
Diversity of Common Bean (*Phaseolus vulgaris* L.) Landraces and the Nutritional Value of their Grains

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Abstract

Grain legumes are considered major sources of dietary proteins, calories, certain minerals and vitamins, and they are the most widely cultivated and consumed crops worldwide. Among them are the common beans, whose major production volumes came from landraces cultivated in traditional farming systems. The objective of this study was to evaluate the phenotypic diversity of a set of common bean landraces from Mexico based on the agromorphological traits and nutritional composition of the grain in the context of traditional farming systems. Different field and laboratory data were collected and complemented with secondary information published in refereed journals and research reports. The results showed that there are significant differences in the morphological and physiological traits of the plant, pod and grain among groups of common bean landraces of different geographic origins, which were associated with different indigenous groups. Similar patterns were observed in the contents of anthocyanins, polyphenols, flavonoids and minerals as well as antioxidant activity. In the evaluated population groups in each region, there are outstanding populations in terms of agromorphological traits and the nutritional value of the grain that can enable a participatory breeding initiative guided by regional objectives. Some populations from Sierra Norte, Oaxaca, presented higher values in Zn and Fe, and populations from Estado de Mexico exhibited high polyphenol and flavonoid values but stable agronomic behaviour.

Keywords: Biochemical characterization, crop evolution, local seed systems, morphological traits, on farm conservation

1. Introduction

The greatest genetic diversity of wild and cultivated beans is distributed throughout the Americas from northern Mexico through Central America and the Andes to northwest Argentina [1]. Domesticated beans are commonly separated into Andean and Mesoamerican gene pools [2], but Mexico has been established as the centre of origin, diversification and domestication of the common bean based on archaeological, ethnobotanical, morphological, biochemical, genetic and isoenzyme evidence [3–6]. The distribution pathways of beans into and across Europe were very complex and occurred through several introduction events from the New World combined with direct exchange between European and Mediterranean countries [5].

Currently, the common bean is distributed in Europe, Asia and Africa, where it presents similarities to Andean and Mesoamerican gene pools or forms hybrids between both gene pools. For example, it was determined that there is a high hybridization frequency in central Europe but low frequencies in Spain and Italy [5]. In Africa, the landraces are frequently grouped into Andean and Mesoamerican gene pools with few introgressions among these groups [6], and this pattern of diversity was also detected in China and India [7, 8]. However, the diversity of the common bean has been studied less in Asia and Africa than in Europe and the Americas.

The landrace concept is useful for naming or distinguishing among cultivated varieties through simple traits that are locally adapted to traditional farming systems [9]. In this context, we use the landraces of the common bean as the unit of diversity of the farm or farm-managed population, which farmers select and sow during every crop cycle. In Latin America, the bean landraces contribute 70–90% of the seed planted by farmers for the production of food grain [10], and according to the Asian Pacific Seed Association, the seed saved by farmers accounts for 80–90% of all of the seeds used in Asia [11]. Therefore, it is important to understand the contribution of such landraces to phenotypic and genetic diversity as well as their contribution to on-farm conservation of diversity and traditional diets.

The phenotypic and genetic diversity of common bean landraces is typically evaluated through morphological traits, phaseolin seed proteins, allozymes, the biochemical-nutritional traits of the grain and DNA markers, with the local populations that are preserved on-farm as references, to describe the population structure, to understand diversification processes and biogeographic distributions, and to define strategies for conservation and utilization [5, 6, 7, 12]. Farmers manipulate common bean populations through the use of the traits of the plants or seeds, which influences the population structure as well as grain quality, i.e., chemical composition [13]. Despite the increasing use of DNA-based markers to estimate the genetic

diversity of different landrace collections, the evaluation of phenotypic variation is still crucial for determining the adaptation and agronomic potential as well as the breeding and nutritional values of landraces.

South-central Mexico is part of the Mesoamerican region that is considered one of the world's biodiversity hotspots, and 28 ethnic groups are concentrated in this region, including the Otomi, Mazahua, Nahuatl, Popolucas, Zapoteco, Mixteco, Mixe, Amuzgo, Triqui, Mazateco, Chinanteco, Mayas, Chontales, Huaves, Chatino, Cuicateco, Chontal, Tzetzal, Tzotzil, Purepecha, Totonaco, Ocuilteco and Matlazincas among others. Various studies of common bean in this region have indicated that it contains the greatest genetic diversity of *Phaseolus vulgaris* in a biocultural diversity context [14–16], a fact documented by the diversity hotspot designation [17]. According to passport data from Mexican genebanks and genetic diversity studies, the highest *P. vulgaris* genetic diversity is being preserved in the fields of indigenous farmers distributed along the south-central part of the region, which includes the Mesoamerican, Jalisco and Durango races.

A wide variety of nutritional compounds with multiple positive effects for human health are contained in bean seeds with the high contents of protein, fibre, polyphenols, flavonoids, carotenoids, saponins, oligosaccharides, condensed tannins, lectins, trypsin inhibitors and phytic acid considered to be the most important components. Polyphenols, anthocyanins and flavonoids, among other phytochemical compounds, are particularly related with antioxidant biological activities and preventive effects against cardiovascular or chronic degenerative diseases, such as cancer, obesity and diabetes as well as other conditions related to the metabolic syndrome, triglycerides and cholesterol [18–23].

In East Africa, the per capita consumption rate of the common bean is above 40 kg/year [24], and in Mexico, it is 10.38 kg/person a year with an overall food intake of 5.43 g protein/person a day [25, 26]. As reported by Aguirre-Arenas et al. [27], an annual per capita consumption ranging from 9.8 to 25.9 kg has been estimated in four communities from Morelos, Tamaulipas, San Luis Potosí and Michoacán, Mexico. Additionally, the highest bean production (86.4%) comes from marginal agrosystems with lower fertility, unirrigated soils on slopes where the landraces are usually planted by small-scale farmers [28].

Interest in the use of grain legumes and their constituents in food is growing in many developed countries, and the factors contributing to this trend include access, legumes are cultivated in almost all climatic conditions, as well as their reported nutritional and health benefits. Despite changes in consumer preferences, pulses have a long history of use as human food in many developing countries from the Mediterranean region, Africa, Latin America and Asia, and in some cases, the demand exceeds national production volumes. Peas, chickpeas, lentils, beans, soybeans, mung beans, faba beans and other grain legumes are important sources of food proteins, amino acids, minerals and bioactive substances (phenolic compounds, lectins, enzyme inhibitors, phytates, oligosaccharides), all of which have functional properties that benefit human health and are modified by processing or physical treatments [29–31]. It is necessary to know the nutritional composition and to test these functional properties of the common bean landraces as well as their contribution to traditional rural diets to increase the consumption volume. The main objective of this research was to evaluate the phenotypic

diversity of a set of common bean landraces from Mexico through agromorphological traits and the nutritional composition of the grain in the context of traditional farming systems and on-farm seed selection.

2. Diversity of common bean landraces using agro-morphological traits and the criteria of farmers

Diverse researchers around the world use local populations or samples of common bean landraces as reference sets to study their genetic diversity and population structure [6, 7, 32, 33, 34]. Nevertheless, such on-farm crop genetic diversity is highly dynamic as a result of the agroecological conditions of cultivation, the preferences of farmers in seed selection and the management of seed lots, among other factors, that have important impacts on the population structure and chemical composition of the grain, which change across time [5, 24, 33, 35]. In Latin America, from 70 to 90% of the common bean seed that is planted is produced by farmers [10], and in Asia, from 80 to 90% of all seeds used by farmers came from local supplies instead of seed companies [12]. In this context, farmers play an important role in the evolutionary process of common beans under domestication, and it is necessary to understand the reasons and criteria for the on-farm management of the bean landraces. In cases where the study samples came from genebanks, such diversity remained static for years, and the genetic diversity estimators differ from those of places where on-farm population dynamics exist, which are primarily in the centres of genetic diversity.

The current genetic and phenotypic variation in the common bean in Mexico in terms of plant and physiological characters and grain and chemical composition is based on the genetic diversity preserved by pre-Colombian cultures, contemporary farmers and the gene pools of related wild species [14, 34, 35]. The variety of the shapes, sizes and colours of the grains in several regions where beans are grown is an example of the still poorly documented genetic diversity in the fields of traditional farmers that is usually characterized by agro-morphological descriptors [36], molecular markers [37], and protein [38], anthocyanin [39] and polyphenol [40] contents among others.

The characters that are most commonly used by farmers to differentiate their landraces include grain colour, colour brightness (shiny black, dirty black, etc.), growth type when planted alone (type I and II) or with corn (growth III and IV), time from planting to the harvest of green beans and grain, and the size, shape and colour of the grain and pod. Other more accurate descriptive characters are sometimes used by farmers aiming to distinguish their landraces that are most commonly related to field and post-harvest behaviour, such as high yield, the quantity of harvested pods, tolerance to biotic and abiotic factors, grain hardness and grain-cooking time, among others. This is all local information related to the knowledge shared by local farmers concerning their landraces.

An agromorphological characterization was required to describe the phenotypic variability in native beans collected from populations from different states and regions in Mexico as well as the phenotypic differences among and within the sources of the different landraces. As

revealed by the results, significant differences exist among bean landraces from different geographical origins as well as within each geographical location (**Table 1**). Consequently, despite the phenotypic similarities in colour and seed dimensions, the different common bean populations are subject to patterns of isolation in addition to artificial selection, which leads to divergence in the characteristics of agronomic importance.

| Descriptive traits | Mexican states (5) | Populations/states | CV (%) | Min. | Max. | Average |
|----------------------------|--------------------|--------------------|--------|-------|-------|---------|
| Days to flowering | 193.43** | 66.4** | 5.6 | 49.3 | 74.3 | 63.7 |
| Pod length (cm) | 8.72** | 4.84** | 10.4 | 9.0 | 15.4 | 12.8 |
| Pod width (cm) | 0.30** | 0.07** | 7.9 | 0.8 | 1.6 | 1.14 |
| Grains/pod | 11.06** | 4.22** | 6.4 | 3.9 | 8.9 | 6.5 |
| Number of pods/plant | 557.31** | 149.7** | 17.2 | 2.7 | 36.7 | 19.5 |
| Number of pods/exp. parcel | 488499** | 115605** | 16.7 | 19.7 | 900.0 | 471.5 |
| Wet yield/parcel (kg) | 144.82** | 38.34** | 18.4 | 0.20 | 17.2 | 7.4 |
| Dry yield/parcel (kg) | 3.06** | 0.83** | 18.6 | 0.03 | 2.31 | 1.12 |
| Wet weight/pod (g) | 51.88** | 37.7** | 14.0 | 3.91 | 20.81 | 14.9 |
| Dry weight/pod (g) | 1.27** | 0.88** | 10.3 | 0.59 | 3.16 | 2.3 |
| Wet yield/plant (g) | 164898.4** | 58479** | 19.2 | 26.7 | 694.0 | 299.1 |
| Dry yield/plant (g) | 3173.88** | 1257.1** | 18.8 | 4.2 | 88.6 | 45.7 |
| Wet weight/30 pods (g) | 46719.49** | 33999** | 14.0 | 117.3 | 624.3 | 446.4 |
| Dry yield/ 30 pods (g) | 1147.61** | 799.2** | 10.3 | 17.3 | 94.7 | 68.6 |

**Significant at $P < 0.01$.

Table 1. Mean squares of the analyses of variance, coefficients of variation (CV), minimums, maximums, and average values of agromorphological traits evaluated in common bean landraces from five Mexican states.

An average of 6.5 grains per pod were quantified among the landraces in Mexico, which exceeds the 3.9 grains per pod estimated in 25 native bean populations from different regions of Italy [41], 4–5 grains per pod from 14 common bean varieties in Turkey [42], and 4.2 grains per pod from different varieties of Andean origin in Asturias, Spain [43]. Such observations indicate that most of the landraces evaluated in this study have the dual purpose of consumption as green pods or as dry grain, depending on the length and number of grains per pod, and they are in high demand in regional markets. The level of demand is very important to farmers because they have opportunity to sell their surplus in local markets after fulfilling their food needs.

Overall, there is great variability in the various morphological traits reported for 49 bean populations from different regions of Mexico, and significant differences were detected in bean populations grouped by their state of origin as well as within each state, such as Oaxaca, Puebla, Tlaxcala, Guerrero and the State of Mexico (**Table 2**). In particular, there are differences in plant vigour and the number of days to flowering (from 49 to 74 days), which influence the

timing from planting to first harvest. For instance, the populations with a shorter time from planting to harvest were those from Puebla and Guerrero, and this precocity was observed in all of the Puebla bean populations evaluated by Ramírez-Pérez et al. [44] with flowering intervals ranging from 41 to 57 days. The results showed that one fraction of the genetic and phenotypic diversity of common bean landraces is preserved in every region of Mexico, and this diversity is being increased through agro-morphological and physiological traits such as time to flowering, yield per plant and plant development.

| Descriptive traits | Mexican states | | | | |
|------------------------------------|----------------------|----------------------|----------------------|--------------------|----------------------|
| | Oaxaca | Puebla | Tlaxcala | Guerrero | Mexico |
| Days to flowering | 62.1 ^b | 66.0 ^a | 60.3 ^b | 66.4 ^a | 62.6 ^b |
| Pod length (cm) | 12.7 ^{a,b} | 12.4 ^b | 12.4 ^b | 13.6 ^a | 12.6 ^b |
| Pod width (cm) | 1.0 ^d | 1.1 ^c | 1.2 ^b | 1.1 ^c | 1.3 ^a |
| Grains/pod | 7.2 ^a | 6.6 ^b | 5.9 ^c | 6.6 ^b | 5.7 ^c |
| Number of pods/plant | 20.4 ^a | 21.0 ^a | 14.4 ^b | 24.5 ^a | 14.7 ^b |
| Number of pods/experimental parcel | 474.1 ^b | 456.6 ^{b,c} | 349.0 ^{c,d} | 653.2 ^a | 345.0 ^d |
| Wet yield/exp. parcel (kg) | 7.0 ^b | 6.7 ^b | 5.3 ^b | 10.7 ^a | 5.8 ^b |
| Dry yield/exp. parcel (kg) | 1.03 ^b | 1.06 ^b | 0.85 ^b | 1.60 ^a | 0.88 ^b |
| Wet weight/pod (g) | 13.1 ^c | 14.3 ^{b,c} | 14.8 ^{a,b} | 16.3 ^a | 15.7 ^{a,b} |
| Dry weight/pod (g) | 2.0 ^c | 2.2 ^b | 2.4 ^{a,b} | 2.4 ^a | 2.4 ^a |
| Wet yield/plant (g) | 281.7 ^{b,c} | 308.1 ^b | 212.9 ^c | 404.0 ^a | 242.7 ^{b,c} |
| Dry yield/plant (g) | 42.5 ^{b,c} | 48.4 ^{a,b} | 34.9 ^c | 60.0 ^a | 37.0 ^{b,c} |
| Wet weight/30 pods (g) | 392.6 ^c | 428.9 ^{b,c} | 443.5 ^{a,b} | 488.4 ^a | 472.4 ^{a,b} |
| Dry yield/30 pods (g) | 59.0 ^c | 67.3 ^b | 71.7 ^{a,b} | 73.3 ^a | 72.7 ^a |

In rows, means with similar letters are not significantly different (Tukey's test, $P < 0.05$).

Table 2. Comparison of the means of agromorphological traits evaluated in common bean landraces from different Mexican states.

The bean populations originating in Guerrero had a greater pod length (12.7 cm) than those from Mexico, which had the greatest width (1.3 cm). Hence, the highest numbers of pods per plant were yielded in the Oaxaca, Puebla and Guerrero landraces and ranged from 20.4 to 24.5. It is noteworthy that the highest average quantity of grains per pod was reported in the Oaxaca populations (7.2), from which higher pod and grain yield expectations were derived (**Table 2**). The Tlaxcala, Guerrero and Mexico populations had a statistically higher average weight, both fresh and dry, per pod (> 14.5 g), which yielded higher pod and grain yields (**Table 2**). This means that the Oaxaca bean grains are thinner and smaller than those reported in other states, as classified by Espinosa-Pérez et al. [28] using a collection of native common bean populations from the south-central region of Mexico. The common beans from Tlaxcala

and Guerrero have a high potential for use in a breeding programme or for direct consumption and regional cultivation, but the Oaxaca beans can be used as sources of genes due to their resilience in environments with limited soil moisture.

One of the limitations to grain legume performance is the low flower sets in environments with moisture stress in the soils and coldness. In addition to the flower sets being low, approximately 70–80% in the floral phase of the buds, the pods fall prematurely with only a fraction reaching maturity. A decrease in the number of pods per plant and final yield occurs in these cases, which affects the adaptability of a bean population to different agroecological production niches [45].

A principal components (PC) analysis was performed once the population morphological characterization from the different states of Mexico had been completed, and 74.9% of the total phenotypic variance in the bean populations was captured in the first two PC. The traits that described the first component (PC1) were pod number and weight per plant, both fresh and dry, and pod width and the weight of 30 pods for PC2. The spatial distribution of the bean population with the highest pod number and weight per plant is in the upper and lower right quadrant (II and III) in **Figure 1**, corresponding to the landraces from Guerrero, Puebla, and Oaxaca as well as some others from the State of Mexico. The phenotypic divergences among geographic groups, shown in **Figure 1**, confirm the previous results in the context of the biogeographic and cultural manipulation of the traditional farming systems by the farmers. For example, the indigenous groups from Oaxaca have a particular form of cultivation related to rainfall conditions and the sowing depth, among other practices, that differ from the management by the farmers of Puebla and Guerrero.

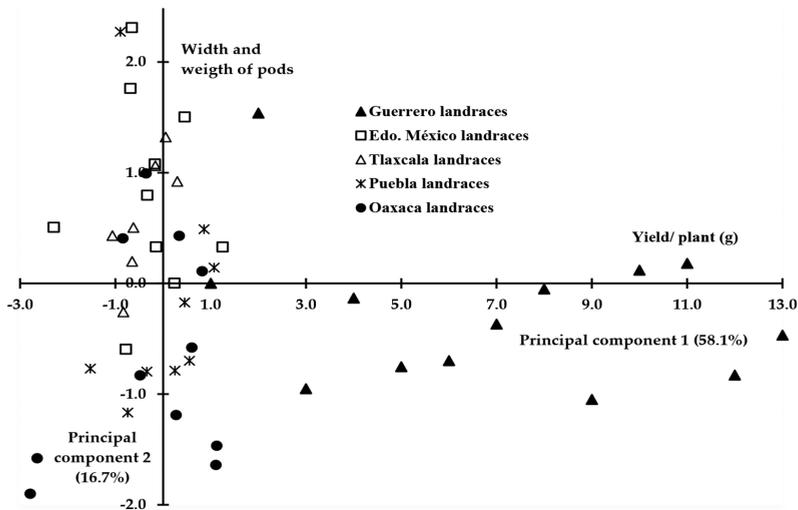


Figure 1. Dispersion of populations of common bean landraces in the states of Oaxaca, Puebla, Tlaxcala, Guerrero and Estado de Mexico based on two principal components of agromorphological traits.

A total of 70 native common bean populations from different geographical regions of Oaxaca, Mexico, which are occupied by the Zapotec, Mixtec, Mixes and Chinantec indigenous groups, were evaluated and compared with 10 improved varieties. Significant differences were detected in the common bean landraces both among and within the geographical regions of origin. Distinctive plant and grain characters were revealed in the bean populations originating from the Mixtec region and cultivated by the Mixtec indigenous group when compared to those grown in the Central Valley (Zapotecs of the Valley) and Sierra Norte (Zapotecs of the Sierra), indicating that differences among native common bean populations are induced by the natural and artificial selection pressures exerted by indigenous groups (**Table 3**). The result highlights the differences in management practices among regions inhabited by indigenous groups that are conferred to their common bean landraces because the agroecological conditions are different in each region.

| Descriptive traits | Regions of Oaxaca (5) | Populations/ regions | CV (%) | Min. | Max. | Average |
|----------------------------------|-----------------------|----------------------|--------|------|-------|---------|
| Days to flowering | 15247.1** | 609.3** | 7.4 | 38.2 | 101.0 | 79.6 |
| Pod length (cm) | 143.1** | 11.70** | 6.8 | 9.8 | 17.5 | 13.8 |
| Grains/pod | 52.79** | 7.85** | 10.3 | 3.4 | 8.9 | 6.8 |
| Dry weight of 60 pods (g) | 0.040** | 0.004** | 17.1 | 40.0 | 240.0 | 136.2 |
| Dry weight of grains/60 pods (g) | 0.024** | 0.002** | 18.2 | 30.0 | 170.0 | 101.0 |
| No. of pods/experimental parcel | 215499.7** | 37456.5** | 33.2 | 44.5 | 502.7 | 235.4 |

**Significant at $P < 0.01$.

Table 3. Mean squares of the analyses of variance, coefficients of variation (CV), minimums, maximums, and average values of agromorphological traits evaluated in common bean landraces from different regions of Oaxaca, Mexico.

| Descriptive traits | Landraces of | | | | Improved varieties |
|----------------------------------|---------------------|--------------------|---------------------|--------------------|--------------------|
| | Sierra Sur | Sierra Norte | Valles Centrales | Mixteca | |
| Days to flowering | 92.7 ^{a,1} | 87.8 ^b | 84.7 ^{b,c} | 81.7 ^c | 44.3 ^d |
| Pod length (cm) | 15.5 ^a | 12.9 ^c | 15.2 ^a | 14.0 ^b | 10.9 ^d |
| Grains/pod | 7.8 ^a | 6.1 ^c | 7.7 ^a | 6.9 ^b | 5.1 ^d |
| Dry weight of 60 pods (g) | 145.9 ^a | 149.5 ^a | 138.9 ^a | 144.7 ^a | 77.5 ^b |
| Dry weight of grains/60 pods (g) | 109.1 ^a | 106.5 ^a | 107.6 ^a | 107.8 ^a | 55.1 ^b |
| No. of pods/experimental parcel | 279.0 ^a | 234.9 ^a | 278.4 ^a | 247.3 ^a | 104.3 ^b |

In rows, means with the same letter are not significantly different (Tukey's test, $P < 0.05$).

Table 4. Comparison of the means of agromorphological traits among common bean landraces from different geographic origins in Oaxaca, Mexico.

It is noteworthy that the bean populations from different regions of Oaxaca were ranked significantly higher in terms of several agronomic and morphological characteristics in comparison with 10 improved varieties used by commercial producers (**Table 4**). The bean populations from the Sierra Sur were late to flower, but they have a similar pattern to that of the bean populations from the Central Valley in relation to grain number per pod and pod length, with averages of 7.8 and 15.5, respectively. These values are higher than those estimated in 15 bean populations from different regions of Jalisco and Nayarit, as reported by Lépiz et al. [35], and moreover, they exceeded the average calculated for 21 common bean genotypes from Tabasco of 4.2 grains per pod [37]. Therefore, the quality of the bean populations from Oaxaca significantly exceeded that of the improved varieties, which means that there is high variability in their agronomic traits, so these populations may be useful as raw materials for a breeding programme.

Additionally, a PC analysis was also carried out to evaluate the overall variability, and in this case, 81.2% of the total variation was captured in the first two PC (**Figure 2**). The descriptive variables of the first component were days to flowering and dry grain weight, and for the second component, they were grain number per pod and average dry weight of 60 pods. Hence, in addition to there being phenotypic differences among bean populations from different states, significant divergences are also denoted among bean populations located in different geographic regions within the same state (such as Oaxaca). All of the local bean populations represent a feasible strategy for bean planting and harvesting by small farmers who plant less than 3 ha in the south-central and south-eastern regions of Mexico. Regionally, the zone of origin of each common bean landrace determines its adaptability; subtropical and tropical row materials have difficulty adapting and producing grain in temperate regions and vice versa.

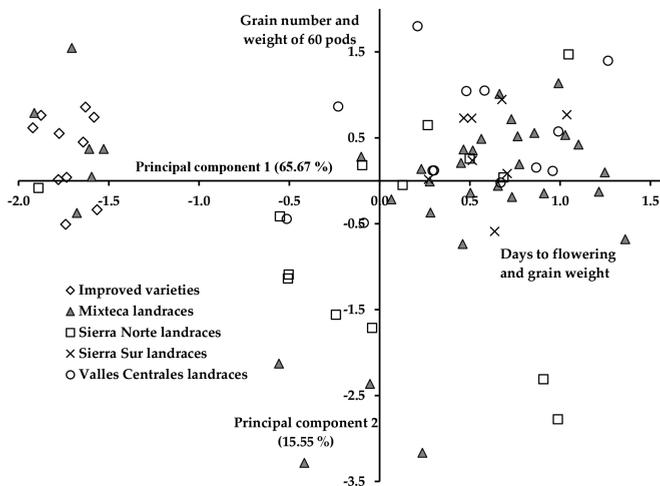


Figure 2. Dispersion of common bean landraces and improved varieties from different regions of Oaxaca, Mexico, based on two principal components of agromorphological traits.

3. Grain nutritional composition in common bean landraces

In terms of the chemical composition of the common bean, it is an outstanding protein source with a low carbohydrate level. Thus, approximately 15 % of the required daily protein intake for a 70-kg adult [46] is provided by a 100-g daily portion of beans. The amino acid content differs from one genotype to another, and it also depends on the ecological conditions for planting, farm management and grain storage conditions, among other factors [23, 47].

The proximal analysis of the common bean indicates that grains contain 14–33% protein, 1.5–6.2% lipids, 14–19% total fibre (from 10.1 to 13.4% insoluble and from 3.1 to 7.6% soluble), 2.9–4.5% ash and 52–76% carbohydrate [48]. Derived and non-derivative (dietary fibre) polysaccharides plus a variety of mono-, di- and polysaccharides are among the carbohydrates that occur in greater proportions. Thus, the grain contains a variety of low and non-digestible carbohydrates, but their functional structure changes through soaking and cooking, increasing the amount of soluble fibre and the digestibility [49, 50].

As assessed by cooking time, there is high variability in protein content and grain hardness among improved varieties and landraces. The protein content in native beans from Hidalgo, Mexico, ranged from 16.0 to 26.9%, as reported by Muñoz-Velázquez et al. [38], with variations in cooking time from 43 to 81 minutes for wine- and creamy yellow-coloured beans, and higher protein content plus a 95% *in vitro* digestibility rate was observed in light brown Canario and Flor de Mayo varieties. Protein contents ranging from 16.3 to 29.2% with cooking times from 50 to 141 min were reported by Ramírez-Pérez et al. [44] in local, brown-coloured bean populations from Puebla, and protein levels ranging from 21.0 to 25.8% with cooking times from 54 to 118 minutes were reported in local bean varieties from Guerrero by Solano-Cervantes et al. [51]. Certain variations are induced by agroecological or grain management conditions, but such changes are not significant. A constant high protein content through cultivation cycles and years is a characteristic of outstanding genotypes [52].

Regarding essential amino acid content, it has been reported previously that the limiting amino acids in corn grain are apparently complemented by those contained in beans. Phenylalanine, isoleucine, leucine, lysine, methionine, cysteine, threonine, tryptophan and valine are among the main essential amino acids in beans with a range from an average of 1.2 to 1.5 g methionine/100 g of protein and 4.9 to 9.9 g cysteine/100 g of protein. Most amino acids in the grain are found in sufficient quantities to meet the daily requirements of 1.1–6.6 g/100 g of protein [48], and it is noteworthy that the amounts of isoleucine, leucine, lysine, methionine, phenylalanine, threonine and valine contained in the grain do not change significantly after cooking [49].

A rather important and underestimated input provided by human consumption of beans is the portion of minerals, and several authors have reported that the environment has little influence on the differences from genotype to genotype. Instead, differences likely correspond to genetic diversity among and within improved varieties, either wild or cultivated, and landraces [53–55]. The intake of both macro- and micro-minerals is associated with the prevention of prostate cancer [56], and beneficial effects against colon cancer have also been found experimentally in Sprague-Dawley rats [57]. There are other beneficial effects for human

health [58], yet the inhabitants of rural and urban communities are deficient in Fe and Zn, which are elements that are mainly associated with malnutrition in children and pregnant women [51]. The mineral content in the common bean varies depending on the genetic material, crop management and grain storage conditions [53, 54, 59].

Significant differences with regards to the S, P, Na, K, Mg, Ca, Fe, Zn, Cu and Mn contents among groups of native bean populations of different geographical origins were recently determined in studies carried out by the authors. The contents were evaluated by means of atomic absorption spectrometry and UV-vis using germplasm from Oaxaca that was planted in an experimental plot, and differences among bean populations from the same geographic region were also determined (Table 5). Low S, Na, Ca and Zn contents were presented by the populations originating from the Mixteca region as opposed to the populations from Sierra Norte that had higher S, K, Fe, Zn and Mn contents, which in turn differed from those that originated in the Central Valley with high levels of P, Na, Zn and Cu (Table 5). Hence, a relevant fraction of the Mexican *P. vulgaris* genetic pool is in the Oaxaca regions in Mexico, so the genetic pools of the different Oaxaca regions differ in the contents of both mineral macro- and micro-elements. Therefore, the data suggest that common beans provide an important fraction of essential minerals and not only proteins and carbohydrates, and this information is relevant to consumers because the specialized and organic markets demand products with major contents of these minor dietary components.

| Sources of variation | Groups | Populations/ groups | Error | Coef. var. (%) | Groups (contents in mg/100 g) | | | |
|----------------------|------------|------------------------|--------|-------------------|-------------------------------|--------------------|--------------------|--------------------|
| | | | | | Mixteca | Sierra Norte | Sierra Sur | Valles Centrales |
| Macro-elements | | | | | | | | |
| S | 8094.6** | 667.2** | 11.7 | 7.5 | 39.4 ^d | 67.1 ^a | 41.9 ^b | 40.5 ^{bc} |
| P | 106769.3** | 52431.2** | 137.1 | 3.6 | 341.7 ^b | 266.0 ^c | 267.5 ^c | 359.8 ^a |
| Na | 4327.4** | 1017.9** | 52.3 | 10.1 | 63.9 ^c | 74.2 ^b | 70.6 ^b | 85.1 ^a |
| K | 73606.6** | 26151.9** | 1017.4 | 3.5 | 918.4 ^b | 946.6 ^a | 909.0 ^b | 846.4 ^c |
| Mg | 746.9** | 730.5** | 3.8 | 1.6 | 117.7 ^b | 118.6 ^b | 125.9 ^a | 113.7 ^c |
| Ca | 998.3** | 1353.7** | 2.8 | 7.2 | 91.3 ^d | 98.3 ^b | 93.6 ^c | 100.1 ^a |
| Micro-elements | | | | | | | | |
| Fe | 1.83** | 2.22** | 0.1 | 6.4 | 5.24 ^a | 5.11 ^a | 5.11 ^a | 4.87 ^b |
| Zn | 4.11** | 0.90** | 0.17 | 9.7 | 4.1 ^b | 4.5 ^a | 4.0 ^b | 4.7 ^a |
| Cu | 6.89** | 0.97** | 0.01 | 7.4 | 1.23 ^b | 1.14 ^c | 1.25 ^b | 2.02 ^a |
| Mn | 0.17** | 0.10** | 0.001 | 2.9 | 1.24 ^b | 1.32 ^a | 1.17 ^c | 1.18 ^c |

**Significant at P < 0.01. ¹ In rows, means with the same letter are not significantly different (Tukey's test, P < 0.05).

Table 5. Significance of the mean squares of the analyses of variance and comparison of means among groups of common bean landraces from Oaxaca, Mexico, in relation to the mineral contents in the grain.

Significant differences among collections from the groups of different origin were determined by a canonical discriminant analysis (Pillai's trace $F = 3.36$, and Wilks' lambda $F = 3.52$; $P < 0.01$). The collection dispersion in reference to the first two canonical discriminant functions is shown in **Figure 3**, and the patterns of differences by geographic origin indicate divergences. For instance, the populations from the Mixteca region are dispersed in the lower left quadrant, very close to those of the Sierra Sur; those from the Sierra Norte are in the lower right quadrant, and the Central Valley has a higher dispersion in all the quadrants. It is also relevant that the samples with high Fe, Cu, Ca, P, S, Mn and K contents exist in the upper right quadrant (**Figure 3**). As a result, the outstanding samples with high mineral contents might be used in a breeding scheme as proposed by Welch and Graham [60], Welch et al. [61] and Teixeira et al. [62] in *P. vulgaris* germplasm. Therefore, as suggested by these authors, more than high yields and adaptability ought to be the main criteria for bean selection.

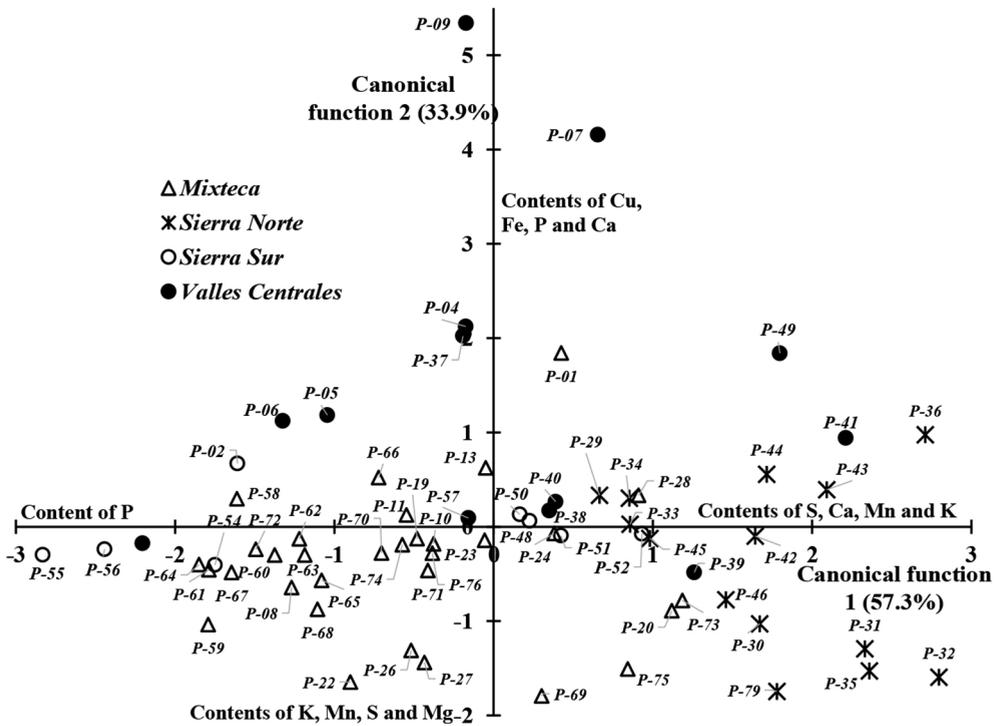


Figure 3. Scatterplot of common bean landraces from different regions of Oaxaca based on two principal canonical functions and the mineral contents in the grain.

The dispersion of the evaluated populations based in the amount of total macro- and microelement content is shown in **Figure 4**. A total of four scenarios for the populations of particular interest were generated by the creation of four quadrants based on the average content of both macro- and micronutrients. For instance, populations with a higher microelement content are

scattered in the upper left quadrant, but these were low in macronutrients. On the other hand, populations that are scattered in the lower right were high in macro- but low in micro-elements. The outstanding populations with higher averages of both macro- and micro-elements are located in the right upper quadrant, where populations from the Mixtec, Sierra Norte and Central Valleys appear. Specifically, the P-06 population is characterized by a high content of both micro- and macro-elements, whereas the P-60, P-67, P-75 and P-79 contain a higher amount of only macro-elements. Consequently, we believe that a set of native bean populations with high macro- and micro-element contents can be identified in every region of Mexico, and they are preserved by farmers and used directly as food (Figure 4).

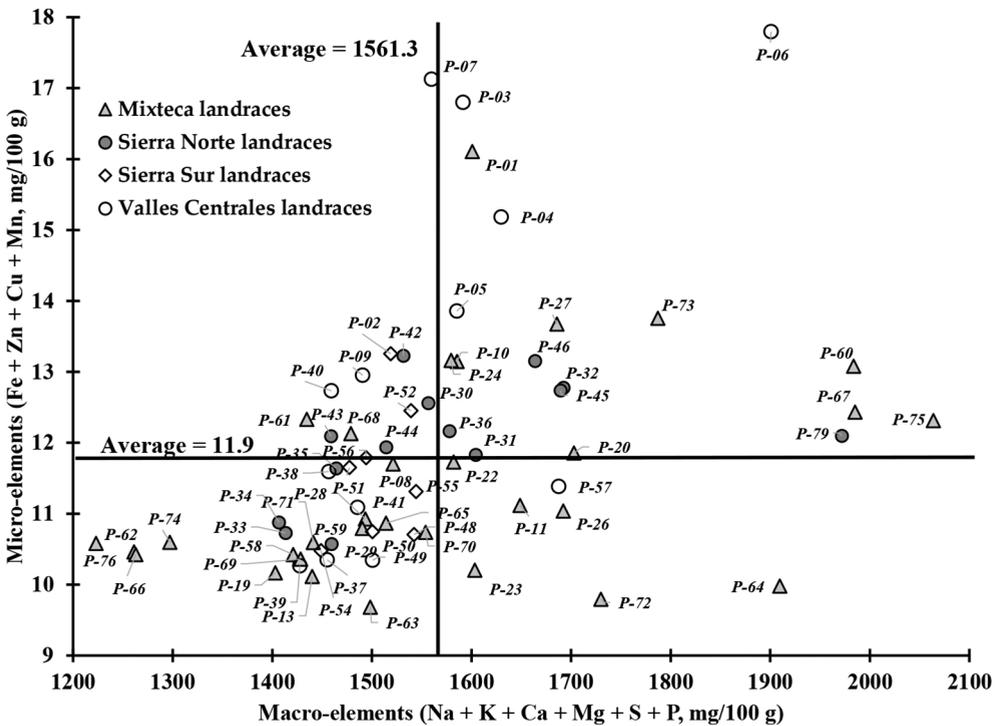


Figure 4. Dispersion of common bean landraces from different regions of Oaxaca in relationship to the total contents of the macro- and micro-elements in the grain.

Another relevant aspect of the bean is its functional compounds and potential nutraceutical content, so 25 native bean populations were collected from Oaxaca, Mexico and experimentally cultivated. At harvest time, a sample ranging from 200 to 500 individuals per population was taken and analysed in a laboratory for the contents of monomeric anthocyanins, polyphenols and flavonoids as well as antioxidant activity by DPPH and a colour index (Table 6).

| Accession ¹ | An ² | Seed coat | | | Seed | | | | Seed colour | | |
|-------------------------------------|-------------------------|-------------------------|-------------------------|--------------------------|------------------------|-------------------------|-------------------------|-------------------------|--------------------------|-------------------------|--|
| | | Po | Fl | AA | Po | Fl | AA | L* | Chrome | h° | |
| EDOMEX-011-11 ^P | 0.04 | 82.2 | 20.9 | 564.5 | 2.5 | 0.70 | 13.8 | 59.5 | 8.0 | 46.2 | |
| EDOMEX-011-7 ^{mc} | 0.04 | 94.6 | 9.3 | 751.3 | 2.5 | 0.37 | 14.1 | 53.5 | 17.1 | 58.6 | |
| EM-01-01 ^{pr} | 1.13 | 89.5 | 12.3 | 667.9 | 2.7 | 0.40 | 11.8 | 54.4 | 10.2 | 50.7 | |
| <i>Average-Mexico</i> | <i>0.4^{c2}</i> | <i>88.7^c</i> | <i>14.2^b</i> | <i>661.2^c</i> | <i>2.6^a</i> | <i>0.49^a</i> | <i>13.2^b</i> | <i>55.8^b</i> | <i>11.7^{ab}</i> | <i>51.8^a</i> | |
| GRO-01-103 ^{pr} | 0.41 | 67.9 | 12.8 | 621.7 | 2.1 | 0.33 | 12.0 | 51.6 | 9.4 | 33.7 | |
| GRO-011-15 ^c | 0.05 | 61.2 | 6.5 | 132.5 | 2.3 | 0.30 | 13.8 | 68.2 | 10.7 | 65.3 | |
| GRO-011-16 ^c | 0.25 | 55.7 | 16.8 | 610.1 | 2.6 | 0.78 | 13.5 | 50.5 | 15.5 | 51.7 | |
| GRO-01-118 ^{pr} | 0.25 | 92.5 | 12.9 | 724.4 | 1.3 | 0.33 | 10.4 | 36.9 | 5.1 | 21.5 | |
| GRO-011-19 ^{pr} | 0.34 | 51.0 | 12.8 | 512.9 | 2.7 | 0.77 | 11.0 | 56.7 | 8.9 | 47.0 | |
| GRO-011-20 ^f | 0.07 | 57.9 | 14.1 | 520.7 | 1.6 | 0.18 | 7.1 | 50.0 | 9.7 | 42.5 | |
| GRO-011-23 ^p | 0.22 | 51.2 | 19.6 | 639.4 | 1.3 | 0.63 | 16.6 | 59.7 | 9.5 | 40.8 | |
| GRO-10-120 ^p | 0.53 | 70.2 | 15.0 | 631.4 | 2.3 | 0.32 | 13.1 | 48.1 | 11.4 | 43.6 | |
| GRO-10-129 ^c | 0.42 | 80.9 | 8.5 | 735.9 | 2.5 | 0.48 | 10.9 | 53.4 | 7.6 | 35.2 | |
| GRO-10-87 ^r | 0.59 | 62.1 | 21.5 | 779.2 | 1.4 | 0.61 | 10.2 | 49.1 | 12.4 | 40.3 | |
| GRO-10-99 ^r | 0.24 | 52.2 | 11.6 | 459.7 | 2.3 | 0.42 | 9.1 | 60.7 | 6.3 | 36.4 | |
| <i>Average-Guerrero³</i> | <i>0.3^d</i> | <i>63.9^d</i> | <i>13.8^c</i> | <i>578.9^d</i> | <i>2.0^c</i> | <i>0.47^b</i> | <i>11.6^c</i> | <i>53.2^b</i> | <i>9.7^{ab}</i> | <i>41.6^b</i> | |
| OAX-011-07 ^{pr} | 0.38 | 87.9 | 15.7 | 750.8 | 2.7 | 0.56 | 8.3 | 47.8 | 11.6 | 44.9 | |
| OAX-011-12 ^y | 0.37 | 71.4 | 10.0 | 615.7 | 3.3 | 0.54 | 20.3 | 47.7 | 13.1 | 48.7 | |
| OAX-011-28 ^b | 2.14 | 57.0 | 5.9 | 534.7 | 1.9 | 0.38 | 10.5 | 51.7 | 5.6 | 67.7 | |
| OAX-011-29 ^{mc} | 1.54 | 108.2 | 7.3 | 1021.7 | 2.3 | 0.30 | 15.9 | 63.6 | 7.7 | 61.2 | |
| OAX-011-30 ^b | 3.47 | 127.0 | 11.0 | 973.8 | 1.9 | 0.35 | 12.5 | 49.1 | 4.8 | 81.3 | |
| <i>Average-Oaxaca</i> | <i>1.6^b</i> | <i>90.3^b</i> | <i>9.9^c</i> | <i>779.3^b</i> | <i>2.4^b</i> | <i>0.43^c</i> | <i>13.5^b</i> | <i>52.0^b</i> | <i>8.6^b</i> | <i>60.7^a</i> | |
| PUE-011-13 ^p | 0.25 | 104.5 | 15.7 | 713.4 | 2.0 | 0.27 | 11.2 | 48.5 | 12.1 | 35.7 | |
| PUE-011-14 ^y | 0.04 | 39.2 | 8.9 | 389.4 | 1.3 | 0.10 | 7.4 | 62.1 | 25.4 | 72.1 | |
| PUE-011-15 ^{cp} | 9.07 | 27.7 | 7.9 | 321.6 | 5.4 | 0.64 | 32.4 | 59.5 | 11.1 | 62.0 | |
| PUE-011-20 ^b | 1.94 | 31.3 | 8.0 | 240.4 | 1.3 | 0.28 | 23.0 | 45.5 | 4.8 | 79.4 | |
| PUE-011-34 ^{mc} | 1.32 | 80.2 | 11.1 | 728.0 | 1.5 | 0.32 | 25.3 | 56.3 | 9.2 | 64.1 | |
| PUE-11-33 | 0.05 | 70.6 | 9.8 | 603.6 | 2.7 | 0.49 | 15.9 | 53.7 | 10.5 | 41.4 | |
| <i>Average-Puebla</i> | <i>2.1^a</i> | <i>58.9^c</i> | <i>10.2^d</i> | <i>499.4^c</i> | <i>2.4^b</i> | <i>0.35^c</i> | <i>19.2^a</i> | <i>54.3^b</i> | <i>12.2^a</i> | <i>59.1^a</i> | |

| Accession ¹ | An ² | Seed coat | | | Seed | | | | Seed colour | |
|--|------------------|--------------------|-------------------|--------------------|------------------|-------------------|-------------------|-------------------|-------------------|-------------------|
| | | Po | Fl | AA | Po | Fl | AA | L* | Chrome | h° |
| TLA-10-5 ^c (average-Tlaxcala) | 0.2 ^c | 123.4 ^a | 14.8 ^a | 985.3 ^a | 2.6 ^a | 0.41 ^d | 13.4 ^b | 62.2 ^a | 9.8 ^{ab} | 60.6 ^a |
| DHS-Tukey | 0.02 | 1.03 | 0.21 | 5.9 | 0.10 | 0.02 | 0.65 | 5.01 | 3.0 | 7.52 |

¹Origin of groups: EDOMEX/EM= Estado de México; GRO = Guerrero; OAX = Oaxaca; PUE = Puebla; TLA = Tlaxcala.

²An = anthocyanins (mg of Cynidin-3-Glucoside-C3G-/g DW); Po = polyphenols (mg gallic acid equivalents-GAE-/g DW); Fl = flavonoids (mg catequine equivalents -CE-/g DW); AA = antioxidant activity (μmol ETrolox/g DW).

³among groups, means with the same letter are not significantly different (Tukey's test, P < 0.05). Visual colour of the grains: P = pink; ^{abc}= mixture of seed colours; ^{pr} = pink-red; ^c = cream; ^{cp} = cream pink; ^r = red; ^b = black; ^y = yellow.

Table 6. Average values of anthocyanins, polyphenols, antioxidant activity and colour index in a Mexican collection of common bean landraces.

The variation among populations in the monomeric anthocyanin content in grains ranged from 0.04 to 9.07 mg cyanidine-3-glucoside (C3G)/g on a dry basis, and among groups, the highest average was presented by samples from Puebla (2.1 mg C3G/g) followed by the Oaxaca group (1.6 mg C3G/g) and Tlaxcala (0.2 mg C3G/g). The variation in anthocyanins among the study populations was slightly greater than that described by Gola-Masum-Akond et al. [63] in 29 common bean genotypes of different colours: 0.05 to 0.45 mg C3G/g. Although no specific determinations of anthocyanin types were carried out in this study, it was evident that collections of intense black and red as well as multicoloured beans (a grain mixture of different colours) presented a higher anthocyanin content (>1 mg C3G/g); these included EM-01-01, OAX-011-28, OAX-011-29, OAX-011-30, PUE-011-15, PUE-011-20 and PUE-011-34. As determined by Tsuda et al. [64], delphinidin-3-O-β-D-glucoside, petunidin-O-β-D-glucoside and malvidin-3-O-β-D-glucoside were mostly associated with black bean anthocyanins. However, as reported by Xu et al. [65], the dephinidin-3-glucoside and petunidin-glucoside were the compounds most commonly related to the black grain bean. The highest anthocyanin content in red grain beans was of pelargonidin 3-glucoside, as reported by Choung et al. [66], and higher anthocyanin content was reported in brown, black spotted and pinto grain beans (0.45 a 0.59 mg C3G/g) by Dzomba et al. [67]. As a result, the highest anthocyanin contents in the common bean are associated with beans with a dark seed coat with brown, red and black grain variations.

The anthocyanin contents in black beans reported in this study (1.94 to 3.47 mg C3G/g) were higher than those reported by Salinas-Moreno et al. [39] in 15 black bean varieties, which varied from 0.38 to 0.72 mg C3G/g. Variations are partly attributed to the types of laboratory procedures used, yet differences among genotypes can not be ignored. This was confirmed by the evaluation performed by Xu and Chang [68], who did not find any anthocyanins in the pinto variety but identified delphinidin-3-glucose, malvidin-3, 5-diglucose, petunidin-3-glucose, malvidin-3-galactoside, and malvidin-3-glucose in the black variety (Turtle Eclipse).

Regarding polyphenol and flavonoid contents, important differences were found among the types of seed coats and seeds without seed coat, and the first was favoured in both cases. Among population groups, polyphenol content varied from 58.9 to 123.4 mg GAE/g and from

2.0 to 2.6 mg GAE/g, respectively, plus the variation in flavonoids among groups differed from 9.9 (Puebla) to 14.8 (Tlaxcala) mg CE/g and from 0.35 to 0.49 mg CE/g. These higher polyphenol and flavonoid concentrations provided major antioxidant activity in the seed coat (499.4 to 985.3 $\mu\text{mol ETrolox/g}$) than in the seed (11.6 a 19.2 $\mu\text{mol ETrolox/g}$), **Table 5**.

These patterns of high antioxidant activity were repeatedly found among populations within groups such as the PUE-011-15 (27.7 $\mu\text{mol ETrolox/g}$) and PUE-011-20 (31.3 $\mu\text{mol ETrolox/g}$) collections, which had the lowest polyphenol contents in the seed coat. Nevertheless, they were higher than the highest seed contents of 20.3 and 32.4 $\mu\text{mol ETrolox/g}$ in the OAX-011-12 and PUE-011-15 collections, respectively (**Table 5**).

Regarding flavonoid contents among populations, the variation ranged from 5.9 (OAX-011-28) to 21.5 (GRO-10-87) mg CE/g in the seed coat and from 0.1 (PUE-011-14) to 0.77 (GRO-011-19) mg CE/g in the seed (**Table 5**). Consequently, the greatest flavonoid content and highest antioxidant activity in the seed coat made us conclude that, with regard to nutraceutical properties, attention should be focused on this fraction, as well as on the grain covering, because of its high potential.

The variation in the total polyphenol content in the grain ranged from 1.3 to 5.4 mg GAE/g in this work, which was slightly lower than that reported by Golam-Masum-Akond et al. [63] in different bean varieties (from 5.9 to 14.1 mg GAE/g) and even lower than the contents in the seed coat (from 27.7 to 127.0 mg GAE/g). These latter values are similar to those reported by Espinosa-Alonso et al. [40] in different common bean populations in Mexico, which ranged from 49.6 to 131 mg GAE/g. Differences in the laboratory methodology could have influenced the results, but populations with potential nutraceutical value due to high flavonoid content in both the seed coat and seed were still detected, such as the OAX-011-29 and TLA-105 among others.

A variation in total flavonoid content ranging from 0.82 to 10.6 mg CE/g in 62 bean populations, both wild and cultivated, was reported by Espinosa-Alonso et al. [40]. The lowest values were similar to those determined for grain but, in several cases, were higher than those revealed for the seed coat for a group of 15 populations, up to 11 mg CE/g. An estimated variation in flavonoids ranging from 0.6 to 1.2 mg CE/g was reported by Boateng et al. [69]. Regardless of the differences in methodology and the estimate derived from the results, the populations under evaluation have important flavonoid levels in the seed coat compared to other genotypes, both cultivated and wild. This fact indicates that the farmers in the study area have a deep knowledge of their bean seeds and continue cultivating the most valued landraces.

The use of combined grain colour indexes (L^* : chromaticity, and h° : tone) helps to differentiate populations by the colour of the seed coat or any other characteristic that can be visually appreciated, such as the luminosity index (L^*). These indexes became rather useful in the present study for distinguishing the visual colours: pink, cream, yellow or red from other visual variants. Those denominated red and those denominated black were distinguished by the Chroma index, but the tone hue index (h°) was the most accurate because a gradient value was assigned to each colour or variant. Thus, all of the evaluated bean pop-

ulations were classified in a quantitative way, and in this case, the lowest values correspond to perceptions of pink or red and the highest to black (**Table 5**). These indexes can be used as physical parameters to differentiate between local bean varieties of different grain colour.

The antioxidant activity in the seed coat (132.5 a 1021.7 $\mu\text{mol ETrolox/g}$) was considerably higher compared to that reported in the seed (7.1 a 32.4 $\mu\text{mol ETrolox/g}$). It was significantly correlated ($r > 0.36$, $P < 0.05$) with total polyphenol content in the seed coat and seed as well as to the anthocyanins in the grain. As a result, the differentiation among bean groups of origin and bean populations was rather clear. As confirmed by the results of this study, anthocyanins and polyphenols confer high antioxidant activity to the bean grain and seed coat; similar results were reported by Golam-Masum-Akond et al. [63], Dzomba et al. [67], and Oomah et al. [70].

4. Contribution of farmers to on-farm conservation of common bean germplasm

The on-farm conservation of common bean landraces by Mexican small farmers is a basic survival strategy aimed at meeting the daily feeding requirements of rural families. As a consequence, the strategic conservation *in situ* landraces within indigenous, non-indigenous and marginalized communities becomes a way to access food that is not discussed but only conducted to grow and produce beans to eat. However, when there are surpluses, they are sold through either local or regional markets [15, 16, 71]. In several cases, landraces are only regionally or sporadically known nationwide [28] even when remarkable potential has been fully identified in local genetic pools through agronomic, molecular and biochemical assessments [36, 72, 73].

The cultivated wild species *Phaseolus* sp., *Zea mays* ssp. *parviglumis* H. H. Iltis & Doebley (teosinte) and *Cucurbita* sp. [74–77] are also distributed in the Mexican region within Mesoamerica. Possibilities for crossing or genetic flow are generated by the spatial convergence of the genetic pools of wild and cultivated species despite some degree of geographical isolation, differences in flowering time or low crossing rates (<1%). This occurs in beans [78], even though crosses are sometimes high (20–70%) when large numbers of pollinators prevail in the agroecosystems [79].

Beans are grown under different agroecological conditions and for multiple purposes, as we documented in different visits through several regions in the south and southeast of Mexico. The cultivation variants depend on growth rate, both fresh and dry harvest purposes and the levels of precocity. For instance, bean population types III and IV of indeterminate growth, which are most commonly referred to as either climbers or ‘frijol de guía’, are usually associated with corn and harvested as fresh green beans or dry grain. In these cases, the bean climbs and tangles itself in the corn plant, which being a late flowering and fruiting plant supports the bean. Determinate growth bean types I and II are grown in small plots or backyard gardens to harvest in green beans, and a pink, purple, green with mottled burgundy or simply green

colourations characterize the pods, depending on the landraces sold in the local and regional markets. Dry cultivation is performed, and higher yields per unit area are also obtained in such cases.

The bean populations referred to as bush bean plants or determinate growth type I and II are preferred for monoculture planting, most frequently in large areas and in northern Mexico. They are precocious, and the populations display more uniform flowering and fruiting. The grain colour is uniform solid to mottled and variegated, pale white, pink purple, marbled, cream, red, wine, brown, grey, black, white, as well as mottled in different combinations, and it is not surprising to find farmers planting different physical seed mixtures in terms of colour and species. *P. vulgaris* with *Phaseolus coccineus* and *P. vulgaris* with *Phaseolus lunatus* are among the most productive mixtures. All of these observations are consistent with the management of *Phaseolus* sp. diversity described by Worthington et al. [80] and Soleri et al. [81] in Oaxaca, Mexico.

The local bean supply system differs from region to region and from one community to another, and it was revealed through field trips that beans are planted in larger areas by the farmers in the north-central region (>3 ha/producer) than in the south-southeast region (<3 ha/producer) of Mexico. As a consequence, the seed requirement for improved varieties or landraces in both volume and diversity are different in such cases. Improved varieties, and sometimes landraces, are most commonly used by north-central farmers, and often in contrast, landraces, and sometimes improved varieties or even a mixture of both, are most commonly used by the farmers located in the south-southeast. It is a rather common practice for farmers to turn to other communities or regions to obtain seed in years when losses occur due to weather events, such as droughts, storms, floods or hurricanes, or even buy improved varieties. However, they are always looking to find germplasm that suits their agroecological niches [82].

Estimates have been made concerning the movement of seeds within communities in Oaxaca, Mexico, and it was revealed that over 90% of farmers either keep and cultivate their own landrace seed or obtain it from their neighbours or farmers in nearby communities or from traditional local markets [80].

More than a single local bean population has been planted in each agricultural cycle by farmers in Yucatan and some other states in the south-eastern region of Mexico. Some of the reasons underlying the decisions regarding which bean landraces to grow include growth type (I, II, II or IV) because it is directly related with the number of management practices that need to be performed (e.g., Type IV requires more practices); days from planting to the harvest of green beans or dry grain pods; the adaptability to the ecological conditions of the plots or backyard of the producer; tolerance to soil water deficits or low temperature; consumption of fresh forms (as green beans) or dry forms, flowers and/or dry pods; tolerance to insects during storage; grain hardness or consistency with regard to cooking time and flavour and the related organoleptic characteristics, among others [83]. It is appropriate to note that such seed exchange systems are not closed because new seed lots always arrive in the communities being sown, but the sowing continuity of such batches relies on both adaptability and productivity levels in the new places where they are used.

The local seed beans from small farmers are often stored in closed plastic containers and packages, and occasionally, the seed is treated with calcium hydroxide (lime), ash, dried epazote plants (*Dysphania ambrosioides* (L.) Mosyakin et Clemants), chilli pods (*Capsicum* sp.) and chemical insecticides. Additionally, the bean grain is handled differently depending on the harvest volume and the need for storage in the medium term; when only small amounts are harvested (<100 kg), it is generally used for immediate consumption. As a consequence, bags are used and placed in dry spots that are regularly used in the kitchen, but when the harvest is good (>100 kg), the surplus is usually sold at either local or regional markets or even stored in plastic containers with capacities of 100–200 kg that must be perfectly closed. The necessary seed treatments are applied in such cases.

Frequently, farmers from a given region in Mexico or a community have apparently similar bean populations because the beans are alike in grain coat colour, size, shape, growth type, flower and even the local name, as when the Spanish names, such as “negro delgado”, “frijol de milpa” or “frijol de cerro”, are used or when the local names are used, such as “daá yel-la”, “daá laá”, “daá tupii” and “daá ya-áá” [81] in the Zapoteca de la Sierra language; “xcolibu’ul” and “tzamá” in the Mayan language [83]; “ndutji” in Mixtec; “etl”, “iztac etl”, “yahoetl”, “pitzahuaqetl” or “itza acaletl” in Nahuatl; “tatsuniutul” in Purepecha; “tsjúú” in Mazahua; “chenek” in Tzotzil; “m’jnai” in Chinanteco; “rune” in Triqui [84], among other indigenous languages. This means that even if the beans are visually or morphologically equal or identified by the same landrace name, they cannot be assumed to be from similar populations. Additionally, the landraces in the *Phaseolus* regions and communities of geographical origin cannot be assumed to have low levels of genetic diversity, mainly in the region known as Lerma-Santiago where a high genetic diversity prevails, based on the documented genetic profiles, geographical origin, phylogeny and ethnohistory of the local bean populations.

The south-southeast regions of Mexico are recognized as the centres of the origin, domestication and genetic diversity of the common bean [4, 77, 85] and where, even today, in indigenous communities, knowledge of the germplasm, crop and seed management [16] is transferred from parents to their children. As a result, the management of genetic diversity in the hands of farmers has established a certain group of features in each bean population that is adapted to each particular agro-ecological niche that is influenced by consumer preferences [85]. Some evidence of such facts was confirmed by the analysis of genetic diversity among different seed samples from farmers in the region of Santa Maria Jaltianguis in the state of Oaxaca, México, where, using SSRs and RFPs markers, significant differences (F_{ST}) were revealed among farmers with similar bean seed lots of the Mesoamerican and Jalisco races [80, 81].

The bean gene pools in Mexico can be classified into four groups: a) a total of 85 improved varieties that are currently registered in the Catalogo Nacional de Variedades Vegetales del Sistema Nacional de Inspección y Certificación de Semillas [86] for marketing to farmers; b) approximately 7000 Mexican *P. vulgaris* accessions that are mainly preserved in the germplasm banks from the Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP), Universidad Autónoma Chapingo (UACH) and Universidad de Guadalajara; c) out of the 70 *Phaseolus* wild and cultivated species that are distributed in Mexico, the Mexican germplasm banks have the seed of 28 wild species that are distributed throughout the country

from sea level to an altitude of 3000 m (Table 7). It should be considered that even though both wild and cultivated species exist, five species have already been domesticated in the region including *P. vulgaris*, *P. coccineus*, *P. lunatus*, *P. acutifolius* and *P. dumosus* [35, 87]. d) Finally, the gene pools composed of wild species, landraces and heirlooms in the hands of farmers from different Mexican regions; a single farmer may usually hold from 1 to 3 landraces [81, 83]. Now, taking into account that there were 609,342 small family bean production units in 2008 [88], it can be estimated that there are currently 609,342 to 1,828,026 seed lots with a certain degree of differentiation induced by the handling that each farmer provides to his bean populations. As a consequence, each seed lot is designated as the unit of physical diversity that is shaped by all of the bean grains used by each farmer for the next crop, which is treated as independently reproducing a particular type of bean [89, 90]. The highest *P. vulgaris* genetic diversity, which is generally classified as the Mesoamerican, Jalisco and Durango races, is preserved in the fields of small Mexican farmers [2, 4, 14, 77, 91].

| <i>Phaseolus</i> species ¹ | <i>Phaseolus</i> distribution by Mexican state |
|---------------------------------------|---|
| <i>xanthotrichus</i> | Hidalgo, Chiapas |
| <i>vulgaris</i> | Most of the country |
| <i>tuerckheimii</i> | Chiapas |
| <i>ritensis</i> | Chihuahua, Durango |
| <i>polymorphus</i> | Aguascalientes, Coahuila, Durango, Guanajuato, Jalisco, Nuevo León |
| <i>pluriflorus</i> | Durango, México, Jalisco, Michoacán, Morelos, Nayarit, Sinaloa |
| <i>pedicellatus</i> | Guanajuato, Guerrero, Hidalgo, Jalisco, México, Michoacán, Morelos, Nayarit, Querétaro, San Luis Potosí, Tamaulipas, Veracruz |
| <i>pauciflorus</i> | Chihuahua, Durango, Guerrero, Jalisco, México, Michoacán, Morelos, Nayarit, Sinaloa, Sonora, Zacatecas |
| <i>parvulus</i> | Chihuahua, Durango, Nayarit, Sinaloa, Sonora, Zacatecas |
| <i>oligospermus</i> | Chiapas |
| <i>oaxacanus</i> | Oaxaca |
| <i>nesonii</i> | Chiapas, Jalisco, México, Michoacán, Oaxaca, Zacatecas |
| <i>neglectus</i> | Nuevo León, Tamaulipas |
| <i>microcarpus</i> | Chiapas, Guanajuato, Durango, Guerrero, Jalisco, Michoacán, Oaxaca, Puebla |
| <i>micranthus</i> | Jalisco, Michoacán, Nayarit, Sinaloa, Sonora |
| <i>maculatus</i> | Aguascalientes, Chihuahua, Coahuila, Durango, Guanajuato, Hidalgo, Puebla, Querétaro, San Luis Potosí, Sonora, Tlaxcala, Zacatecas |
| <i>lunatus</i> | Baja California, Campeche, Chiapas, Colima, Guerrero, Jalisco, México, Michoacán, Morelos, Nayarit, Oaxaca, Sinaloa, Tabasco, Tamaulipas, Veracruz, Yucatán |

| | |
|----------------------|--|
| <i>leptostachyus</i> | Chiapas, Chihuahua, Colima, Durango, Guanajuato, Guerrero, Hidalgo, Jalisco, México, Michoacán, Morelos, Nayarit, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sinaloa, Sonora, Tamaulipas, Veracruz, Zacatecas |
| <i>jaliscanus</i> | Jalisco, Nayarit, Sinaloa, Michoacán |
| <i>hintonii</i> | Oaxaca, Morelos, Michoacán |
| <i>grayanus</i> | Chihuahua, Coahuila, Durango, San Luis Potosí, Sonora, Zacateca |
| <i>glabellus</i> | Chiapas, Hidalgo, Oaxaca, Puebla, San Luis Potosí, Tamaulipas, Veracruz |
| <i>filiformis</i> | Baja California, Chihuahua, Coahuila, Sonora |
| <i>esperanzae</i> | Hidalgo, México, Michoacán, Puebla |
| <i>coccineus</i> | Template regions from states of México, Chiapas, Oaxaca, Guerrero, Morelos, Puebla, Veracruz, Tlaxcala, Hidalgo, Guanajuato, Michoacán, Jalisco, Nayarit, Zacatecas, Durango, Nuevo León, Tamaulipas, Sinaloa |
| <i>chiapasanus</i> | Chiapas, Oaxaca |
| <i>albescens</i> | Jalisco, Michoacán |
| <i>acutifolius</i> | Baja California, Chihuahua, Durango, Sonora, Sinaloa, Nayarit, Jalisco, Querétaro, Colima, Coahuila, Guerrero, Michoacán, Oaxaca, Chiapas, Veracruz, Tabasco |

¹Species with seed available at the INIFAP germplasm banks, Universidad Autonoma Chapingo and/or Universidad de Guadalajara.

Table 7. Gene pools of wild species of *Phaseolus* distributed in Mexico [34, 73, 91].

5. Perspectives on the implementation of strategies for the participatory breeding of landraces at the community level

Common bean landraces are an important component of Mexican small-scale farms, and there are numerous landraces that are often highly variable in the plant, physiological, seed, biochemical, genetic and nutritional traits and which usually distinguished by local names or characters. The landraces have particular properties or reputational characteristics for adaptation to local climatic conditions and consumer demand for regional dishes.

The demand for seeds by local farmers depends on the market demand for each improved variety. Improved varieties of grains with light colours are regularly demanded by farmers in the north-central region (i.e., Flor de Mayo, Flor de Junio, Bayo, Cacahuate, Canario, Garbanillo, Mayocoba, Ojo de Cabra, Pinto and some others), and dark-coloured or black varieties (i.e., Jamapa, Negro, etc.) are less likely to be in demand. Small farmers in the south-central-southeastern communities, on the other hand, request a higher number of landraces than improved varieties because they farm plots with a great diversity of agroecological, orographic and altitudinal production niches where improved varieties do not usually thrive. Specific

genetic differences have been determined among the seed lots of farmers in the same community [80, 81], who thus provide a high genetic diversity grouped in three common bean races, which are the Mesoamerican, Jalisco and Durango, that are conserved *in situ* by small farmers [2, 4, 78].

Efforts to supply improved bean varieties to farmers who have their products sold in domestic and international markets are being made by INIFAP, research centres and universities. Such farmers can pay from \$20 to \$100 dls for the amount of seed required to sow a single hectare with a last generation variety or imports. Conversely, small farmers in the south, central and south-eastern regions of Mexico lack economic resources to buy the seeds of improved bean varieties and are more likely to supply themselves with their own seed or to borrow it from their neighbours in either the same community or nearby [81, 82, 92]. Therefore, decentralized plant breeding or a strategy different to the traditional scheme is required to improve bean landraces, which means that breeding programmes need to be either participatory or collaborative to implement *in situ* breeding with the cooperation of breeders and farmers or farmer communities to achieve local and regional objectives in the fields of local farmers. A relevant lack of genetic improvement programmes prevails in Mexico because there is also a lack of bean breeders.

Unique opportunities to use the gene sources of more than 20 wild species distributed throughout Mexico are offered by the many *Phaseolus* landraces and heirlooms and wild or cultivated germplasm gene pools, even though the interspecific crossings have not yet been tested. There are also ways to break through the barriers that prevent crosses among species or any other gene transfer strategies of agronomic and biochemical-nutritional relevance among related or different species in terms of genetic divergences. These underutilized or underexplored opportunities require further study. Genetic markers help to both locate and identify specific groups of genes of agronomic and nutritional biochemistry importance, thus making the genetic selection more efficient. However, investment in laboratory infrastructure as well as equipment and human resources is still required to make assisted breeding with genetic markers a reality. Recent improvements include the generation of advanced lines with varying degrees of resistance to pests and diseases through interspecific hybridization [93].

Evidence of the nutritional and nutraceutical potential of landraces as protein sources (essential amino acids), carbohydrates, minerals and polyphenols (anthocyanins, flavonoids, phenols, carotenoids and some other compounds) with high antioxidant activity were previously above. Small farmers, in several cases, take direct advantage of landraces despite little knowledge of the enormous nutritional contribution that comes from the consumption of common bean landraces. The data generated in universities and research centres must be disseminated to consumers because of the decreasing tendency in *per capita* consumption in Mexico from 18.9 kg in 2000 to 10.2 kg/person/year in 2008 [85, 94]. Important progress was achieved by Welch et al. [61], Blair et al. [95] and Gelin et al. [96] with regards to common bean improvement with the selection of elite germplasm with high Zn and Fe contents. However, despite having a quantitative inheritance, such characters interact with the environment and crop management. The most remarkable outcomes were realized using germplasm from the Andes and Mesoamerica.

One challenge for common bean breeding is the generation of improved varieties, which requires the exploitation of genetic variability and the application of local knowledge. At local and regional levels, a farmer is aware that genotypes or landraces respond favourably to abiotic and biotic stresses, including future scenarios of climate change. As previously reported, most breeding for drought resistance has been within the Mesoamerican gene pool and based on grain yield under stress. The sources for drought resistance originated from Jalisco and Durango, Mexico [97]. The impacts of both abiotic and biotic stresses on the common bean crop are influenced by interactions with other environmental components, such as soil texture characteristics, organic matter content, the degree to which aggregate stability affects water infiltration, soil water-holding capacity, and the ability of the roots to acquire moisture and nutrients.

The highest phenotypic and genetic diversity of the landraces is in the custody and preserved in the plots, backyards and homes of small farmers in Mexico. Such self-generated seed producers are able to exchange this diversity among neighbours and relatives who require only small quantities, which is a different scheme than that employed by seed companies or institutions that provide improved seed varieties because the demand in the communities is lower than the minimum required by a business aiming to multiply the improved varieties. Furthermore, the latter are not always adapted to the agroecological niches of small traditional producers, so the local seed exchange systems become the only sources of supply for small farmers, who require different breeding strategies than those used in commercial agriculture.

6. Conclusions

To understand the diversity of common bean landraces, to take advantage of the nutritional value of the grain, and to promote strategies for on-farm conservation and utilization, it is necessary to characterize and evaluate the phenotypic and genetic variation managed by traditional farmers, which provides us with a better understanding of the dynamic and structure of cultivated populations. The farmers modify landrace diversity through management practices in accordance with the diverse reasons or criteria used to satisfy their food needs, the agroecological production conditions, cultural factors and, sometimes, market demands.

The results of this study showed that two patterns of diversity in the common bean landraces can be distinguished in Mexico in terms of the geographic area being represented; at the level of states and regions within a state, the landraces are defined by the agromorphological characteristics and chemical composition of the grain, such as the contents of minerals, flavonoids, polyphenols and antioxidant activity as well as grain colour indexes (L^* , chrome and hue). The agroecological conditions of cultivation and farm management influence the high variability in the agromorphological and chemical composition of the grain in the common bean landraces.

In each collection of the evaluated common bean landraces, populations were detected with high agronomic and grain composition potential. For example, there were populations with a

high number of grains and yield per plant and/or populations with high contents of micro- and macro-elements, polyphenols, flavonoids and antioxidant activity within each level of diversity represented, the Mexican states and the regions in the state of Oaxaca. Therefore, there is germplasm available at both diversity levels to start a breeding programme at the national level or for on-farm seed selection. In addition, different populations were identified with a dual purpose, the production of both green and dry beans.

In developing countries such as Mexico, consumer preferences are changing towards a decrease in the consumption of common beans, but contradictorily, the incidence of diabetes, obesity and others chronic degenerative diseases is increasing in the population. Therefore, in countries with the major genetic diversity of the species, the common bean is losing its social role. Currently, different researchers are publishing articles demonstrating the protective effect of green or dry beans in the prevention of diverse diseases, including cancer, and other research groups are demonstrating the functional properties. However, there is scarce or no research oriented towards solving the social problem of malnutrition, which is also associated with the reduction in the information available to consumers and non-experts. Today, it is not enough to demonstrate that high genetic diversity exists in common beans with the accompanying nutritional and nutraceutical potential; we must test its utility to solve social problems.

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