Intraspecific Diversity and Morpho-Phenological Variation in *Phaseolus lunatus* L. from the Yucatan Peninsula, Mexico[1]

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Martínez-Castillo, J., Zizumbo-Villarreal, D. *(Centro de Investigación Científica de Yucatán, Calle 43 No. 130 Col. Chuburná de Hidalgo, Mérida, Yucatán, México 97200),* **Perales-Rivera, H.** *(El Colegio de la Frontera Sur, División de Sistemas de Producción Alternativos, Unidad San Cristóbal) and* **Colunga-GarcíaMarín, P.** *(corresponding author, Centro de Investigación Científica de Yucatán, Calle 43 No. 130 Col. Chuburná de Hidalgo, Mérida, Yucatán, México 97200; email pcolunga@cicy.mx).* Intraspecific Diversity and Morpho-Phenological Variation in *Phaseolus lunatus* L. from the Yucatan Peninsula, Mexico. *Economic Botany 58(3):354–380, 2004. The genetic diversity of* P. lunatus *in the Yucatan Peninsula was assessed on the basis of its morphological and phenological characters. Our results were then discussed in relation to ethnobotanic information obtained about the intraspecific diversity recognized by farmers, their selection criteria, agronomic management, production purpose and percentage of cultivated area. Research was undertaken in one of the cultural subareas of Mesoamerica, the Lowland Maya area, where traditional agriculture has been more persistent and where high diversity of* P. lunatus *landraces has been recorded. Four of the 13 cultural-geographic zones established for the origin of this culture were included, 160 farmers from 12 localities were interviewed, and 149 seed samples of* P. lunatus *germplasm were collected and analyzed using six characters. A subset of these samples was grown under ex situ uniform growth conditions and analyzed using 28 characters. Ethnobotanical and morpho-phenological data indicated 30 putative distinct landraces, two wild, and two weedy variants, suggesting gene flow among them. Richness and diversity estimates were greatest, and evenness lowest, where there was: 1) minimal agricultural intensification, 2) wild and weedy populations, and 3) greater persistence of traditional culture. Results underscored the importance of establishing in situ conservation programs in these areas.*

Diversidad Intraespecifica y Variacion Morfo-Fenologica de *Phaseolus lunatus* L. en La Peninsula de Yucatan, Mexico. *Se estimó la diversidad genética de* P. lunatus *en la Península de Yucatán con base en caracteres fenológicos y morfológicos, y se discute en relación a la información etnobotánica obtenida acerca de la diversidad intraespecífica reconocida por los campesinos, sus criterios de selección, su manejo agronómico, el destino de la producción y el porcentaje de área cultivada. La investigación se llevó a cabo en una de las subáreas culturales de Mesoamérica en donde la agricultura tradicional ha sido más persistente y en donde se ha reportado alta diversidad de cultivares de* P. lunatus*: las Tierras Bajas Mayas. Cuatro de las trece zonas geográfico-culturales establecidas en el origen de esta civilización fueron incluídas, 160 campesinos de 12 localidades fueron entrevistados y 149 muestras de semilla del germoplasma de* P. lunatus *fueron analizadas con base en 6 caracteres. Un subconjunto de estas muestras se cultivó bajo condiciones homogéneas de crecimiento ex situ y se analizó usando 28 caracteres. Los datos morfológicos y etnobotánicos indicaron 30 cultivares putativos, dos variantes silvestres y dos arvenses, y sugirió flujo génico entre ellas. La riqueza y la diversidad fue mayor, y el predominio menor, donde hubo: 1) menor intensificación agrícola, 2) poblaciones silvestres y arvenses de* P. lunatus, *y 3) mayor persistencia de cultura tradicional. Los resultados resaltan la importancia de establecer programas de conservación in situ en estas áreas.*

Key Words: *Phaseolus lunatus*; intraspecific diversity; Maya lowlands; in situ conservation; genetic resources; morpho-phenological variation; gene flow; traditional agriculture.

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Lima bean (*Phaseolus lunatus* L.), one of the major cultivated species of the genus *Phaseolus,* is an important source of proteins for rural populations in South America and Africa (Lioi et al. 1998) and an important commercial species for countries such as the USA, where 20 400 ha were harvested and 17 200 tons were exported in 2002 (Lucier and Plummer 2003). Analyses of genetic variation and relationships among cultivars, landraces, and wild populations (based upon morphological, biochemical, and molecular markers) have suggested the existence of two major gene pools for *P. lunatus*: the Mesoamerican gene pool and the Andean gene pool, and a minor group of intermediate genotypes (Caicedo et al. 1999; Fofana et al. 1997; Fofana et al. 2001; Lioi and Galasso 2002; Lioi et al. 1998).

In the Mesoamerican part of Mexico, the lima bean is cultivated on lowland slopes adjacent to the Pacific Ocean and the Gulf of Mexico. It is a common cultivar in traditional cropping systems and is cultivated by diverse ethnic groups (Ballesteros 1999). In the Mexican part of the Yucatan Peninsula, *P. lunatus* is integrated into the *milpa* production system, an ancestral Mesoamerican dry land farming system based on human energy in which vegetation is cyclically slashed and burned in order to plant a group of basic crops, such as corn (*Zea mays* L.), squash [*Cucurbita moschata* (Duch) Duch ex Poir; *C. argyrosperma* Huber], and beans (*P. vulgaris* L., *P. lunatus* L.). Alongside these basic crops, other secondary species are cultivated, such as *Capsicum* spp., *Ipomoea batatas* L., and *Solanum esculentum* L. After two to four years of cultivation (depending on soil fertility), the land is allowed to rest for a period of five to 15 years before a new cycle is begun (Hernández-Xolocotzi 1952; Pérez-Toro 1945). The conservation of patches of vegetation that are cyclically cultivated is, in turn, the mainstay of the *milpa*'s productivity, as it assures the recovery of soil fertility and maintains the habitat for a large part of the plant genetic resources integrated into the *milpa* agroforestry production system (Colunga-GarcíaMarín and May-Pat 1992; Hernández-Xolocotzi 1992; Zizumbo-Villarreal 1992). The *milpa* system is the nucleus of a much larger, agroforestry production system involving multiple activities for appropriating natural resources. In the Mayan lowlands, the *milpa* has survived over the centuries due, in part, to the rocky and shallow soils that have limited the introduction of: 1) agricultural machinery, 2) other cereals, and 3) broadcast sowing. Another significant factor contributing to the persistence of the *milpa* system has been the cultural resistance offered by the Mayan people who have maintained this agricultural system as the material basis of their culture for many generations (Zizumbo-Villarreal 1992).

At present, there are four geographic areas in the Mexican part of the Yucatan Peninsula where the *milpa* continues to be the most important economic activity. The locations of these areas and their agroecological characteristics are shown in Fig. 1 and Table 1, respectively. These areas correspond to four of the 13 cultural-geographic zones established by Adams and Culbert (1977) for the origin of the Maya lowland civilization. These four areas have their own particular physiographic, vegetational, and agroecological features (Duch-Gary 1991; Orellana et al. 1999), and have followed their own specific cultural and economic trajectories since the arrival of the Europeans. They include: 1) northeastern Campeche, in "Los Chenes" zone. In this area, a series of low-to-tall hills alternate with interspersed plains, including floodplains. Vegetation includes savanna, seasonally-flooded low tropical deciduous forest, and medium tropical semi-evergreen forest; 2) southern Yucatan, in the "Puuc" zone. This area is characterized by hillock formations, continuous stretches of long, elevated hills and variable-sized plains, favorable for intensive agriculture that runs between them. In terms of vegetation, this region is noted for low tropical deciduous forest and medium tropical sub-deciduous forest. This is the area where the influence of commercial agriculture has most recently been the greatest; 3) southeastern Yucatan, located within the "Northern Plains" zone. Undulating plains with hillocks and shallow bottomlands characterize the physiography of this region. Vegetation consists of medium tropical sub-deciduous forest. The most traditional Mayan communities in the state of Yucatan are encountered here; and, 4) central eastern Quintana Roo, within the "Río Bec" zone. This area corresponds to the region currently known as the "Mayan Resistance Area" (Bartolomé and Barabas 1977). It is comprised of human populations that emigrated from the southeastern part of the state of Yucatan during the Caste Wars (*Guerra de Castas*) in the 19th

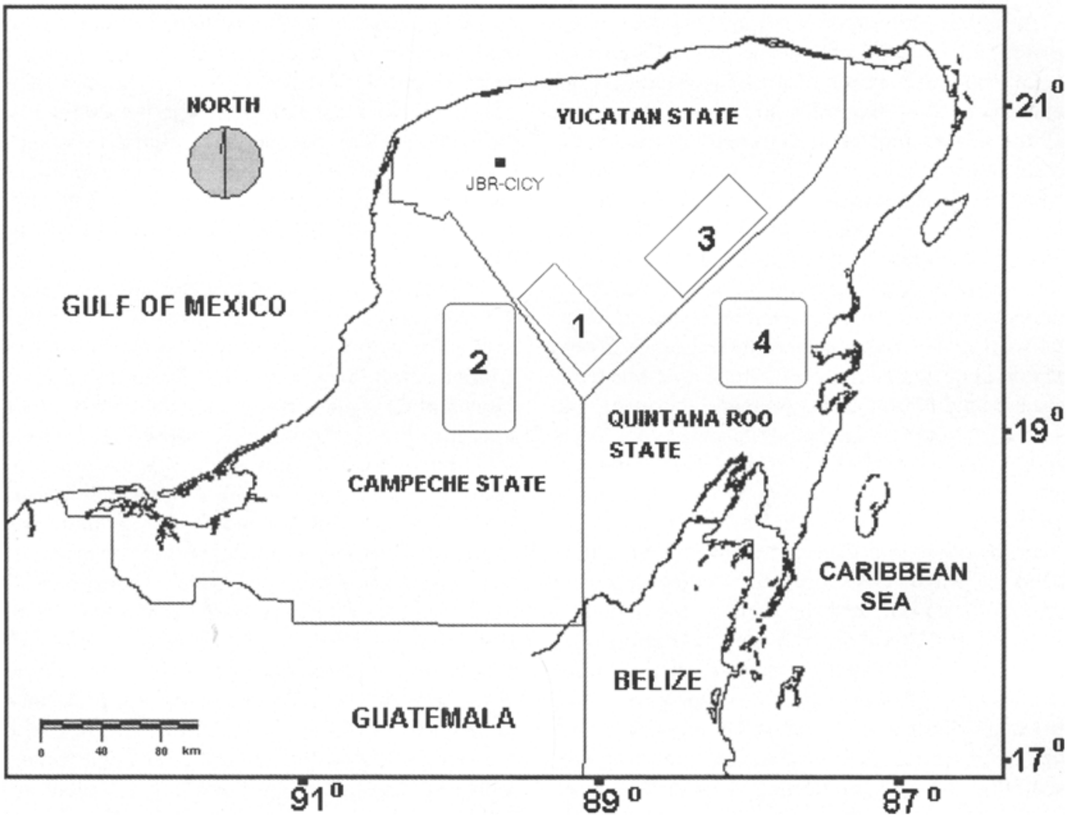

Fig. 1. Site of the ex situ characterization and the four studied areas. Southern Yucatan (1), Northeastern Campeche (2), Southeastern Yucatan (3), Central eastern Quintana Roo (4).

TABLE 1. ENVIRONMENTAL CHARACTERISTICS AND AGRONOMIC MANAGEMENT OF THE EX SITU CHARACTERIZATION SITE AND THE FOUR STUDIED AREAS IN THE MORPHO-PHENOLOGICAL VARIATION AND INTRASPECIFIC DIVERSITY ANALYSIS OF *P. LUNATUS* IN THE PENINSULA OF YUCATAN, MEXICO.

	Southern Yucatan	Northeastern Campeche	Southeastern Yucatan	Central eastern Quintana Roo	JBR-CICY
Temperature (°C)	26.4	26.3	25.3	26.1	25.5
Average annual rainfall (mm)	1094	1078	1158	1290	950
Rainfall/Temperature	41.4	41.6	45.8	49.4	37.3
Vegetation types[1]	1–3	2-4-5	3	4	1
Soil types[2]	r-cl	r	4-l	l-r	l-r
Average years of fallow period	0	0	8	15	—
Agricultural management[3,4]	m (70%) m-lb (30%)	m-lb (80%) pc (20%)	pc	Pc	—
Use of herbicide and fertilizer (%)	100%	100%	70%	70%	—

[1] 1 = low tropical deciduous forest, 2 = seasonally-flooded low tropical deciduous forest, 3 = medium tropical subdeciduous forest, 4 = medium tropical semievergreen forest, 5 = savanna.

[2] r = rendzine, l = litosol, cl = cromic luvisol.

[3] m = monoculture of maize, m-lb = maize with lima bean; pc = maize with lima bean and other species.

[4] Percentages are based on 160 peasants interviewed.

century. These populations remained independent until the beginning of the 20th century. The dominant vegetation in this area is the medium tropical semi-evergreen forest.

In spite of its importance, studies on the diversity of *P. lunatus* in this region are few. In 1979, Debouck collected 101 cultivated accessions in the northeast of the state of Campeche and in the south of Yucatan, corresponding to 21 local names. He also collected 11 wild populations and two weedy populations in the northeast of Campeche. These accessions are deposited in the Bean Collection of the Centro Internacional de Agricultura Tropical (CIAT), where the greatest number of *P. lunatus* accessions in the world are found, 225 in all. Of these, 124 belong to the Peninsula of Yucatan: 114 collected by Debouck (1979), plus 10 accessions from the state of Yucatan, collected by Murruaga-Martínez (1981) (http://www.ciat.cgiar.org/urg/beans.htm). The material in this bank has been characterized under the conditions of the Valle del Cauca in Colombia, basically in relation to the seed characteristics (Maquet 1991; Debouck and Toro 2003, pers. comm.). This characterization indicates a wide variation in the color pattern of the testa and in the seed mass. Color pattern includes seeds with solid colors such as red, white, black, and grey, as well as diverse combinations of these colors. Seed mass can range between 23 and 47 g/100 seeds in the case of the cultivated accessions, from 9 to 14 g/100 seeds in the wild, and from 19 to 22 g/100 seeds in the weedy accessions. In relation to the HCN content, the wild germplasm shows a greater concentration in comparison with the cultivated. Regarding the variation of the electrophoretic pattern in the storage protein of the seed, all of them presented the pattern of the Mesoamerican gene pool, where we can observe four subtypes of patterns: M1, M6, M8, and M9. Type M1 is found only in cultivated accessions and the others only in the wild and weedy accessions. All accessions evaluated were susceptible to attack from weevils of the *Zabrotes* genus. This susceptibility was less in the case of attack from weevils of the *Acanthoscelides* genus, where the wild accession showed resistance to this organism. Characterization of the germplasm in this collection is still underway, as is the analysis to demonstrate the differences between the variants collected in this region of Mexico (Debouck 2003, pers. comm.).

Hernández and Delgado (1992) found a wide variety of color and shape in the cultivated germplasm of *P. lunatus* in the eastern part of the state of Yucatan. They did not record the local names for each variant and the material was grouped according to the primary color of the testa, in brown, black, red and white variants. By also considering solid or combined colors and flat or globular shapes, these authors registered 21 variants, the most common being a white, spherical seed. Also in this area, Nahal (1993) reported three different seed shapes among the cultivated variants, flat, globular, and kidney-shaped, as well as a variant with small, dark-colored seeds similar to those of wild populations. In 1999, Ballesteros undertook a botanical exploration of Mexico. He recorded the highest diversity of cultivated variants of *P. lunatus* (in terms of seed characters) in the Yucatan Peninsula, included in 25 local names. These cultivated variants included the two cultigroups (cv-gr.) previously described by Baudet (1977) for Mesoamerica: the cv-gr. "Papa" with small, globular seeds weighing 0.24 to 0.40 g/seed, named the "Maya" type by Ballesteros (1999); and the cv-gr. "Sieva" with flat, medium-sized seeds weighing 0.40 to 0.70 g/seed, named the "Meso-Caribbean" type by Ballesteros (1999). He also reported intermediate forms among these cultigroups, including medium-sized, kidney-shaped seeds. Finally, he reported cultivated variants characterized by small, flat, dark-colored seeds, weighing 0.10 to 0.15 g/seed, that were similar to the wild types. These were called the "Pseudo-wild" seed type.

The repercussions of human population growth and socio-economic changes occurring in rural areas of the Yucatan Peninsula during the last 50 years have resulted in major modifications of the *milpa* system. Among the most evident changes have been a greater production specialization, the introduction of agricultural inputs (such as herbicides), and shorter fallow periods for farmlands. These changes, in turn, have been related to a decreased planting of the crops associated with corn, and a loss of the vegetational areas next to the *milpa*, where wild relatives have been traditionally allowed to develop with domesticated species (Zizumbo-Villarreal 1992).

Establishing guidelines for conserving native germplasm in the Maya area of the Yucatan Peninsula is of great relevance. This region is one of the Mesoamerican sub-areas with the greatest cultural continuity and historical persistence of its traditional farming practices. However, in recent times it has been suffering from an accelerated process of modifications to the *milpa* system.

Within the context presented above, the main objective of this study was to assess the genetic diversity of *P. lunatus* in the Yucatan Peninsula on basis of morphological and phenological characters, and to discuss the results in relation to the ethnobotanic information about the intraspecific diversity recognized by the traditional peasant farmers, their selection criteria, agronomic management, product destination, and percentage of cultivated area.

Materials and Methods

Ethnobotanical Research

This survey was undertaken during 2000 and 2001 in eight two-week field trips, two trips for each region studied, following the methodology approach proposed by Hernández-Xolocotzi (1970). Three agricultural communities were selected from each one of the four study areas. In each community, 13 to 14 peasant farmers (40 per study area) were randomly chosen from a list provided by local civil authorities. Appendix 1 shows the semi-structured interview applied to each farmer which focused on the following information associated with wild, weedy, and cultivated variants of *P. lunatus*: Mayan name, morphological and phenological characters used for traditional classification, selection criteria, agricultural management practices, production purpose, and percentage of area cultivated of each variant in relation to the total area cultivated of *P. lunatus*. Data obtained through the semi-structured interviews were complemented with data obtained through participative observation during the agricultural works at the *milpa* done by peasants.

Samples of all variants cultivated and recognized as different by each farmer were collected from existing seed stock in the farmer's barns. The quantity collected per sample was of 0.5 kg. For the collection of germplasm from the wild and weedy populations, botanical explorations were conducted in the agricultural areas of each community visited, with the participation of peasant farmers. From each wild and weedy population, samples were collected that included an average of 10 pods from 20 to 30 individuals. A total of 149 samples were collected: 133 cultivated, 14 wild, and two weedy. In this work, we have considered the wild and weedy populations of *P. lunatus* to be those that grow spontaneously without the intervention of the farmers. They do not recognize these populations as part of their cultivated germplasm. The difference between these populations lies in the fact that the former do not grow within the *milpas* (or in adjacent areas), while the weedy populations do, sharing the space with the cultivated germplasm of *P. lunatus*. Botanical vouchers were collected with the help of the interviewed farmers, and deposited in the CICY herbarium.

Patterns of Morphological Variation in Seeds

Statistical analyses were undertaken with the Statistical Analysis System software Release 6.12 (SAS 1997) following Colunga-García-Marín, Estrada-Loera and May-Pat (1996). The following seed attributes were utilized: 1) primary and secondary colors (two qualitative characters), which were determined by a table of colors (Maquet 1991), and 2) mass, length, width, and length/width (four quantitative characters). Seed length was measured along the hilar region and seed width was measured at the level of the seed hilum, in centimeters (cm). Ten seeds from each of the 149 samples obtained during the ethnobotanical survey were evaluated for the six characters. Tests of normality were carried out on the residual values for all variables ($\alpha = 0.05$), pooling over all samples using the UNIVARIATE procedure. Seed length and seed width were normally distributed, whereas seed length/seed width and seed mass were normalized using the functions $\sqrt{x}$ and $\ln(x + 1)$, respectively. Two multivariate clustering techniques and a series of one-way analyses of variance were performed.

An agglomerative hierarchical analysis was carried out with the CLUSTER procedure based on the matrix of means for the six characters of the 149 samples. The elements of the matrix were standardized to mean 0 and standard deviation 1. Clustering was undertaken using the unweighted pair-group method with arithmetic averages (UPGMA). Clusters were represented by a dendrogram that used the standardized average distance as height. A series of five Principal Components Analyses (PCA) were undertaken with the PRINCOMP procedure, one for each of those farmers' recognized variants represented by more than 13 samples. Procedures were based on the correlation matrix of the four quantitative variables. The first two standardized principal components were plotted and visually inspected to determine clusters. A series of one-way analyses of variance (ANOVA) for the four quantitative characters were also performed for those farmers' recognized variants represented by two or more samples. The GLM procedure for unequal sample sizes was employed. Alpha significance levels were adjusted using the Bonferroni's inequality to account for the simultaneous inferences made for each group of analyses ($\alpha = 0.05/4$) (Miller 1981). Comparisons of means were made with the Tukey's test, using an adjusted alpha significance level (Zar 1999). Based upon the results obtained with these four statistical techniques, the variants traditionally recognized by farmers were classified into putative landraces. Those groups of samples that were morphologically different but received the same traditional name were identified as different landraces by adding the suffix 1 or 2 to the traditional name. Samples that were morphologically identical but received different traditional names were grouped into a same landrace identified by the most common used traditional name.

Once the number of putative different landraces and wild and weedy variants was defined (30 cultivated, 2 weedy, and 2 wild), the UPGMA and PCA procedures described above were repeated, using them as OUT/146/s.

Richness, Geographic Distribution, Relative Abundance, Diversity and Dominance

Based upon the results obtained from the analysis of the patterns of morphological variation in seeds, as well as from the ethnobotanical research, the following parameters were estimated for each study area: 1) richness (i.e., the absolute number of putative landraces and wild and weedy variants), 2) geographic distribution, 3) relative abundance, calculated as the number of hectares cultivated with each putative landrace in relation to the total cultivated hectares for the species in the four study areas, according to reports from the farmers, 4) Diversity, using Shannon's index (Shannon and Weaver 1949, $H' = -\Sigma\ p_i \ln p_i$), and 5) dominance, utilizing Simpson's index (Simpson 1949, $D = \Sigma\ p_i^2$). In calculating the Shannon and Simpson indices, p_i represented the percentage of the area cultivated per putative landrace. These indices were calculated using the Biodiversity Professional software Release 2.0 (McAleece 1997).

Morphological and Phenological Variation in Putative Landraces under Uniform Ex Situ Growth Conditions

In order to define the morphological and phenological differences of the variants traditionally recognized by the peasant farmers, eliminating the environmental variation of the conditions in which they were collected, a sample of these variants was planted during a productive cycle (June 2001–February 2002) under uniform growth conditions in the Regional Botanical Garden of the Centro de Investigación Científica de Yucatán (JBR). The JBR is located north of the city of Merida in the Mexican state of Yucatan, at an altitude of 8 m above sea level. The terrain is flat with a complex microrelief. Soils are classified as young and very rocky, corresponding to Litosols and Rendzines (FAO/UNESCO 1972). The average annual temperature is 25.5°C and the rainfall is 950 mm. The original vegetation corresponds to a tropical deciduous forest (Colunga-GarcíaMarín, Campos-Rios and Escalante-Rebolledo 1990) (Table 1).

The sample comprised 17 variants, corresponding to 17 of the 30 putative landraces resulting from the analysis of morphological variation of the seed, and originating from the four regions studied. These variants were selected because they showed the characteristic coloring patterns, shape, and size of their corresponding landrace, without indication of segregation, since the donor farmers had protected the purity of their germplasm. Furthermore, these variants are those that, when taken together, covered the full range of morphological variation encountered in the *P. lunatus* germplasm cultivated in the region. Ten seeds of each variant were planted under uniform moisture and soil conditions, each in its own pot filled with rendzine soil. Each variant occupied a single row with a one-meter distance between plants and rows, following the design used by Nienhuis et al. (1995), with hand irrigation each four days and hand weeding when necessary.

Twenty-eight characters were recorded in 10 plants per variant. Appendix 3 shows 23 quantitative characters, the other five are color characters and are not included in this Appendix. The characters recorded are: 1) seven characters taken from the phenological guide for *P. vulgaris* published by the Centro Internacional de Agricultura Tropical (CIAT 1983), including the number of days that each plant needed to reach the following phases: emergence of cotyledonal leaf at soil surface (emergence of seedling), presence of unfolded primary leaf of the plant, presence of unfolded first trifoliate leaf, presence of unfolded third trifoliate leaf, presence of first flower bud (preflowering), opening of first flower (flowering), and presence of first pod with the corolla of the flower hanging or separated (pod formation), and 2) 21 morphological descriptors (vegetative, seed, fruit, and flower characters) proposed for *P. lunatus* by the International Board for Plant Genetic Resources (IBPGR 1982), evaluated considering the mean of 10 structures per character in cm (leaflet, seed, pod, and flower bud). Seed characters were measured as described previously in the seed morphological variation section, pod length was measured as the longest straight line from base to tip of a mature pod, pod width as the largest width of a mature pod, flower bud length as the longest straight line from sepal base to tip of bud, leaflet length was measured on the terminal leaflet of third trifoliate leaf from pulvinus to leaf tip, and leaflet width was measured as the largest width of the terminal leaflet. Patterns of variation were analyzed by PCA (PRINCOMP procedure; quantitative characters only) and UPGMA (CLUSTER procedure; qualitative plus quantitative characters) (SAS 1997). The variables days to flowering and days to pod formation were analyzed by a series of analyses of variance (ANOVA). Tests of normality were carried out on the residual values for all variables ($\alpha = 0.05$), pooling over all samples using the UNIVARIATE procedure. The variables days to seedling emergence, number of locules per pod, and number of seeds/number of locules could not be normalized using any of the functions recommended by Zar (1999). However, these variables were ultimately incorporated into the PCA because neither their inclusion nor exclusion altered the number or composition of the groups. The variable days to first trifoliate leaf was normalized using the function $1/x$.

Results

Ethnobotanical Research

Traditional Classification of Diversity.— From the total of 149 seed samples of *P. lunatus* collected during the ethnobotanical research, 14 samples were obtained from wild populations and two samples were obtained from weedy populations. In traditional nomenclature, both wild and weedy populations were called *ib-cho* (*ib* rat) because according to farmers, rats consumed the seeds of these plants. Both types of populations showed obvious differences in size, shape, and color (Fig. 2), however, in spite of these differences, the peasants did not give them different names. The term *ib-tuul* (*ib* rabbit) reported by Ballesteros (1999) was not recorded. The term *ib-cho* was also applied to species of the genus *Vigna* showing leaf characteristics similar to *P. lunatus.*

Table 2 shows the cultivated variants traditionally recognized by the peasants interviewed in the Yucatan Peninsula, Mexico. From the total of 149 seed samples of *P. lunatus* collected during the ethnobotanical survey, 133 corresponded to 25 cultivated variants traditionally recognized by peasants, who used two morphological characters and one phenological character to differentiate them: 1) Seed shape. The variants with globular-to-elliptical seeds pertaining to the cv-gr. "Papa" were called *x-uolis ib* (*ib* ball) or "*mulición*" (*ib* birdshot). The variants with seeds that are flat and kidney-shaped pertaining to the cv-gr. "Sieva" were called *petch* (flat). 2) Seed color pattern. Variants with seeds of only one color, such as *chak-ib* (*ib* red), *box-ib* (*ib* black), and *sac-ib* (*ib* white) were named by their color. Variants whose seeds showed combinations of colors often received names related to the things, plants, or animals that they resembled, such as the variant *madza-kitam* (*ib* wild boar eyebrows) and *pool-santo* (*ib* saint's head). The variation found in these two morphological characters is shown in Fig. 2. 3) Production cycle. Variants also received names related to the duration of the plant's production cycle, such as *mejen-ib* (*ib* short cycle; a variant with a three to four months production cycle) and *nuk-ib* (*ib* long cycle; a variant with a seven to eight months production cycle). The combination of these three characteristics is used to distinguish among cultivated variants. For example, the variant with a white seed and short production cycle

Fig. 2. Seed morphological variation of wild, weedy and cultivated variants, recognized by traditional farmers in the Peninsula of Yucatan, Mexico. Lane 1 = flat variants, lane 2 = globular-elliptical variants, lane 3 = wild and weedy populations. Traditional variants not recognized with morphological characters alone: *chakpetch-chakmejen* (cp-cm), *xmejen-nuk* (me-nu), *mulición-sacmejen* (mu-sm). Wild (wi) and weedy (we).

was called *sacmejen,* whereas the variant with a red seed and short cycle was named *chakmejen.* Synonyms for variants' names were encountered on many occasions. One variant might receive more than one name, depending on its different attributes. For example, *sacmejen* could be named by some peasants only by its seed color as *sac* or named by some other only by its productive cycle as *mejen.* Sometimes different variants received the same name if the peasants used only one classification criterion. For example, *chakuolis, boxuolis, putsicasutsuy,* and *mulición* could be named just as *mulición* due to their globular seed.

Selection Criteria, Agronomic Management, Product Destination and Percentage of Area Cultivated.—For the wild and weedy populations, no selection criteria by the peasants were detected, basically because they are not given any use. Only one peasant reported having used wild plants to make cords from the stalks. Some peasants reported that a few people have consumed wild and weedy populations because of their considerable pod production and similarity to the cultivated material, but they stopped doing so when they subsequently became ill. The wild and weedy seeds of *P. lunatus* have a high HCN content which makes them unfit for consumption (Maquet 1991). Some peasants tolerate their presence within the *milpas* when their population density does not affect the correct development of their crops. They were kept under control by: 1) Hand weeding, when the population density was low (< 15 plants). The peasants practice two kinds of hand weeding: *haranchak* and *lochepak,* differentiated by the degree of control applied. The first is more effective as the weeds are eliminated along with their roots. *Lochepak,* on the other hand, eliminates only the aerial part of the plant, allowing a subsequent recovery. With this kind of weeding, the peasants allow the weed population to reach the stage of seed production along with their crops. However, they are not harvested because they are recognized as inedible. 2) Use of herbicides. When the population density was higher (> 50 plants), as in some populations which manage to grow within the corn monoculture, the peasants

TABLE 2. SEED MORPHOLOGICAL CHARACTERISTICS, ENTHNOBOTANICAL DATA AND NUMBER OF ACCESSIONS PER STUDY AREA OF THE TRADITIONALLY RECOGNIZED VARIANTS OF *P. LUNATUS* IN THE YUCATAN PENINSULA, MEXICO. SEED FORM (A); FIRST AND SECOND COLOR OF SEED (B); TIME TO THE HARVEST (C); AGRICULTURAL MANAGEMENT (D); PRODUCTION PURPOSE (E); TASTE (F); COOKING TIME (G); SOUTHERN YUCATAN (G); NORTHEASTERN CAMPECHE (I); SOUTHEASTERN YUCATAN (J); AND CENTRAL EASTERN QUINTANA ROO (K).

Name	A[5]	B[6]	C[7]	D[8]	E[9]	F[10]	G[11]	H	I	J	K
cv-gr. Sieva											
Bacalar	f-t	br-b	l	a	m-s	s	i	0	0	0	14
Balche[1]	f-t	br-b	l	a	m-s	s	i	0	0	0	5
Batun[4]	f-th	c	l	a	s	s	i	0	0	1	0
Boxpetch[4]	f-th	b	l	a	s	sb	i	0	0	0	1
Chakchi[4]	f-th	r-w	s	a	s	s	i	0	0	1	0
Chakmejen[3]	f-t	r	s	a	s-m	s	f	0	1	1	0
Chakpetch[3]	f-t	r	l	a	s-m	s	i	0	1	4	4
Chaksaac[3]	f-t	r-b	l	a	s-m	s	i	0	2	1	0
Chocolate[4]	f-th	br	l	a	s	sb	s	0	0	0	1
Madzakitam[4]	f-t	b-w	l	a	s	sb	s	1	0	0	0
Mejen[3]	f-th	w	s	m	m-s	s	f	6	1	0	0
Nuk[3]	f-th	w	l	a	m-s	s	f	2	0	0	0
Tabaco[4]	f-t	br	l	a	s	b	i	0	0	0	1
cv-gr. Papa											
Balampach[2]	e-g	r-g	l	a	m-s	s	i	0	0	0	1
Boxuolis[4]	g	b	l	a	s	sb	s	0	0	0	1
Chakuolis[4]	g	r	l	a	s	sb	s	0	0	0	4
Kan[4]	e-g	y	l	a	s	s	i	0	0	1	0
Mulición[3]	g-e	w	l	a	m-s	s	f	9	7	2	15
Poolsanto[4]	e	g-b	l	a	s	sb	s	0	0	1	0
Putsicasutsuy	e-g	r-g	l	a	m-s	s	i	1	2	5	2
Sac[3]	e-k	w	l	a	m-s	s	f	0	2	24	2
Sacmejen[3]	g	w	s	a	m-s	s	f	0	0	1	1
Tsisibal[2]	e-g	r-g	l	a	m-s	s	i	0	0	2	0
Tuchasutsuy[2]	e-g	r-g	l	a	m-s	s	i	0	0	1	0
Xananmucuy[2]	e-g	r-g	l	a	m-s	s	i	0	0	0	1

[1] Synonymous of *Bacalar* variant.
[2] Synonymous of *Putsicasutsuy* variant.
[3] Variants that split in two different variants.
[4] Variants that conserve their original status.
[5] f-t = flat-thinned, f-th = flat-thick, e- = elliptic, e-k = elliptic kidneyed, e-g = elliptic-globular, g-e = globular-elliptic, g = globular.
[6] w = white, b = black, br = brown, r = red, g = gray, y = yellow, c = cream.
[7] l = 7 to 8 months, s = 3 to 4 months.
[8] a = polyculture, m = monoculture.
[9] m-s = subsistence and market, s-m = principally subsistence but also market, s = just subsistence.
[10] s = sweet, sb = semibitter, b = bitter.
[11] f = fast, i = intermediate, s = slow.

limited the density with the application of herbicides, but only until the maize plants had reached a point in their development that assured the production of ears. Once the harvest was secured, the peasants allowed these populations to grow freely, eventually covering the whole field. Only in the southeast of Yucatan did the farmers report the elimination of the wild and weedy populations in order to prevent them from "mixing" with the cultivated variants.

Table 3 shows the selection criteria applied to the cultivated germplasm by the peasants interviewed. The peasants indicated taste (27.39%) and color (20.75%) as the main criteria, cooking time was next in importance (12.45%), and finally the production purpose (11.2%). The var-

TABLE 3. SELECTION CRITERIA OF GERMPLASM CULTIVATED OF *P. LUNATUS* AND PERCENTAGE OF PEASANTS THAT APPLIED THE CRITERIA FROM THE 160 FARMERS INTERVIEWED IN THE YUCATAN PENINSULA, MEXICO.

Selection criteria	%
Seed taste	27.39
Seed color	20.75
Cooking time	12.45
Economic value	11.2
Seed form	6.2
Productive cycle short	5.39
Resistance to attack of bruchids	5.39
Seed size	4.15
Resistance to drought	3.32
Seed yield	2.49
Growth in poor soils	1.25

iants identified as having the best taste were *mulición, sac, xmejen, nuk, sacmejen,* and *putsicasutsuy,* the first five with white testa. White as primary color (5 variants) was the most represented among the cultivated variants recognized by the peasants, followed by the red (3 variants). The same color patterns found in this research are in the accessions from Yucatan Peninsula in the CIAT bean collection. In this collection, grey is the primary color seed most common among the cultivated accessions. The variants with white testa were also identified as the fastest cooking (Table 2). In relation to the production purpose, the variants selected for auto-consumption were *boxuolis, boxpetch* and *madzakitam;* the variants selected for auto-consumption but also with some commercial interest in mind were *bacalar, chaksaac,* and *chakpetch. Xmejen, sac, putsicasutsuy,* and *mulición* were selected for the same reasons but with greater commercial interest in mind (Table 2). No variant appeared to be selected exclusively for a commercial interest. Another of the selection criteria was the productive cycle (5.39%); 21 of the 25 variants recognized by the farmers were reported as long cycle variants and only four (*xmejen, sacmejen, chakmejen, chakchi*) as short cycle variants. The preference of a large number of long cycle variants is probably related to their better adaptation to dry land farming.

Concerning the production purpose, we found that, when the production was directed mainly to the market, the white testa variants were preferred, occupying 66.66% of the total cultivated area for this species reported by the farmers (Appendix 2). Of these, *xmejen* reaches the highest prices because of its white testa, larger seeds, and shorter productive cycle, allowing seed production in months when there is no production of other white testa variants such as *mulición* or *sac.* However, this variant does not represent a high percentage of cultivated area (only 3.03%) as its production depends on mechanized systems and irrigation. In relation to the cultivated area, the variants of greatest importance in the region were *mulición* (29.61%) and *sac* (25.12%). One red testa variant, *putsicasutsuy,* also obtained a high value on the market, but it was always lower than that of the white testa variants. However, this variant presents a high percentage of cultivated area (16.5%), only surpassed by *mulición* and *sac.* Commercial production is directed mainly to the markets of Merida and Oxkutzcab, in the state of Yucatan. Other variants such as *bacalar* had a high value but only in the local markets like Felipe Carrillo Puerto in the state of Quintana Roo and in the small rural towns. The *bacalar* variant occupies the fourth place in percentage of cultivated area (5.84%), but it is cultivated only in the central eastern area of Quintana Roo. The production of *P. lunatus* also included a number of variants that were cultivated only for auto-consumption as these were not popular in the market, apparently because of the dark color and semi-bitter taste of the seed. This component of auto-consumption was reflected in the low percentage of cultivated area for this class of variants, as in the case of *boxpetch* (1.85%), *boxuolis* (0.08%), and *chocolate* (0.02%), among others (Appendix 2).

The number of variants cultivated by the peasants ranged from one to seven, with an average of two to three. With the exception of *xmejen,* all the variants were cultivated in polyculture under the *milpa* system, with maize as the main crop and tutor plant for *P. lunatus. Xmejen* was planted with sticks as tutors, in small, mechanized, irrigated areas. When the seed was sufficient and the production had a commercial component, the peasants planted each variant separately in different sections of the *milpa* or in different *milpas* in order to maintain the purity of their germplasm and obtain a better price on the market. When the quantities of seed from each variant were small and the production was destined to auto-consumption, the peasants planted their germplasm in the form of mixed seeds (the planting of seeds from different varieties mixed together in the same part of the *milpa*), regardless of the loss of the particular characteristics of each landrace.

Patterns of Morphological Variation in Seeds

Figure 3 shows the UPGMA carried out with the 149 samples of *P. lunatus* collected. This analysis showed two large groups: 1) "Wild" included 14 populations, and 2) "Cultivated-weedy" was comprised of the cultivated samples plus the two weedy populations. Taking into consideration that the traditional classification gave wild and weedy populations the same name, we undertook a PCA that included the 14 wild populations and the two weedy populations, as shown in Fig. 4. The analysis showed a clear difference between the two weedy populations (groups "A" and "B"), and wild ones were grouped in two clusters (groups "C" and "D"); all groups were remarkably different because of their seed dimensions. Group "C" showed negative values on the second principal component axis, indicating spherical seeds. Group "D" showed positive values, indicating flattened seeds. In this analysis, the first and second principal components account for 78.4 % and 9.8 % of total variation, respectively. This result was confirmed both by the one-way ANOVA's and by the comparison of means tests presented in Table 4. Therefore we catalogued the wild populations as two separate variants: 1) *ibcho*-1, with 10 populations, and 2) *ibcho*-2, represented by four populations; the weedy populations were catalogued as *ibcho*-3 (group "A") and *ibcho*-4 (group "B") (Appendix 2).

This procedure was also used for the 133 samples of the traditionally recognized variants (Table 4, PCA graphs not shown). Results from the four statistical analyses plus information provided by farmers on the length of productive cycle for each cultivated variant indicated that the 133 samples could be grouped in 30 morphologically distinct putative landraces. The importance of the productive cycle as a classificatory criterion was corroborated later by the ex situ analysis. Of the 25 traditionally recognized variants, 10 were divided in two putative landraces each (for example, *bacalar* was divided in *bacalar-1* and *bacalar-2*), four (*xananmcuy, balampach, tuchasutsuy* and *tsisibal*) were considered to be synonymous with another putative landrace (*putsicasutsuy*), and nine were maintained as they had been originally recognized by farmers (for example, *boxpecth, kan,* and *madzakitam*) (Table 2, Appendix 2).

Figure 5 and 6 show the UPGMA and the PCA results respectively, considering the 30 putative landraces, the two weedy variants, and the two wild variants. Both types of analyses showed similar cluster patterns. In both cases, two main groups were observed. The first group, named "A", included the two wild variants plus the small-seeded, weedy variant *ibcho*-4. The second group, named "B" in the UPGMA, included all the landraces plus the large-seeded, weedy variant *ibcho*-3. A third group, "C," present only in the PCA, segregated the landraces with globular-shaped seeds from the other landraces.

For cultivated germplasm, there was no clear differentiation among the cultigroups proposed by Baudet (1977), as the "B" group integrated variants with globular seeds, kidney-shaped seeds, and even those with flat, thick, or thin seeds. Intermediate forms might have resulted from hybridization between landraces belonging to the two sympatric cultigroups. It is worth noting that weedy populations (group "D") occupied an intermediate position between the wild and cultivated populations.

Richness, Geographic Distribution, Abundance, Diversity and Dominance.—Richness: Statistical analyses of seed variation among wild populations showed two morphologically distinct groups indicating low seed morphological differentiation. With respect to the two weedy populations, morphological differentiation was evident as each population was placed in a distinct group. The area richest in putative landraces was southeastern Yucatan (17), followed by central eastern Quintana Roo (14), "Los Chenes" (13), and the "Puuc" region (8).

Geographic Distribution.—The wild popula-

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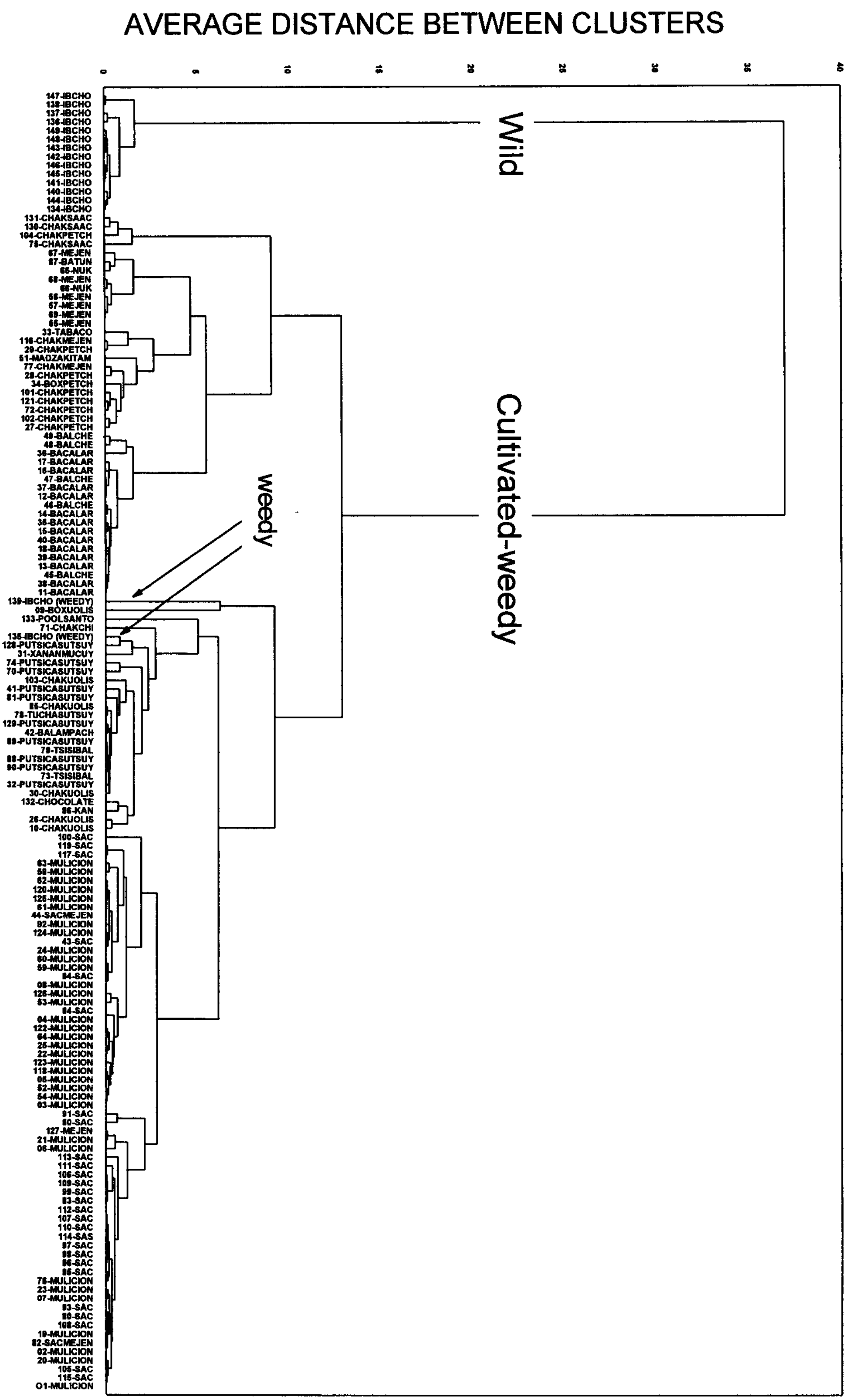
Fig. 3. UPGMA analysis of 149 cultivated, weedy and wild populations of *P. lunatus* in the Yucatan Peninsula, Mexico, based on six morphological seed characters. Number before the name is the accession number.


AVERAGE DISTANCE BETWEEN CLUSTERS
Wild
Cultivated-weedy
weedy

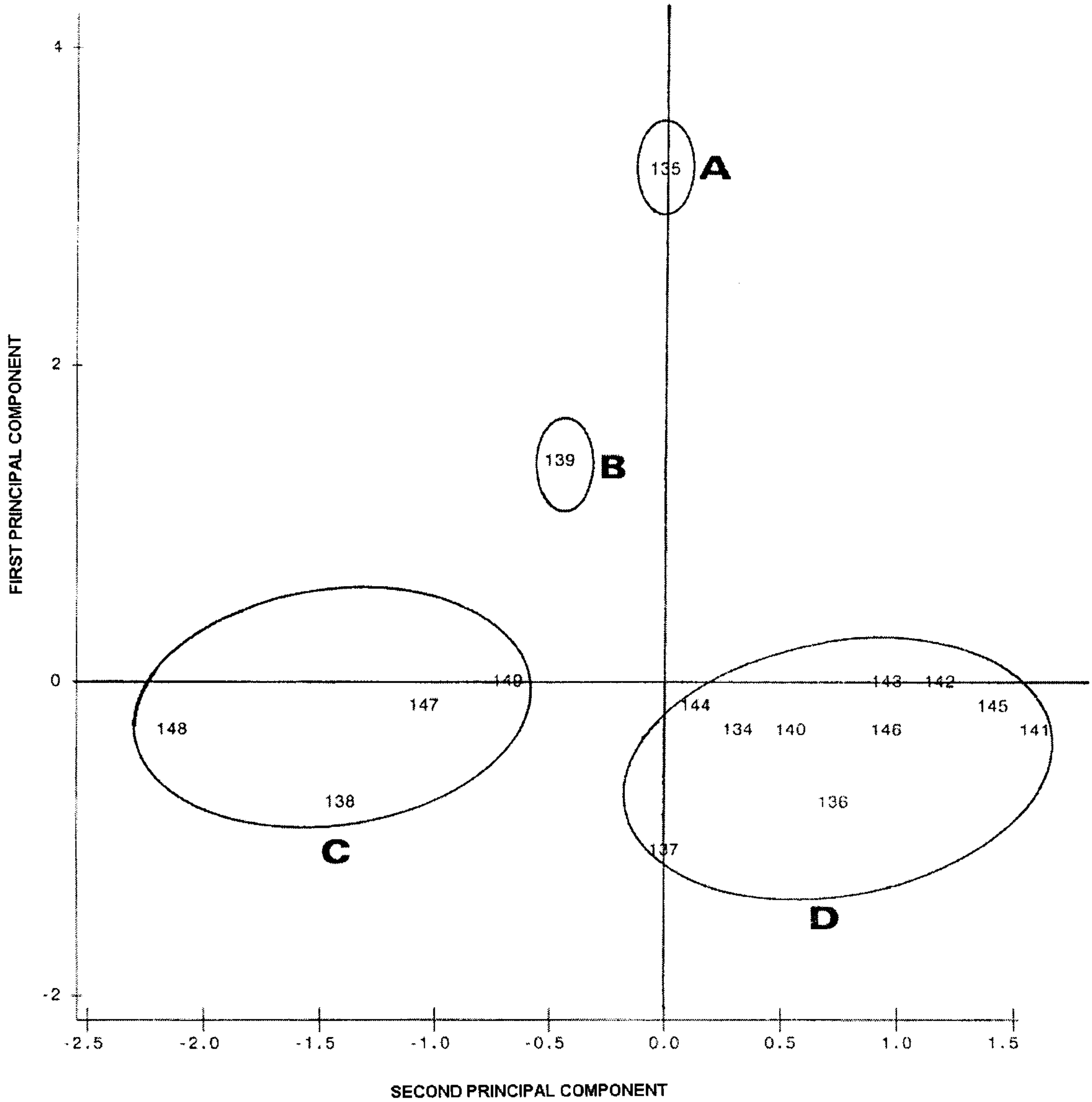


Fig. 4. First and second principal components of the analysis of wild and weedy populations of *P. lunatus* from the Yucatan Peninsula, México, based on four morphological seed characters. Number is the accession number.

tions were located in the four study areas. The two variants recognized by the analysis of morphological variation of seed occur sympatrically only in central eastern Quintana Roo, the area where wild populations also showed more variation in seed color; besides the common gray seeds, there were also black and reddish seeds. The weedy populations were only found in central eastern Quintana Roo and southeastern Yucatan, both populations being different. Landraces of the cv-gr. "Sieva" were distributed within the four study areas, but unlike the broad distribution of this cultigroup, some of its landraces showed very localized distributions. For example, *bacalar*-1, *bacalar*-2, *tabaco,* and *chocolate* were only collected from central eastern Quintana Roo. Landraces belonging to the cv-gr. "Papa" were well represented in central eastern Quintana Roo (Table 2). Eight of the 12 putative landraces that were encountered in this area belong to this cultigroup. This result might be adequately explained if the dispersal of this

TABLE 4. ONE-WAY ANALYSES OF VARIANCE (ANOVA) OF FOUR MORPHOLOGICAL CHARACTERS OF THE SEEDS OF TRADITIONALLY RECOGNIZED VARIANTS OF *P. LUNATUS* FROM YUCATAN PENINSULA, MEXICO, WITH TWO OR MORE ACCESSIONS. NUMBER OF ACCESSIONS (N), MEAN (M), COEFFICIENT OF VARIATION (CV), SIGNIFICANT DIFFERENCES $P < 0.0125$ (**), NO SIGNIFICANT DIFFERENCES (NS).

		Length			Width			Length/width			Mass		
Name	N	M	CV	*F*	M	CV	*F*	M	CV	*F*	M	CV	*F*
cv-gr. Sieva													
Bacalar	19	1.39	5.33	1.98 ns	0.93	6.02	2.83**	1.22	3.07	3.25**	1.55	4.39	7.91**
Chacmejen	28	1.27	3.06	0.08 ns	0.89	7.24	18.6**	1.19	3.42	20.6**	1.49	2.43	11.5**
Chakpetch	9	1.29	7.44	19.1**	0.87	7.24	18.6**	1.21	3.51	4.9**	1.47	5.48	55.3**
Chaksaac	3	1.33	8.64	7.25**	0.88	6.95	5.01**	1.23	3.15	1.05 ns	1.53	5.95	21.2**
Mejen	7	1.24	5.35	11.3**	0.85	4.75	12.18**	1.21	3.38	0.69**	1.46	3.28	12.08**
Nuk	2	1.24	7.32	22.5**	0.87	3.39	23.1**	1.19	3.56	24.1**	1.49	2.76	1.34ns
cf-gr. Papa													
Chakuolis	4	1.05	6.54	3.58 ns	0.78	6.06	2.14 ns	1.16	3.21	0.94 ns	1.41	6.54	9.4**
Mulición	33	0.93	7.81	3.88**	0.74	6.21	4.62**	1.12	4.19	2.33**	1.32	5.69	18.56**
Putsicasutsuy	15	1.08	6.37	3.56	0.79	6.67	4.58**	1.17	3.19	2.60**	1.39	8.39	66.66**
Sac	28	1.04	5.53	3.19**	0.76	6.04	9.1**	1.17	3.09	2.02**	1.40	5.50	18.5**
Sacmejen	2	0.96	9.74	35.5**	0.75	5.77	9.1**	1.13	3.31	16.6**	1.31	5.28	30.2**
Wild-weedy													
Ibcho	16	0.78	9.17	13.93**	0.62	8.97	7.36**	1.12	3.51	4.26**	0.71	12.61	30.07**

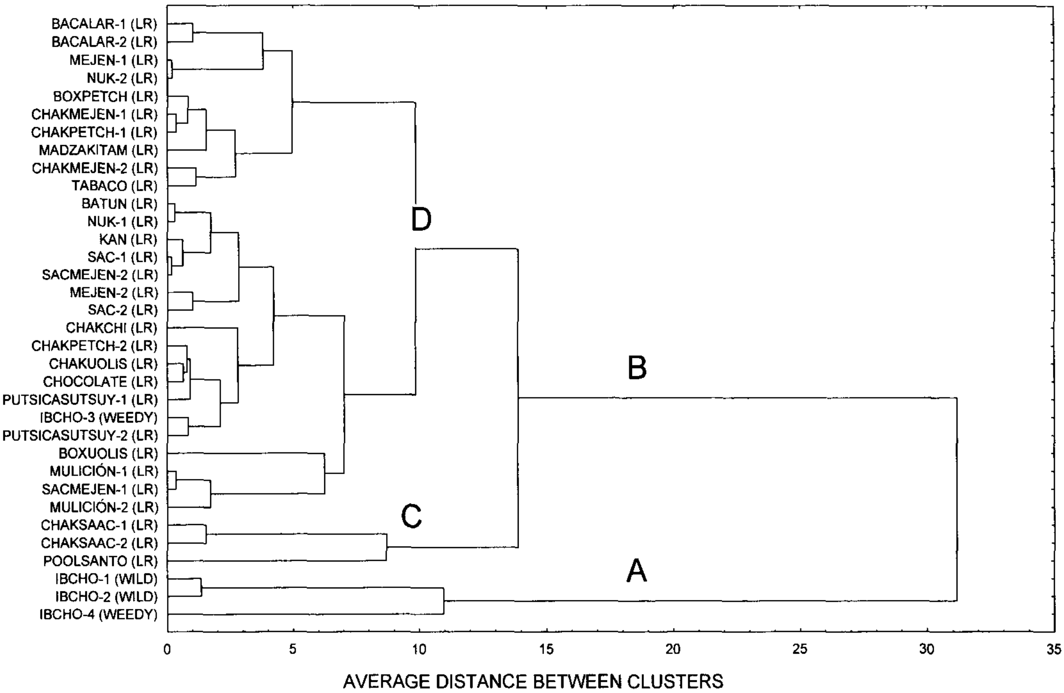


Fig. 5. UPGMA analysis of 30 putative landraces, two weedy and two wild variants of *P. lunatus* from the Yucatan Peninsula, Mexico, based on six morphological seed characters. Landraces (LR).

cultigroup was associated with human migrations around the Caribbean region, as suggested by Makie (1943). In central eastern Quintana Roo a greater number of "rare" landraces were seen ("rare" referred to landraces planted by no more than one peasant of the 40 interviewed in the area).

Abundance.—Wild populations were most abundant in central eastern Quintana Roo and "Los Chenes", where they competed with crops. Weedy populations were only found in central eastern Quintana Roo and southeastern Yucatan, at low population densities. Relative abundances of the 30 putative landraces in the four areas together can be seen in Appendix 2. According to farmers who participated in the survey, the landrace *mulición*-1 occupied 28.73% of the area under cultivation. This was followed by the landraces *sac*-1 (23.31 %) and *putsicasutsuy*-1 (14.3%). The remaining landraces did not surpass 5% of the area cultivated of *P. lunatus,* and 14 of these landraces (e.g. *poolsanto* and *chakuolis*) failed to reach even 1% of this area.

Diversity and Dominance of Landraces.—Central eastern Quintana Roo was the most diverse area (H′ = 0.8), followed by southeastern Yucatan (H′ = 0.76). Tied for third place were "Los Chenes" and the "Puuc" region (both with H′ = 0.71). Central eastern Quintana Roo was also the area with the lowest dominance (D = 0.19), followed by the "Puuc" region (D = 0.22) and southeastern Yucatan (D = 0.25). The area with greatest dominance was "Los Chenes" (D = 0.35).

Patterns of Morphological and Phenological Variation in Cultivated Variants under Uniform Ex Situ Growth Conditions

Appendix 3 shows the means and variation coefficients of 23 quantitative characters used in the ex situ analysis. In this analysis, no segregation was observed between the seeds harvested from each variant selected. This was probably due to the high grade of purity in the seed samples selected for this analysis. Figure 7 shows the UPGMA based upon the 28 characters for the 17 putative landraces. This analysis indicated five main groups. The first hierarchical division separated the "A" group from the rest, fundamentally due to the coloration of floral struc-

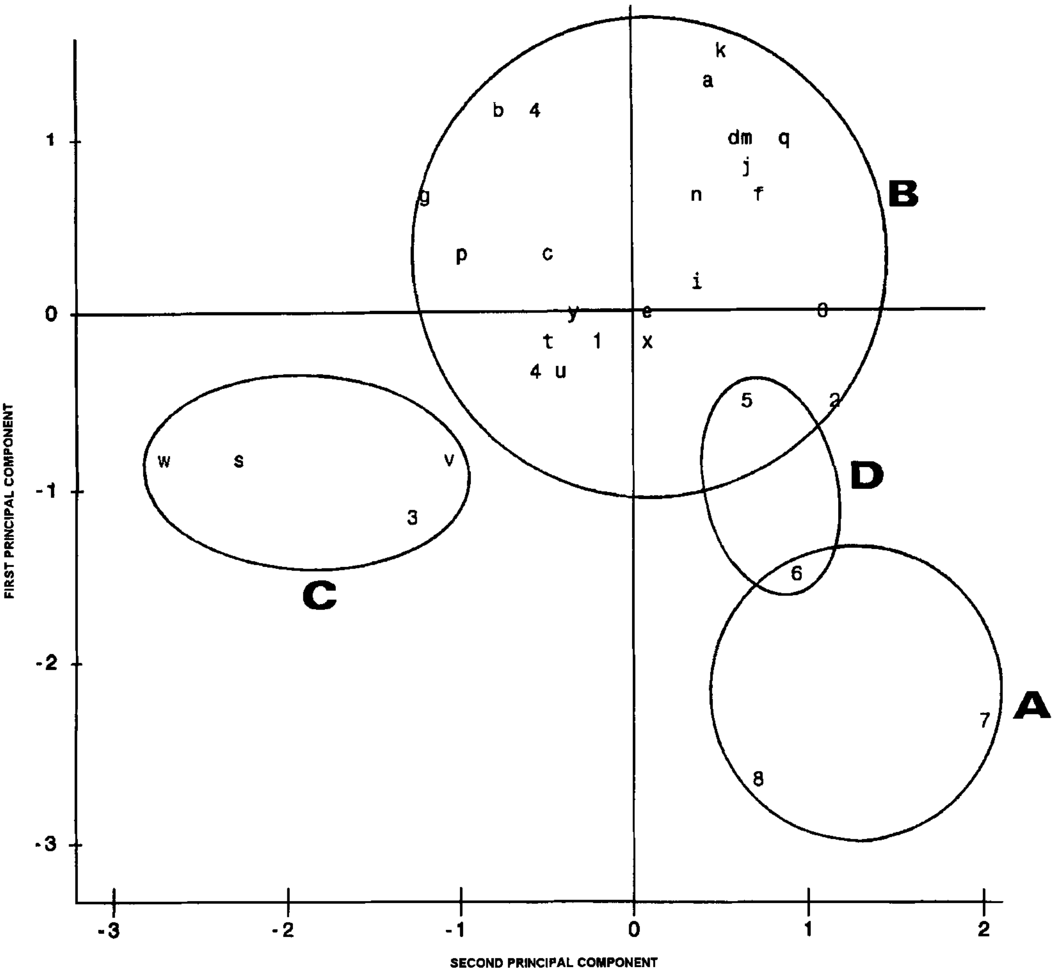


Fig. 6. First and second principal components of the analysis of 30 putative landraces, two weedy and two wild variants of *P. lunatus* from Yucatan Peninsula, Mexico, based on four morphological seed characters. Landraces Sieva = a–r; landraces Papa = s–z and 1–4; Weedy variants = 5–6; Wild variants = 7–8. Key to the letters and numbers is given in Appendix 2.

tures, hypocotyl and seeds. Landraces within the "A" group had lilac-colored flowers, purple standards, red hypocotyls, and black seeds, all characters similar to those found in wild populations. These landraces were among the least valued for consumption, primarily because of the semi-bitter taste of the bean and its slowness to cook (Table 2). The rest of the groups were comprised of landraces with white flowers. The second hierarchical division separated out the "B" group from the other three. The "B" group was represented by the landrace *poolsanto* (elliptical seeds, intermediate between those of the "Papa" and "Sieva" cultigroups). The third hierarchical division separated the "C" group (comprised of "Papa" landraces) from the "D" and "E" groups (which included "Sieva" landraces). In the fourth hierarchical division, the landrace *mejen-1* was segregated from the other "Sieva" landraces ("D" group).

Figure 8 shows the PCA carried out, based on the 23 quantitative characters recorded. The grouping pattern observed in this analysis was, in general, consistent with the UPGMA (Fig. 7). Four instead of five groups can be recognized in the PCA: 1) group "A", represented by the landrace *boxpetch,* 2) group "C," primarily comprised of "Papa" landraces, 3) group "D", represented by *mejen*-1 landrace, and 4) group "E," comprised of the "Sieva" landraces. The first,

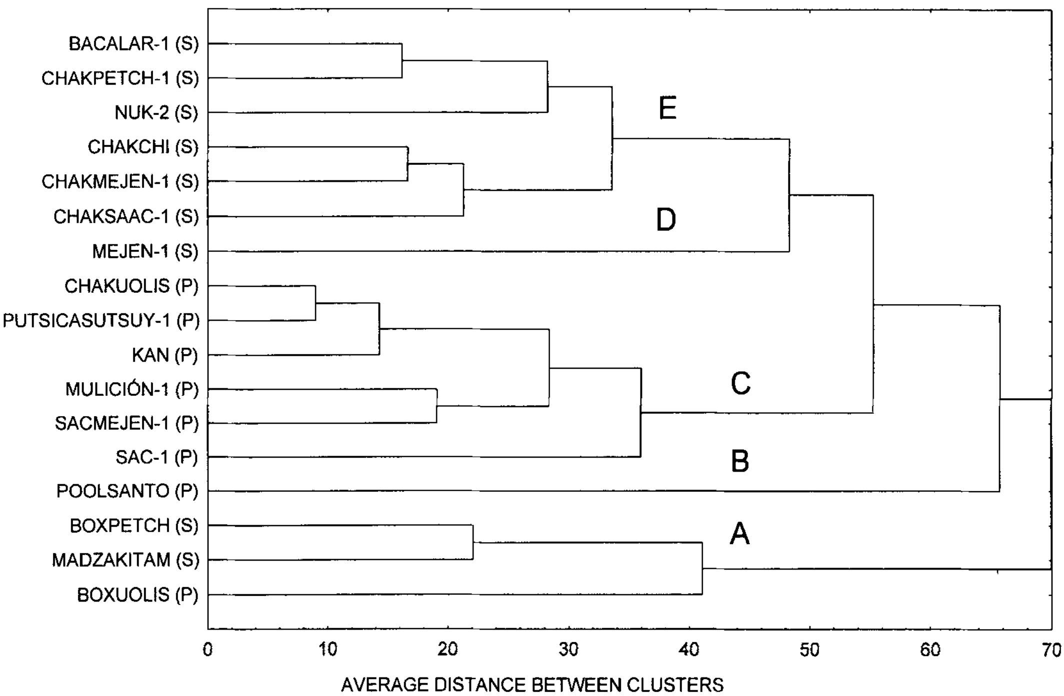


Fig. 7. UPGMA analysis of 17 cultivated variants of *P. lunatus* grown under ex situ conditions in the Yucatan Peninsula, México, based on 28 morphological and phenological characters. Landraces Sieva (S), landraces Papa (P).

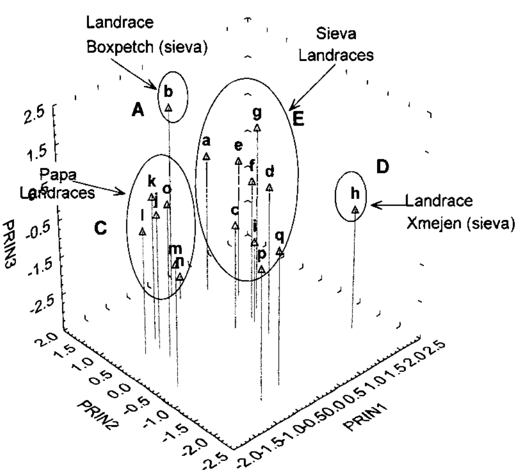


Fig. 8. First, second and third principal components of the analysis of 17 cultivated variants of *P. lunatus* grown under ex situ conditions in Yucatan Peninsula, Mexico, based on 23 morphological and phenological characters. Landraces Sieva = a–i; Landraces Papa = j–q. Key to the letters is given in Appendix 3.

second, and third principal components account for 32.4 %, 19.4 %, and 14.9% of total variation, respectively.

Table 5 shows the analyses of variance carried out for days to flowering and days to pod formation. The results of these analyses showed significant differences among putative landraces. Both analyses indicated an early-to-late gradation for landraces, where the extreme ends of the gradation were represented by *mejen-1* (earliest landrace; 101 days to flowering and 106 days to pod formation) and *kan* (latest landrace; 160 days to flowering and 163 days to pod formation). This situation could be reflecting the result of the selection of germplasm towards a range of cultivated variants presenting different lengths in their productive cycle, as a response to the conditions of random rainfall in the Yucatan Peninsula.

Discussion

In the Yucatan Peninsula of Mexico, we found wild and weedy populations of *P. lunatus,* both given the same Mayan name by peasants interviewed, probably in relation to their null importance as food. Wild populations were found in

TABLE 5. TUKEY'S TESTS OF COMPARISON OF MEANS FOR THE NUMBER OF DAYS TO FLOWERING (FIRST FLOWER OPENED) AND THE NUMBER OF DAYS TO POD FORMATION (FIRST POD WITH THE COROLLA FLOWER HANGING DOWN), IN THE PUTATIVE LANDRACES OF *P. LUNATUS* GROWTH UNDER UNIFORM EX SITU CONDITIONS IN MERIDA, MEXICO. SAMPLE SIZE = 10 PLANTS PER VARIANT.

Days to flowering			Days to pod formation	
Tukey's test*	Mean	Landrace	Mean	Tukey's test*
a	159.6	*Kan*	162.9	a
a-b	156.3	*Chakuolis*	162.1	a
b-c	148.1	*Putsicasutsuy-1*	155.1	a-b
c-d	147.5	*Poolsanto*	152.7	b-c
c-d	145.1	*Mulición*	149.2	b-c-d-e
c-d-e	143.5	*Boxpetch*	152.0	b-c-d
c-d-e-f	139.9	*Bacalar*	146.1	c-d-e-f
d-e-f-g	139.5	*Sac-1*	144.2	d-e-f
e-f-g-h	136.6	*Boxuolis*	141.5	e-f-g
f-g-h-I	131.6	*Chakchi*	135.0	g-h-i
g-h-I	131.3	*Chakpetch-1*	137.8	f-g-h
h-I	129.4	*Sacmejen-1*	134.3	g-h-i-j
i-j	127.8	*Nuk-2*	134.2	g-h-i-j
i-j	127.5	*Chakmejen-1*	131.7	h-i-j
i-j	124.0	*Madzakitam*	127.3	i-j
j	120.4	*Chaksaac-1*	126.2	j
k	101.3	*Mejen-1*	106.3	k

* Landraces with the same letter are not significantly different ($\alpha = 0.05$) for this character.

the four study areas. Statistical analyses of morphological variation in seeds indicated differentiation between two groups of wild populations. They grow sympatrically only in central eastern Quintana Roo. Even though wild and weedy populations were not used, sometimes their growth is permitted within or near the *milpas* where *P. lunatus* is cultivated. This situation could explain the fact that in several wild populations we found seeds with colors, forms, and sizes similar to the cultivated variants, as a consequence, perhaps, of past events of gene flow between wild and cultivated germplasm. The greatest abundance of wild populations and the sympatrical growth of the two morphological variants were found in central eastern Quintana Roo, findings that appear to be correlated with: 1) longest fallow periods, 2) lowest herbicide use, and 3) best soil fertility conditions (Table 1).

Statistical analyses of morphological variation in seeds also indicated differentiation between the two weedy populations sampled and a morphologically intermediate status between wild and cultivated variants. The intermediate status found concurs with existing data on the seed mass of the accessions of *P. lunatus* collected in Campeche and Yucatan by Debouck (1979). This situation might have reflected the existence of gene flow between weedy and cultivated populations. Since the two weedy populations grew within two *milpas* with different seed mixtures of cultivated variants of *P. lunatus,* and in both cases, the weedy plants were controlled with a hand weeding technique (*lochepak*) that allows the simultaneous flowering of weedy and cultivated plants, it is possible for gene flow to occur between both populations. It has been suggested that weedy populations of *P. lunatus* are the product of such hybrid crossing between wild and cultivated populations, as the species can reach high rates of allogamy (approximately 48%) (Baudoin 1998). It has also been suggested that they are the result of regressive mutations, a process seen in various tropical environments (Baudoin 1988). Recent studies conducted on *P. vulgaris* (Papa and Gepts 2003) showed that the weedy populations are genetically intermediate between the wild germplasm and the cultivated one, suggesting a possible hybrid origin.

Weedy populations were only present at low densities in central eastern Quintana Roo and southeastern Yucatan. This situation could be a consequence due to the differential management of the agricultural areas by the farmers. The areas where wild populations grow are preferred for corn monoculture treated with herbicides, since hand picking is not effective in eliminating high-density wild populations. This agricultural management does not permit the existence of species associated with corn as *P. lunatus,* thus the generation of *P. lunatus* weedy populations by gene flow is not possible. So, weedy populations of *P. lunatus* were specifically associated with long fallow periods that allowed the existence of vegetational patches and with traditional weeding practices. The agricultural intensification prevalent in "Los Chenes" and in the "Puuc" region might be contributing to the absence of wild and weedy populations.

Among cultivated germplasm we found a wide variation associated with the traditional Mayan farming system known as the *milpa.* This variation was traditionally recognized and classified by peasants principally through the use of one phenological (length of production cycle) and two morphological characters (seed shape and color). Determining the criteria of traditional classification was very useful in the differentiation of putative landraces, since it allowed us to distinguish variants by the length of their productive cycle, something that would not have been recognized with the morphological analysis of seed alone. The importance of this character was demonstrated by the ex situ analysis. Such is the case of the variant *xmejen,* which is so important in the economy of the peasant farmers but which differs from the variant *xnuk* only in its shorter productive cycle. It has been pointed out that the study of intraspecific diversity based on traditional knowledge is a good starting point for analyzing the genetic diversity of cultivated species (Bellon 1995; Hernández-Xolocotzi 1970). The results obtained in this work give support to this point of view.

Our analyses revealed greater morphological diversity of the cultivated variants than would be expected based upon the traditional names used by peasants. We did not find a clear differentiation between the two cultigroups suggested by Baudet (1977) for the Mesoamerican gene pool, since we found landraces that did not correspond to the "Papa" or "Sieva" groups; a situation already alluded to by Ballesteros (1999). Studies carried out with biochemical and molecular markers (Fofana et al. 1997; Gutiérrez et al. 1995; Lioi and Lotti 1996; Maquet et al. 1997) did not show a clear divergence between these two cultigroups. It is possible that the selection of germplasm present in these groups could have occurred in genetically related ancestral materials that diverged very recently, making a clear genetic differentiation between both cultigroups difficult up to now (Maquet et al. 1997). Although *P. lunatus* has been considered a predominantly autogamous species, gametophytic factors have been reported that prevent self-fertilization, such as the inhibition of pollen tube growth on incompatible style tissues (Allard 1963; Bemis 1959). A high inter-group fertility among landraces has also been reported (Erickson 1982). Allard (1954) showed that distance is one of the main factors limiting the amount of exogamy between the cultivated variants, diminishing rapidly at distances greater than 0.76 m. Other important factors were wind direction and the type of variant. These limiting factors of the amount of exogamy found by Allard (1954) might not be so important in the agriculture of the Peninsula of Yucatan. In this region, the planting distance between individuals of *P. lunatus* is one meter; this distancing eventually disappears given the indeterminate growth habit of the plant. Furthermore, the practice of planting a large number of variants (up to 7) in one *milpa,* either in rows or mixed, favors the possibility of gene flow between one variant and another and subsequently the generation of variation which eventually could have been selected by the peasants.

Ballesteros (1999) and Nahal (1993) reported a "Pseudo-wild" cultivated variant which was not found in this study. However, it is possible that their collections were made at peasants' homes where mixed germplasm was being stored for the next cultivation cycle. If so, these collections might have accidentally included weedy seeds. The "Pseudo-wild" seed type (Ballesteros 1999; Nahal 1993) possibly corresponded to the weedy variant *ibcho*-4 found in this work.

Ex situ analysis indicated a group of putative landraces (*boxuolis, boxpetch,* and *madzakitam*) that shared certain characteristics with wild populations, such as the coloration of the flower, hypocotyl, and seeds. Ethnobotanical information revealed that the seeds of these landraces had a semi-bitter flavor and cooked slowly, thus limiting their commercialization possibilities. These characteristics are probably related to wild traits suggesting genetic infiltration from wild to cultivated landraces. Ex situ analyses also demonstrated that some putative landraces shared characteristics from both the "Sieva" and "Papa" cultigroups, a finding that also suggested gene flow between these cultigroups.

We found differences among our study areas in the richness, diversity and dominance of putative landraces. The highest values for richness and diversity and the lowest values for dominance were associated with central eastern Quintana Roo and southeastern Yucatan. This, in turn, was related to: 1) longest fallow periods and lowest agricultural intensification, 2) greatest traditional culture persistence and human populations isolation, and 3) lowest market pressures. In central eastern Quintana Roo, the gene pool for *P. lunatus* appears to have been enriched by human migrations into the region from different parts of the Yucatan Peninsula during the Caste Wars of the 19th century, as well as by the historical contact that immigrant human populations have maintained with their areas of origin (Bartolomé and Barabas 1977). In central eastern Quintana Roo and southeastern Yucatan, the *boxuolis, boxpetch* and *madzakitam* landraces were collected. These landraces were characterized by flower, hypocotyl, and seed coloration patterns that were similar to wild populations. In addition, wild and weedy populations were collected in these two regions. Taken as a whole, it is clear that these areas support gene complexes of wild, weedy, and cultivated populations.

The differences found in richness, diversity, and dominance of the putative landraces of *P. lunatus* among the four study areas do not seem to be correlated to ecological or agroecological differences. Within the four areas, agriculture is carried out in the same types of vegetation: medium sub-evergreen forest and medium sub-deciduous forest, with mainly rendzina and litosol soils. Although there is a rainfall gradient running from south to north in the Peninsula of Yucatan, making the area of the Chenes and central-eastern Quintana Roo wetter, the results presented in this work do not indicate a correlation between rainfall and richness or diversity of landraces.

At present, there are few landraces of economic value in local and regional markets of the Yucatan Peninsula. Those of greatest value are landraces with a white testa, such as *xmejen-1, mulición*-1 and *sac*-1. Ethnobotanical information indicated that the relatively great abundance of just two landraces, *mulición*-1 and *sac*-1, might be the consequence of market pressures on traditional farmers to produce seeds with a white testa. However, the disproportionately large representation of these variants might also be related to their long production cycle that is highly adapted to the prevailing rainy season. Ballesteros (1999) has indicated that the preference for the white testa variants could be due to a selection pattern imposed by the European colonization. However, this situation may be related to the content of HCN in this type of variants in comparison with the content in variants with other colors of testa. Smart (1988) suggests that white testa genotypes have less HCN content. However, Maquet (1991) found no correlation between coloration of the seed and HCN content in a sampling collected in this region. On the other hand, ethnobotanical information indicates that one of the variants recognized by the peasants as having a better taste is *putsicasusuy,* which has a reddish-grey coloring. The same color patterns found in this research are in the accessions from the Yucatan Peninsula in the CIAT bean collection collected in the period from 1970 to 1980, suggesting that the same variation in color pattern has been maintained by traditional farmers today. The peasants also identified the white testa variants as being the fastest cooking. The cooking time is related to the speed of imbibition of the seed. In an experiment on germination with 17 traditionally recognized cultivated variants of *P. lunatus* (data not shown), the white testa variants presented a shorter imbibition time and the two variants of black seed, *boxuolis* and *boxpetch* presented a longer time. Thus criteria such as taste, color, and cooking time of the seed could be determining the price in the market and, in conjunction, these four criteria could be determining the selection of certain landraces (mainly the white testa) over others. This situation has discouraged many peasants from planting landraces with seed colors other than white; and this, in turn, is limiting the generation of hybrid forms.

The lowest richness of landraces observed in the "Puuc" region appears to have been correlated with a high degree of agricultural intensification and with the incorporation of small-scale farmers into markets. In this area, we encountered almost half the landraces occurring in southeastern Yucatan. Deep soils in the "Puuc" region have allowed the introduction of irrigation and farm machinery into geographically tiny areas. This has favored monocultures and agricultural intensification due to the planting of short cycle landraces (such as *mejen-1*) with high market values. The importance of landraces with shorter productive cycles is reflected in the fact that they have also been selected and maintained in various genetic pools by peasant farmers.

The greatest diversity of *P. lunatus* found in the Yucatan Peninsula by Ballesteros (1999), when compared to the rest of Mexico, could be explained by the results presented in this investigation. The morpho-phenological variation in *P. lunatus* observed suggested the presence of complex genetic pools in the Maya lowlands area that may have resulted from sympatric contact between wild, weedy, and cultivated populations. Such a situation is similar to those described by Beebe et al. (1997) for *P. vulgaris* in the Andean center and by Papa and Gepts (2003) and Zizumbo-Villarreal et al. (2002) for Mesoamerica. In both cases, gene flow between components of the complexes has been considered an important mechanism for generating genetic variability (Beebe et al. 1997; Harlan 1992). Understanding the importance of this, at present we are conducting analyses about diversity and gene flow among the variants recognized in this investigation, using microsatellite markers. Ethnobotanical data suggested that peasants favored the formation and maintenance of these complex genetic pools through: 1) traditional weeding practices that did not totally eliminate weedy plants; 2) side-by-side planting of different landraces; and, 3) sowing mixtures of landraces when seeds were scarce. During collecting, seeds from weedy populations were occasionally found among harvested cultivated seeds. Thus, it is possible that such seeds might eventually be returned to cultivated fields by farmers acting as unconscious dispersal agents. On the other hand, this great diversity of *P. lunatus* in the region could lie in the profound and continuous history of selection pressures and traditional management practices exercised by Mayan farmers over thousands of years. It could also be a result of the complexity of human migrations in the area and the history of germplasm exchange that has been maintained with other subcultural areas in Mesoamerica since the establishment of the first agricultural communities (Colunga-GarcíaMarín et al. 2003).

The results presented in this study indicate the importance of initiating in situ and ex situ germplasm conservation programs for *P. lunatus* in the Yucatan Peninsula, especially given the accelerated pace of agricultural intensification in the region. The fact that central eastern Quintana Roo and southeastern Yucatan had the greatest richness and diversity, the least dominance, and the greatest number of "rare" cultivated varieties, emphasizes that in situ conservation programs would be especially relevant here. Unexpected conditions such as the randomness of rainfall events, relatively few peasants planting "rare" varieties, and the older age of farmers, could lead to significant losses of germplasm even within the span of a single human generation. A similar situation was observed for the *chocolate* and *tabaco* landraces of *P. lunatus.* Only one peasant, in central eastern Quintana Roo, of the 160 interviewed in the ethnobotanical research maintained these stocks. Unfortunately, he lost these seeds during the drought of the 2001–2002 farming season. Additionally, a certain differentiation among wild populations was found in central eastern Quintana Roo.

In situ conservation programs must also include significant cultural reinforcement programs, since the relevant objective is not the conservation of available germplasm by farmers, but that farmers continue to play a dynamic role in the generation of new germplasm.

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Appendix 1

Interview of 160 Peasants in the Yucatan Peninsula, Mexico

Farmer's name:
Name of the community:
Study area:

Traditional classification:
Do you sow *ibes*?
What are the names of your types of *ibes*?
What do these names mean?
What morphological or phenological characters do you use to name your *ibes*?

a) Plant characters:
b) Seed characters:
c) Others characteristics:

Besides your *ibes*, how many types of *ibes* do you know?
How are those *ibes* named?
Why are those types of *ibes* named in this way?
Do you know the wild *ibe*?

How do you name the wild *ibe*?
What does this name(s) mean?
Are there different types of wild *ibes*?
What morphological or phenological characteristics do you use to name the wild *ibes*?
  a) Plant characters:
  b) Seed characters:
  c) Others characteristics:
Selection criteria:
Why do you prefer to plant each of these types of *ibes* and no others?
Of the *ibes* you know but do not plant at present, which would you like to plant?
Why?
Of the *ibes* you plant:
Which tastes better?
Which cooks faster?
Which has the best price on the market?
Which is the largest in size?
Which has the nicest color?
Which has the nicest shape?
Which produces more seeds?
Which can be harvested sooner?
Which resists drought better?
Which resists attack from weevils better?
Do you maintain and select your classes of *ibes* for the reasons mentioned above?
Which reason is most important for you?
Apart from the reasons already mentioned, is there any other reason you choose to plant one type of *ibe* and not another?

Agricultural management:
In what type of *milpa* do you plant your *ibes*?
  a) traditional (slash and burn), b) mechanized with irrigation, c) other (which?)
When (period of the year) do you sow your different class of *ibes*?
When (period of the year) do you harvest your different class of *ibes*?
How many types of *ibes* do you sow?
How many hectares do you plant of each type of *ibe*?
Where do you plant your different types of *ibes*?
  a) in the *milpa*,
  b) in the home garden,
  c) other place (where?)
How do you plant them?
  a) Separately (each type in different *milpas* or different parts of the same *milpa*),
  b) in seed mixtures, c) in other way (which?)
Why do you do it in this way?
How many years of fallow did the *milpa* have where you planted your *ibes*?
Why do you plant in that site?
Do you use fertilizer in your *milpa*?
Why do you use fertilizer?
Do you use herbicide in your *milpa*?
Why do you use herbicide?
What other crops do you plant with your *ibes*?
  a) maize, b) common bean, c) squash, d) others (which?)
Where does the wild *ibe* grow?
  a) within the *milpas,*
  b) alongside the *milpas,*
  c) roadside,
  d) forest (what kind?),
  e) other place (where?)
If plants of wild *ibe* grow in your *milpa,* what do you do with these wild plants?
  a) cut them (*haranchak* or *lochepak*?),
  b) use herbicide,
  c) permit their growth
Why do you do this?

Product destination:
Why do you sow *ibes*?
  a) subsistence, b) market, c) both of them, d) other (which?)
What types of your *ibes* are for subsistence?
Why these types?
What types of your *ibes* are for the market?
Why these types?
Where do you sell your *ibes*?
  a) in the town, b) outside the town (where?), c) both
What types of your *ibes* do you sell more?
What types of your *ibes* are more expensive?
How much does each type of *ibe* cost?
Do you use wild *ibe*?
What do you use this germplasm for?

APPENDIX 2. MEAN (M) AND COEFFICIENT OF VARIATION (CV) OF FOUR SEED MORPHOLOGICAL CHARACTERS AND RELATIVE ABUNDANCE OF 30 PUTATIVE LANDRACES AND TWO WILD AND WEEDY VARIANTS OF *P. LUNATUS* IN THE YUCATAN PENINSULA, MEXICO. (C) CODE OF VARIANT USED IN FIGURE 6, (N) NUMBER OF ACCESSIONS BY VARIANT.

			Length (cm)		Width (cm)		Length/Width		Mass (g)		Relative abundance
Variant number	C	N	M[1]	CV	M[1]	CV	M[1]	CV	M[1]	CV	(%)[2]
cf-gr. Sieva											
Bacalar-1	a	16	1.39	5	0.93	6	1.23	3	1.56	4	4.92
Bacalar-2	b	3	1.36	6	0.96	5	1.19	2	1.58	6	0.92
Batun	c	1	1.16	4	0.85	5	1.17	3	1.43	4	0.74
Boxpetch	d	1	1.30	2	0.86	4	1.23	2	1.56	2	1.85
Chakchi	e	1	1.17	2	0.87	7	1.16	3	1.18	5	0.02
Chakmejen-1	f	1	1.26	4	0.85	6	1.22	3	1.46	3	0.21
Chakmejen-2	g	1	1.27	3	0.94	4	1.16	2	1.51	2	0.11
Chakpetch-1	g	8	1.32	6	0.89	6	1.22	4	1.47	6	1.59
Chakpetch-2	i	1	1.12	4	0.78	5	1.20	2	1.46	3	0.2
Chaksaac-1	j	2	1.28	8	0.86	7	1.22	4	1.48	5	2.81
Chaksaac-2	k	1	1.42	6	0.93	5	1.24	2	1.61	3	1.4
Chocolate	l	1	1.09	4	0.78	8	1.18	3	1.40	1	0.02
Madzakitam	m	1	1.35	4	0.93	6	1.21	3	1.36	6	0.31
Mejen-1	n	6	1.26	6	0.86	5	1.21	3	1.47	4	2.59
Mejen-2	o	1	1.12	5	0.78	5	1.21	3	1.35	3	0.44
Nuk-1	p	1	1.17	6	0.87	4	1.16	3	1.50	2	2.06
Nuk-2	q	1	1.31	4	0.87	3	1.23	2	1.47	3	2.06
Tabaco	r	1	1.35	4	0.95	5	1.19	2	1.54	1	0.16
cv-gr. Papa											
Boxuolis	s	1	0.91	5	0.77	6	1.09	2	1.42	2	0.08
Chakuolis	t	4	1.05	7	0.78	6	1.16	3	1.41	5	0.06
Kan	u	1	1.04	4	0.78	5	1.15	2	1.32	3	1.01
Mulición-1	v	32	0.93	8	0.75	6	1.12	4	1.32	5	28.73
Mulición-2	w	1	0.90	7	0.75	4	1.09	3	1.56	2	0.88
Poolsanto	x	1	1.07	4	0.78	5	1.17	3	1.32	5	0.26
Putsicasutsuy-1	y	13	1.09	6	0.80	6	1.17	3	1.43	7	14.3
Putsicasutsuy-2	z	2	1.04	9	0.73	5	1.19	4	1.21	5	2.2
Sac-1	1	26	1.05	5	0.77	5	1.17	3	1.41	5	23.31
Sac-2	2	2	1.05	6	0.77	5	1.17	3	1.42	5	1.81
Sacmejen-1	3	1	0.88	6	0.73	4	1.10	3	1.26	4	2.39
Sacmejen-2	4	1	1.03	6	0.78	5	1.15	2	1.37	2	2.39
Weedy											
Ibcho-3	5	1	1.05	17	0.75	13	1.17	3	1.20	4	—
Ibcho-4	6	1	0.89	8	0.69	9	1.14	2	0.93	3	—
Wild											
Ibcho-1	7	10	0.75	8	0.59	9	1.13	3	0.64	10	—
Ibcho-2	8	1	0.71	9	0.61	9	1.08	2	0.63	1	—

[1] Mean of 10 seeds per accession.

[2] Planted area of the variant by the farmers interviewed/planted area of *P. lunatus* × 100.

APPENDIX 3. MEAN (M) AND COEFFICIENT OF VARIATION (CV) OF 23 MORPHOLOGICAL AND PHENOLOGICAL QUANTITATIVE CHARACTERS OF 30 PUTATIVE LANDRACES OF *P. LUNATUS* FROM THE YUCATAN PENINSULA, MEXICO GROWTH UNDER UNIFORM CONDITIONS IN JBR-CICY. (C) CODE OF VARIANTS USED IN FIGURE 8. (N) SAMPLE SIZE.

			Emergence of seedling (days)		Primary leaf (days)		First trifoliate leaf (days)		Third trifoliate leaf (days)	
Name	C	N	M[1]	CV	M[1]	CV	M[1]	CV	M[1]	CV
cf-gr. Sieva										
Bacalar-1	a	10	8	10	13.4	10	19.2	9	31.7	7
Boxpetch	b	10	6.9	13	9.9	10	16.9	11	13.6	7
Chakchi	c	10	8	8	10.5	9	15.2	8	25.7	5
Chakmejen-1	d	10	6	11	8.4	10	14.2	6	27.3	5
Chakpetch-1	e	10	6.8	14	10.2	13	13.3	10	32.2	6
Chaksaac-1	f	10	15	13	11.5	11	17.7	10	23.1	7
Madzakitam	g	10	6	8	8.2	8	12.7	5	28.2	5
Mejen-1	h	10	6	11	10.6	9	14.9	10	30.4	8
Nuk	i	10	6	11	10.3	9	14.4	10	48.2	6
cv-gr. Papa										
Boxuolis	j	10	6.1	9	8.6	11	14.7	10	28.7	6
Chakuolis	k	10	16	11	8.3	11	16.1	10	28.9	6
Kan	l	10	5.1	11	8.2	8	13.5	7	26.7	4
Mulicion-1	m	10	5.2	19	9.1	13	13.5	9	30.4	7
Poolsanto	n	10	7.4	14	14	5	29.5	5	36.5	3
Putsicasutsuy-1	o	10	6	8	8.3	10	13.4	6	26.9	5
Sac-1	p	10	5	13	8	8	12.5	16	22.3	23
Sacmejen-1	q	10	5	13	8	10	11.9	6	21	6

[1] Mean of the ten plants.
[2] Mean of ten morphological structures per plant.

APPENDIX 3. EXTENDED.

Preflowering (days)		Flowering (days)		Pod formation (days)		Flower bud length (cm)		Pod length (cm)		Pod width (cm)		Pod length/width	
M[1]	CV	M[1]	CV	M[1]	CV	M[2]	CV	M[2]	CV	M[2]	CV	M[2]	CV
128.4	5	139.9	4	146.1	4	0.6	8	5.7	8	1.5	7	3.9	11
136.7	7	143.5	8	152	8	0.7	7	5.7	8	1.5	8	3.8	10
128.7	4	131.6	4	135	4	0.6	5	5.5	6	1.3	12	4.4	20
125.3	1	127.5	1	131.6	1	0.7	5	5.9	15	1.4	6	4.4	13
128.5	4	131.2	4	137.8	3	0.7	5	6.2	10	1.4	12	4.5	12
115.5	6	120.4	6	126.2	6	0.6	5	4.4	10	1.2	8	3.7	10
121.5	3	124	3	127.3	2	0.7	7	6.4	9	1.5	11	4.3	10
86.2	4	101.3	3	106.3	3	0.7	7	5.5	11	1.5	9	4.2	16
122	6	127.8	6	134.2	6	0.7	5	5.8	9	1.3	10	4.6	13
133.6	5	136.6	5	141.5	5	0.6	5	4.7	6	1.4	7	3.5	7
147.9	3	156.3	3	162.1	2	0.7	3	5.5	9	1.5	14	3.8	7
149.9	4	159.9	3	162.9	3	0.6	7	4.8	6	1.4	10	3.5	9
128.5	2	145.1	2	149.2	2	0.7	8	6.3	10	1.4	11	4.4	6
139.5	2	147.5	2	152.7	2	0.7	5	5.5	12	1.3	6	4.2	13
138.7	4	148.1	4	151.1	3	0.7	6	5.1	5	1.4	11	3.8	6
121.1	2	139.5	2	144.2	2	0.7	7	5.7	7	1.4	9	3.9	10
113.6	1	129.4	2	134.3	1	0.7	4	5.3	12	1.3	9	4.3	18

APPENDIX 3. CONTINUED.

Name	Beak of pod length (cm)		Pod length/ beak length		Seeds number/pod		Locules number/pod		Locules number/ seeds number	
	M^2	CV	M^2	CV	M^2	CV	M^2	CV	M^2	CV
cv-gr. Sieva										
Bacalar-1	0.4	18	0.2	19	1.9	17	2.7	18	1.5	39
Boxpetch	0.3	23	0.2	26	2.9	20	3.1	18	1.1	17
Chakchi	0.4	20	0.2	20	2	24	3	16	1.6	36
Chakmejen-1	0.4	22	0.2	30	2.1	47	3.1	10	1.8	48
Chakpetch-1	0.4	19	0.2	19	2.6	10	2.9	20	1.1	19
Chaksaac-1	0.2	20	0.1	18	2.4	22	2.8	15	1.2	26
Madzakitam	0.4	17	0.2	19	2.5	21	3	16	1.3	28
Mejen-1	0.4	15	0.2	24	2.2	34	2.4	22	1.3	55
Nuk	0.3	30	0.2	24	2.6	27	2.9	11	1.3	51
cv-gr. Papa										
Boxuolis	0.3	14	0.2	14	2.6	20	2.8	15	1.1	19
Chakuolis	0.3	23	0.2	27	2.7	18	3.1	10	1.2	20
Kan	0.3	28	0.2	29	2.3	29	2.6	20	1.2	29
Mulicion-1	0.3	16	0.2	17	2.6	20	3	16	1.2	20
Poolsanto	0.4	17	0.3	18	2.2	42	3.1	10	1.7	45
Putsicasutsuy-1	0.3	24	0.1	26	2.4	29	1.8	23	1.2	28
Sac-1	0.3	22	0.2	26	2.8	28	3	22	1.1	19
Sacmejen-1	0.3	24	0.1	27	2.5	28	2.9	11	1.3	49

APPENDIX 3. CONTINUED. EXTENDED.

Seed length (cm)		Seed width (cm)		Seed length/width		Hypocotyl length (cm)		Leaflet length (cm)		Leaflet width (cm)		Leaflet length/width	
M^2	CV	M^2	CV	M^2	CV	M^2	CV	M^2	CV	M^2	CV	M^2	CV
1.3	8	0.8	10	1.5	6	9.2	10	5.5	16	3.1	19	1.8	9
1.3	4	0.9	4	1.5	5	12.9	11	6.1	8	3.3	10	1.9	6
1.2	6	0.8	6	1.5	5	7	13	5.2	15	2.7	21	1.9	7
1.3	4	0.9	6	1.5	5	8.9	15	5.1	13	2.5	14	2	10
1.4	6	0.9	6	1.5	9	11.1	9	4.8	15	2.7	16	1.9	8
0.9	4	0.7	8	1.3	10	9.1	10	5.3	9	2.7	12	1.9	7
1.3	3	0.9	4	1.5	3	10.2	7	5.9	11	3.2	16	1.9	5
1.4	6	0.9	4	1.6	5	8.2	12	3.7	11	2.1	21	1.8	12
1.3	4	0.9	5	1.5	3	6.3	20	4.1	10	2.4	10	1.7	6
0.9	9	0.8	5	1.2	10	9.5	11	5.2	15	2.9	17	1.7	8
1	5	0.8	6	1.4	8	8.7	13	5.2	7	3.1	10	1.7	11
1	4	0.8	6	1.3	4	7.6	14	4.7	18	2.8	20	1.7	7
1.4	4	0.9	6	1.5	5	9.2	13	4.9	13	2.5	20	1.9	10
1.1	6	0.9	4	1.4	6	7.6	10	3.4	10	2.2	24	1.6	12
1	4	0.8	5	1.4	5	8.5	7	5.6	8	3.2	6	1.8	7
1	8	0.8	6	1.4	6	6.9	8	3.6	19	1.9	26	1.9	16
0.9	6	0.8	6	1.3	5	7.8	6	4.3	19	2.2	26	1.9	14