Biochemical Evidence Bearing on the Domestication of *Phaseolus* (Fabaceae) Beans[1]

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The genus Phaseolus *(Fabaceae) consists of some 50 species, all of which are distributed in the Americas. Four of these contain cultigens.* P. vulgaris *(common bean),* P. lunatus *(lima bean),* P. acutifolius *(tepary bean),* P. coccineus *subsp.* coccineus *(runner bean); and* P. coccineus *subsp.* polyanthus *(no English vernacular name). Biochemical markers—phaseolin seed storage protein and isozymes—have provided new evidence on the organization of the first three species. Domestication has possibly caused a strong reduction in genetic diversity in* P. vulgaris *and* P. acutifolius. *Both* P. vulgaris *and* P. lunatus *cultivars result from at least two independent domestications, in Mesoamerica and in the Andes. These two species consist of two gene pools, each of which includes wild ancestors and their respective cultivated descendants. Our findings suggest the need for additional emphasis on genetic conservation of wild ancestors and their use in breeding programs and for a comparison of inter-gene pool vs. intra-gene pool crosses in breeding programs.*

Información bioquímica acerca de la domesticación de los frijoles *Phaseolus. El género* Phaseolus *consta de unas 50 especies, distribuidas exclusivamente en las Américas; cuatro de estas especies incluyen a formas cultivadas:* P. vulgaris *(frijol común),* P. lunatus *(frijol lima),* P. acutifolius *(frijol tepari o escomite),* P. coccineus *subsp.* coccineus *(frijol ayocote),* y P. coccineus *subsp.* polyanthus *(frijol acalete). El uso de marcadores bioquímicos—faseolina e isozimas—ha producido nueva información acerca de la distribución de la variabilidad genética en las tres primeras especies. El proceso de domesticación causó una reducción marcada en la variabilidad genética para faseolina en* P. vulgaris *y* P. acutifolius. *Las formas cultivadas de* P. vulgaris *y* P. lunatus *resultaron de por lo menos dos domesticaciones distintas, en Mesoamérica y en los Andes. Estas dos especies constan de dos grupos de genotipos, cada cual incluye tanto a las formas silvestres ancestrales como a sus progenies cultivadas respectivas. Nuestros resultados sugieren que se ponga más énfasis tanto en la recolección y la preservación del germoplasma silvestre ancestral como en su uso en programas de mejoramiento; también sugieren que se compare en forma más detenida las cruzas entre grupos de genotipos con las cruzas adentro de estos grupos.*

Over the ca. 100 yr since the first publication of *L'origine des plantes cultivées* by De Candolle (1882), the study of crop evolution has made significant progress in identifying the wild ancestors of our crops. De Candolle (1882) suggested that archaeological, botanical, historical, and linguistic evidence could shed light on the origin of a crop. Of those four types of evidence, archaeological and botanical data are probably the most reliable ones, providing different but complementary types of information. Archaeological evidence on *Phaseolus* (Fabaceae) domestication has recently been reviewed by Kaplan and Kaplan (1988). In this review, I will discuss the most recent botanical (in a broad sense) evidence on the domestication process of *Phaseolus* beans.

The taxonomic status of *Phaseolus* beans has recently been clarified by a number of studies (Delgado Salinas 1985; Maréchal et al. 1978; Verdcourt 1970). These studies consider a *Phaseolus* genus of limited size (some 50 species) and distributed exclusively in the Americas. The genus, in addition to wild-growing species, contains four (or five depending on the taxonomic treatment) cultivated species, i. e., species consisting of a wild ancestral progenitor and the domesticated descendant. These four cultivated species are: the common bean (*P. vulgaris* L.), the lima bean (*P. lunatus* L.), the runner bean (*P. coccineus* L. subsp. *coccineus*), *P. coccineus* subsp. *polyanthus* (Greenman) Maréchal, Mascherpa, & Stainier (no English vernacular name), and the tepary bean (*Phaseolus acutifolius* A. Gray). Together these four species form a group of cultigens contrasted by their life cycle (perennial vs. multiannual vs. annual), reproductive system (cross- vs. self-pollinated), geographic distribution of the wild ancestor and the cultigen (regional vs. world-wide), and degree of domestication (incipient vs. advanced) (reviewed in Gepts 1988).

Traditional information on the domestication process of *Phaseolus* beans has relied on three types of data: age and geographic distribution of archaeological findings, geographic distribution of the presumed wild ancestor, and morphological diversity within the cultigen (e.g., Burkart and Brücher 1953; Evans 1973, 1976; Kaplan 1965, 1981; Mackie 1943). More recent evidence, reviewed here, has relied on biochemical markers, such as phaseolin and isozymes. Phaseolin is the major seed storage protein in *Phaseolus* sp. It accounts for some 35–50% of total seed nitrogen and as a consequence is a major determinant of both quantitative and nutritional characteristics of *Phaseolus* bean seed protein (Brown and Bliss 1983; Gepts and Bliss 1984; Osborn 1988). Isozymes have been abundantly used in the plant sciences to address a variety of questions (reviewed in Simpson and Withers 1986). Qualitative variability identified by electrophoresis for both phaseolin and isozymes has been reported primarily in *P. vulgaris* (e.g., Brown et al. 1981; Wall and Wall 1975; Weeden 1984). My collaborators and I have used this qualitative biochemical diversity to answer several questions regarding the process of domestication in *Phaseolus* beans: (1) What are the actual ancestors of cultivars?; (2) What is the effect of domestication on genetic diversity?; (3) Is there gene flow between wild and cultivated forms?; and (4) Can we identify gene pools, i.e., groups of related genotypes? Most of our information regarding these questions has been gained with common bean; when applicable, information from tepary and lima beans will also be presented. The advantage of both types of traits is that, although they are phenotypic traits, they are relatively free of environmental influence and their genetic control is simple. Phaseolin has the added advantage that the molecular basis for its diversity is particularly complex, ensuring the evolutionary uniqueness of each phaseolin variant (Gepts 1984).

IDENTIFICATION OF THE ACTUAL ANCESTORS OF *PHASEOLUS* BEANS

The mere presence of a wild-growing plant that resembles a cultigen morphologically and yields viable and fertile hybrids when crossed to it, does not provide sufficient evidence with regard to the identity of the actual ancestral populations that gave rise to the cultigen. This is particularly well illustrated by the wild ancestor of *P. vulgaris,* whose distribution extends from northern Mexico to north-

TABLE 1. GEOGRAPHIC DISTRIBUTION OF PHASEOLIN DIVERSITY IN WILD AND CULTIVATED COMMON BEANS (FROM GEPTS ET AL. 1986; GEPTS AND BLISS 1986; KOENIG ET AL. 1990).

Region	Wild	Cultivated
Mexico	'S', 'M'*[a]	'S' ('T', 'M')
Central America	'S', 'M'	'S', 'B'
Northern Andes[b]	'CH,'* 'B', 'I'	'S', 'T', 'C', 'B'
Southern Andes[c]	'T', 'C', 'H', 'J'*	'T', 'C', 'H', 'A'

[a] The asterisk indicates a heterogenous class of phaseolin types.
[b] Includes Colombia and northern Peru.
[c] Includes southern Peru and Argentina.

western Argentina in mountainous areas between 1500 and 2500 m (Brücher 1988; Delgado Salinas et al. 1988). Where did common bean domestication occur along this distribution area? In Mesoamerica or in the Andes or in both regions? A survey of phaseolin diversity in wild and cultivated common beans has allowed us to answer this question (Table 1). Wild common beans of different geographic origins could be distinguished by their particular phaseolin type, each of which was characteristic of its own region (i.e., a given phaseolin type did not appear in more than one region). Cultivars displayed a phaseolin distribution that was parallel to that of wild types: e.g., the 'S' phaseolin pattern found in Mexican wild beans was also the most abundant pattern among Mexican cultivars. This parallel distribution has been interpreted to indicate multiple domestications of the common bean along the extended distribution range of the wild ancestor (Gepts et al. 1986; Gepts and Bliss 1986). Two major domestication centers were identified, one in Mesoamerica leading to 'S' phaseolin cultivars and the other in the southern Andes leading to 'T', 'C', and 'H' cultivars (Gepts et al. 1986; Koenig et al. 1990). A minor domestication center appears to be located in Colombia (or perhaps in Central America) leading to 'B' phaseolin cultivars (Gepts and Bliss 1986; Koenig et al. 1990).

Recent investigations with isozymes have confirmed these findings (Schinkel et al. 1988). A survey of some 100 wild lines and 500 cultivars showed that Mesoamerican and Andean genotypes displayed alternate alleles at several isozyme loci. Among wild types, the Colombian populations showed isozyme profiles similar to those of Mesoamerican populations. An accession from northern Peru appeared to be intermediate between the Mesoamerican populations (including the Colombian populations) and the southern Andean populations (from southern Peru to Argentina). Cultivars displayed the same subdivision into two major groups, one from Mesoamerica and the other from the Andes.

It should be noted here that phaseolin and isozymes displayed high levels of association. For example, the 'S' phaseolin type tended to be associated primarily with the 'F' allele of ribulose biphosphate carboxylase oxygenase (rubisco) and shikimate dehydrogenase. Conversely, the 'T', 'C', and 'H' phaseolins were often associated with the 'S' allele of the aforementioned enzymes. The associations occur in the absence of any genetic linkage between the phaseolin and isozyme loci and are testimony to the presence of extensive multilocus associations in common bean.

Phaseolin has also been used as a marker to trace the dissemination of common

bean cultivars from their respective areas of domestication. Cultivars of the Meso-american area have been introduced into the Andean area and vice versa (Gepts et al. 1986). Colombia appears to be a meeting place for the two types of cultivars; the country displays a geographic gradient with Mesoamerican cultivars more abundant in the northeastern half of Colombia's bean growing region and Andean cultivars at a relatively higher frequency in the southwestern half (Gepts and Bliss 1986). Mesoamerican and Andean cultivars have been dispersed to many con-tinents; however, Mesoamerican beans came to predominate in lowland South America (Brazil and Venezuela) and in southwestern U.S.; Andean cultivars pre-dominate in northeastern U.S., Europe, and Africa (Gepts and Bliss 1988; Gepts et al. 1988). We have recently established a similar division into a Mesoamerican and Andean group in lima bean on the basis of phaseolin results.

One of the chief characteristics of phaseolin (and other seed storage protein markers) is the complexity of the molecular basis for genetic variability. Each pattern of polypeptides observed by electrophoresis arises from a complex series of events at the molecular level. These events include, principally, gene duplication and divergence by nucleotide substitutions and insertions/deletion, and co- and post-translational glycosylations (reviewed in Gepts 1984 and Osborn 1988). Be-cause of its complexity, it is unlikely that a given pattern would have appeared repeatedly in the evolutionary history of the species. In other words, each pattern is unique and traces back to a single ancestor. If this holds true, one should be able to trace the phaseolin patterns observed among cultivars to a single or limited number of wild ancestors in a well-circumscribed region. This turns out to be the case for the 'S' phaseolin type characterizing Mesoamerican cultivars. Out of some 90 wild bean populations, only five exhibited the 'S' phaseolin type (and did not show any signs of gene flow with cultivars). These five populations are located in a well-defined area in west-central Mexico represented by what is today the state of Jalisco (Gepts 1984; Gepts and Debouck n.d.).

EFFECT OF DOMESTICATION ON GENETIC DIVERSITY

Phaseolin data indicate that domestication may have represented a strong bot-tleneck in genetic diversity, especially in Mesoamerica. Of the at least 16 patterns observed among wild common beans in that region only one is represented among cultivars (Gepts et al. 1986). In the Andean region, domestication has also induced a reduction in phaseolin diversity, although a much smaller one possibly because of the much lower levels of phaseolin diversity among wild beans in that region (Gepts et al. 1986; Koenig et al. 1990). A similar reduction in phaseolin diversity has been observed in the tepary bean, which is distributed in Mexico, Central America, and the southwestern U.S. Whereas wild teparies displayed 15 different phaseolin variants, cultivars showed a single variant (Schinkel and Gepts n.d.).

This reduction in phaseolin diversity stands in marked contrast with the increase in morphological diversity observed upon domestication. Cultivars are noticeably more diverse with regard to growth habit, pod type, seed type, and photoperiod adaptation (Gepts and Debouck n.d.). This contrasting trend in diversity raises the issue of representativity of the markers used to characterize genetic diversity. The aforementioned morphological traits may have a fairly atypical genetic control. They are usually controlled by a limited number of genes with major phenotypic

TABLE 2. GENETIC CONTROL OF TRAITS DISTINGUISHING WILD AND CULTIVATED COMMON BEANS (FROM GEPTS AND DEBOUCK N.D.).

Trait	Number of genes	Source
Growth habit:		
Determinacy	1	Norton (1915)
Twining	1	Norton (1915)
Internode length	1	Norton (1915)
Basal internode length	1, 1	Lamprecht (1947)
Node number	2	Cheah (1973)
Pod dehiscence	3	Prakken (1934)
Seed color	9	Leakey (1988)
Seed color pattern	9	Leakey (1988)
Seed size	Polygenic	Johannsen (1909); Motto et al. (1978)
Photoperiod sensitivity	1–3	Leyna et al. (1982); Wallace (1986)

effect. One exception is seed size, which appears to be under quantitative control (Table 2). The characteristic shared by all traits, however, is their high heritability, even for seed size whose heritability reaches 0.7–0.9 (Motto et al. 1978). The major phenotypic effect and the high heritability may reflect the actual domestication process. It is only if a variant was clearly distinguishable that it would have been selected by the earliest farmers (or latest hunter-gatherers) and it is only if this variant was highly heritable that the earliest farmers could have recovered it in the progenies. Because biochemical traits are also highly heritable, their main difference with morphological traits is that the latter can be selected for at the whole plant level. Therefore, the following scenario can be suggested with respect to the fate of genetic diversity during and after domestication. The actual process of domestication would have induced a strong reduction in genetic diversity, as witnessed by phaseolin diversity; during and subsequent to domestication, selection of newly arising morphological variant by farmers would have increased morphological diversity.

Because of their small number, their strong phenotypic effect, and the high heritability of their expression, morphological traits may therefore not constitute a representative sample of the entire genome. Other traits may only have a small phenotypic effect and may not be as highly heritable, yet, in evolutionary times, they may also play a role. Identification of additional highly polymorphic markers and characterization of the variability of these markers in wild and cultivated common beans is needed to resolve this issue of representativity.

Another question that can be raised is why domestication should specifically lead to a reduction in phaseolin diversity. It may be that this reduction is the consequence of a stochastic process involving the selection to a new environment in a small population (i.e., single or limited number of domestications). Alternatively, the phaseolin locus may be linked to one or more loci determining the cultivated phenotype ("hitchhiking effect"). Thirdly, the phaseolin locus may be under direct selection during the domestication process; for example, phaseolin types may have been selected that are more easily broken down during germination

in a cultivated seed bed or digested during passage in the human digestive tract. We are currently investigating the linkage relationship between the phaseolin locus and the loci for morphological traits.

GENE FLOW BETWEEN WILD AND CULTIVATED COMMON BEANS

Based on phaseolin data, Gepts (1984) determined that 20 out of 70 Mexican wild bean populations may have been subjected to gene flow originating in cultivars. Available phaseolin data do not indicate a substantial gene flow from wild to cultivated populations. In a sample of 115 Mexican cultivars, only one displayed a 'M' phaseolin characteristic of wild populations in Mexico (Koenig et al. 1990).

This apparent asymmetry in gene flow between wild and cultivated types raises several issues. Common bean is known as a predominantly self-pollinating species. Yet, a high level of outcrossing is not needed to explain the apparently high frequency of a marker characteristic of cultivars among wild populations. Rare outcrosses during a period of over 7000 yr (age of the earliest cultivated common bean in Mexico's archaeological record; Kaplan 1967) may be sufficient to account for this frequency. In addition, it has recently been shown that under certain genotypes × environment interactions, outcrossing in common bean can reach levels as high as 70% (Wells et al. 1988). The apparently low levels of outcrossing from wild to cultivated common beans are not well understood. This low apparent frequency could be explained by a low frequency of outcrossing in contradiction with data indicating higher levels of gene flow from cultivars to wild populations. It could also be attributed to a strong natural selection or selection by the farmer against any off-types in times of growth habit and seed type; this selection would be further strengthened because of the dominance of wild-type traits in the F_1 generation. Alternatively, the phaseolin locus is linked to one or more loci determining the cultivated phenotype. Selection against wild-type trait would lead to selection against phaseolin patterns characteristic of wild populations. Additional markers and a better knowledge of the linkage relationships between the phaseolin locus and loci for morphological traits are desirable to elucidate this question.

IDENTIFICATION OF GENE POOLS

A gene pool can be defined as a set of genotypes characterized by (1) specific allele frequencies, (2) similar allele associations, (3) differential adaptation to environmental conditions, (4) a defined geographical distribution, and possibly (5) reproductive isolation with genotypes of other gene pools (Gepts and Bliss 1985; Gepts and Debouck n.d.). This definition can be applied at several hierarchical levels. It can be applied at the species level to distinguish, for example, *P. vulgaris* from *P. coccineus.* It can also be applied at a subspecific level to distinguish Mesoamerican vs. Andean common bean genotypes on the basis of several lines of evidence (Table 3). Morphological data indicate that Mesoamerican genotypes have smaller seeds (and correlated smaller leaves and shorter internodes) than Andean genotypes (Evans 1973, 1976; Gepts et al. 1986). Certain alleles of seed color pattern genes are confined to one or the other gene pool. For example, the recessive alleles at the T and E loci (*tt E* determining the "eye" pattern and *tt ee* determining the "soldier' pattern) are found only among Andean

genotypes (Leakey 1988; P. Gepts, unpub.) Preliminary data on bean rust (*Uromyces phaseoli*) resistance, indicate that the two gene pools may contain different genes for rust resistance (Stavely 1982, 1984). Cultivar 'Compuesto Chimalteco 2', which exhibits resistance against the widest known range of rust strains, displays a combination of Andean and Mesoamerican isozyme markers. Its presumed hybridity might explain its broad resistance spectrum. Genetic data also provide evidence for divergence between Mesoamerican and Andean genotypes. As mentioned earlier, genotypes of the two groups exhibit alternate alleles at many isozyme loci. In addition, strong multilocus associations have been observed between isozyme and phaseolin loci, even though these loci are unlinked. The associations point to a restriction of recombination which would be due to several causes. It could be attributed to either the predominantly self-pollinated nature of the species and the geographical isolation between Mesoamerica and the Andes or to selection of specific and different genotypic combinations in the two regions. (This last possibility does not necessarily imply a selective role for isozymes or phaseolin in common bean.) Various forms of reproductive isolation have been identified within common bean; they appear to arise, without exceptions so far, in crosses involving a Mesoamerican and an Andean parent (Coyne 1966, 1967; Gepts and Bliss 1985; Singh and Gutierrez 1984). Genotypes of the two gene pools may also have different adaptations to environmental conditions as illustrated by the work of Ghaderi et al. (1982). Kidney beans (of Andean origin) show an environmental adaptation that is distinctly different from that of navy, tropical black, red Mexican, and pinto beans (of Mesoamerican origins). The existence of two large gene pools seems therefore well established, each of which consists of the wild and cultivated genotypes of their respective regions. This reflects the fact that the cultivars of one region are more similar at the biochemical level to their wild ancestors in the same region than to, for example, their cultivated counterparts in the other region. Phaseolin data suggest the *P. lunatus* may also consist of a Mesoamerican and an Andean gene pool. The situation in the common bean (and the lima bean) contrasts with that described in many other species, where the primary gene pool consists of a single sub-gene pool for the cultivars and another sub-gene pool for the wild ancestors (Harlan and de Wet 1971). It resembles, however, the situation in rice where two large groups of cultivars, japonica and indica, have been identified, presumably resulting from independent domestications (Glaszmann 1987; Second 1982). By analogy with the rice case, a *mesoamericanus* and *andinus* group could be identified in common bean.

Additional research is underway to examine whether these two large gene pools can be further subdivided into smaller entities. Nienhuis and Singh (1988) were able to distinguish between small-seeded and medium-seeded Middle American cultivars on the basis of their combining ability for yield: medium-seeded genotypes grown in the Mexican highlands had a higher yield combining ability than their small-seeded counterparts of the Mexican lowlands. Singh (1988) further proposed a classification in 10 gene pools based on growth habit, mean growing temperature, crop cycle, duration and yield potential. Recently, we have identified two minor 'S' phaseolin variants that show a distinct geographic distribution and are associated with (without necessarily being involved in) several agronomic traits (Koenig et al. 1990). The 'Sd' phaseolin type is found in cultivars of the Mexican highlands, with a prostrate growth habit, medium-sized seeds, good

TABLE 3. EVIDENCE SUGGESTING A MIDDLE AMERICAN AND AN ANDEAN GENE POOL IN COMMON BEAN.

Type of evidence	Source
1. Morphology	
Seed size and correlated effect on leaf size and internode length	Evans 1973, 1976; Gepts et al. 1986; Kaplan 1956
Seed color pattern	Leakey 1988
2. Phytopathology	
Dominant I gene for BCMV resistance	S. Temple, pers. comm.
Rust (*Uromyces phaseoli*) resistance	Stavely 1982, 1984
3. Biochemistry	
Isozymes	Bassiri and Adams 1978
Phaseolin	Gepts et al. 1986; Gepts and Bliss 1986; Koenig et al. 1990
4. Genetics	
Reproductive isolation	Gepts and Bliss 1985
Chlorophyll mutability	Coyne 1966, 1967
5. Adaptation	
Environmental reaction measured by yield	Ghaderi et al. 1982

combining ability for yield (see above) and drought tolerance. The 'Sb' phaseolin type is found in cultivars from Brazil with small seeds, early maturity, and tolerance to low soil acidity. These first data on the existence of net gene pools in common bean are encouraging but additional research is needed to identify additional markers and associations of traits.

SIGNIFICANCE FOR GENETIC RESOURCES CONSERVATION AND BREEDING PROGRAMS

The present distribution of genetic diversity among the cultivars of common bean and other *Phaseolus* beans is the result of evolutionary processes that have affected these species before, during, and after domestication up to today. A better knowledge of this evolutionary history will give us a better understanding of their current genetic diversity, which, in turn, should lead to more efficient germplasm conservation and breeding programs.

For example, our finding that domestication may have strongly reduced genetic diversity in common bean leads us to suggest that more emphasis should be placed on exploration and maintenance of wild ancestor germplasm. The *Phaseolus* world collection at the Centro Internacional de Agricultura Tropical (Cali, Colombia) includes only some 500 accessions of the wild ancestors of the five *Phaseolus* cultigens vs. 35,500 cultivated *Phaseolus* accessions. Likewise, breeding programs should place additional emphasis on the evaluation of wild germplasm and its incorporation into advanced cultivars. The potential benefit of this approach is illustrated by the discovery of resistance to the *Zabrotes subfasciatus* seed weevil in wild common bean populations from Mexico; all cultivars had until then proven to be susceptible (Van Schoonhoven and Cardona 1982; Van Schoonhoven et al. 1983). This resistance is due to the presence of the arcelin storage protein in the

seeds (Romero Andreas et al. 1986; Osborn et al. 1986, 1988) and is now being transferred into cultivars (R. Harmsen and F. A. Bliss, pers. comm.; J. Kornegay and C. Cardona, pers. comm.).

A second major observation is that of a strong divergence between Mesoamerican and Andean genotypes and independent domestications in both areas. This suggests that germplasm of both regions should be maintained with equal priority. It also raises interesting issues with respect to breeding programs. Given the divergence between the two groups, should separate breeding programs be organized for each region or should breeders attempt to bridge or circumvent the gap between the two gene pools? It should be investigated whether with an appropriate breeding methodology a more substantial progress from selection can be achieved in inter-gene pool cross compared to intra-gene pool crosses. Similarly, it would be worthwhile investigating whether heterosis is higher in the former type of cross compared to the latter. This is especially relevant as cytoplasmic male sterility has been identified in common bean (H. Bannerot, pers. comm.) as well as high levels of outcrossing (Wells et al. 1988).

CONCLUSION

The use of biochemical markers—phaseolin seed storage protein and isozymes— has provided significant new evidence on the organization of genetic diversity of *Phaseolus* beans, principally *P. vulgaris*. Two major findings are: (1) the possible strong reduction in genetic diversity upon domestication in *P. vulgaris* and *P. acutifolius*; and (2) the existence of two major gene pools—Mesoamerican and Andean—in *P. vulgaris* and *P. lunatus* each resulting from an independent domestication. These two findings have important consequences for the management of *Phaseolus* germplasm conservation and breeding programs.

ACKNOWLEDGMENTS

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