

## Genetic Diversity of Lima bean in Relation with Phytoecography in the New World

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**Abstract:** *Phaseolus lunatus* L., known as Lima bean, is a Neotropical food legume adapted to a wide range of ecologies, including temperate, humid and semi-arid tropical conditions. This adaptation is the consequence of the large distribution of the wild Lima bean populations in the various natural areas of the New World, involving both lowland and highland areas, as well as distinct vegetation types and climates. These wild materials have given rise to landraces of specific ecological properties, according to the origins of the ancestral wild populations in the two main centers of diversity: Mesoamerican and Andean regions. In order to exploit the potential of this food legume, it is essential, first, to know the genetic organization of the diversity of this cultigen at the intra- and inter-specific levels, and, second, to examine the phytoecography of the wild forms and the landraces in the New World. A state of knowledge is given on the taxonomy and the phylogeny of the genus *Phaseolus* and Lima bean. Special attention is devoted to the primary and the alien gene pools of *P. lunatus*. Data on phytoecography on both wild populations and landraces throughout Latin America help in determining the ecological requirements and potentials of this food legume in the traditional farming systems of the tropics. Current results or progress in these areas are useful to preserve the gene pools of this promising, but neglected, species through *in situ* and *ex situ* approach, and to develop, on the basis of this diversity, improved and productive cultivars of Lima bean.

**Key words:** *Phaseolus lunatus*, Lima bean, genetic diversity, phytoecography, *in situ* conservation.

For plant genetic resources, more attention is now given to the ancestral wild populations and landraces of the cultigens. This interest is due to their poor representation in germplasm collections, their high values as a reservoir of genetic variation, and as a source of novel variants for plant breeding (Frankel, 1974; Harlan, 1976; Brown, 1978; Delgado-Salinas *et al.*, 1988; Marshall, 1990; Bianchi-Hall *et al.*, 1993; Debouck, 2000a; Baudoin, 2001). However, these materials (particularly the wild populations) are not easy to maintain in gene banks. The limited

information available on the ecogeographic distribution of these populations and the necessity of assembling genetic stocks sufficiently representative of the total genetic variability displayed by such materials are among the major reasons for this difficulty. Further-more, seed dispersal and variation in both seed ripening and dormancy among individual plants and populations are also additional constraints for an adequate *ex situ* storage of wild populations (Debouck *et al.*, 1993; Ehrman and Cocks, 1990; Marshall, 1990).

In order to circumvent such obstacles, *in situ* conservation, e.g., in the environment in which wild populations or landraces evolve, is regarded as a dynamic conservation system which ensures the preservation of representative populations throughout their natural geographic range and facilitates the continuing evolution of the crop gene pool. It maintains the genetic integrity and the potential of adaptation of each population and complements also *ex situ* conservation avoiding the inadequate field sampling of ecotypes for storage in gene banks (Ingram and Williams, 1984; Altieri and Merrick, 1987; Maxted *et al.*, 1987; Brush, 1991; Astley, 1992).

In order to preserve plant genetic diversity on the basis of the two *in situ* and *ex situ* conservation approaches, a prerequisite is a good knowledge of the genetic diversity and the phylogeny of the target species, but also of the phylogeography of the ancestral wild forms and landraces of the cultigen. In particular, phylogeography provides valuable information on the diversity of ecological niches and, consequently, on the genetic variability resulting from any change in the environment, on the evolution and damage of vegetation structure and on the risk of genetic erosion (Maquet and Baudoin, 1997). This discipline gives an estimation of the different ecologies where the species is naturally distributed, on its plasticity and, therefore, on the plant breeding potentialities.

Purpose of this paper is to examine the genetic organization and the

as Lima bean, on the basis of data gathered mainly in the New World.

### Phylogeny and Taxonomy of *Phaseolus*

A good understanding of the phylogenetic relationships among species within crop gene pools is of great importance both to germplasm curators and plant breeders. Phylogenetic studies are useful in identifying the wild progenitors and other relatives of domesticated species (Pages and Holmes, 1998), and in clarifying the composition of their secondary and tertiary gene pools. This will help to define both sampling strategies for *ex situ* collections and management approaches for *in situ* conservation, as well to prioritize material for utilization. Gepts (1996) suggests that determining the closest relatives of cultivated beans, for example, has important implications for crop breeding because domestication has caused a genetic bottleneck in all *Phaseolus* cultigens. Furthermore, breeding programs that involve inter-specific crosses are particularly important in *Phaseolus* (Hucl and Scoles, 1985).

The genus *Phaseolus* (subtribe Phaseolinae, tribe Phaseoleae, family Leguminosae) has a complex taxonomic and nomenclature history, which is well illustrated by *P. lunatus*, the Lima bean (Maquet, 1995). Recent phylogenetic investigations strongly support a monophyletic *Phaseolus*. In this modern circumscription, *Phaseolus* is strictly of New World origin, concentrated in tropical and warm temperate America, between

upon by most legume taxonomists, the exact number of species within the genus is still debated (Debouck, 1999). However, there are probably around 50 species in the genus, of which five are domesticated: common bean (*P. vulgaris* L.) which is the most economically important cultigen of the genus, Lima bean (*P. lunatus* L.) which ranks second in economic importance, scarlet runner bean (*P. coccineus* L.), tepary bean (*P. acutifolius* A. Gray), and year bean (*P. polyanthus* Greenm.). In the five cultigens, wild ancestral forms have been identified; they all had a wide distribution before domestication. In the case of common bean and Lima bean, wild forms are distributed in both northern part of America (Mexico and Central America) and southern part of the continent. This situation is reflected by the presence of two groups of material for each of these two cultigens: the Mesoamerican and Andean groups (Debouck, 2000b).

The five *Phaseolus* domesticated species belong to two distinct lineages. The *P. vulgaris* group includes *P. vulgaris*, *P. coccineus*, *P. polyanthus* and *P. acutifolius*. The fifth cultivated species, *P. lunatus*, is part of a very well-defined clade that includes the South American and oceanic island diversification of *Phaseolus*, i.e., *P. augusti* Harms, *P. bolivianus* Piper, *P. lignosus* Britton, *P. mollis* Hook, *P. pachyrrhizoides* Harms, *P. rosei* Piper, and *P. viridis* Piper (Caicedo *et al.*, 1999; Delgado Salinas *et al.*, 1999).

A clade containing *P. viridis* (from Oaxaca, Mexico) and *P. lignosus* (from Bermuda) is sister to the rest of the primarily South American group. The Andean *P.*

*pachyrrhizoides*, *P. augusti* and *P. bolivianus* form a monophyletic group that is sister to a lineage containing both Mesoamerican and Andean accessions of *P. lunatus*, as well as one accession of *P. mollis*, a species endemic to the Galapagos Islands. A Peruvian accession of *P. lunatus* and *P. mollis* are resolved as a sister group, suggesting a mainland origin for the Galapagos species. *P. rosei* collected at the type locality (Chimborazo and Ecuador) falls within the Andean group of wild Lima beans; *P. rosei* could be an Andean wild form of Lima bean (which would make its correct name *P. lunatus*) (Toro Chica *et al.*, 1993; Caicedo *et al.*, 1999).

#### Taxonomy of *P. lunatus*

The latest available taxonomic treatment of *P. lunatus* is by Baudet (1977). A botanical variety, *P. lunatus* var. *lunatus*, was created for all the cultivated genotypes and a var. *silvester* for the wild form. The var. *lunatus* includes the three cultigroups defined by Mackie (1943): cv-gr. Sieva with medium-sized, flat seeds; cv-gr. Potato with small, globular seeds; and cv-gr. Big Lima bean with large, flat seeds. This classification, however, is far from reflecting the whole range of seed diversity and genetic variability among the cultivated materials due to free gene flow occurring between the three cultigroups (Baudoin, 1988). The primary gene pool of *P. lunatus* comprises the wild populations and the landraces of Lima bean, which can be grouped into two main races: the Andean and the Mesoamerican. Each race is characterized by distinctive morphological characters (Maquet, 1995; Debouck *et al.*, 1987), ecological adaptation (discussed later), seed

storage proteins (Debouck, 1989; Lioi, 1994; Gutierrez Salgado *et al.*, 1995; Maquet, 1995), allozymes (Maquet *et al.*, 1997; Lioi *et al.*, 1998) and molecular markers (Nienhuis *et al.*, 1995; Fofana *et al.*, 1997; Caicedo *et al.*, 1999; Lioi *et al.*, 1999; Fofana *et al.*, 2001). Escaped forms and weedy forms (natural hybrids between the wild form and a landrace) are observed throughout Latin America. In addition, several collections from northern Peru have shown that either more cultigroups of native varieties should be defined, or the concept of cultigroup is becoming obsolete because of the great diversity found in the field (Debouck *et al.*, 1987). Hawkes (1986) suggested avoiding Latin names at the intra-specific level for cultivated species. The best taxonomic treatment may be to use the binary combination, i.e., *P. lunatus* L., with some additional indication of the biological status of the material, e.g., wild, weedy, hybrid, landrace, etc. (Debouck, 1991; Maquet, 1995).

#### Origin, Domestication and Genetic Diversity of *P. lunatus*

Central America, where approximately 40-50 *Phaseolus* species occur today, is considered the centre of origin of the genus (Sousa and Delgado Salinas, 1993). *Phaseolus* species are numerous along the mountainous systems of the Sierra Madre Occidental and the Eje Volcánico Transversal of Mexico, which were formed during the Oligocene-Miocene and Later Tertiary or Pliocene, respectively. Therefore, current *Phaseolus* diversity may stem from the Oligocene or later (Delgado Salinas, 1985).

With regard to *P. lunatus*, the existence of a secondary gene pool in the Andes,

with taxa such as *P. pachyrhizoides*, would indicate a centre of speciation in this region, more recent in comparison to that of Central America. This is supported by evidence from seed protein and isozymes studies presented by Maquet (1995), Maquet and Baudoín (1996) and Maquet *et al.* (1999). An Andean origin was also suggested by Fofana *et al.* (1999), Caicedo *et al.* (1999) and Sparvoli *et al.* (2001) using RAPD, AFLP and lectins and lectin-related proteins, respectively. A wild Lima bean with small seeds has long been reported from several parts of Central America (Standley and Steyermark, 1946). However, another wild type with slightly larger seeds was more recently discovered in north-western Peru (Debouck *et al.*, 1987). Two separate domestication events have since been demonstrated, from two different wild forms, with different distribution ranges and distinct ecologies (Gutierrez Salgado *et al.*, 1995; Maquet, 1995; Fofana *et al.*, 1997). Due to the restricted distribution of the large-seeded wild type, it is assumed that one domestication event occurred within the southern Andes of Ecuador and the north-western Andes of Peru. By contrast, the range of the small-seeded wild Lima bean is huge, and a precise location for the domestication of the small-seeded cultivated Lima beans has still to be determined.

Lima beans seem to be an ancient crop, although some dates have been revised downward (Kaplan and Lynch, 1999), and more ancient in South America than in Central America. The earliest records are from the Central Andes of Peru and date to 3,000 years BP (revised date), although a pod from the coast of Peru has been