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Root Sprouts of Domesticated *Phaseolus coccineus* L. Overwinter Plants and the Environment at Its Collection Sites

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Abstract

Buds emerge from the roots of domesticated runner bean plants (*Phaseolus coccineus* L.) as sprouts and give the crop its persistence. This particularity of the species seems to be associated with the environment where the species was cultivated during long time. Data on regrowth traits were recorded on 70 accessions of domesticated *P. coccineus* after overwintering at a site in the central highlands of Mexico. The characteristics recorded included fresh weight of vegetative regrowth, root length, root crown diameter, and diameter of the main root. Most accessions that sprout the following spring, after the grain harvest of the previous year, come from temperate and semi-cold sites with cambisol and andosol soils in mixed Quercus pine forest and high mountain fir trees. Those that do not sprout are from sites of semiarid temperate climate, haplic phaeozem soil in shrub grasslands with deciduous broadleaved trees, and semiwarm subhumid climate, eutrophic regosol soil in deciduous broadleaved forest. Two types of roots were differentiated: branched and thickened taproots, also associated with a different climate, and the type of soil of the collection sites.

Keywords

P. coccineus Distribution, Vegetation-Environment Interactions, Drought-Alternative Species, Root-Regrowth

1. Introduction

Since the 1930s, according with Vavilov [1], the mountain chains of Central and

South America were the center of origin of a large number of cultivated plants such as the common bean (*Phaseolus vulgaris*), runner bean (*P. coccineus*), tepary (*P. acutifolius*) and the year bean (*P. dumosus*). Further studies had shown that the center of origin of the runner bean is the humid highlands of Mesoamerica [2], particularly at the Trans-Mexican Volcanic Belt [3] and is cultivated in Mexico as an annual in sub-humid climates with frost in winter, or as a perennial in hot, sub-humid climates in frost-free areas [4].

In 2008-2013, when the Mexican collection of domesticated runner bean was planted, it was observed that the perennity was given by shoots that emerge from buds on the root. In Spanish, the word "renuevo" is defined as the offshoot or stem that the plant develops anew [5] and is a synonym of re-sprout and "hijuelo". Plant conservation and evolution is focused on de novo replacements such as seed germination and dispersal methods, whereas sprouting is a persistence form in diverse ecosystems [6]. Regrowth is a reproductive strategy that has evolved in response to the severity of the environment, and "provides tissue replacement of the parent genotype after the canopy of a perennial plant is destroyed" [7].

The geographical location of Mexico as well as its variety of physiographic conditions and climates has fostered its rich flora [8]. In this case, differential botanical geography indicates that some species traits coincide with specific geographical areas [9]. A plant capable of reproducing the next generation of its lineage without dependence on seeds, has adaptive advantages that support its development in a wide range of environments. We propose that cultivars of the runner bean with capacity to regrow are a useful propagation alternative in sites where rainfall is delayed, because it allows the plant to survive with moisture and carbohydrates accumulated in its roots.

The objectives of this study were: 1) To identify the materials of the Mexican collection of domesticated runner beans (known as ayocote in Mexico) that have the capacity to regrow and their relationship with the climate, soil and vegetation of the collection sites.; 2) To characterize the runner beans root by measuring its external structures (length, crown diameter and widest portion diameter).

2. Materials and Methods

Geographic data was recorded as an integral component of the Network of Conservation Centers of the National System of Phytogenetic Resources (SINAREFI for its Spanish acronym). Project "Collection and regeneration of bean genetic resources in Mexico", subproject "Diagnosis and increase of the collection of *Phaseolus coccineus* L. for its conservation and utilization in Mexico".

2.1. Experimental Location

Valley de Mexico Experimental Station, sited at Coatlinchan, Texcoco, Mexico at an altitude of 2250 m, in the coordinates 19˚26'44" Northern and 98˚54'02" Western (**Figure 1**).

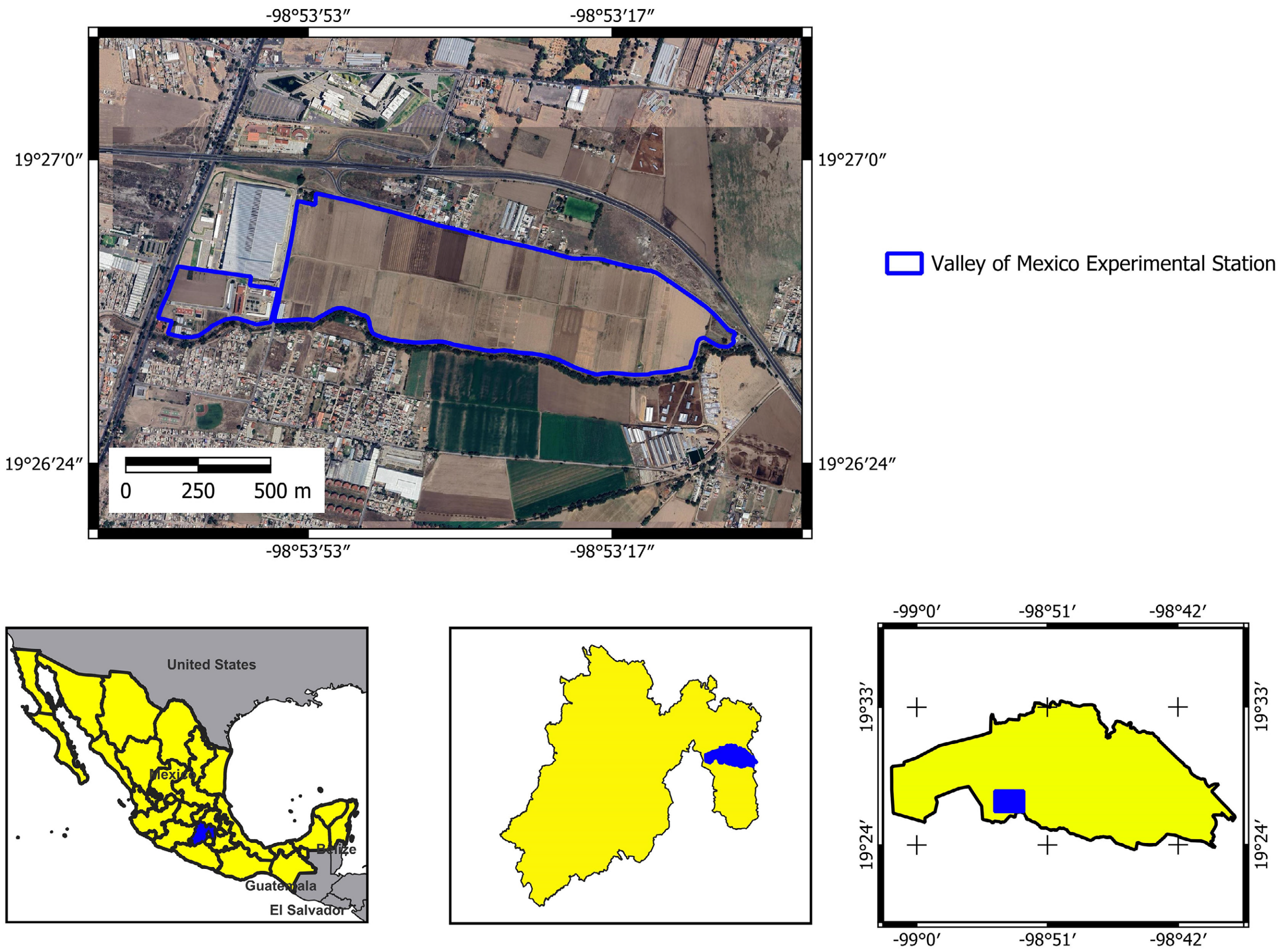

Figure 1. Location of valley of Mexico experimental station.

2.2. Experimental Design

The experimental plot per accession was a 4 m long furrow with a interrow spacing of 0.80 m, leaving one free row in between each accession. Three seeds were sown every half meter, so that there were seven bushes per row.

2.3. Plant material

70 accessions of runner bean of the National Research Institute of Forestry, Agriculture and Livestock (INIFAP by its acronym in Spanish). This germplasm was collected in the 1960s in the states of Guanajuato, Querétaro, Mexico, Hidalgo, Tlaxcala, Oaxaca, and Puebla [10]. The range of geographic coordinates of original collection sites is from 16˚N to 21˚N and 96˚W to 102˚W. We sow seed harvested the previous year.

2.4. Planting Date and Sampling

On April 22, 2013 sowing was done with seed increased in 2012. No chemical seed treatment or fertilizer were applied to the soil, and supplementary irrigations were applied on May 3, and July 31. The grain was harvested in September and October 2013, and non-destructive sampling of root sprouts was carried out on 10 March 2014.

2.5. Plant Traits

The identification of accessions with sprouts was made by visual observation of those that already displayed foliage. Fresh weight sprouts: Three plants per accession were extracted from the soil. Immediately after extraction, the fresh weight of the root and sprouts was measured with an Ohaus Compass CX electronic scale with a precision of 1 g. Root architecture and dimensions: Root length was measured with a simple 1 m ruler. Root crown diameter and Root thickened section diameter were measured with a Scala INOX 222A 6-inch vernier. Two types of taproots were identified by visual observation: slender taproot and thickened taproot.

2.6. Climatic Variables at the Experimental Location

Data were gathered from a nearby climatological weather station. We used information on accumulated precipitation and average minimum and maximum temperature per month during the growing season.

2.7. Information from the Collection Sites

The geographical coordinates of the collection sites were obtained from the passport data of the *Phaseolus* spp. germplasm catalogue [10]. Climate type and mean annual minimum and maximum temperature from [11] and [12], predominant vegetation from [13], and type of soil from [14]. The data was processed with QGIS® version 3.34 software [15].

2.8. Statistical Analysis

Objective 1. Identify materials by their ability to resprout, and their association to climate, soil and vegetation type of collection sites in the domestication center. Accessions with and without regrowth were identified by visual observation. To find out the altitude and specific climatic conditions (minimum and maximum annual mean temperature) of collection sites, we searched for information on climate, soil and vegetation type of collection sites. A principal component analysis (PCA) was carried out to reduce the size of the database to explain the presence or absence of regrowth. This analysis was performed with SAS version 9.3 [16]. The variables that contributed to the differentiation of landraces with and without regrowth were selected. In accordance with the values of the first three principal components, four groups of cultivars were established and plotted in quadrants with the Sigma Plot® software.

Objective 2. To characterize the runner beans root by measuring its external structures (length, crown diameter and widest portion diameter). For the variables shoot weight and root dimensions of the 70 varieties, a one-way analysis of variance (ANOVA) and a Tukey test were performed to evaluate whether significant differences existed ($\alpha < 0.05$) [17]. Variables that did not meet the assumptions of homogeneity of variance and normality were log transformed.

3. Results

Experimental location. Total rainfall in the crop cycle was 545 mm, the lowest minimum temperature (7˚C) and the lowest maximum temperature (21˚C) occurred from 9 to 18 September. The period from grain harvest to sprout sampling was 137 days. No frost occurred in the growing season or from harvest to sprout sample.

3.1. Recognition of Varieties with Shoots

Shoots emerged from root sprouts close to the soil surface, in the middle portion, or in the thickened root zone. Different sprout growth rates were observed, from initial underground (**Figure 2(a)**) to extensive with foliage (**Figure 2(b)**).

3.2. Collection Site Variables

3.2.1. Geographic Coordinates

The 70 runner beans came from 25 sites: 42 with sprouts, from 16˚82'N to 21˚45'N and 96˚67'W to 100˚87'W; 28 without sprouts from 16˚78'N to 21˚30'N and 96˚67'W to 102˚30'W (**Figure 5**).

3.2.2. Climate, Soil and Vegetation Type

These 70 accessions came from temperate, semi-warm and semi-arid climates in a wide range of soils and vegetation types: The 42 sprouting varieties were grouped according to climate, soil and vegetation of their collection sites:

(a) (b)

Figure 2. (a) Initial underground sprout, and (b) Advanced sprout with foliage. Photos were taken in the Valley of Mexico Experimental Station in April 2014.

1) Temperate and semi-cold climates: 26 cultivars from temperate sub-humid climate in: Cambisol and Andosol soils in mixed *Quercus* and pine forest, and high mountain spruce formation; Phaeozem in shrub grasslands and semi-desert vegetation; and Leptosol in mixed *Quercus* and pine forest.

2) Semi-arid temperate climate: eight accessions collected in Leptosol soil with deciduous broadleaf forest and semi-desert vegetation; Phaeozem in shrub grassland with deciduous broadleaves; and Umbric Andosol with high mountain spruce formation.

3) Semi-warm sub-humid climate group C: eight accessions collected in Leptosol and deciduous broadleaf forest or semi-desert vegetation, in Eutrophic Cambisol and cloud forest; and Leptosol in evergreen broadleaf forest.

The 28 no sprouting runner beans were also grouped according to climate, soil and vegetation type of their collection sites:

1) Temperate climates: 12 accessions collected in Andosol Umbric and high mountain sprouce formation; and Eutrophic Cambisol in mixed *Quercus* and pine forest.

2) Semi-arid climates: 11 accessions collected in Phaeozem haplic or Umbric Andosol in shrub grasslands with deciduous broadleaved trees, or Eutrophic Regosol in deciduous broadleaved forest with trees <15 m (100% deciduous).

3) Semi-warm climate group C: five accessions collected on Regosol eutrophic soil in deciduous broadleaf forest.

3.3. Plant Variables

3.3.1. Root Architecture

Once the soil was excavated, and the underground and aerial portions of sprouts extracted, two different architectural root types were distinguished: pivoted branched taproot in 55 accessions (79%) and pivoted thickened taproot in 15 (21%) (Figure 3). Four root areas were identified: the closest to the stem or crown, the area where the secondary roots emerge, the one where the ciliary roots emerge, and the tip. This describes an axonomorphic root with a preponderant axis and secondary ones less developed compared to the main one [5].

(a) (b)

Figure 3. Two root types in runner bean: (a) Pivoted branched, accession no. 8329 from San Luis de la Paz, Gto., and (b) Pivoted thickened, accession no. 8212 from Tlatlauquitepec, Pue. Photos were taken in the Valley of Mexico Experimental Station in April 2014.

3.3.2. Statistics of the Analyzed Variables

Plant fresh weight, root length, crown diameter and diameter of thickened portion, met the assumptions of homogeneity of variance and normality (Table 1).

Plants with regrowth had significantly 34% more fresh weight than plants without regrowth, and five cm more of root length. Differences in crown diameter and in the widest portion diameter of root were not significant (Table 2).

3.3.3. Runner Bean Accessions Grouped by Root Architecture and Collection Site Variables

The two proposed root architecture types for *Phaseolus coccineus* L. accessions were associated to distinct climate, and soil type of collection sites.

Of the 70 cultivars, 79% had taproots and 21% had thickened taproots, and both root types came from locations with cambisol, andosol, phaeozem and leptosol soils, and semi-cold, templates, semi-warm and semiarid climates.

Accessions with taproots were preferentially from sites with temperate and semi-cold climate (80%) and cambisol soils (25%); those with thickened taproots from temperate climate sites (47%), mainly in cambisols soil type (60%), but also in andosols (20%) and including leptosols (13%) soil types.

Accessions with thickened root and also root sprouts are native from Amozoc, Atempan, Tlaltlauquitec and Zacapoaxtla, Puebla, La Dieta Mich., Tlaxcala, Tlax., and San José Villa de Allende, Méx., located between 19˚01'N to 19˚52'N, and 97˚27'W to 100˚12'W, in sites with cambisol eutrophic soil, mean annual minimum temperature from −2˚C to 0˚C, mean annual maximum temperature from 26˚C to 28˚C, and total annual precipitation from 800 to 1000 mm.

Table 1. Variables measured for runner bean accessions.

Variable	N	Mean	Std Dev	Min	Max	Skewness	Kurtosis
Fresh weight (root and foliage) (g)	69	111.0	106.9	12.5	538.3	2.4	6.5
Length (cm)	68	35.1	6.5	16.0	50.5	0.0	0.3
Crown diameter (cm)	69	1.0	0.2	0.6	1.9	1.2	2.3
Thickest diameter	69	2.4	0.6	1.1	4.4	0.5	0.6

Table 2. Comparison of sprout weight and root dimensions of runner bean accessions with and without sprouts.

Variable	Sprout	N	Mean	Sd	Minimum	Maximum
Fresh weight	with	29	187.76 a	168.97	35.00	850.00
	without		63.45 b	45.02	15.00	155.00
Root longitude	with	40	36.97 a	6.35	17.83	50.5
	without		32.06 b	6.01	16.00	45.00
Crown diameter	with	41	1.07 a	0.37	0.60	2.36
	without		0.97 a	0.20	0.65	1.50
Thickest diameter	with	41	2.52 a	0.65	1.50	4.40
	without		2.31 a	0.56	1.00	3.17

Sd = standard deviation.

3.3.4. Runner Bean Accessions Grouped by Plant Variables and Collection Site's Characteristics

Principal component analysis that included geographical coordinates and temperature of collection sites, as well as resprouts (root and shoot) fresh weight, and root dimensions explained 70% of the variability (Table 3). The first component explained 34% by geographic coordinates, mean annual minimum temperature of collection sites, and root length; the second, 25% by sprout fresh weight and the broadest portion diameter of root; and the third, 11% by crown diameter (Figure 4).

The spatial distribution based on the first two components revealed two main distinct groups (Figure 4).

Table 3. First three principal component values describe collection site, root weight and root dimensions of 70 native Mexican runner bean.

Variable	Component		
	1	2	3
N Latitude	**0.490**	−0.001	0.107
W Longitude	**0.478**	−0.114	0.288
Minimum mean annual temperature	**−0.459**	−0.084	0.004
Sprout fresh weight	−0.141	**0.515**	0.057
Root thickest portion diameter	−0.055	**0.563**	0.058
Root crown diameter	−0.101	0.232	**0.858**
Root length	**0.478**	−0.114	−0.288

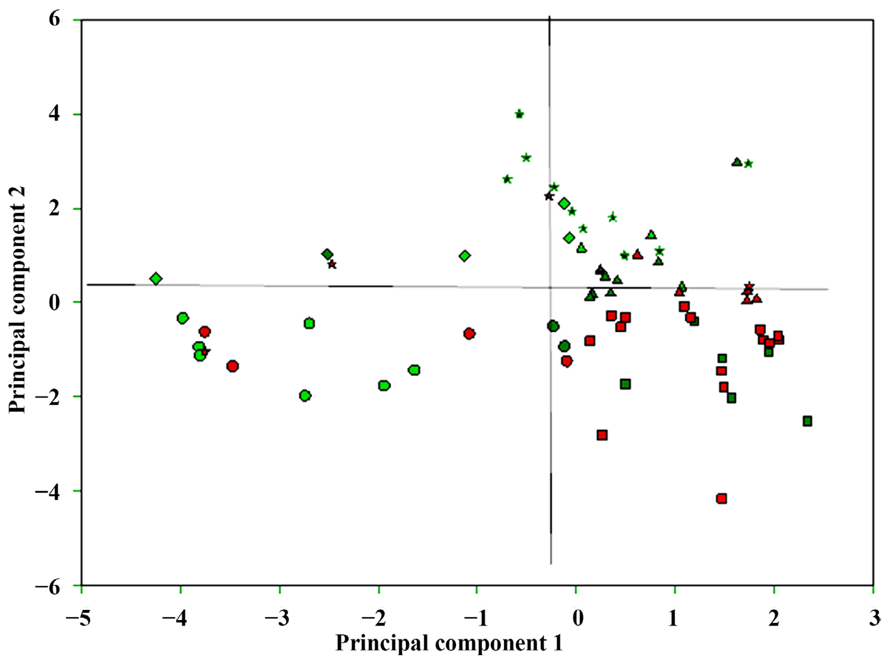

Figure 4. PCA-based spatial distribution of 70 native runner beans varieties. Green color represents cultivars with sprouts, and red ones without sprout. Cultivars with thickened taproot and sprout are represented by green stars, and red ones represent cultivars with thickened taproot without sprout.

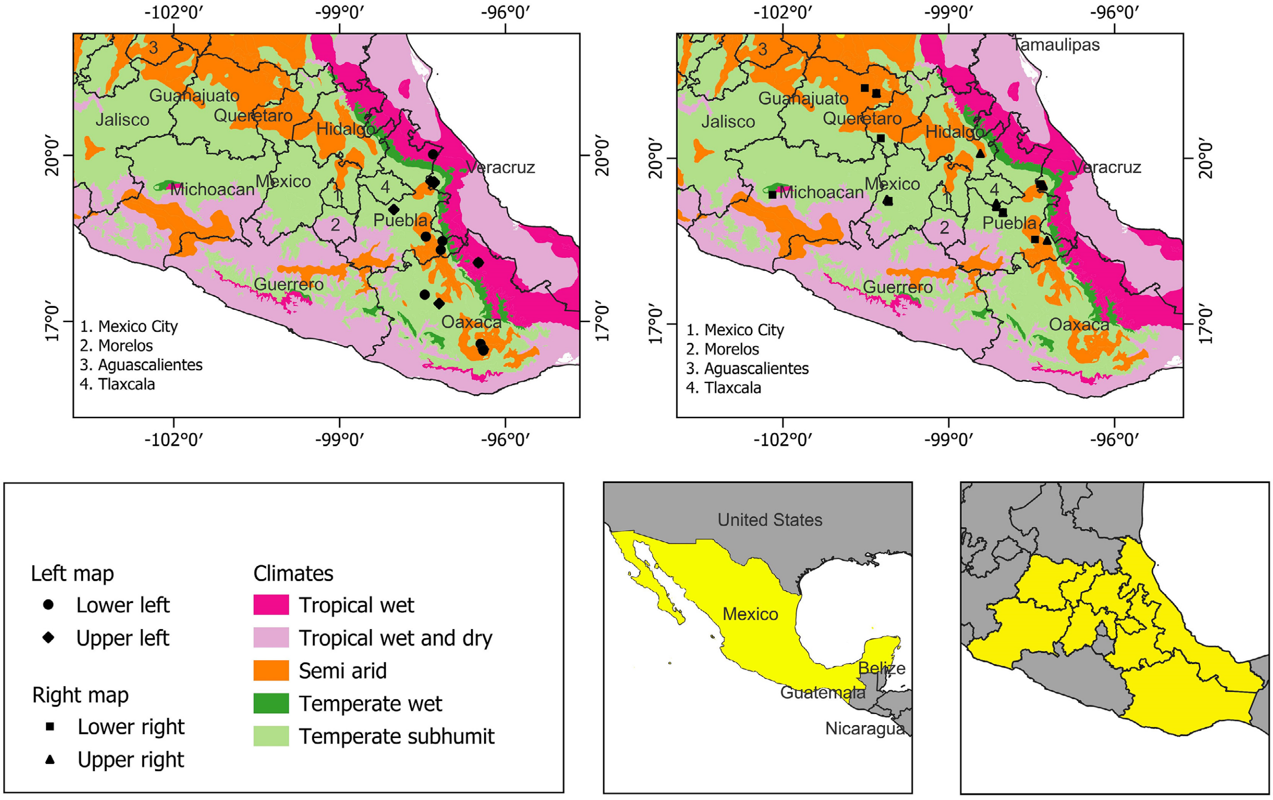

Figure 5. Distribution of 70 runner bean accessions (*Phaseolus coccineus* L.) in different climatic zones. Symbols per quadrant of the PCA graph; circles, lower left quadrant; diamonds, upper left; squares, lower right; triangles, upper right.

The right quadrants grouped the runner beans collected further north, also from the temperate zone, including those from the arid zone of northern Guanajuato, central Puebla, western Estado de Mexico, and those from Michoacán, Tlaxcala and Querétaro, between 18˚52'N and 21˚27'N and 97˚22'W and 102˚19'W, with mean annual minimum temperatures ranging from −3˚C to 1˚C (Figure 5).

Cultivars with regrowth were mainly distributed in both left quadrants, in semi-warm sub-humid and humid of group C climates, and in the upper right one, in temperate sub-humid, and temperate humid (geometric shapes in green). In contrast, cultivars without regrowth came mainly of semi-arid temperate and sub-humid temperate climates (geometric shapes in red). Cultivars with pivoted thickened root and regrowth came from temperate humid and sub-humid climates (green stars). Only four cultivars with pivoted thickened root had not regrowth (red stars).

4. Discussion

Plant biodiversity includes wild relatives, landraces, and modern cultivars. Landraces are dynamic populations of domesticated plants that have historical origin and distinct identity and lack formal improvement, as well as often being genetically diverse, locally adapted and associated with traditional farming systems [18]. According to reference [19], *Phaseolus coccineus* is distributed on mountain systems from north of Mexico to Central America, escaped plants down to Colombia; three forms of populations of the species can be recognized: the wild, the cultivated, and the escaped, all of them with tuberous roots. They describe dozens of different vernacular names in most of the native languages across different regions in the highlands of Mexico.

Landraces are a valuable genetic resource for crop improvement and a reliable local source of food diversity. Such is the case of traditional landraces of runner bean in the Central highlands of Mexico [20]. Furthermore, results of reference [21] and [20] clearly show that landraces in their Mesoamerican center of origin are scarcely differentiated from their wild relatives since the gene flow between them is high and continuous, a fact that indicates a wealth of genetic diversity. Reference [20] also mention that the domestication bottleneck might be less severe for perennials than for annual plants, because perennial species frequently have a cross pollination mating system and overlapping generations. Although in many areas of central Mexico the runner bean is commonly cultivated as an annual crop, its subterraneous organs are kept for the next agricultural cycle [2].

P. coccineus L., is cultivated as an annual in sub-humid and semiarid climates with frost in winter, or as a perennial crop in hot, sub-humid climates in frost-free areas [4]. Most accessions have a perennial life cycle, with large tap roots characteristic of their wild ancestors [2] and their size is dependent on age and environmental factors. Results suggest that plant perennity in the runner bean is due to root reserves and capacity for resprouting, a plant survival mechanism through vegetative reproduction, related to the climatic conditions on the sites of origin, where the species evolved and became domesticated. Reference [22] pointed out that root diversity in morphological traits declines sharply across the sequence of tropical, temperate, and desert biomes, presumably due to inhospitable environment. According to these authors, root traits have evolved by two contrasting strategies, one ancestral conservative in which root thick plants depends on symbiosis with mycorrhizal fungi for soil resources, and a more opportunistic strategy in which thin roots enable the plants to efficiently leverage photosynthetic carbon for soil exploration. Therefore, root traits facilitate plant's adaptation to its environment, and its evolutionary history determines the arrangement of its functional traits [22].

Our observations revealed that after the grain was harvested, the root did not die over the winter, became dormant, and in the spring, when exposed to favorable conditions (warm temperature), sprouted again and resume plant growth. The root remained active and, in the first phase of resprout growth, before it reaches the soil surface and sunlight to initiate photosynthesis, acted as a reserve storage organ. Plants with a storage root are specifically adapted to store products photosynthesized in the shoot [23]. Species from temperate and cold climates had developed this capacity to withstand cold after exposure to environmental stimuli, such as low temperatures and short days [24]. But the absence of frost through the growing cycle, and between grain harvest and root removal, suggested that resprout emergence is not an immediate response to frost, but an adaptive mechanism towards a shorter growth cycle [25].

The root contributes to the adaptation of the runner bean plant to its environment; cultivars with resprout were preferentially associated to collection sites with temperate climate with typical mountain soils, like Cambisol with a high degree of saturation, Andosol having volcanic origin, and Phaeozem, rich in organic matter (more favorable environments, in terms of moisture availability). Reference [25] conducted a study in Southern Colombia where they interviewed 60 farmers and among the species grown in the area, three Phaseolus species stand out, *P. vulgaris*, *P. coccineus* and *P. dumosus*, the first of annual growth cycle and the other two perennials, and they considered them as semi-domesticated. In this area, farming is non-mechanized and pre-dominantly subsistence-oriented, with small quantities produced for local markets. They found out that in *P. coccineous* its fleshy roots are not the only organ able to resprout, but also the lower part of the stem, which may be due to the high humidity of the environment in the area. They pointed out that the perennially trait allows for the generation of an extensive root network that contributes to soil conservation and maintenance of soil biota. An important finding was that when the plant resprout, its growing cycle is shorter, reaching production in about 4 to 5 months rather than 9 to 10. In the highlands of Central Mexico, although resprouting its present, the perennially trait in domesticated populations of *P. coccineus* diminish in the number of individuals in few years due to a harsher environment than in Southern Colombia where farmers indicated the presence of 30 years old plants. In Mexico the slow loss of the perennial trait towards Northern drier semiarid areas may be also indirectly due the advance in domestication towards a short growth cycle in annual cropping.

In Chile, Reference [26] studied landraces and improved genotypes of *P. coccineus* and found out that fifty percent of the genotypes had fibrous (fasciculate) roots, which can be classified as annual variants, whereas the rest had tuberous roots that can be multiplied vegetatively and have the potential for resprouting the following year and are classified as perennials. Among the draw conclusions, Reference [26] indicated that soil characteristics such as structure, porosity, and aeration, among others, can influence the shape and size of the root system. In the present study, the observed root systems, although the landraces were grown outside its original niches, its characteristics were freely displayed in a cropped soil.

Reference [23] indicated that root architecture is about the shape of the root in the soil, is concerned with an entire root system of an individual plant and varies within plant species. We found that within the same species and domestication form (runner bean landraces) there were different root architecture types, most probably related to the environment, evolution, and domestication sites of the species. Exploitation of this variation could improve crop root adaptation to climate change in semi-arid lands [27]. Runner bean plant are known by Mexican rural communities as a soil improver because its root erodes hard pan soils and contributes to soil formation, a feature that can be useful in stony areas of shallow soils.

Future studies of the runner bean root phenotypic variation may contribute to escape drought and global warming effects in specific areas, increase crop productivity and make food available in countries that need it most. Frequently, along with the vegetative resprout, inflorescences are also observed early during resprouting. We propose future research to: investigate the optimal and suboptimal range of the runner bean root temperature for resprouting; the soil volume both root types are able to explore; and find out if the thickened taproot, with sprouts and plants coming from resprout, can be adapted to different climatic conditions. In addition, since few reports mention the consumption of *P. coccineus* leaves, flowers, and roots (after a long boiling time), its nutritious value must be determined.

5. Conclusion

The overwinter resprout in *P. coccineus* seems to be widespread, but more prevalent from accessions that come from temperate and semi-cold sites with Cambisol and Andosol soils in mixed Quercus-pine Forest and high mountain fir trees. These environments within and around the Mexican Trans Volcanic Belt have been mentioned as drivers of wide diversification and local persistence of biodiversity [28]. The fact that resprout is widespread may be related to an increased capacity for colonizing diverse niches in a temperate-humid environment. After domestication, the resprout trait was carried along during the dispersion of the crop, but it is being eroded or of none use in harsh semiarid environments where the crop is used as short-lived annual species.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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