

dated to 5,600 years BP (Kaplan, 1994). The evolution of the cultivated species under domestication has been reviewed recently (Debouck and Smartt, 1995; Debouck, 1999). As in most crops, increases in the size of pods and seeds are the most striking differences between the cultivated forms and their wild ancestors. Reduction in hardness, dormancy and anti-nutritional factors (i.e., antitrypsin factors, cyanide glycoside) has also occurred. Most landraces contain low levels of linamarin (Baudoin *et al.*, 1991).

White-seeded cultivars have been selected. This mutation appears from time to time in wild populations, for example in Yucatan, Mexico (Debouck, 1999). The loss of seed dispersal mechanism is also a common feature of crop domestication. Major evolutionary changes have occurred in growth habit. The original climbing habit with profuse branching, observed in the wild form, was selected for a quick harvest, leading to the bushy determinate growth habit and annual landraces. In addition to these changes in plant habit, some selection has been undertaken for photoperiod insensitivity. As pointed out by Koinange *et al.* (1996), most of the evolutionary changes in beans are due to mutations of just a few genes, the increase in seed size being one noteworthy exception.

Domestication has taken place from a limited number of wild populations and is generally associated with an overall reduction of genetic diversity, contrasting with an increased diversity in morphological traits (mostly ones under direct, conscious selection by farmers). The reduction of

demonstrated with molecular markers, which are thought to be neutral to selection. Using seed-protein markers, Maquet *et al.*, (1990), Gutierrez Salgado *et al.* (1995) and Maquet (1995) showed reduced genetic diversity among the small-seeded Mesoamerican landraces, and also among large-seeded Andean landraces though not to the same extent and in different markers. As a consequence of this "founder effect", much of the genetic diversity has been left out of the domesticated stocks; possibilities are to be explored in terms of unrealized potentials from the wild forms.

Allozyme studies complement the data obtained from seed-proteins. The total gene diversity of the Lima bean at the species level ($H_{es} = 0.26$) is similar to that of *P. acutifolius* (Schinkel and Gepts, 1989) and *P. coccineus* (Escalante *et al.*, 1994), but higher than that of wild *P. vulgaris* forms ($H_{es} = 0.13$) (Koenig and Gepts, 1989). On the basis of allozyme data, the genetic diversity of the Lima bean is evenly distributed between the Mesoamerican and the Andean gene pools (Maquet *et al.*, 1997). This confirms the results obtained by Nienhuis *et al.* (1995) using RAPD markers. Allozyme data also showed that wild and cultivated forms of the Lima bean are characterized by similar levels of gene diversity and are not differentiated within each gene pool. However, Fofana *et al.* (1997) showed using RAPDs that the wild form and landraces of each gene pool were indeed genetically differentiated. Such discrepancies between studies could result either from the different nature of the markers or from the sample used.

Internacional de Agricultural Tropical (Cali and Colombia): the cultivated forms represent around 90% of this germplasm bank, the remnant being wild and weedy forms (Maquet and Baudoin, 1997). Although some disparities are observed in the geographic distribution of the accessions, more landraces are present in South America than in Central America while the opposite situation occurs with the wild forms. Seed multiplication and rejuvenation of this base collection on the field have to take into account not only the ecological requirements of each accession, but also the reproductive biology of the plant. *P. lunatus* is a self-compatible annual or short-lived perennial species with a mixed mating system, i.e., predominantly self-pollinating, but with a fair amount of outcrossing (Baudoin, 1991). Within the primary genetic reservoir of Lima bean, gene diversity is mainly distributed among rather than within accessions ($GST = 0.755$) (Maquet *et al.*, 1997). Lima bean germplasm is characterized by a high inbreeding coefficient ($f = 0.891$). In spite of this, and a low rate of gene flow, the intrapopulation gene diversity estimated from the CIAT collection ($Hs = 0.032$) is significantly different from zero and higher than that of other selfing species, such as *P. acutifolius* ($Hs = 0.0004$) (Schinkel and Gepts, 1989) and *P. vulgaris* (Koenig and Gepts, 1989).

Because of the wide distribution of their wild ancestors and multiple domestication events, cultivated common bean and Lima bean probably have a wider genetic base than the other cultigens of the genus, *P. acutifolius*, *P. coccineus* and *P. polyanthus* (Debouck, 1999). This can perhaps partly

explain the vast ecological expansion of these two beans, in comparison to the limited success of the other three species.

Currently, no natural inter-specific hybrids involving *P. lunatus* have been reported. Nevertheless, the Lima bean, *P. lunatus*, has a high genetic diversity beyond the intra-specific level (Baudoin, 1991; Maquet *et al.*, 1997). Studies of inter-specific hybridization (reviewed by Debouck, 1999) were carried out to investigate relationships between Lima bean and its wild allies from Mesoamerica in the context of the gene pool concept of Harlan and de Wet (1971), as modified by Smartt (1990).

The secondary gene pool of the Lima bean probably consists of the South American species (i.e., *P. augusti*, *P. bolivianus*, *P. pachyrrhizoides*). These species differ very little (Caicedo *et al.*, 1999; Delgado Salinas *et al.*, 1999) and may in fact constitute a single species with geographic variants.

The tertiary gene pool of *P. lunatus* includes the following species from the USA and/or Mexico with varying levels of relationships and compatibility (Baudoin, 1991; Debouck, 1999; Delgado Salinas *et al.*, 1999; Delgado Salinas, 2000): *P. jaliscanus* Pipet, *P. juguilensis* Delgado, *P. maculatus* Scheele, *P. marechalii* Delgado, *P. polystachyus* Britt., Stern & Pogg, *P. ritensis* Jones, *P. salicifolius* Pipet, *P. sonorensis* Standley, *P. xolocotzii* Delgado. Two variants of *P. polystachyus* are usually recognized: *P. sinuatus* Nutt. and *P. smilacifolius* Pollard.

All attempts to cross *P. lunatus* with *P. vulgaris* have failed to produce a viable

and fertile hybrid (Al-Yasiri and Coyne, 1966; Mok *et al.*, 1978; Leonard *et al.*, 1987; Kuboyama *et al.*, 1991). Early success claimed by Honma and Heeckt (1959) with the use of heterozygous parents is problematic, as mentioned by Hucl and Scoles (1985). The reciprocal cross *P. lunatus* x *P. vulgaris* is even more difficult to obtain (Rabakoarihanta *et al.*, 1979). The difficulty in obtaining fertile viable hybrids between common and Lima beans confirms their distinct taxonomic positions in the genus. Some species could fall between these two extremes, but most have not been studied in sufficient detail so far.

In conclusion, *P. lunatus* shows high levels of intra-specific genetic diversity, distributed between Mesoamerican and Andean gene pools and also between wild and cultivated forms. In addition, the cultigen is characterized by a wide alien gene pool, covering at least 12 species present in both Mesoamerican and Andean regions of the New World.

Wild Lima bean populations can still be found in the centers of diversity, from Mexico to Ecuador, and in different ecologies. *P. lunatus* thus gives us the possibility of observing the mechanism contributing to the maintenance of genetic diversity over many generations, and to obtain reliable data as a model system of relevance not just to the more critically threatened *Phaseolus* species, but also for other species with similar botanical characteristics.

Phytogeography

Phytogeography in the New World

While *Phaseolus* species are found in

the rainfall pattern coincides with favorable conditions of temperature and photoperiod for growth and reproduction; a dry season follows that allows for seed dispersal and conservation in the soil during period of less favorable temperatures. Survival is mainly in the form of seeds, although tuberous roots can also play a role in the *in situ* preservation of some *Phaseolus* species (Debouck, 2000b). As mentioned above, wild forms of common bean and Lima bean are present in both Central and South America. Both are floristic elements of climax forests: subhumid premontane and lower dry tropical forests in the case of the wild Lima bean, subhumid montane forests in the case of wild common bean. Their ecological success and adaptation in disturbed habitats has been a positive factor in their domestication.

The wild form of *P. lunatus* is only found in the Americas, while the cultivated form is widely distributed all over the tropical world and in some temperate regions (i.e., Bulgaria, Italy, USA, Canada, etc.). In particular, some short-cycle breeding lines are cultivated in southern Canada and northern USA. Weedy forms or escapes have been reported in the Democratic Republic of Congo. Despite this extensive distribution, we restrict our discussion to the New World, the centre of origin and of primary diversity of *P. lunatus*. With regard to the cultivated form, only the landraces are considered here due to their major importance in current improvement program and on-farm conservation projects (Altieri and Merrick, 1987; Brush, 1995).

The geographic distribution of wild and cultivated Lima beans extends from the

to the tropical humid climate of the Amazonian region in Ecuador and Peru, to the temperate climates of highland areas 2,500 m above sea level (masl).

Wild forms

The studies of Maquet and Baudoin (1997) and Debouck (2000b) provide a good knowledge on the distribution and ecologies of the wild Lima bean populations in the New World. Tables 1, 2 and 3 (adapted from these studies) indicate, respectively,

and drier regions. In this zone, rainfall varies from 800 mm to 1,500 mm per year, with a well-defined dry season of 3-5 months. At mid-altitudes (800-2,000 msl), the *Tierra templada* is covered with evergreen forests with a T_m varying from 17° to 22°C. Temperature is a critical factor and excessively low temperatures (temperature of the coldest month <14°C) restrict the geographical distribution of wild *P. lunatus* populations in altitude and latitude.

Table 1. Ecological habitats colonized by wild *Phaseolus lunatus* in the Neotropics

Geographic area	Vegetation types
Mexico	Lowland tropical deciduous forests and scrubs
Central America	Lower tropical dry and subhumid forests
South America	Colombia, Venezuela: lower tropical dry forest; South Ecuador, Peru: western humid lower mountain forest

Vegetation types according to Rzedowski, 1978 (for Mexico); Holdridge, 1967 (for Central America); Cabrera and Willink, 1973 (for South America).

the ecological habitats of the wild *P. lunatus* in the New World, and characteristics of natural distribution areas in Meso-America and in the Andes for these wild materials.

The small-seeded wild form of *P. lunatus* extends at low altitudes from Sinaloa, Mexico (23°-26°N) to Salta, Argentina (25° S°) and through the Caribbean Islands (Maquet and Baudoin, 1997). Wild populations are mainly distributed along the Pacific slopes of the mountains of Mexico and Guatemala, but are found exclusively on these slopes further south in Meso-America. Caducifoliolate and semi-deciduous forests characterize the region at low altitudes (<800 msl), often referred to as *Tierra caliente*, with an annual average temperature (T_m) higher than 22°C. These forests are the transition between very humid

Both small- and large-seeded wild populations are present in South America, but not in the same ecologies. Small-seeded populations are distributed along the east slope of the Andean cordillera in central-northern Colombia, central-southern Peru and northern Argentina. The large-seeded wild form of *P. lunatus* extends in the Andean region from Cajamarca, Peru to Imbabura, Ecuador, and possibly into Colombia (Toro Chica *et al.*, 1993). In Ecuador and northern Peru, caducifoliolate forests become steppic (*Matorral*) due to low rainfall. This could suggest that large-seeded wild populations are best adapted to drier conditions. In addition, these populations are tolerant of lower temperature (T_m around 15°C). No wild populations have been collected in the