as was expected (Fig. 2). Among the wild beans, those from both Mesoamerica and Northern Peru separated widely from the wild beans from the Southern Andes. Likewise, within the Andean gene pool of wild beans, a group from Central and Southern Peru was distinct from a group from Bolivia and Argentina. Thus, the pattern of separation into groups was by and large consistent with that observed previously with a wild bean core collection (Tohme et al., 1996). This indicates that the AFLP did in fact reveal genetic diversity where this was known to exist.

Andean Diversity

MCA of AFLP data indicated that most cultivated accessions formed a single relatively compact group in any combination of dimensions (Fig. 2). About 9% of landrace accessions appeared as outlier, and these occupied the space between the Andean cluster and the Mesoamerican check cultivar (Fig. 2). The analysis was repeated without the wild beans and after eliminating outlying accessions, but no discrete groups emerged from the large group of Andean accessions. Within this larger group were included beans of all growth habits; both dry bean and ñuña types; landraces from both primary and secondary centers of diversity; and races Nueva Granada, Peru, and Chile, on the basis of morphological traits. The dendrogram created by UPGMA with Nei's similarity index confirmed the result of the MCA analysis regarding the narrow genetic base of most of the landraces (Fig. 3). One large group included 172 of the landraces that were at least 80% and mostly 90% similar, while 16 landraces separated from the larger group. The Mesoamerican check ICA Pijao formed a third group. The use of bootstrapping confirmed that these three groups were distinct, and that no other nodes of the dendrogram were significantly different (Fig. 3). This indicates that there were no subgroups within the larger group of 172 landraces which included representation of the three Andean races.

These results confirm the narrow genetic base of the Andean gene pool. Working with a smaller group of accessions, Becerra and Gepts (1994) found narrow differences among groups of Andean accessions previously classified as pertaining to races Nueva Granada, Peru, and Chile. In the present study no prior classification of accessions was performed, and a tendency to form discrete races was not detected. In this study we chose a sizable sample of the bean core collection which in turn was sampled systematically for morphological traits and agroecological origins across a wide geographical range. We consider that the present sample reflects the diversity of the Andean pool available in gene banks today. We must therefore conclude that the cultivated

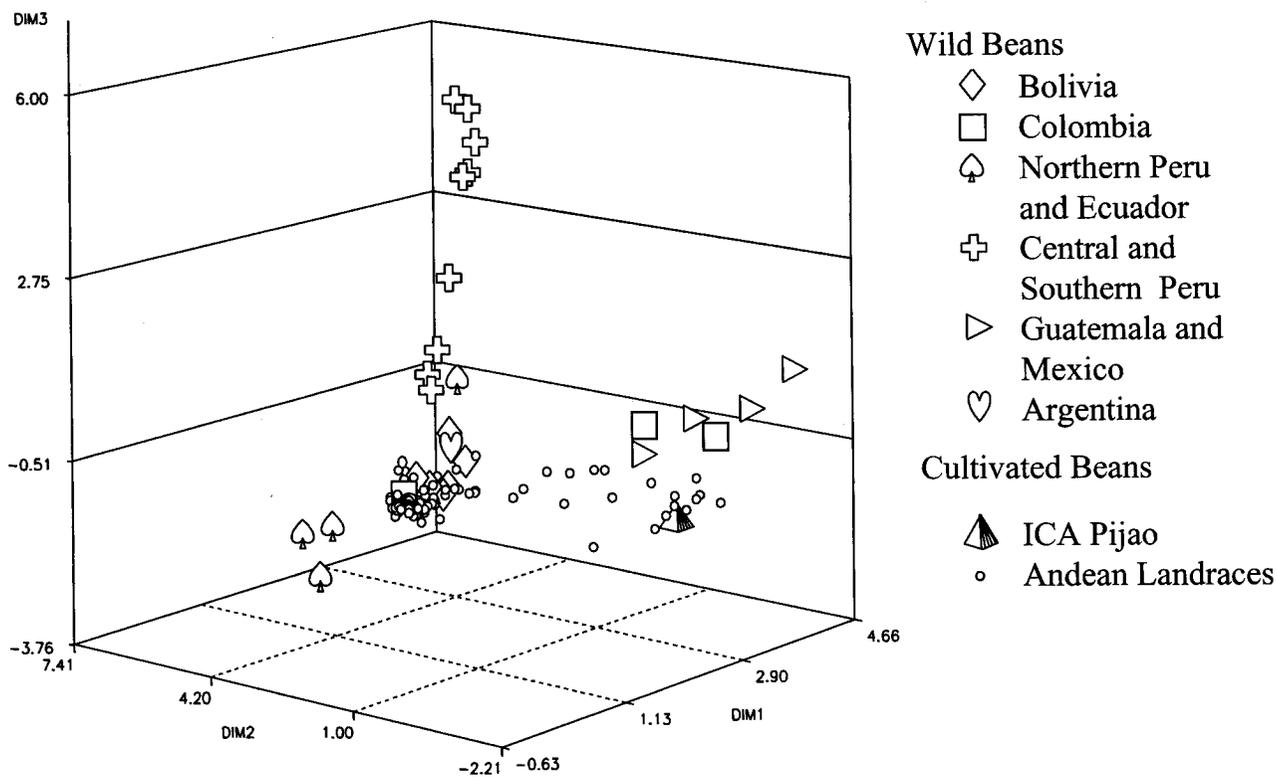


Fig. 2. Relationships among accessions of common bean landraces derived from the Andean gene pool, and selected accessions of wild bean, as revealed by multiple correspondence analysis.

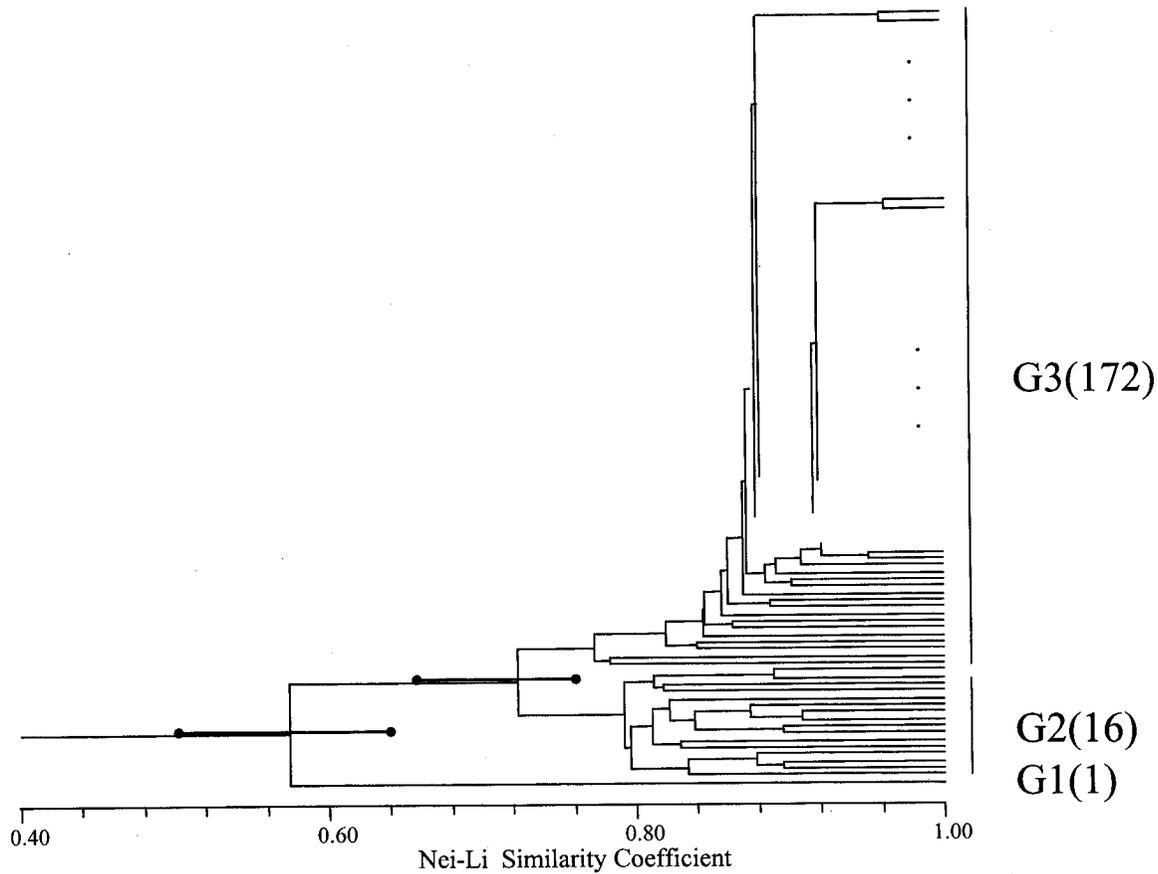


Fig. 3. Grouping of accessions of common bean landraces derived from the Andean gene pool and one Mesoamerican check cultivar by unweighted pair group method with arithmetic mean. Number in parentheses indicates total number of accessions in the respective group. The two lines in bold around key nodes denote 95% confidence intervals for those nodes, as revealed by a bootstrap analysis.

Andean gene pool in the primary center of diversity as a whole has a very narrow genetic base. We continue to investigate possible subtle patterns of diversity within the Andean pool associated with growth habit, but differences are by no means discrete. This contrasts strikingly with the Mesoamerican gene pool, which presents well-defined races that are distinguished as discrete groups by molecular markers, with some structure even within races (Beebe et al., 2000).

We expected to find more genetic variability among the Andean landraces, on the basis of the great morphological and adaptational variability among Andean beans (Singh et al., 1991a) and the existence of unique germplasm such as ñuñas (Tohme et al., 1995). Races Nueva Granada, Peru, and Chile of the Andean gene pool were defined essentially on plant morphology and differences in adaptation regimes. Our results suggest that all three races might have a common origin, in which case these races would have resulted essentially from intensive human intervention and selection for these traits. Several traits that are important in domestication, including photoperiod and temperature adaptation, are probably under simple genetic control (Koinange et al., 1996; Kornegay et al., 1993; White et al., 1996). Thus it is not out of the question that from a narrow initial base, adaptation to a wider range of growth environments across altitudes and latitudes could be selected. Indeed, the intensity of the selection pressure for morphological variability in Andean beans is again underscored by the contrast with Middle American landraces. Compared with beans in the Middle American gene pool, Andean beans present grain types that are relatively more distant from wild beans with respect to seed size, and range and intensity of grain colors, in spite of a narrower genetic base. Pre-Colombian plant cultivators of the Andean zone may have been avid plant selectors to create such variability. This is testified as well by the great diversity of minor crops domesticated in the Andean zone in pre-Colombian times (National Academy of Science, 1989).

Our expectation that Andean beans would express wide genetic variability was also on the basis of the fact that Andean landraces present several phaseolin types, even more than Middle American landraces. Although the Middle American gene pool presents diverse and discrete races on the basis of DNA analysis (Beebe et al., 2000), it is quite uniform for phaseolin, having mostly S and S type variants of phaseolin (Gepts, 1988b) and a few M types (Beebe et al., 2000). In contrast, Andean landraces are characterized by T, C, and H type phaseolin (Gepts, 1988b), followed by numerous minor types such as A, Ca, Pa, K, Ko, and Tca (Koenig et al., 1990; Tohme et al., 1995), in spite of narrow DNA diversity as indicated by this study. Thus, the Andean pool presents the opposite of the situation found in the Middle American pool. Beebe et al. (2000) suggested that in the Middle American pool, S phaseolin had displaced other phaseolin types found in wild beans through a wild-weed-crop complex, whereby S phaseolin was introduced into local populations of wild bean or local domesticates. In the Andean pool, a similar but reverse

effect could have occurred, whereby wild type phaseolins were introduced into landraces through a wild-weed-crop complex. For example, C phaseolin was found segregating in a complex in Cuzco-Apurimac, Peru (Beebe et al., 1997), and this may have been the mechanism whereby C phaseolin was introduced to cultivated bean. This implies that subsequently the greater part of the original cultivated Andean genome would have been reselected, to result in the narrow genetic base observed in the present report. This could be explained by reselection of cultivated traits such as seed color or size. Such an effect was noted in a breeding program because of the selection of red seed color in crosses with black beans, in which selection pressure for red color had apparently recovered a broad part of the genome of the red seeded parents, supposedly through linkage drag (Beebe et al., 1995).

Introgression

Among the outliers in the two analyses, many of these presented phaseolins that are atypical of Andean beans, such as 'S' (Mesoamerican) or 'CH' (Northern Andean). Some outliers also possessed the dominant I gene for BCMV resistance, which is very uncommon in true Andean beans. The outliers in the correspondence analysis appeared to result from introgression from Mesoamerican beans, on the basis of phaseolin data and the intermediate position of the outliers between the Andean beans and the Mesoamerican check. An examination of the band constitution of the outliers likewise confirmed that they possessed many bands present in ICA Pijao but absent or at very low frequency in the large group of Andeans. The existence of introgressed accessions is not surprising considering that Mesoamerican beans have been grown in the Andean zone since pre-Colombian times (Kaplan and Kaplan, 1988; Towle, 1961). Several accessions from Chile were included among the outliers. Paredes and Gepts (1995) reported similar evidence of introgression in Chilean landraces. Genetic segregation has been observed in many cultivar mixtures grown by traditional farmers in Colombia and Peru (Beebe et al., 1997), implying that significant outcrossing occurs in farmers' fields. In cases in which the farmer is not market oriented and is unconcerned with a specific grain type for commercialization, he will often not cull out variant grain types that result from genetic recombination. In this situation, introgressed types are more likely to be maintained in the farmers' mixtures than would occur with market-oriented bean cultivators. This could explain the relatively high frequency of introgressed types among the accessions conserved in the gene bank. It should also be noted that in the formation of the core collection from which the present sample was drawn, unusual grain types were given preference to capture the broadest possible diversity, thus favoring non-commercial grain types.

When H was calculated for the larger cluster of 172 landraces in the UPGMA analysis, a value of $H = 0.07$ was found, while the outliers presented a value of $H = 0.17$. These two values of H are statistically different as

indicated by a *t*-test. The entire group presented a value of $H = 0.10$. Thus, introgression appears to have broadened the genetic base of Andean beans modestly. Of the total variability, 83.5% was found to reside between the two groups, and only 16.5% within groups.

Domestication

When the wild beans were viewed in relation to the cultivated beans in the MCA, several of the Bolivian wild bean accessions actually overlapped in the correspondence analysis with the very compact group of landraces, as did one wild accession from Colombia. Random wild accessions such as the Colombian, which group with cultivated bean, could reflect introgression from cultivated bean into local wild populations, as has been observed in Colombia (Beebe et al., 1997). Among the remaining wild beans, the other Bolivian accessions, together with the one Argentinean accession, grouped very closely to cultivated bean and were interspersed with other landraces on the margin of the tight group of cultivated bean. Wild beans from southern Peru, Mesoamerica, and northern Peru were fairly distant. This suggests that, among the several sites in the Andean zone where wild bean populations have been collected, eastern Bolivia or northern Argentina are the most likely candidates as the primary domestication site of the Andean gene pool of domesticated common bean. A conclusive identification of a primary domestication site cannot be determined based solely on genetic similarity and would require other sorts of evidence such as archaeological data. However, the identification of Bolivia as a possible domestication site invites comparison with other possible sites that harbor wild beans.

The narrow genetic base suggests that domestication of Andean beans occurred within a rather narrow wild population. During much of this long process of domestication and intensive selection, the Andean landraces must have been isolated from other wild bean populations that could have served as sources of variability through a wild-weed-crop complex during incipient domestication (Beebe et al., 1997). In general, the topography of the Andes has served to isolate wild bean populations (Tohme et al., 1996), and in this regard any of the populations might have resulted in a narrow genetic base had they been domesticated within their respective regions.

One group of wild bean is centered in Argentina (Tohme et al., 1996). In the MCA plot, a wild accession from Argentina graphed relatively close to cultivated bean, but slightly more distant than some of the Bolivian wild beans. The Argentinean populations are found in environments that are relatively isolated from agricultural settings. Indeed, these are some of the very few wild populations that are to be found in a primary forest environment, such that no weedy types have ever been observed in Argentina (D.G. Debouck, 2000, personal communication). It does not seem likely that bean would have been domesticated from the populations known at present in Argentina.

Southern Peru was an important center of pre-Colom-

bian civilization. Another group of wild bean is centered in southern Peru, in Cuzco, and Apurimac provinces at altitudes of 1800 to 2800 m above sea level (Tohme et al., 1996; Beebe et al., 1997). Multiple correspondence analysis grouped these wild beans quite distantly from cultivated beans. The AFLP data do not support a Peruvian domestication site, although one important caveat must be added. The Peruvian province of Ayacucho has not yet been explored for wild bean although it is suspected to exist there. A final judgment on the possibility of a Peruvian domestication site must await an evaluation of other populations from Peru. However, with regard to wild beans available at present from Cuzco-Apurimac, if this population had been domesticated, it would have been difficult to generate the broad variability in temperature adaptation found in Andean beans within a limited area. Although the valleys of Cuzco and Apurimac lead to the lowlands of the Amazon basin and to diverse and warmer environments including the tropical rainforest (Johnson, 1976), common bean does not adapt to such hot, humid environments. Furthermore, the descent to the Amazon basin is abrupt, such that the land on the eastern slopes of the Peruvian Andes that is propitious to agriculture is limited, and relatively few human settlements are found on these slopes. Thus, mid and low altitude environments that are otherwise amenable to common bean are not readily accessible from Cuzco-Apurimac. To adapt bean to lower altitudes, it would have been necessary to transport cultivated bean out of its original isolation in the Cuzco-Apurimac valleys to other environments even more distant, perhaps to regions where it could have come into contact with other wild bean populations.

In Bolivia, by contrast, the eastern slopes of the Andes descend gradually to the plains to the south of the Amazon basin. This topography would have permitted beans that were domesticated at mid- to high altitudes to be moved gradually into warmer environments, while still maintaining the isolation from other wild bean populations, and resulting in the narrow genetic base observed today. Furthermore, eastern Bolivia is subject to more seasonal variability in rainfall and temperature than southern Peru, and offers access to a wider range of growth environments. Thus, Bolivia could have afforded conditions more propitious than those in southern Peru for the development of the agromorphological variability within a narrow genetic base. Furthermore, some Bolivian populations of wild bean display good ability to produce seed at moderately high temperatures in Cali, Colombia (about 23°C average) (Orlando Toro, 1997, personal communication). Thus, ancient domesticated beans derived from these populations may have adapted to the lowlands relatively easily. It is also noteworthy in this regard that traditional Brazilian germplasm of Andean origin is particularly diverse among Andean bush beans for several traits: indeterminate bush growth habit; photoperiod insensitivity; moderate tolerance to low soil phosphorus availability; grain colors including black, purple speckled, cream, yellow, cream and red mottled, and purplish red; and a seed striping pattern called "zebra," which is common in

Africa but relatively rare in the New World. These accessions might be the remnants of the first germplasm adapted to low altitudes that descended from the Bolivian highlands to the lowland plains.

In light of a possible domestication event in Bolivia, it is ironic that beans are no longer important on a wide scale there. In spite of this, landraces are remarkably diverse with regards to uses: Besides dry bean for cooking, popping beans are still to be found, as well as spherical beans called chuies used in children's games (Tohme et al., 1995).

It is instructive to compare the domestication of Andean common bean with that of peanut (*Arachis hypogaea* L.). It is widely accepted that peanut was domesticated in lowland Bolivia or Paraguay (Krapovickas, 1969), or northern Argentina (Kochert et al., 1996). Tetraploid peanut presents a situation that is less ambiguous than the Andean common bean with regard to its domestication site, since one of its putative wild diploid ancestors, *A. ipaensis*, has been found only in southern Bolivia (Kochert et al., 1996). From this region the domesticated peanut evidently spread rapidly throughout the Andean zone and into the Caribbean and probably even to Mexico. This case illustrates several important points that are relevant for common bean. First, an agricultural civilization existed in the region with a well-developed capacity to domesticate crops and to practice selection on phenotypic variability. In this regard it is significant that peanut also presents wide morphological variability and a narrow genetic base (Halward et al., 1992; Kochert et al., 1996), similar to the Andean common bean. This may be more evidence of intensive selection activity across long periods by pre-Columbian cultivators in this same general region. Second, the case of peanut demonstrates that the means for dispersal of crops from this region to other regions were available. The peanut was apparently cultivated in Mexico in pre-Columbian times, on the basis of linguistic (Estrada Lugo, 1989) and archaeological evidence (Smith, 1967). In fact, the peanut had spread to many of the same regions as Andean beans, including the Caribbean basin (Leon, 1984). How Andean beans came to be established there is a mystery (Beaver, 1993). However, the same means that served to establish peanut in the Caribbean could have also carried Andean beans there. Linguistic similarities are consistent with a hypothesis that the Arawak Indians could have been an element in the distribution of peanut (Krapovickas, 1969). Similarly, cassava (*Manihot esculenta* Crantz) and pineapple (*Ananas comosus* (L.) Merr.) are crops of South American origin that had spread to the Caribbean basin in the pre-Columbian era (Leon, 1984), confirming the links between the two regions.

These findings on the narrow genetic base of Andean landraces are significant for the genetic improvement of Andean beans. Typically, Andean beans have been more difficult to improve for yield potential (White et al., 1992; Kornegay et al., 1992). This may reflect the lack of genetic diversity among Andean types. It is obviously important to broaden the genetic base of the Andean beans. Crosses with Mesoamerican beans are an obvious

strategy to attain this objective, but such crosses often produce poor progeny (Gepts and Bliss, 1985; Singh, 1995). What other sources of diversity might be explored? One option could be landraces that already display introgression of Mesoamerican genes, such as those observed in this study and classified as group 2. Such germplasm originated in Chile (Paredes and Gepts, 1995), Peru, Ecuador, and Colombia, and has been observed in Africa. Another possibility could be wild-weed-crop complexes, specifically one observed in Cuzco-Apurimac in southern Peru by Debouck (Beebe et al., 1997). On the basis of present results, it appears that these local wild populations were probably not involved in the primary domestication of common bean, and that the weedy types collected there may therefore represent variability not present in cultivated bean. Other schemes for broadening the genetic base through crosses with wild ancestors of crops have been developed for tomatoes (*Lycopersicon esculentum* L.) and rice (*Oryza sativa* L.) (Tanksley and McCouch, 1997) and are being tested for common bean, including wild populations that were apparently not involved in domestication or gene flow, on the basis of present results.

Given the possibility that Andean common bean was domesticated in Bolivia, it would be of interest to pursue a comparison of other Bolivian wild beans with the cultivated bean. Debouck (1988) carried out additional explorations of wild bean in Bolivia. These collections should be the object of additional study in light of present results.

CONCLUSIONS

In spite of vast diversity in plant and grain morphology and in agroecological adaptation, Andean landraces of common bean proved to have a very narrow genetic base on the basis of AFLP analysis, although introgression from Middle American beans has served to broaden the genetic base slightly. This implies that Andean landraces were derived from one or a few similar wild populations, possibly on the eastern slopes of the Andes in Bolivia, and that the morphological variability that exists among landraces was introduced through farmer selection. Thus, races in the Andean gene pool of common bean probably reflect human intervention and not ancestral traits. Broadening the genetic base of Andean beans is therefore a high priority.

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