



REVIEW ARTICLE

ORIGIN, DISTRIBUTION, TAXONOMY, BOTANICAL DESCRIPTION, GENETICS AND CYTOGENETICS, GENETIC DIVERSITY AND BREEDING OF LIMA BEAN (*Phaseolus lunatus* L.)

K.R.M. Swamy

Retd. Principal Scientist & Head, Division of Vegetable Crops, ICAR-Indian institute of Horticultural Research, Bangalore-560089

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*Corresponding author: K.R.M. Swamy

ABSTRACT

Lima bean belongs to the family Fabaceae, subfamily Faboideae, genus *Phaseolus* and species *Phaseolus lunatus*. Lima beans or butter beans or sieva beans are some of the most common legumes that are consumed all over the world. The beans are actually the seeds of this plant, but their large size and dense nutrient profile make them an excellent sustenance crop. The larger varieties of these beans are typically lima beans, while smaller-seeded varieties are sieva beans, but they are actually the same species. Lima beans and fava beans (*Vicia faba*) have a somewhat similar appearance once they're both shelled and dried. However, fava bean pods are typically bumpy while lima bean pods are smooth. Lima beans also tend to be starchier with a more mild flavor than fava beans, which some say have a cheese-like taste. Lima beans, also known as butter beans, are a type of legume that belongs to the same family as common beans, such as kidney beans and black beans. They are named after Lima, a city in Peru, where the beans were first discovered and cultivated. Lima beans are characterized by their flat, kidney-shaped seeds and come in both a green and a cream-colored variety. *P. lunatus* is a fast-growing herbaceous vine, attaining up to 6 m in length, that can become weedy in the wild. It can rapidly colonize degraded areas and secondary vegetation forming dense thickets which displace native vegetation. In addition, *P. lunatus* has deep rooting, drought tolerance, and wide environmental adaptation, which are traits that help it to colonize new habitats including degraded and infertile areas. It has been listed as invasive in Cuba, Puerto Rico, Fiji, Philippines, New Caledonia, and New Zealand. In this review article on Origin, Domestication, Taxonomy, Botanical Description, Genetics and Cytogenetics, Genetic Diversity, Breeding of Lima Bean are discussed.

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INTRODUCTION

Lima bean belongs to the family Fabaceae, subfamily Faboideae, genus *Phaseolus* and species *Phaseolus lunatus* (Rojas-Sandoval and Acevedo-Rodríguez, 2015; Wikipedia, 2024). Lima beans or butter beans or sieva beans are some of the most common legumes that are consumed all over the world. The beans are actually the seeds of this plant, but their large size and dense nutrient profile make them an excellent sustenance crop. The larger varieties of these beans are typically lima beans, while smaller-seeded varieties are sieva beans, but they are actually the same species (Staughton, 2024). Lima beans and fava beans (*Vicia faba*) have a somewhat similar appearance once they're both shelled and dried. However, fava bean pods are typically bumpy while lima bean pods are smooth.

Lima beans also tend to be starchier with a more mild flavor than fava beans, which some say have a cheese-like taste (Iannotti, 2022). Lima beans, also known as butter beans, are a type of legume that belongs to the same family as common beans, such as kidney beans and black beans. They are named after Lima, a city in Peru, where the beans were first discovered and cultivated. Lima beans are characterized by their flat, kidney-shaped seeds and come in both a green and a cream-colored variety (Fareeha, 2024). *P. lunatus* is a fast-growing herbaceous vine, attaining up to 6 m in length, that can become weedy in the wild. It can rapidly colonize degraded areas and secondary vegetation forming dense thickets which displace native vegetation. In addition, *P. lunatus* has deep rooting, drought tolerance, and wide environmental adaptation, which are traits that help it to colonize new habitats including degraded and infertile areas. It has been listed as invasive in Cuba, Puerto Rico, Fiji,

Philippines, New Caledonia, and New Zealand (Rojas-Sandoval and Acevedo-Rodríguez, 2015). International Common Names (Rojas-Sandoval and Acevedo-Rodríguez, 2015) are in

English: bean (Lima), Burma bean, butter bean, haricot bean, Madagascar bean, sieva bean, sugar bean,

Spanish: frijol de luna, frijol lima, haba, habichuela, judía de Lima, Judion, pallar, poroto de Lima, poroto de manteca,

French : haricot de Lima, haricot du Cap, pois du Cap,
Chinese: mian dou,

Portuguese: fava-Belém, feijão-de-Lima,

India: bakla. Lima bean are also known as Lima bean, butter bean, sieva bean, sugar bean, Madagascar bean, butter bean, Java bean [English]; haricot de Lima, haricot du Cap, pois du Cap [French]; feijão de Lima, fava belém [Portuguese]; frijol de luna, haba lima, judía de Lima, pallar, garroñón, guaracaro [Spanish]; kacang kratok [Indonesian]; Limabohne, Mondbohne [German]; fagiolo di Lima [Italian]; pwachouk [Haitian Creole]; patani [Tagalog] (Heuzé *et al.*, 2015; Wikipedia, 2024). Common bean (*P. vulgaris*) and lima bean (*P. lunatus*) are the most important crop species from the genus *Phaseolus*. Both species have the same chromosome number ($2n = 22$) and previous cytogenetic mapping of BAC clones suggested conserved synteny. Nevertheless, karyotype differences were observed, suggesting structural rearrangements. In this study, comparative cytogenetic maps for chromosomes 3, 4 and 7 were built and the collinearity between the common bean and lima bean chromosomes was investigated. Thirty-two markers (30 BACs and 2 bacteriophages) from *P. vulgaris* were hybridized *in situ* on mitotic chromosomes from *P. lunatus*. Nine BACs revealed a repetitive DNA pattern with pericentromeric distribution and 23 markers showed unique signals. Nine of these markers were mapped on chromosome 3, eight on chromosome 4 and six on chromosome 7. The order and position of all analyzed BACs were similar between the two species, indicating a high level of macrocollinearity (Almeida and Pedrosa-Harand, 2013). Lima bean (*Phaseolus lunatus* L.) is an important source of protein for the human diet, especially in warmer and drier regions where common bean does not grow well. This species is very similar to the common bean (*P. vulgaris* L.) in that both species share similar wild distribution and domestication in two independent regions: Andean and Mesoamerican. Both species have $2n = 22$, similar genome sizes (637 Mbp in *P. vulgaris* and 622 Mbp in *P. lunatus*) and a predominance of metacentric and submetacentric chromosomes. Differences in chromosomemorphology have led to the suggestion that rearrangements such as inversions, duplications and translocations have occurred in the genus (Almeida and Pedrosa-Harand, 2013). In this review article on Origin, Domestication, Taxonomy, Botanical Description, Genetics and Cytogenetics, Genetic Diversity, Breeding of Lima Bean are discussed.

ORIGIN AND DISTRIBUTION

Columbus on his first voyage of discovery found beans under intensive cultivation by the Indians in Cuba.

Other early Spanish explorers likewise encountered cultivated beans. English and French explorers, following the Spanish, found beans along the whole Atlantic Coast as far north as Virginia. The lima bean, however, appeared to be restricted to the area south of the Potomac River in Virginia, where it is still found in close resemblance to the original primitive forms of the inhabited islands of the West Indies, Brazil, Colombia, Peru, Central America, the western coast of Mexico, and northward to the Hopi pueblos in the southwestern United States. The antiquity of these lima beans is further confirmed by the extensive discoveries of large lima beans of various colors in the tombs of ancient Peruvian cultures and in excavations of pre-Columbian ruins of the southwestern agricultural Indians. It is evident from the records of explorers and botanists that the lima beans have been distributed by man. From these early bean cultures, the lima beans have escaped into the jungles and have established themselves in a wild state where they are recovered at the present time. In North and South America these escaped lima beans are undoubtedly of pre-Columbian origin, but similar escapes are found throughout the world in tropical countries where they have been introduced in post-Columbian times. The origin of the lima bean has been confused. The origin of the large lima has been placed in the Amazon Valley by Bentham and accepted by deCandolle in his studies on the origin of cultivated plants (Mackie, 1943).

Lima bean, has been domesticated at least twice in the Americas, once in the Andean region and at another time in Mesoamerica; however, the domestication history of this crop in the latter region remains unclear. A phylogeographic analysis of DNA polymorphisms in the internal transcribed spacer (ITS) region of the ribosomal DNA from a collection of wild and domesticated accessions was applied to establish where and how many times in Mesoamerica Lima bean was domesticated. The results showed evidence for two wild Mesoamerican gene pools with contrasting geographical distributions. While the MI gene pool occurs in central western Mexico, including the Pacific coastal range, the MII gene pool is widespread and occurs toward

the Gulf of Mexico, the Yucatan peninsula, and Central and South America. In a cluster analysis, all Mesoamerican landraces clustered together with wild accessions from the MI gene pool (L haplotype) suggesting a unique domestication event in central western Mexico. The most likely domestication region is an area of the states of Nayarit–Jalisco or Guerrero–Oaxaca and not areas such as the Peninsula of Yucatan where the crop is currently widespread and diverse (Serrano-Serrano *et al.*, 2012).

The genus *Phaseolus* comprises about 105 species, mostly distributed across the Americas. The species *Phaseolus lunatus* has a Neotropical origin with at least two centres of domestication (Gutiérrez-Salgado *et al.*, 1995): 1. Central America (Mexico through Guatemala) for the small-seeded types. 2. South America (mainly Peru) for the large-seeded types. This distinction coincides with a classification into two types: Mesoamerican and Andean, based on morphological, ecological, protein and molecular characters. The Andean wild populations have a very limited geographic distribution (Ecuador and northern Peru), while the Mesoamerican wild types extend from Mexico to Argentina through the east side

of the Andes. Recent discoveries have led to the proposition of three primary centres of genetic diversity, two of which are also domestication centres: (1) a centre of genetic diversity and domestication on the western slope of the Andes in southern Ecuador and northern Peru; (2) a centre of genetic diversity and domestication in Central America; and (3) a centre of genetic diversity in the region covering northern Peru, northern Colombia, northern Ecuador and western Venezuela. Currently, wild and cultivated types have been distinguished as *P. lunatus* var. *silvester* and *P. lunatus* var. *lunatus*, respectively. Within the cultivated types three cultivar groups have been distinguished: 1. Sieva Group with medium-sized flat seeds. 2. Potato Group with small globular seeds, also known as Fordhook types. 3. Big Lima Group with large flat seeds (Rojas-Sandoval and Acevedo-Rodríguez, 2015).

P. lunatus is native to tropical and subtropical America, from northern Mexico to southern Argentina and Paraguay. It has been widely cultivated around the world and can now be found cultivated and naturalized in the West Indies, Asia, Africa, Europe, and on several islands in the Pacific Ocean (Rojas-Sandoval and Acevedo-Rodríguez, 2015). *P. lunatus* has been widely cultivated in tropical and subtropical regions of the world, facilitating its establishment and naturalization. In post-Columbian times, this species spread throughout the Americas. Spaniards took seeds across the Pacific to the Philippines and from there it spread to other parts of Asia, mainly Java, Myanmar, and to Mauritius. The slave trade introduced *P. lunatus* from Brazil into Africa, particularly to the western and central parts. Some large-seeded types from the Peruvian coast were distributed to south-western Madagascar and southern California. Currently, the USA is the largest producer of Lima bean with about 21,000 ha under cultivation (mainly in California, Delaware, Maryland, and Wisconsin) (Rojas-Sandoval and Acevedo-Rodríguez, 2015).

Lima bean originated from Guatemala, Mexico and Peru. Once domesticated, it spread throughout the Americas, and the Spaniards imported it to the Pacific Islands and the Philippines. It later spread to South-East Asia while the slave trade resulted in the introduction of the lima bean to Western and Central Africa. Lima bean is now widely naturalized in the tropics. It is found in humid, sub-humid and semi-arid tropical climates as well as warm temperate climates. In humid climates, lima bean is often intercropped with cereal crops, root crops or other crops, while in drier climates it tends to be used as sole crop (Heuzé *et al.*, 2015). Lima bean is believed to be originated in the general area of Guatemala, Mexico and Peru. The distribution routes were from the Pacific foothills of Mexico, through the Central and South Americas to Southern Canada. It was later spread to Southern Asia and through the slave trade, extended to West and Central Africa. It was asserted that Lima bean entered the African continent through the Portuguese explorers, particularly to the Central and Western parts of Africa from Brazil during the slave trade (Nasir *et al.*, 2021). The domestication process in lima bean involves two independent events, within the Mesoamerican and Andean gene pools. This makes lima bean an excellent model to understand convergent evolution. The mechanisms of adaptation followed by Mesoamerican and Andean landraces are largely unknown. Genes related to these adaptations can be selected by identification of selective sweeps within gene pools. Previous genetic analyses in lima bean have relied on

Single Nucleotide Polymorphism (SNP) loci, and have ignored transposable elements (TEs). Here we show the analysis of whole-genome sequencing data from 61 lima bean accessions to characterize a genomic variation database including TEs and SNPs, to associate selective sweeps with variable TEs and to predict candidate domestication genes. A small percentage of genes under selection are shared among gene pools, suggesting that domestication followed different genetic avenues in both gene pools. About 75% of TEs are located close to genes, which shows their potential to affect gene functions. The genetic structure inferred from variable TEs is consistent with that obtained from SNP markers, suggesting that TE dynamics can be related to the demographic history of wild and domesticated lima bean and its adaptive processes, in particular selection processes during domestication (Lozano-Arce *et al.*, 2023).

Lima beans, also known as butter beans, have a fascinating history that dates back thousands of years. These legumes are believed to have originated in South America, specifically in the region that is now Peru. The name "Lima" actually comes from the capital city of Peru, where the beans were first discovered. Archaeological evidence suggests that lima beans were cultivated by the indigenous people of Peru as early as 6000 BC. They were an important staple in their diet, providing a rich source of protein, fiber, and essential nutrients. Over time, lima beans spread to other parts of the world through trade and exploration. During the 16th century, Spanish explorers brought lima beans to Europe, where they quickly gained popularity. They were embraced for their versatility and nutritional value. From Europe, lima beans made their way to other continents, including Africa and Asia, becoming a beloved ingredient in various cuisines (Savory Suitcase, 2023).

Lima bean is one of the five species of the genus *Phaseolus* that was domesticated in the Americas. The species is composed of wild (*P. lunatus* var. *silvester*) and domesticated populations (*P. lunatus* var. *lunatus*). Although most of the *Phaseolus* species originated in Mesoamerica, DNA molecular markers indicate that wild Lima bean originated in the northern Andes. Phylogeographic studies also suggest that wild Lima bean experienced a process of range fragmentation, that lead to the migration of the species into Mesoamerica and the eastern slope of the central-southern Andes to reach its current widespread distribution from northern Mexico to northern Argentina. Given their geographic and environmental widespread distribution, wild Lima beans display a large range of ecological adaptations that go from semiarid to humid areas and from hot regions at low elevation in Central America to cooler regions at high elevation in the Andes. The populations of domesticated Lima beans also show a wide range of ecological adaptations and therefore are an important genetic resource that will enable adaptation to current and future challenges associated to climate change. To better understand the importance of Lima bean genetic resources, it was assembled the first genome of Lima bean that was collected from a landrace in Colombia. Additionally, they performed a comprehensive analysis based on a large set of SNP markers derived from GBS (Genotyping-by-Sequencing) data, for almost 500 wild and domesticated accessions. These and previous analyses have shown that wild Lima bean is

structured into four non-overlapping major gene pools: i) the Mesoamerican MI pool at the northern end of the distribution range mainly in northern and central-western Mexico, ii) the Mesoamerican MII pool distributed from southern Mexico to northern Argentina, iii) the Andean AI pool restricted to the western slope of the Andes of Ecuador-northern Peru, and iv) the Andean AII pool found in central Colombia. Understanding the phylogeography of wild Lima bean has also improved understanding of its domestication process. Molecular markers confirm that Lima bean underwent two independent domestication events. One domestication occurred from the AI gene pool and gave rise to the large-seeded Andean landraces known as "Big Lima". Another domestication occurred in central-western Mexico from the MI gene pool and gave rise to the small-seeded Mesoamerican landraces known as "Sieva" and "Potato". Demographic inferences based on GBS data indicated that the genetic bottleneck due to domestication was stronger during the Mesoamerican than in the Andean domestication. Although Lima bean was domesticated twice, the Mesoamerican and Andean landraces show phenotypic convergence in traits related to the domestication syndrome such as loss of pod dehiscence (the natural seed dispersal mechanism), pod and seed gigantism, loss of seed dormancy, increased yield, changes in growth habit, and phenology, among others (Martínez-Castillo *et al.*, 2023).

Phaseolus lunatus is found in Meso- and South America. Two gene pools of cultivated lima beans point to independent domestication events. The Mesoamerican lima bean is distributed in neotropical lowlands, while the other is found in the western Andes. They were discovered in Peru and may have been the first plant that was brought up under civilization by the native farmers. The Andes domestication took place around 2000 BC and produced a large-seeded variety (lima type), while the second, taking place in Mesoamerica around 800 AD, produced a small-seeded variety (Sieva type). By around 1300, cultivation had spread north of the Rio Grande, and, in the 1500s, the plant began to be cultivated in the Old World. The small-seeded (Sieva) type is found distributed from Mexico to Argentina, generally below 1,600 m (5,200 ft) above sea level, while the large-seeded wild form (lima type) is found distributed in the north of Peru, from 320 to 2,030 m (1,050 to 6,660 ft) above sea level (Wikipedia, 2024). The origin of the lima bean has been studied for quite some time. In a 1943 publication Mackie described the plant originating from the jungles of Guatemala and to have descended into three lines: "(1) the Hopi, or northern branch, (2) the Carib, or West Indies, branch and (3) the Inca, or southern, branch" (Marsh, 2024). These important beans are believed to have been cultivated in South America as long as 4,000 years ago, and then at other times throughout history in North and Central America. This has resulted in these beans being a staple crop for indigenous people, and a relatively easy crop to cultivate, even in harsh conditions (Staughton, 2024). Archaeological excavation on the coast of Peru unearthed proof that *Phaseolus vulgaris* and *P. lunatus* were cultivated in the Americas since pre-Columbian times. Lima beans themselves were important to the Incan diet. Ceramics and woven textiles from ancient Peruvians are known to depict the lima bean. The capital city of Peru, Lima, is named after this bean. The small-seeded types, also called sieva beans, are native to Mexico and Central America, and appear in the

archeological record around 800 A.D. Large-seeded types are from the Andes of South America, carbon dated back 3,500 years (Allaire and Brady, 2024).

TAXONOMY

Lima bean belongs to the family Fabaceae, subfamily Faboideae, genus *Phaseolus* and species *Phaseolus lunatus* (Rojas-Sandoval and Acevedo-Rodríguez, 2015; Wikipedia, 2024). Lima bean is composed of two botanical varieties: var. *silvester* for the wild material and var. *lunatus* for the domesticated one. Studies have indicated the existence of three major gene pools: One Andean gene pool (A) and two Mesoamerican gene pools (MI and MII); with one domestication event in each of them: 1) for A, the mid-altitude western valleys between Ecuador and Peru in South America; 2) the central eastern region from Mexico for MI; and 3) the region located between Guatemala and Costa Rica for MII. Recent evidence from microsatellite markers have suggested another possible domestication event in South America, but lack of wild lima bean collections from South America limits explore this hypothesis. Within the var. *lunatus*, the existence of three cultigroups: 1) Sieva, with medium-sized and flat seeds; 2) Potato, with small globular seeds; and 3) Big lima, with large flat seeds. Big Lima represents the A gene pool, while Sieva and Potato represent the MI and MII gene pools. Lima bean has a high level of polymorphism, mainly related to seed traits. This aspect was firstly used to recognize the main gene pools and later to characterize the genetic diversity of this species. As a crop, lima bean is the second most important legume of the genus *Phaseolus* on the world. It is an important source of protein for rural populations in South America and Africa. In Brazil, lima bean is known as fava, favabelém or feijão-de-lima, and it has considerable importance in the Northeast of Brazil, where it is used as a food and an alternative income source for the local population. Collections obtained from Brazil have shown that the genetic diversity, reflected in the number of landraces and morphological variation of seed, could be as high as that reported in the Yucatan Peninsula, a region considered as a center of diversity for the Mesoamerican gene pool (Silva *et al.*, 2017).

According to the taxonomy, the bean belongs to the genus *Phaseolus*, which includes approximately 35 species of which 4 are cultivated: *P. vulgaris* L.; *P. lunatus* L.; *P. coccineus* L., and *P. acutifolius* L. (Arias-Restrepo *et al.* 2007). *Phaseolus lunatus* L. belongs to the Fabaceae family, and there are two domesticated genetic stocks from two different wild forms with two seed morphologies, small and large. The small seeds are known as *ib.*, patashete and futuna (Yucatan, Chiapas, and Jalapa, Mexico, respectively), caballero bean (Cuba), ixtapacal (Guatemala), chilipuca (El Salvador), haba (Puerto Rico and Panama), sieva and comba (Colombia), and guaracaro (Venezuela), among others. The large seeds are known as lima, layo and pallar (Peru), torta (Colombia), palato (Bolivia), and manteotto (Argentina) (Sandoval-Peraza *et al.*, 2020). Morpho-agronomic characterization studies aiming at the discrimination and classification of lima bean accessions in relation to the centers of domestication and biological status have been of great importance for conserving the biodiversity of this species. For this purpose, researchers have widely used the multivariate analysis called discriminant analysis, which is not always capable of producing satisfactory results.

Computational intelligence-based classifiers are additional tools for understanding complex classification problems. In this study, the objective was to test the use of the decision tree in the classification of lima bean according to the centers of domestication and biological status (cultivated and wild), based on eight phenotypic traits of the seed. Sixty accessions of lima bean from the *Phaseolus* Germplasm Bank of Universidade Federal do Piauí (BGP / UFPI) were evaluated, and classification was performed using two approaches: conventional statistics with discriminant analysis of principal components (DAPC) and computational intelligence through decision tree (DT). The results showed that the use of DT was efficient to identify patterns in the classification of lima bean accessions, due to its comprehensibility. Seed weight was one of the main descriptors used to explain the origin and diversity of the species. The results found will be useful for studies that involve the conservation of genetic resources, mainly for the maintenance of germplasm banks and in breeding programs. In addition, it is recommended to integrate machine learning algorithms in studies aimed at classifying lima bean (Almeida *et al.*, 2021).

The species *Phaseolus lunatus* L., popularly referred to as lima beans, can be found in the form of two botanical varieties: *P. lunatus* var. *lunatus*, which includes domesticated populations, and *P. lunatus* var. *silvester*, made up of wild populations. Classification of this species is carried out according to its geographical origin and seed characteristics. Studies conducted from the chloroplast DNA of 109 lima bean accessions, pointed to two major domestication centers: 1) Andean (A), located in Ecuador and northern Peru, in which the plants have large seeds and are adapted to high altitudes; and 2) Mesoamerican (M), which extends from central-western Mexico to Honduras, where plants have small seeds and occur at lower altitudes. Discrimination of populations has been of great importance for biodiversity conservation and the development of breeding programs. Thus, analyses of genetic diversity, through phenotypic or genetic characteristics, have guided the choice of appropriate parents in breeding programs, leading to the optimization of selective gains, due to the variability found in the offspring of crosses between divergent groups (Almeida *et al.*, 2021). The lima bean is a domesticated species of economic and cultural importance worldwide, especially in Mexico. The species has two varieties. The wild variety is *silvester* and the domesticated one is *lunatus*. Like many beans, raw lima beans are toxic (containing *e.g.* phytohaemagglutinin) if not boiled for at least 10 minutes. Canned beans can be eaten without having to be boiled first, as they are pre-cooked. The lima bean can contain anti-nutrients like phytic acids, saponin, oxalate, tannin, and trypsin inhibitor. These inhibit absorption of nutrients in animals and can cause damage to some organs. In addition to boiling, methods of roasting, pressure cooking, soaking, and germination can also reduce the antinutrients significantly (Wikipedia, 2024).

Other Scientific Names are (Rojas-Sandoval and Acevedo-Rodríguez, 2015):

Dolichos tonkinensis Bui-Quang-Chieu
Phaseolus bipunctatus Jacq.
Phaseolus ilocanus Blanco
Phaseolus inamoenus L.
Phaseolus limensis Macfad.

Phaseolus limensis var. *limenanus*
Phaseolus lunatus var. *macrocarpus* (Moench) Benth.
Phaseolus macrocarpus Moench
Phaseolus portoricensis Spreng.
Phaseolus puberulus Kunth
Phaseolus rosei Piper
Phaseolus saccharatus Macfad.
Phaseolus tunkinensis Lour.
Phaseolus vexillatus sensu Blanco, non L.
Phaseolus viridis Piper
Phaseolus vulgaris sensu Blanco, non L.
Phaseolus xuaresii Zuccagni

Synonyms asre (Heuzé *et al.*, 2015):

- **Phaseolus falcatus** Benth. ex Hemsl., nom. nud.,
- **Phaseolus inamoenus** L.,
- **Phaseolus limensis** Macfad.,
- **Phaseolus lunatus** var. **lunatus**,
- **Phaseolus lunatus** var. **macrocarpus** (Moench) Benth.,
- **Phaseolus lunatus** var. **silvester** Baudet,
- **Phaseolus macrocarpus** Moench,
- **Phaseolus tunkinensis** Lour., **Phaseolus viridis** Piper.

Synonyms are (Wikipedia, 2024)

- *Dolichos tonkinensis* Bui-Quang-Chieu
- *Phaseolus bipunctatus* Jacq.
- *Phaseolus ilocanus* Blanco
- *Phaseolus inamoenus* L.
- *Phaseolus limensis* Macfad.
- *Phaseolus lunatus* var. *macrocarpus* (Moench) Benth.
- *Phaseolus macrocarpus* Moench
- *Phaseolus portoricensis* Spreng.
- *Phaseolus puberulus* Kunth
- *Phaseolus rosei* Piper
- *Phaseolus saccharatus* Macfad.
- *Phaseolus tunkinensis* Lour.
- *Phaseolus vexillatus* Blanco, nom, illeg, non L.
- *Phaseolus viridis* Piper
- *Phaseolus xuaresii* Zuccagni.

BOTANICAL DESCRIPTION

Life cycle lima bean: The seed of a lima bean plant is that lima bean itself. You can cook and eat it, but if you wish, you can plant it and give yourself a crop of lima beans for future use. Germination begins when the bean (we'll refer to it as a seed from here on) soaks up some water. Water acts as a catalyst, as its presence triggers the release of gibberellins. These hormones regulate how a plant grows, and at this stage of the lima bean's germination, the gibberellin hormones encourage the seed to produce a radicle root. Ideal germination conditions include a soil temperature of between 23°-29° C. The radicle root is an embryonic element of the seed. In this incarnation, it won't play a large role in the life of the mature plant, but immediately following germination, it will stretch out into the soil to absorb more water. The radicle root will eventually grow to become the plant's root system, but it's no more a root system at this point than a stack of uncut wood is a coffee table— things need to happen for it to develop into that. The hypocotyl stem is the first indication of something

breaking through the soil and reaching up for the sunlight. This tiny stem is the lima bean plant's first shoot. The hypocotyl stem bears little resemblance to the plant that will eventually appear after maturation. However, as it lifts the first couple of cotyledon leaves toward the sky, it's critical to the plant's development. These leaves are often called "seed leaves" because they survive largely on nourishment from the seed, much as a fetus draws nourishment from the placenta. Cotyledon leaves act as solar panels for the burgeoning plant, giving the seed and the hypocotyl stem energy so they can produce the larger leaves we expect to see on a lima bean plant. The following stage of the life cycle of the lima bean is flowering. Once a more mature stem has grown and larger leaves have sprouted, the lima bean plant has full access to the nutrients in the soil and water around it, and it is fully capable of photosynthesis. It becomes a mature plant when it begins producing flowers. Flowers contain a stamen and pistil—the flower's male and female reproductive. Once these appear and mature, the lima bean plant can get pollinated. Following successful pollination, the flower will eventually wither and fall to the ground as bean pods begin to grow. These bean pods are why you planted your lima bean plant in the first place, as they produce seeds, also known as beans. An adult lima bean plant producing seeds is said to be fruiting, meaning it's bearing fruit (in this case, lima beans). If the beans get harvested, then they probably get eaten. If they don't get harvested, they can fall from the flower and into the soil, where they can sprout and begin creating another lima bean plant (Fig. 1 and 2) (Staff Writers, 2022).

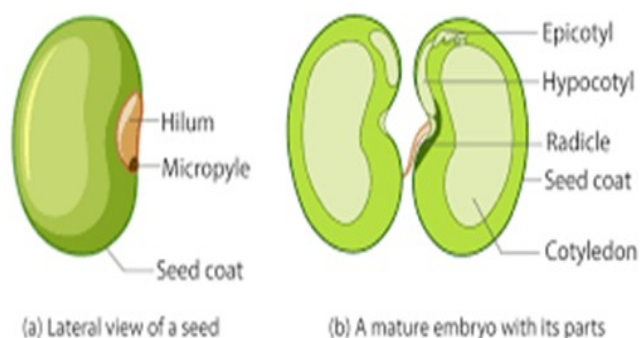


Fig. 1. Parts of Lima bean seed

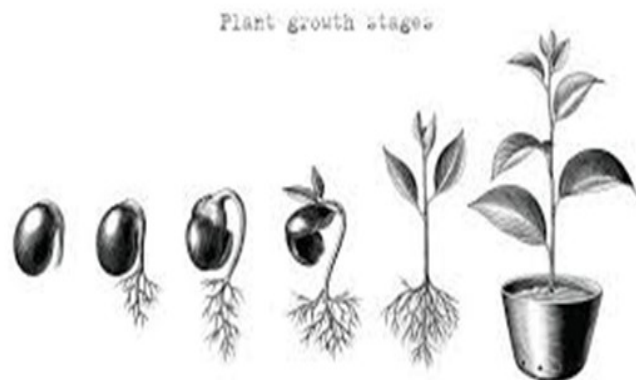


Fig. 2. Plant growth stages

Herbaceous vine, twining, attaining 5-6 m in length. Stems obtuse-pentagonal or cylindrical, puberulent. Leaves alternate, trifoliolate; leaflets chartaceous, the apex acute or short-

acuminate, the margins sinuate; upper surface dark green, dull, glabrous, with slightly prominent venation; lower surface pale green or glaucous, glabrous, with the primary and secondary venation prominent; terminal leaflet 5.5-11 × 3.5-7.5 cm, rhombic or deltate, the base cuneate or truncate; lateral leaflets asymmetrically deltate, the base truncate; petiolules thickened, 3-5 mm long, pubescent; rachis 1.5-2.5 cm long; petioles 6.5-9 cm long, sulcate, puberulent, the base slightly broadened. Inflorescences of axillary pseudoracemes, erect, 3-30 cm long, the flowers in groups of 2 per node of the inflorescence; pedicels 6-9 mm long, pilose; bracteoles minute, oblong. Calyx 2-2.5 mm long, green, campanulate, pilose, the sepals deltate, subequal; corolla white or lilac, pink or bluish, the standard semicircular, 7-10 mm long, abaxially pilose, the wings obovate, unguiculate, as long as the standard, the keel spirally twisted, ca. 1 cm long; stamens 10, diadelphous, the vexillar stamen broadened at the base; ovary with hispidulous pubescence, intermingled with uncinat hairs. Fruit an oblong-falcate legume or in the form of a half-moon, flattened, 5-7 × 1-2 cm, puberulent with uncinat hairs or glabrescent, dehiscent by valves that open in a spiral containing 2-4 seeds. Seeds reniform, flattened, approximately 7 mm long, reddish brown, with dark spots (Rojas-Sandoval and Acevedo-Rodríguez, 2015).

Lima bean is a tropical and subtropical legume cultivated for its edible seeds. There are wild and cultivated types of *Phaseolus lunatus*, generally referred to as *Phaseolus lunatus* var. *silvester* Baudet and *Phaseolus lunatus* var. *Lunatus* respectively. Lima bean is a herbaceous plant with two main types of growth habit. The perennial form is an indeterminate, vigorous, climbing and trailing plant, up to 2-6 m tall, with axillary flowering only. It has swollen and fleshy roots up to 2 m long. Annual lima bean is a pseudo-determinate, bushy plant, 0.3-0.9 m tall with both terminal and axillary flowering. It has thin roots. The stems may be up to 4.5-8 m long. The leaves are alternate and trifoliolate with ovate leaflets, 3-19.5 cm long x 1-11 cm broad. Inflorescences are 15 cm long and bear 24 white or violet bisexual flowers. The fruits are 5-12 cm long, dehiscent pods with 2 to 4 seeds. Seeds are very variable in size, shape and colour. Cultivar groups have been distinguished according to seed differences (Heuzé *et al.*, 2015). Botanical description of Lima bean is given in Fig. 3.

Floral biology: The white or cream-colored, legume-type flower of the lima bean is borne at the end of a pedicel on a 2 to 4 inch-long raceme. Usually, only a small percentage of the flowers on a raceme set. Various reasons for this failure have been given, including high temperature and low humidity, improper soil moisture, and inadequate pollination. In the flower itself, the keel is elongated into a spirally twisting beak. The style, which follows the spirals of the keel, is also twisted. It is bearded below the stigma. The stigma, and a portion of the spirally twisted style with pollen adhering to the brush of hairs, projects from the tip of the keel petal when this is depressed and returns again when the pressure is removed. The anthers surround the style and shed their pollen upon it, but the stigma is never dusted before it is exerted. If the stigma is pollinated by the insect visitor before it is touched by its own pollen, cross-pollination can result. Anthesis occurs between 7 and 8 a.m. The flower never closes, but the corolla is shed after a few days.














		
Sowing	Grminated seed	Grminated seed
		
Field	Field	Field
		
Flowers and pods	Flowers	Flowers
		
Pods	Pods	Pods
		
Pods	Pods	Pods
		
Pods and seeds	Pods and seeds	Seed pods

Fig. 3. Botanical description

Nectar is secreted at the base of the corolla and is the source of a fine quality honey. Bees also visit the plant for its pollen. Nectar secretion seems to be greatest when plants first come into bloom, and it remains intense for about a week - then tapers off (Fig. 4) (LSA, 2024).

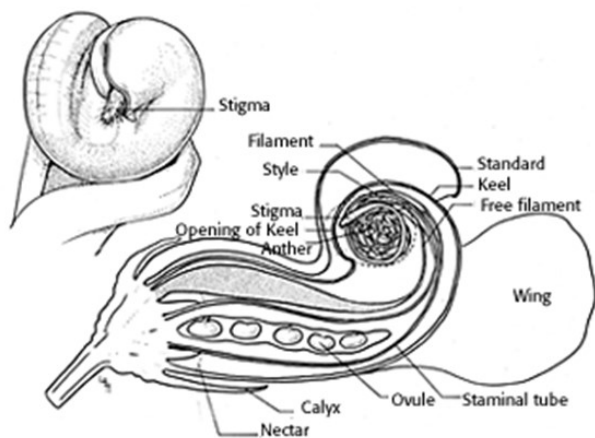


Fig. 4. Parts of flower of Lima bean

Pollination: *P. lunatus* is a bisexual species in which autogamy is favoured by the synchronized maturity of pollen grains and stigma in its flowers, as well as the proximity within the bud. However, outcrossing rates of 0.02% up to 48% have been reported, depending on genotype, growth conditions, distance between plants, wind direction, and local pollinating insect populations. In Puerto Rico, *P. lunatus* has been collected in flower and fruit from December to June. *P. lunatus* has both photoperiod-insensitive types that flower in day-lengths up to 18 hours, and short-day types that require a day-length as short as 11–12.5 hours to initiate flowers (Rojas-Sandoval and Acevedo-Rodríguez, 2015). Lima bean plants are self-pollinated (Iannotti, 2022). Pollination is a vital process in the reproduction of plants, including lima beans. It is the transfer of pollen from the male reproductive organ (stamen) to the female reproductive organ (pistil). While lima beans are typically self-pollinating, it doesn't hurt to lend nature a helping hand to ensure a bountiful harvest. In this article, we will discuss the importance of pollination for lima bean plants and provide you with steps on how to pollinate them effectively. Pollination plays a crucial role in the development of lima beans. Without proper pollination, plants may produce fewer pods or fail to bear any fruit altogether. Lima beans are primarily self-pollinating, meaning they have both male and female reproductive organs within each flower. However, external factors such as lack of pollinators or adverse weather conditions can hinder successful pollination. By manually pollinating your lima bean plants, you can increase the chances of achieving a higher yield. Before we delve into the process of pollination, it's important to distinguish between male and female flowers on lima bean plants. Male flowers have long, slender stalks called stamens that contain pollen. Female flowers have shorter stalks called pistils, which lead to the ovary where pod development occurs (PLB, 2023).

Choose a time when the weather conditions are favorable for pollination – preferably when there is little to no wind and the temperature is around 21–27°C. This will increase the chances of successful pollination. Keep an eye on your lima bean

plants as they start flowering. Look for open flowers that are ready for pollination. Male flowers typically appear before female flowers, so you may need to wait for the female flowers to fully develop. To manually pollinate lima bean plants, you will need to collect pollen from the male flowers. Gently tap the stamen of a male flower over a clean container to release the pollen. Alternatively, you can use a small brush or cotton swab to brush against the stamen and collect the pollen. Take the collected pollen and transfer it to the stigma of a female flower. The stigma is located at the top of the pistil. Gently brush or dab the pollen onto the stigma, ensuring good contact between the two. Continue collecting pollen from multiple male flowers and transferring it to different female flowers on your lima bean plants. This will increase cross-pollination and enhance your chances of a successful yield. After pollinating, it's important to protect your flowers from external factors that may interfere with pollination. Covering the plants with a fine mesh or using netting can keep unwanted insects away while still allowing airflow. Regularly monitor your lima bean plants after pollination. Ensure they receive adequate water, sunlight, and nutrients for optimal growth. Remove any damaged or diseased pods to prevent them from affecting other healthy pods (PLB, 2023).

GENETICS AND CYTOGENETICS

Knowledge of the genetics of the Lima bean is incomplete, although it remains a prerequisite for crop improvement. Studies conducted on North American varieties led to the identification of 23 monogenic plant and seed characters and four independent linkage groups. The characters and their genetic symbols are given by Baudoin. Inheritance of seed size has been diversely interpreted by many authors. Results reflect an intricate system of genotype × environment interaction, seed size acting as a component in the adaptive value of the genotypes within a population. Two dominant gametophytic factors were identified preventing self-fertilization by inhibiting pollen tube growth on incompatible stylar tissue. Although screenings have demonstrated considerable genetic diversity for photoperiod reactions and many yield components (number of racemes and pods per plant, plant size or vigour, growth duration, root/top ratio, leaf shape, days to first flowers, length of pod-filling period, seed size), no studies of inheritance have been undertaken with these attributes. However, variability differs according to the growth habit. Determinate bush forms show little diversity for erectness, branching pattern and growth duration. In contrast, indeterminate prostrate or climber forms which predominate particularly in the tropics show a wide range of diversity. In trials conducted in Nigeria with climbing varieties, dry-seed production was positively correlated with number of pods per plant, threshing percentage and number of seeds or ovules per pod. The yield was, however, negatively correlated with earliness in flowering and maturity, seed and pod size, and 100-seed weight. The negative correlations were attributed to the poor performance of the large-seeded forms (Big Lima) in a savannah region of Nigeria where the trials were carried out. Molecular markers are very useful for a better understanding of the genetic organization of the whole gene pool and for crop breeding. Investigations have been undertaken with *P. lunatus*. Up to now results based on electrophoresis of seed storage proteins revealed two major patterns: a Central American pattern extending from Mexico to Argentina along the eastern

slopes of the Andes, and an Andean pattern prevailing in Peru and Ecuador. Big Lima seed morphotype is frequently associated with the Andean pattern, while the Sieva and Potato morphotypes are associated with the Central American pattern. These data support the idea of separate domestications of the crop. They also open new directions for genetic improvement, focusing the efforts to assess the total genetic diversity and divergence both within and between the subgene pools (Baudoin, 1993).

The common bean (*Phaseolus vulgaris*) and lima bean (*P. lunatus*) are among the most important legumes in terms of direct human consumption. The present work establishes a comparative cytogenetic map of *P. lunatus*, using previously mapped markers from *P. vulgaris*, in association with analyses of heterochromatin distribution using the fluorochromes chromomycin A3 (CMA) and 4',6-diamidino-2-phenylindole (DAPI) and localization of the 5S and 45S ribosomal DNA (rDNA) probes. Seven BACs selected from different common bean chromosomes demonstrated a repetitive pericentromeric pattern corresponding to the heterochromatic regions revealed by CMA/DAPI and could not be mapped. The subtelomeric repetitive pattern observed for BAC 63H6 in most of the chromosome ends of common bean was not detected in lima bean, indicating lack of conservation of this subtelomeric repeat. All chromosomes could be identified and 16 single-copy clones were mapped. These results showed a significant conservation of synteny between species, although change in centromere position suggested the occurrence of pericentric inversions on chromosomes 2, 9 and 10. The low number of structural rearrangements reflects the karyotypic stability of the genus (Bonifácio *et al.*, 2012). Lima bean is diploid ($2n=22$) and propagated by seed (Nasir *et al.*, 2021). Lima bean, one of the five domesticated *Phaseolus* bean crops, shows a wide range of ecological adaptations along its distribution range from Mexico to Argentina. These adaptations make it a promising crop for improving food security under predicted scenarios of climate change in Latin America and elsewhere. In this work, we combine long and short read sequencing technologies with a dense genetic map from a biparental population to obtain the chromosome-level genome assembly for Lima bean. Annotation of 28,326 gene models show high diversity among 1917 genes with conserved domains related to disease resistance. Structural comparison across 22,180 orthologs with common bean reveals high genome synteny and five large intrachromosomal rearrangements. Population genomic analyses show that wild Lima bean is organized into six clusters with mostly non-overlapping distributions and that Mesamerican landraces can be further subdivided into three subclusters. RNA-seq data reveal 4275 differentially expressed genes, which can be related to pod dehiscence and seed development. We expect the resources presented here to serve as a solid basis to achieve a comprehensive view of the degree of convergent evolution of *Phaseolus* species under domestication and provide tools and information for breeding for climate change resiliency (Garcia *et al.*, 2021). Lima and common bean are both diploid species ($2n=2x=22$ chromosomes; DNA: ~622 Mbp/1C) with high levels of homozygosity throughout their genomes because of predominant autogamy. Previous cytogenetic research confirms a high degree of synteny between the two species (Garcia *et al.*, 2021).

Lima bean is a crop that stands out for its economic and social importance throughout the world, including in Northeast Brazil. Evidence points to high levels of genetic diversity in this crop in this region. Monitoring the levels of genetic diversity in lima beans is necessary for predicting the possible processes of genetic erosion. In this study, we compared the genetic diversity of 12 lima bean genotypes collected in the 1980s with that of 42 genotypes collected in 2014–2016 in Northeast Brazil, using eight microsatellite loci (SSRs), to assess the occurrence of genetic erosion. The genetic diversity (H_E) for the genotypes collected in 2014–2016 ranged from 0.144 to 0.47, indicating a wide diversity among the lima bean germplasm cultivated in Northeast Brazil. The Garza–Williamson index showed values below 0.70 for both the periods (1980s and 2014–2016). Moreover, the results obtained suggest a recent genetic bottleneck for the 2014–2016 genotypes, which may be related to the management and production techniques used by farmers owing to the growing market demand for improved lima bean varieties in recent years (Lustosa-Silva *et al.*, 2022).

GENETIC DIVERSITY

It has a high degree of phenotypic variation for seed traits, which are important for understanding the genetic diversity and origin of this crop (Fig. 5) (Silva *et al.*, 2017). In Fig. 5 genetic variability for seed shape, color and size in Lima bean is given. Seed variation appears on their shape, size, color, and color pattern of the seed skin (Fig.6). Based on the size of the length, width, and thickness of the seeds the types of seed consist of four types of seeds. They are *big type* is the accession that belongs to the large seed group, the medium type that dominates in this grouping. It is divide into *medium-big type* and *small-medium type* and the last *small type*. The color of seeds and the color pattern of lima seeds showed a very high variation. In his research, the color that dominates is a brownish-yellow color and the second color is dark brown (Bria *et al.*, 2019).

The results of this study showed that lima seed shells have a primer color of seeds and a second color that forms a certain pattern. The primer color of the seeds varies widely are white, yellow, brown, maroon, purple-reddish, and black. The second color on the body of the beans that form the color pattern are white, dark brown and red. Color patterns formed in the form of lines, dots, stains/spots, and mixtures. Based on the morphological characteristics of the color and the color pattern that associated with the seed hilum areas in seed terminology, lima bean are grouped into three groups, (1) Plain seed (Fig. 7-A), seeds have one color only without any color patterns; (2) color with hilum seed (Fig. 7- B1,2,3), seeds have hilum eye is associated with other pattern parts in the presence of spots and points on the seed body; (3) color with unclear hilum (Fig. 7- B 4,5), seeds have unclear eyes with spots on the seed body (Bria *et al.*, 2019). Striking annual variations in seed size were shown by six populations of lima beans grown under optimal conditions in an apparently stable climate. The response of each population to each year was unique, indicating that the genotype of each population is affected differently by subtle environmental influences occurring in differing years.



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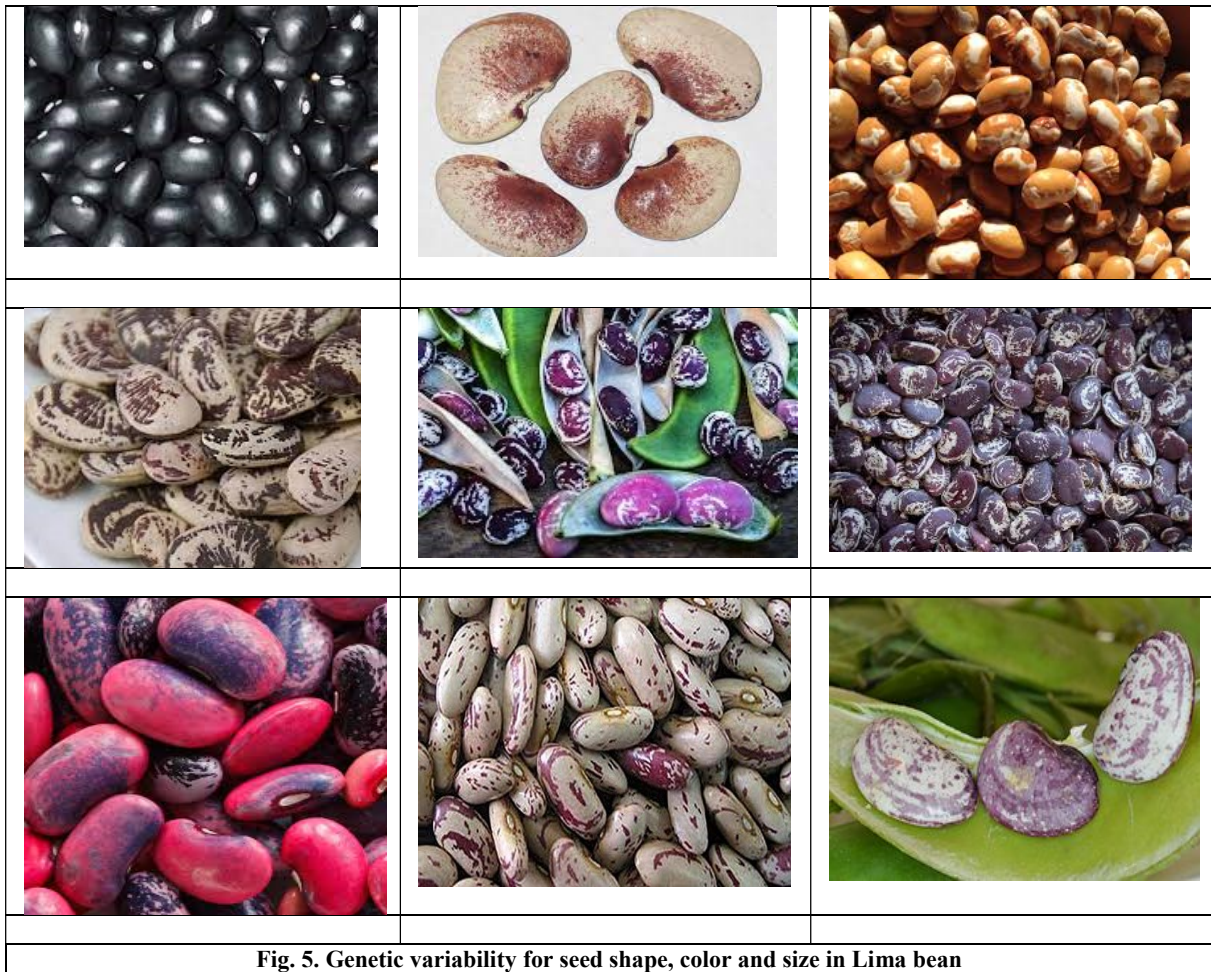


Fig. 5. Genetic variability for seed shape, color and size in Lima bean

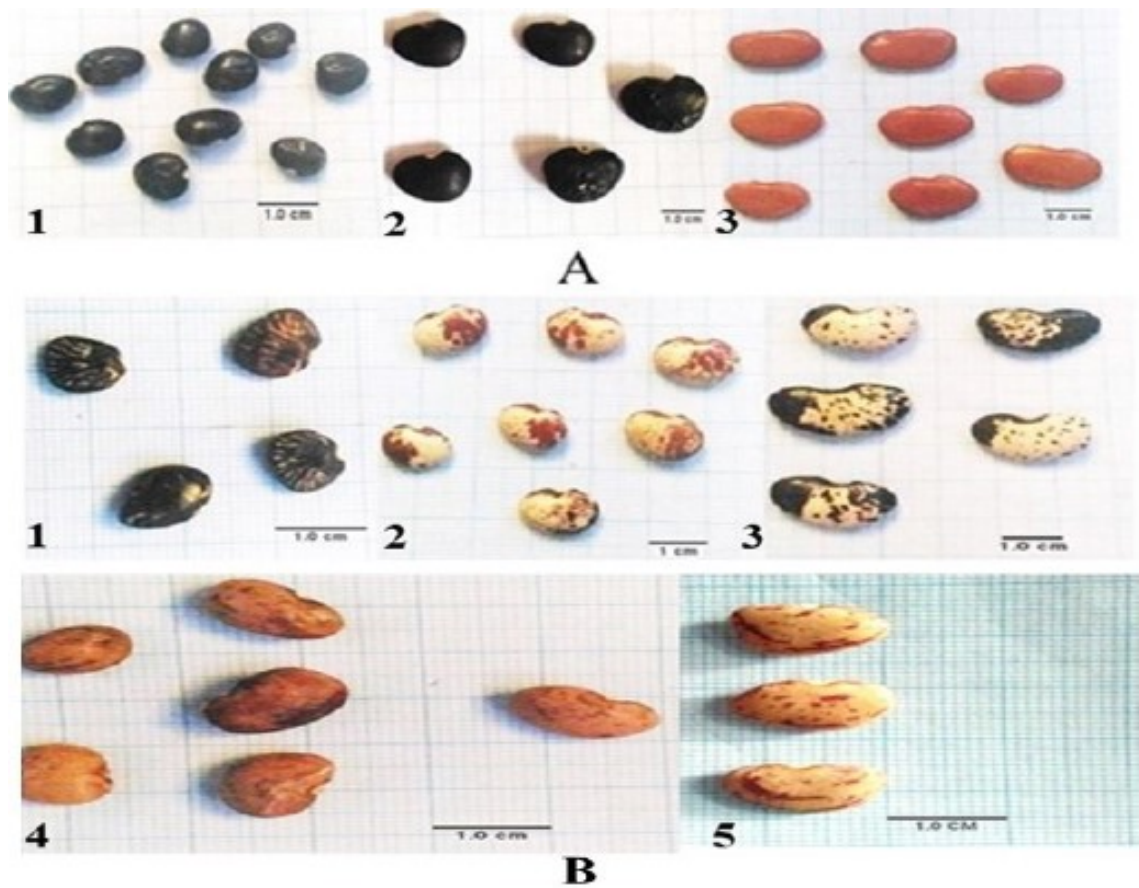


Fig.6. Variation of seed shape and color. (A) Seed without secondary color and pattern, (B) Seed with secondary color and pattern

Specific "genotypes", as identified by marker genes conditioning easily recognisable seed-coat colour differences, tended to behave similarly within each population. Occasional inconsistencies indicated that interactions with environment occurred between different "genotypes" within the same population. The seeding rates used produced moderate competition between plants within a population. However, when competition between plants is eliminated by wide spacing, seed size remains constant over years; *i.e.* genotypic-environmental interactions do not occur. Thus, even under an apparently constant environment, seed size in lima beans is a complex character made up of complicated interactions between genotype and micro-environment. There is some evidence that seed size is one of the components of fitness in lima beans. The apparently fortuitous seasonal fluctuations in seed size observed in this study may therefore be a mechanism contributing to genetic variance for fitness in populations of this species (Parsons and Allard, 1959).

It is a common observation that identical genotypes show drastic differences in phenotypic expression of quantitative characters when an organism is grown under widely different environmental conditions. More interesting to the evolutionist and breeder are such conspicuous fluctuations in phenotypic expression within apparently homogeneous environments. Genotypic-environmental interactions of this latter type, which presumably result from subtle but nevertheless important variations in micro-environment, have received increasing attention in recent years, both experimentally and analytically.

Striking annual variations in seed size were shown by six populations of lima beans grown under optimal conditions in an apparently stable climate. The response of each population to each year was unique, indicating that the genotype of each population is affected differently by subtle environmental influences occurring in differing years. Specific "genotypes", as identified by marker genes conditioning easily recognisable seed-coat colour differences, tended to behave similarly within each population. Occasional inconsistencies indicated that interactions with environment occurred between different "genotypes" within the same population. The seeding rates used produced moderate competition between plants within a population. However, when competition between plants is eliminated by wide spacing, seed size remains constant over years; *i.e.* genotypic-environmental interactions do not occur. Thus, even under an apparently constant environment, seed size in lima beans is a complex character made up of complicated interactions between genotype and micro-environment. There is some evidence that seed size is one of the components of fitness in lima beans. The apparently fortuitous seasonal fluctuations in seed size observed in this study may therefore be a mechanism contributing to genetic variance for fitness in populations of this species (Parsons and Allard, 1959). Lima bean is an important source of protein for people as it contributes all of the essential amino acids necessary for humans. In Brazil, lima bean has a great relevance, mainly in the Northeast, where it is an alternative income in addition to a food source. It has a high degree of phenotypic variation for seed traits, which are important for understanding the genetic diversity and origin of this crop.

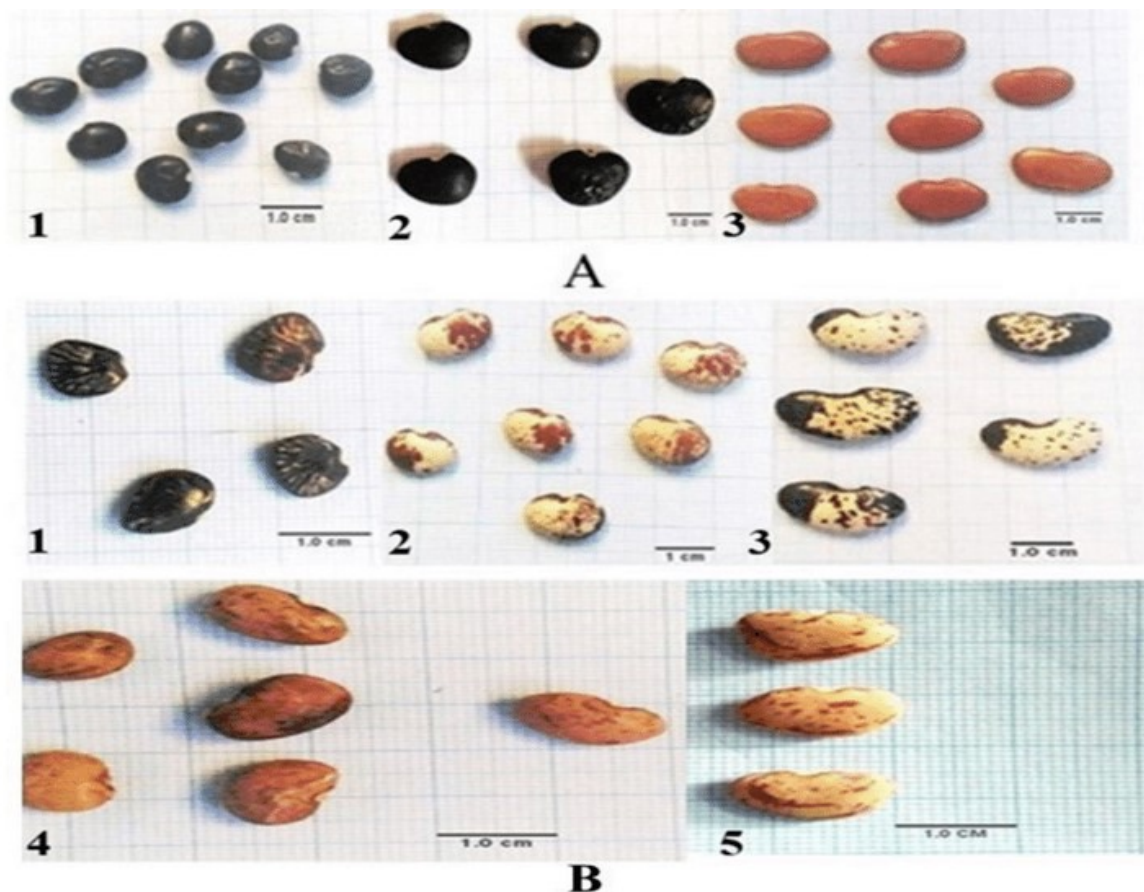


Fig. 7. Variation of seed shape and color in Lima bean (A) Seed without secondary color and pattern, (B) Seed with secondary color and pattern

We aimed to characterize 166 accessions of cultivated lima bean from Brazil using qualitative and quantitative descriptors through the Ward MLM (Modified Location Model) in order to analyze the organization of the genetic diversity and the origin of this germplasm. High genetic variability was detected and seed length and width characteristics were the main contributors to genetic divergence among the accessions. Results showed the presence of accessions with characteristics typical of the Mesoamerican and Andean gene pools, and another group with intermediate characteristics of these two gene pools. Our results will be useful to breeding programs, since currently there is little information on the genetic diversity and the origin of the lima bean landraces cultivated in Brazil (Silva *et al.*, 2017).

Lima bean is a species of beans which originating from the regions of Central America and Andes Mountains. Lima bean in Timor Island is underutilized although these plant growth there and have many variations. This study aims to determine the diversity of lima beans on Timor Island based on morphological characters. Samples were collected by survey methods from three districts on the island of Timor. Morphological traits related to the vegetative and flowering stages and mature seeds morphology were scored using the International Plant Genetic Resources Institute lima bean descriptors with a soft modification. The similarity index is calculated using the General Similarity Coefficient Gower formula. The dendrogram is generated from cluster analysis using the *Unweighted Pair Group Methods using Arithmetic Average* (UPGMA) method. Furthermore, *Principal Component Analysis* (PCA) was used to determine the role of each morphological character used. The dendrogram shows that 23 collected accessions are divided into two main clusters with a 57% similarity index. The two clusters are distinguished based on the presence or absence of secondary colors and secondary patterns in the seed organs. Then, each main cluster is divided into two subclasses based on the character of the pigmentation stem, the length of the terminal leaflets, flower color, and seed type (Bria *et al.*, 2019).

A total of 96 landrace were collected from five administrative zones of Ethiopia from which 106 clear bands were detected. About 95 (88.7%) of the bands were polymorphic. The genetic diversity analyses result revealed that landrace collected from West Wellega showed the highest (0.1864) genetic diversity. AMOVA demonstrated highly significant ($P=0.00$) genetic diversity among and within populations. A considerable proportion (66%) of the total genetic diversity was distributed among populations and 34% within populations. In addition, the calculated F_{st} value was high ($F_{st} = 0.66$), associated with a low gene flow value ($N_m=0.27$) indicating lower differentiation of the populations, which, in turn, implied no significant exchange of planting materials among farmers in the studied populations and the nature of the crops that Lima bean is 52% self pollinated crop. UPGMA, STRUCTURE and PCoA analysis showed very strong grouping among individuals collected from the same zones and geographically distinct zones. Overall, genetic diversity achieved from this study could be used as pioneer information about the existing genetic resource for future Lima bean conservation and improvement strategy in Ethiopia (Nasir *et al.*, 2021).

Lima bean is one of the important legume vegetables in Indonesia. However, genetic information for these plants is

still minimalized, especially on Timor Island. This study aims to analyze the genetic diversity of lima beans from Timor Island based on ISSR molecular markers. A total of 4 accessions of lima beans were analyzed using 3 ISSR primers to produce 15 polymorphic bands with an average of 68.18% polymorphism. The cluster analysis results use the Unweighted Pair Group Methods using Arithmetic averages (UPGMA) method to create a dendrogram that produces two main clusters. There were plain seed and pattern seed group with a similarity coefficient of 0.52. These results indicated that the genetic variation of the lima beans from Timor Island was high. Moreover, the result provides a suitable method for evaluating the genetic diversity of lima beans using the ISSR marker and important information of future lima bean breeding programs (Bria and Bani, 2021).

We evaluated the role of gene flow and wild-crop introgression on the structure and genetic diversity of Lima bean in the Yucatan Peninsula, an important Mesoamerican diversity area for this crop, using a genotyping-by-sequencing approach (15,168 SNP markers) and two scales. At the local scale, STRUCTURE and NGSEP analyses showed predominantly crop-to-wild introgression, but also evidence of a bidirectional gene flow in the two wild-weedy-crop complexes studied (Itzinté and Dzitnup). The ABBA-BABA tests showed a higher introgression in Itzinté (the older complex) than in Dzitnup (the younger one); at the allelic level, the wild-crop introgression in Itzinté was similar in both directions, in Dzitnup it was higher from crop-to-wild; and at the chromosomal level, introgression in Itzinté was from wildto-crop, whereas in Dzitnup it occurred in the opposite direction. Also, we found HE values slightly higher in the domesticated accessions than in the wild ones, in both complexes (Itzinté: wild D 0.31, domesticated D 0.34; Dzinup: wild D 0.27, domesticated D 0.36), but $\% P$ and $_$ estimators were higher in the wild accessions than in the domesticated ones. At a regional scale, STRUCTURE and MIGRATE showed a low gene flow, predominantly from crop-to-wild; and STRUCTURE, Neighbor-Joining and PCoA analyses indicated the existence of two wild groups and one domesticated group, with a marked genetic structure based in the existence of domesticated MI and wild MII gene pools. Also, at the regional scale, we found a higher genetic diversity in the wild accessions than in the domesticated ones, in all estimators used (*e.g.*, HE D 0.27 and HE D 0.17, respectively). Our results indicate that gene flow and introgression are playing an important role at the local scale, but its consequences on the structure and genetic diversity of the Lima bean are not clearly reflected at the regional scale, where diversity patterns between wild and domesticated populations could be reflecting historical events (Heredia-Pech *et al.*, 2022).

BREEDING

Germplasm

Lima bean (*Phaseolus lunatus* var. *lunatus*) is the second most cultivated and consumed species, from *Phaseolus* genus, in Brazil as compared to common bean (*Phaseolus vulgaris*). This plant species can be found widely and with high diversity in all ecogeographic regions, highlighting the Northeastern,

Brazil, where lima bean presents greater genetic diversity in landrace genotypes. Unfortunately, national surveys do not discriminate *P. lunatus* and *Vicia faba* (known as “fava”). Thus, the available information become unclear how are the representativeness and importance of each of these legume species in Brazil. The highest diversity of beans, in general, is found in the Northeastern region, Brazil. Since this region is considered as the poorest region, beans are an important part of diet to population, mainly due to their high content of protein. However, there are particularities about lima bean, such as its representativeness in regions of high altitude, being mostly the main source of protein. In other regions, lima bean usually represents a special type of food. Regarding the origin of the Brazilian germplasm of lima bean, studies indicate the presence of genotypes from three known gene pools, and the geographic location of Brazil favors this assumption. It can support the hypothesis that Brazil is a center of domestication. There is information about wild genotypes collected in the Central region of Brazil. In terms of *ex situ* conservation, the Active Germplasm Bank of Phaseolus from Federal University of Piauí (BGP/UFPI) was established in 2003, and conservates landraces obtained from local smallholders and sellers. Currently, the BGP/UFPI has 1,345 genotypes (updated in February 2020) mainly obtained in Brazil (Lopes, 2022).

Lima bean is widely distributed in the Americas and has been widespread in the Tropics since it was first introduced to the Old World in 1493 after the voyage of Columbus. However, this crop has low commercial value (except for as a specialty export) in many of the countries where it is cultivated, which has represented a great challenge for the conservation of Lima bean genetic resources. *Ex situ* conservation. The Alliance of Bioversity International and CIAT in Colombia is the most important genebank in the world that conserves Lima bean accessions. This genebank conserves 3,301 accessions that were sampled from 63 countries, most of them from America, Africa and Asia. This collection is made up of 3,028 cultivated accessions (82% are landraces), 259 wild forms, 53 weedy and one escaped genotype. Notwithstanding some gaps in coverage, the collection contains accessions adapted to a broad range of temperature, altitude and moisture conditions. As for the *P. vulgaris* collection maintained in genebanks, the Lima bean collection is an asset for breeders, given the wide variety of accessions adapted to conditions that could be important in relation to global warming. This collection will be moved to a new facility at Future Seeds genebank, a platform that innovates in genomics and big data to improve the use of germplasm collections for adaption of crops to climate change and increase the nutritional value of plants. Another collection that stands out in America is the Regional Plant Introduction Station of the University of Washington with more than 1,100 accessions. In Latin American countries, other genebanks focus on the conservation of their native germplasm. Outside the Americas, the Bogor-Indonesia collection at the RDCB (Research and Development Center for Biology) is a large gene bank containing more than 3,800 accessions, mostly of Asian origin (Martínez-Castillo *et al.*, 2023).

Breeding

It is well-known that plant breeding aims to develop new plant varieties with desirable traits. However, this process promotes the loss of certain genetic traits, such as nodulation by

indigenous rhizobia in soils. Therefore, this study aimed to assess the potential effect of lima bean breeding on root nodulation by indigenous rhizobia. Five genotypes were utilized in this experiment, following the steps of lima bean breeding, including two parent plants (P_1 and P_2) and three segregating generations (F_2 , F_7 , and F_8). The plant growth and nodulation traits were evaluated during the flowering period, which varied depending on each genotype. The results of the multivariate analysis clearly separated the parent plants from the segregating generations based on nodulation traits. Nodulation by indigenous rhizobia varied across the evaluated genotypes and generally decreased as the generations advanced. The highest nodulation traits were found in P_1 and P_2 , while they decreased in F_2 and were undetectable in F_7 and F_8 , indicating a loss of ability to nodulate in this region with the advancement of generations. This study demonstrated that lima bean breeding has a negative impact on the ability of indigenous rhizobia to nodulate lima bean genotypes during the advance generations (Brito *et al.*, 2023).

The lima bean is an important food crop that is cultivated in temperate, arid, and semiarid tropical regions. It is a source of dietary protein for millions of people living in low-income countries. However, the genetic variability available for breeding programs is still poorly understood, which limits its productive potential. Knowledge of landrace germplasm through molecular and agromorphological markers could facilitate future breeding gains. Therefore, we evaluated the genetic variation of agromorphological and molecular markers in a lima bean collection. Twelve quantitative traits and microsatellite markers (SSRs) were used to determine genetic polymorphisms and differentiation among the 26 lima bean accessions. Considerable diversity was observed in traits related to agronomic performance, such as pod width, seed length, and seed width. At the molecular level, the expected mean heterozygosity ($He = 0.486$) was greater than the observed value ($Ho = 0.128$), indicating a deficiency of heterozygotes, which is a result of the reproductive system of the species. Although having a mixed system of reproduction, the lima bean is predominantly autogamous. The polymorphic information content (PIC) ranged from 0.04 to 0.67. Loci BM211 and BM156 were highly informative and are indicated for further studies with lima beans. The UFPI accessions 222, 234, 237, 228, 264, 230, and 251 showed the highest levels of similarity, while UFPI 230 and UFPI 276 were genetically distant and complementary in their traits; therefore, they could be used in crosses. Furthermore, the pairs of accessions UFPI 121/UFPI 173, UFPI 274/UFPI 276, and UFPI 271/UFPI 134 were duplicates found in the lima bean germplasm collection (de Melo *et al.*, 2023).

Although Lima bean is cultivated in many countries of America, just a few research groups have developed breeding programs. In Brazil, the Agricultural Science Center research group of the Federal University of Piauí (UFPI) has conducted a pioneering plant breeding program to generate improved cultivars that have a determinate growth habit, upright posture, uniform maturation, short cycle, resistance to anthracnose and a commercial grain pattern for agribusiness. They are also developing cultivars with indeterminate growth habit for smallholders, as an option to be used under intercropping with maize. In 2019, the program was extended to include aspects related to growth habit, as well as reaction to anthracnose and

seed patterns with populations advanced by the modified bulk method. The resulting lines will be evaluated soon. In the United States of America, the Dry Bean Breeding Program (DBBP) at the University of California, Davis is developing Lima bean varieties for growers in California. In recent years, the region has dedicated approximately 8,100 hectares to the cultivation of Lima bean, harvested each year, with a nearly even split between white, large-seeded varieties and white small-seeded varieties of both determinate and indeterminate growth habit (USDA 2018). To serve this industry, the DBBP is screening new varieties for seed color, seed size, growth habit, pest resistance, and other adaptation traits necessary for high yields in the Central Valley of California. In conjunction with this work, the Gepts Lab at UC Davis has undertaken a series of scientific investigations to improve our understanding of Lima bean genetics and the inheritance of agronomic traits. This lab group created a population of recombinant inbred lines which were used for linkage mapping during the development of the *P. lunatus* reference genome and has conducted several quantitative trait locus and genome wide association mapping studies of seed dimensions, cyanogenesis, and tolerance to the insect pest *Lygus hesperus*. Additionally, the Gepts lab group has carried out studies of high throughput phenotyping for insect tolerance with novel autonomous insect sensors. In Peru, the breeding of Lima bean is carried out at the Cotton and Bean Breeding Department of the Ica Farmers Association, which is responsible for obtaining improved cultivars with early-cycle determinate and indeterminate growth patterns as well as semi-late or intermediate cycle. The National Institute of Agrarian Research (INIA) also played an important role in the development of improved cultivars, until it was dismantled more than 20 years ago. Breeding began on one landrace named "Pallar de Ica", characterized by white seeds belonging to the Lima bean cultigroup, which already has its denomination of origin. More than 70% of the Lima bean consumed in Peru comes from the Ica region and from this variety. With the support of the Universidad Nacional Agraria La Molina, they have also carried out i) the molecular characterization of a wide number of genotypes, including those with colored seeds, ii) the analysis of the nutritional and hydrocyanic acid content of colored-seeds genotypes and iii) the evaluation of the correlation between the hydrocyanic acid content and their phytosanitary response. At present, both research groups are evaluating and selecting genotypes with high nitrogen fixation potential and are searching for the optimization of the legume-rhizobia symbiosis. In Mexico, the Technological Institute of Conkal research group has evaluated landraces of Lima bean from the Yucatan Peninsula and managed to identify 12 important morphological and physiological leaf traits for selecting accessions with high yields to achieve sustainable, environmentally safe crop production. In Ecuador, it was evaluated one Lima bean landrace under two different conditions of temperature and humidity and recorded data for 32 traits related to plant architecture, flower and seeds characteristics and yield, and 17 events in the phenology of the plants. They found that Lima bean is more tolerant to changes in environmental conditions compared to *P. vulgaris* landraces; they also found that the Lima bean was very productive and it might be considered as a potential species that could be grown in greenhouses, replacing other economically less attractive crops (Martínez-Castillo *et al.*, 2023).

Cultivars

Both bush and pole (vine) cultivars exist; the latter range from 1 to 5 metres in height. The bush cultivars mature earlier than the pole cultivars. The pods are up to 15 cm long. The mature seeds are 1 to 3 cm long and oval to kidney-shaped. In most cultivars, the seeds are quite flat, but in the "potato" cultivars, the shape approaches spherical. White seeds are common, but black, red, orange, and variously mottled seeds are also known. The immature seeds are uniformly green. Lima beans typically yield 2,900 to 5,000 kg of seed and 3,000 to 8,000 kg (6,600 to 17,600 lb) of biomass per hectare (Wikipedia, 2024).

Bush types (Wikipedia, 2024).

- 'Henderson' / 'Thorogreen', 65 days (heirloom)
- 'Eastland', 68 days
- 'Jackson Wonder', 68 days (heirloom, seeds brown mottled with purple)
- 'Dixie Butterpea', 75 days (heirloom, two strains are common: red speckled and white seeded)
- 'Fordhook 242', 75 days, 1945 AAS winner

Pole types (Wikipedia, 2024)

- 'Carolina Sieva', 75 days (heirloom, suffered a seed crop failure in the years 2011 and 2012 causing this variety to still not be widely sourced ten years later)
- 'Christmas' / 'Chestnut' / 'Giant Speckled' / 'Speckled Calico', 78 days (heirloom, seeds white mottled with red)
- 'Big 6' / 'Big Mama', 80 days^[14]
- 'Willow Leaf', 80 days (heirloom, there are white-seeded and variously mottled strains)^[15]
- 'Mezcla', 82 days
- 'King of the Garden', 85 days (heirloom)

Lima beans are of very great commercial value, but are not sufficiently appreciated as a table food because it is not generally known that in a dry state they can be used in practically the same manner as are the common beans. In reality they are richer and more delicate in flavor than the common beans, and can be used in as many different ways. The virtues of these types as green beans need only a passing mention, and their value as an accompaniment of corn in succotash is well known to every consumer of canned goods. Of the pole types of white lima beans, the small-seeded Carolina, or Sieva, is probably the most dependable, although its quality is only fair. King of the Garden is a large-seeded variety of high quality, but under many conditions it is less productive than Sieva. Florida Butter is a purple-and-buff speckle-seeded kind popular in the South. Henderson Bush is the most important dwarf lima; it is the one grown most for canning and as dry baby lima beans. It is a dependable bearer, but only fair in quality. Green-seeded strains of this type are now available. Fordhook and Burpee are favorite large-seeded dwarf kinds of high quality, but they frequently are unproductive under adverse conditions. Early Market and Fordhook 242, two new varieties having medium-sized seeds and high quality, are more productive than Fordhook and Burpee in the middle part of the country (Marsh, 2024).

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