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Management, phenotypic patterns and domestication of *Polaskia chichipe* (Cactaceae) in the Tehuacán Valley, Central Mexico

A. Carmona, A. Casas*

Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México (Campus Morelia), Apartado Postal 27-3 (Xangari), Morelia, Michoacán 58089, Mexico

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Abstract

Polaskia chichipe, a cactus endemic to Central Mexico, is valued for its edible fruits and branches used as fuel wood. This plant occurs in the wild in thorn-scrub forests, in disturbed areas and in home gardens. Our study documented that this plant species was manipulated through management in situ of wild populations in disturbed areas, where the better phenotypes with larger and sweeter fruits were spared and enhanced by vegetative propagation and transplanting of young plants. Manipulation was also conducted by cultivation in home gardens where the better phenotypes were propagated by branches or seeds or by transplanting complete young plants. Morphological variation was compared among wild, managed in situ and cultivated populations to examine how human manipulation might have influenced modifications in phenotypic patterns. Fruits, seeds and some flower parts of managed populations were, on average, larger than in wild populations, and even larger in cultivated populations. The results suggest that the better phenotypes, from a human perspective, were more abundant in managed in situ and cultivated populations due to artificial selection, and that domestication resulted from both types of management.

Keywords: Columnar cacti; Domestication; *Polaskia chichipe*; Morphological variation; Tehuacán-Cuicatlán Valley

*Corresponding author.
E-mail address: acasas@oikos.unam.mx (A. Casas).

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1. Introduction

The Tehuacán-Cuicatlán Valley, Central Mexico (Fig. 1), is recognized as one of the sites where agriculture first developed in the New World (MacNeish, 1967, 1992). For more than 10,000 years, prehistoric and current human cultures of this region have used a broad spectrum of wild and incipiently manipulated plant resources for subsistence that have complemented agriculture significantly (MacNeish, 1967; Casas et al., 2001). Cacti are among the main plant resources used by people since the earliest phases of human occupation of the region (MacNeish, 1967; Smith, 1967)

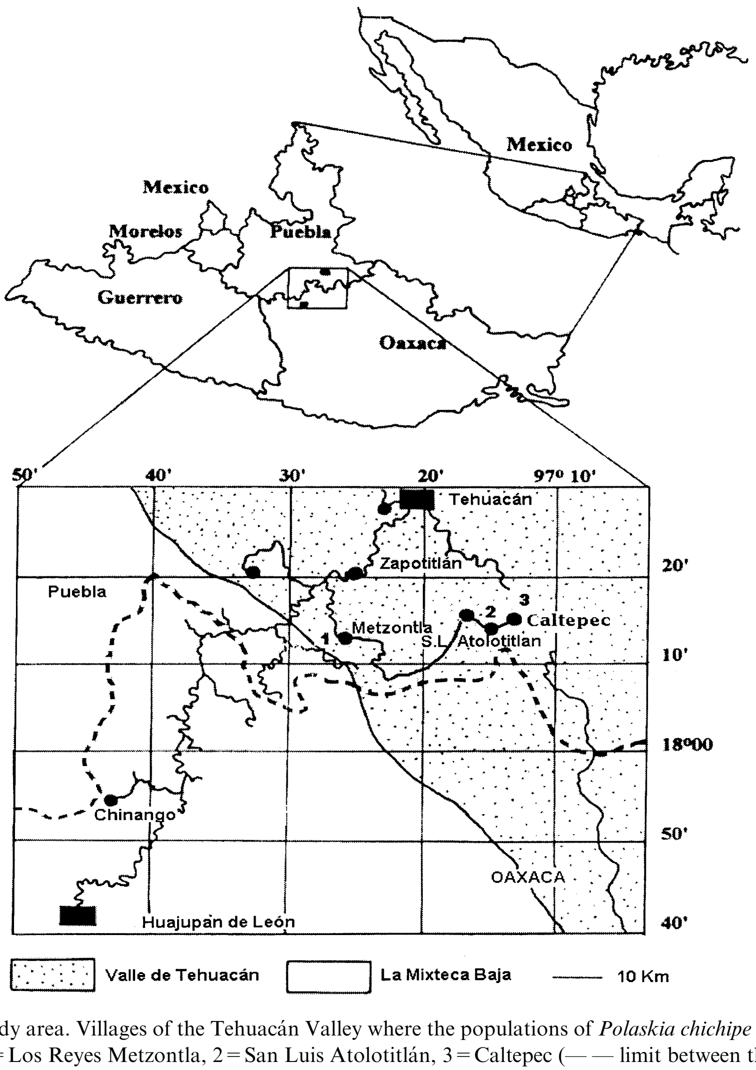

Fig. 1. Study area. Villages of the Tehuacán Valley where the populations of *Polaskia chichipe* studied are located. 1 = Los Reyes Metzontla, 2 = San Luis Atolotitlán, 3 = Caltepec (— — limit between the states of Puebla and Oaxaca.

and, according to Casas et al. (1999a), columnar cacti, including 20 species important for sources of food, medicine, fodder, material for construction, living fences and fuel wood, have been crucial resources for local people because of their diversity and abundance in the vegetation types covering most of the area.

At present, people of the region gather products of columnar cacti from wild populations. Some species are also cultivated in home gardens and terraces, mainly by vegetative propagation, but also by transplanting young plants and sowing seeds. The principal cultivated species are *Myrtillocactus schenkii* (J. Purpus) Backeb., *Pachycereus hollianus* (F.A.C. Weber) F. Buxb., *P. marginatus* (D.C.) Britton and Rose, *Polaskia chichipe* (Glosselin) Backeberg, *Stenocereus pruinosus* (Otto) F. Buxb., and *S. stellatus* (Pfeiffer) Riccob. (Casas et al., 1999a). Additionally, people practice forms of management of wild populations in situ by sparing and enhancing numbers of particular plant species during clearing of natural vegetation for agriculture (Casas et al., 1999a,b). Casas and Barbera (2002) report that *Escontria chiotilla* (F.A.C. Weber) Rose, *Myrtillocactus schenkii*, *M. geometrizans* (C. Martius) Console, *Pachycereus hollianus*, *Polaskia chende* (Gosselin) Gibson and Horak, *P. chichipe*, *Stenocereus pruinosus*, and *S. stellatus* are among the species managed in situ. But management in situ may also involve selective sparing and enhancing of particular desirable phenotypes of those species which are advantageous over other non-desirable phenotypes to people. Both cultivation and management in situ appear to involve domestication in some columnar cacti species (Casas et al., 1999a,b), considering as domestication the evolutionary processes guided by humans (see Darwin, 1859, 1868; Harlan, 1992). Such processes involve alteration of the genetic structure of populations determined by the manipulation of morphological and physiological variation of plant populations by artificial selection, resulting in divergence between wild and manipulated populations.

In a review on domestication of cacti in Mesoamerica, Casas and Barbera (2002) found that fruits were predominantly used by people, and that characteristics such as fruit size, pulp colour and flavour, peel thickness, and thorniness were considered when the quality of fruits was assigned. Similarly, these characters were used by people to select individuals to preferably spare and enhance through vegetative propagation, transplant, and/or sow seeds. This form of artificial selection is intense in home gardens, where individuals are continually replaced by others with better attributes, but it is also practiced in managed in situ populations (Casas et al., 1997, 1999a).

Our study analyses the morphological variation of *Polaskia chichipe*, popularly known as "chichipe", in the context of processes of domestication. Arias et al. (1997) described *P. chichipe* as an arborescent plant, 2–4 m height, with a well-defined stem and numerous green branches with 9–12 ribs. Areoles are separated by 1–1.5 cm; flowers are 3 cm long with tepals white-yellowish with a reddish strip in the middle. Fruits are red, small, and spherical, with black seeds 1.3 mm long. Endemic to the Tehuacan Valley and markedly restricted to soils derived from volcanic rocks in elevations of $\sim$1600–$\sim$2300 m, it is a dominant element of the particular thorn-scrub vegetation "chichipera" (Valiente-Banuet et al., 2000). Some wild populations are under in situ management, and there is cultivation in home gardens. According to Casas et al. (1999a), propagation of this species by humans is conducted by vegetative propagation of branches, or by sowing seeds from the desirable phenotypes. However, it is a common practice that people tolerate seedlings and young plants of this plant species (derived from seeds in bird or human faeces) in wild populations managed in situ and in home gardens. People let the most vigorous seedlings grow and decide to leave or remove the resulting plants after reaching reproductive stage (approximately 10 years) depending on the presence of favourable or unfavourable characteristics. *P. chichipe* is one of the columnar cacti of the region with higher economic importance. Its fruits are used fresh or dry as human food, in preparing jams, and are sold commercially. Fruit peel and branches are a source of fodder, whereas wood is used as fuel wood for manufacturing pottery (Casas et al., 1999a).

In the field, *P. chichipe* was observed with conspicuous variation in fruit morphology, particularly their size. Fruits from manipulated populations appeared to be generally larger than those from the wild. Some primary questions were whether this trend in variation was real, if it was due to environmental differences among sites, or due to human manipulation through artificial selection for larger fruits.

Patterns of morphological variation resulting from environmental differences and/or forms of management were studied previously in other cacti, particularly *Opuntia* species (Colunga-García et al., 1984; Felker and Russel, 1987; Felker et al., 2002; Pimienta-Barrios, 1994), *Stenocereus stellatus* (Casas et al., 1999b), *S. queretaroensis* (Pimienta-Barrios and Nobel, 1994; Nobel and Pimienta-Barrios, 1995), *S. pruinosus* (Luna and Aguirre, 2001), *Escontria chiotilla* (Arellano and Casas, 2003), and *Polaskia chende* (Cruz and Casas, 2002). These studies revealed that environment influenced morphology of individuals, and some of them revealed that, in addition, under various management regimes within a given environment the plants have morphological differences, especially in characters targeted by artificial selection. It was found that managed in situ and cultivated populations were particularly abundant in plants with larger fruits of sweeter flavour, less spiny and thinner peel, higher proportion of pulp, and more and larger seeds (see Casas and Barbera, 2002) for a review on this topic). Previous research also focused on the relationship between the process of domestication of columnar cacti and reproductive biology in *S. stellatus* (Casas et al., 1999c), *Polaskia chende* (Cruz and Casas, 2002), and *P. chichipe* (Otero-Arnaiz et al., 2003). Otero-Arnaiz et al. (2003) found that, whereas wild populations of *P. chichipe* had a predominantly self-incompatible breeding system, the managed in situ and cultivated populations were 24–27% self-compatible. These authors also found phenological differences between wild and manipulated populations which apparently favour reproductive isolation. Furthermore, the authors found that seeds from managed in situ and cultivated individuals germinated significantly faster than those from the wild. These results suggest that artificial selection favoured a higher frequency of self-compatible individuals producing seeds with faster germination.

Polaskia chichipe thus appears to be under process of domestication by which people practice artificial selection favouring survival and propagation of desirable phenotypes. In this study we hypothesized that artificial selection favoured the abundance of phenotypes which produce fruits of better quality (larger size, with higher amount of pulp, sweeter flavour, thinner peel, and less spiny) in the managed in situ and cultivated populations (as found in *Stenocereus stellatus*, *Polaskia chende* and *Escontria chiotilla*). Phenotypes with larger fruits and seeds were expected to be significantly more abundant in cultivated populations than in managed in situ populations, and, in turn, more frequent than in unmanaged wild populations. In this form, selection determined a morphological differentiation among populations under different management regimes. The purpose of this study was to test this hypothesis and to determine its meaning in the context of the process of domestication.

2. Materials and methods

2.1. Study area

The study was conducted in the area comprising the territory of the neighbouring villages of San Luis Atolotitlán, Caltepec, and Los Reyes Metzontla, Puebla, in the Biosphere Reserve Tehuacán-Cuicatlán, Mexico (Fig. 1). Annual mean temperature and annual rainfall in the climatological station of Caltepec is 18.2°C and 655.3 mm, respectively (García, 1981). Wild, managed in situ and cultivated populations were included in the analysis. Wild populations were in natural environments where useful products were gathered. Managed in situ populations were those found in vegetation disturbed for agricultural fields, whereas cultivated populations were located in the home gardens of the villages studied. Each group included three populations from which 30 individuals were sampled, respectively (a total of 270 individuals in nine populations). Wild population 1 was located at Cerro Tocotín at elevation 2100 m, within the forested area of San Luis Atolotitlán; wild population 2 was close to San Luis Atolotitlán on the road to Metzontla at elevation 2070 m; and wild population 3 was located on the edge of the territory of Caltepec and San Luis Atolotitlán at 2020 m. Vegetation was categorized as "chichipera" (Valiente-Banuet et al., 2000), in which *Polaskia chichipe* was one of the dominant species. The managed in situ population 1 was located in the valley neighbouring Cerro Tocotín at elevation 2000 m; the managed in situ population 2 was close to the limit between San Luis Atolotitlán and Caltepec at an elevation of 2100 m; and the managed in situ population 3 was in Metzontla at 1940 m. These were open areas for cultivation of maize where spared and enhanced individuals of *P. chichipe* were found. Cultivated population 1 included individuals of *P. chichipe* within home gardens of the village of San Luis Atolotitlán at 1890 m; cultivated population 2 was in the home gardens of the village of Metzontla at 1850 m; and the cultivated population 3 was in the home gardens of Caltepec at 1900 m.

2.2. Ethnobotanical studies

A total of 90 structured interviews were conducted among peasant families of the villages studied (30 interviews per village) to obtain information on uses of *Polaskia* *chichipe*, the perception of its morphological variation by people, the different uses of variants, the forms of management, as well as mechanisms and targets of artificial selection.

2.3. Morphometric studies

In each population, 30 individual plants of reproductive age were sampled over transects 10 m wide per 50 m or more long. Individuals were labelled and 3–5 flowers and fruits were sampled from each. The flowers were transported in jars with 70% ethanol and measured in the laboratory. The fruits were transported in plastic bags in a portable cooler and measured also in the laboratory. A calliper was used to measure flowers and fruits. Pulp and peel were weighed with a precision balance Ohaus, whereas the seeds, after they were cleaned and counted, were weighed in a precision balance Mettler Toledo AG245. Vegetative characters were measured in the field. With the exception of height (measured with a metric stick), and stem diameter (measured with a forestaff), vegetative characters included 5 measures per individual (measured with a calliper). A total of 34 morphological characters were analyzed (Table 1).

2.4. Statistical methods

Patterns of morphological similarity and differences among individuals and populations were analyzed by multivariate methods and one-way ANOVA, similarly to studies of Colunga-García et al. (1996) and Casas et al. (1999b). Multivariate methods included cluster (CA), principal component (PCA) and discriminant function analyses (DFA), in order to visualize the consistency of classification patterns under different methods.

A basic data matrix was constructed with characters as variables and individuals sampled as operational taxonomic units (OTUs). Another data matrix was constructed with the mean values per character per population and the populations as OTUs. The data matrices were standardized by the algorithm $Y' = (Y - a)/b$, where Y' is the standardized value, Y is the real value of that character, a its mean value, and b its standard deviation (Rohlf, 1993). Cluster and principal component analyses were performed by NTSYS 1.8 (Rohlf, 1993), and discriminant function analyses by SYSTAT 7.0 (SYSTAT, 1997). CA was conducted by calculating the dissimilarity among populations through the Euclidean Distance coefficient and by computing an UPGMA analysis (Sneath and Sokal, 1973). For PCA, a correlation matrix between characters was calculated from the standardized matrix, and from it the eigenvectors were computed. The eigenvectors were multiplied by the standardized matrix to plot the individuals and populations in the space of the first two principal components. The DFA was performed from a standardized matrix including the 15 characters with higher contribution to explain the variation in PCA. A multiple analysis of variance (MANOVA) was conducted to test significance of differences between wild,

Table 1
Characters analyzed and eigenvectors resulting from PCA of the morphological variation among wild, managed in situ and cultivated populations and individuals of *P. chichipe*

Characters	Measure	Populations		Individuals	
	Units	PC1	PC2	PC1	PC2
Fruit length	mm	0.930	0.278	0.913	0.208
Fruit diameter	mm	0.909	0.310	0.918	0.210
Number of areoles in fruits	number	0.192	0.699	0.918	0.052
Density of areoles in fruits	number/cm^2	−0.394	0.518	−0.979	−0.030
Fruit weight	g	0.939	0.263	0.835	0.303
Weight of fruit peel	g	0.886	0.310	−0.970	−0.104
Thickness of fruit peel	cm	−0.146	0.842	−0.984	−0.196
Weight of fruit pulp	g	0.954	0.211	0.957	−0.059
Seed weight	g	0.913	0.283	0.912	−0.595
Number of seeds	number	0.927	0.141	0.774	0.878
Pericarpel length	mm	0.443	−0.244	0.971	−0.053
Pericarpel diameter	mm	0.496	−0.453	0.899	0.004
Tepals length	mm	−0.101	0.058	0.975	−0.018
Perianth diameter	mm	0.792	−0.210	0.945	−0.013
Ovary length	mm	0.235	0.029	0.999	0.014
Ovary diameter	mm	0.042	0.365	0.711	1.006
Nectarious chamber length	mm	−0.371	0.425	0.934	0.386
Nectarious chamber diameter	mm	0.431	−0.817	0.990	0.018
Pistil length	mm	0.252	0.296	0.815	0.157
Pistil diameter	mm	0.734	−0.350	−1.008	0.022
Number of stigma lobes	number	0.451	−0.390	0.623	−0.043
Stigma lobes length	mm	0.108	−0.422	−0.928	0.203
Stamens length	mm	0.443	−0.761	0.947	−0.060
Anther length	mm	0.302	−0.076	−1.000	0.038
Anther diameter	mm	−0.588	0.403	−1.007	0.023
Plant height	m	−0.160	−0.260	−0.992	0.066
Stem diameter	cm	0.111	0.489	0.925	−0.034
Number of ribs	number	0.587	0.628	0.725	0.173
Rib width	mm	−0.377	−0.781	0.953	−0.135
Rib depth	mm	0.127	−0.750	0.989	−0.067
Number of spines per areole	number	0.590	−0.401	0.480	0.150
Central spine length	mm	0.776	0.126	0.721	−0.182
Central spine diameter	mm	0.669	0.413	−1.009	0.011
Distance between areoles	mm	−0.113	−0.013	0.381	−0.342

PC = principal component.

managed in situ and cultivated populations considering all morphological characters analysed.

One-way ANOVAs were conducted with non-standardized values of the morphological characters per individual grouped in their populations. Multiple range test were performed by Tukey method at 95% of confidence (Sneath and Sokal, 1973) using SYSTAT 7.0.

3. Results

3.1. Ethnobotany

All 90 of the peasant families interviewed consumed fruit of *P. chichipe* and collected its branches for fuel wood for cooking their meals. In Metzontla, families also used the fuel wood for firing traditional pottery, which was sold commercially and constituted the basis of their economy. Ripe fruits of this plant species were harvested during May and June but dead branches were collected throughout the year. Fruits were consumed fresh, as jams, or other products. Nearly 7% dry the fruits as raisins to consume or to prepare in the traditional sauce called "mole". Some families (~6% of the total interviewed) sell or exchange fresh fruits for maize. Fruits were also consumed as fodder by goats and cows. All people interviewed said that the amount of fruit produced by chichipe depends on the amount of rain during the rainy season prior to the reproductive season (which occurs during the dry season). In some cases fruit production was depleted by freezing temperatures.

Nearly 91% of the persons interviewed indicated that the differences in fruit size among populations were well known, and all of them noted that plants producing large fruits occurred in wild as well as in managed in situ and cultivated populations. But they indicated areas where those plants were more abundant, generally being managed in situ and cultivated populations. People distinguished three pulp colours (red, purple, and dark red). According to people, the most abundant pulp colour was red, only 13% had observed fruits with purple pulp. None of those interviewed distinguished differences in peel thickness. Most people recognized that fruits may be insipid, sour or sweet, and they preferred the sweet ones. Only ~11% of persons interviewed observed differences in the amount of spines on the fruit peel, and they preferred collecting the ones with fewer spines.

Nearly 20% of people interviewed propagated chichipe, primarily by planting young branches (15–20 cm long) cut at the branching point, but also by transplanting complete young individuals. Propagation of branches and young individuals commonly occurred in areas cleared for agriculture, where people enhanced the abundance of chichipe, especially those producing better fruits. These were also areas where people relocated young individuals to facilitate agricultural activities. Sometimes branches and young individuals from fields and home gardens were propagated in the home gardens, although people said that was not common because in the homegardens seedlings and young individuals were continually established from seeds propagated by birds and humans. Furthermore, the space available for new individuals in the homegardens was limited.

Nearly 90% of the people interviewed said that when they cleared land for agriculture, they spared individuals of chichipe, and that this was promoted and warded by the local authorities. When sparing individuals of chichipe, ~28% of people favoured only those individuals more productive which produced better fruits. According to those interviewed younger chichipe were the best for producing better fruits, but this was lost in older individuals. Nearly 18% of people leave all the chichipe plants in agricultural fields, whereas ~44% leave only those plants that do not interfere with agricultural activities. Irrigation, fertilization or prunings of chichipe plants were not practiced.

3.2. Cluster analysis

The phenogram resulting from this analysis (Fig. 2) clustered populations into two main groups. One group was comprised of the wild populations, whereas the other group included the managed in situ and cultivated populations together. Managed in situ and cultivated populations were in turn classified in subgroups.

3.3. Principal component analysis

The principal component analysis comparing the nine populations (Fig. 3) produced results similar to cluster analysis. There was a clear separation of wild populations, managed in situ populations and cultivated populations. Table 1 indicates, according to the eigenvectors of principal component 1, that those variables with the highest contribution to explain the variation have positive values, and they were fruit characters (fruit length, diameter and weight, weight of peel and pulp, as well as seed number and weight), diameter of perianth and length of the central spine. The most relevant variables of principal component 2 were peel thickness (with positive values), and diameter of nectarious chamber and pistil, as well as rib width and depth (all with negative values). In the principal component 3, the most important variables were length of pericarpel and stigma lobes (with positive and negative values, respectively), and diameter of the ovary (with positive value).

Fig. 4 shows the 270 individuals of *P. chichipe* analyzed in the space of the first principal component. Individuals were distributed in a continuous gradient with the wild individuals predominant in the left part of the plot, and cultivated individuals in the right part. The central part of the plot included predominantly individuals from managed in situ populations, but they are mixed with both wild and cultivated individuals. Table 1 lists the eigenvectors resulting from PCA of individual plants,

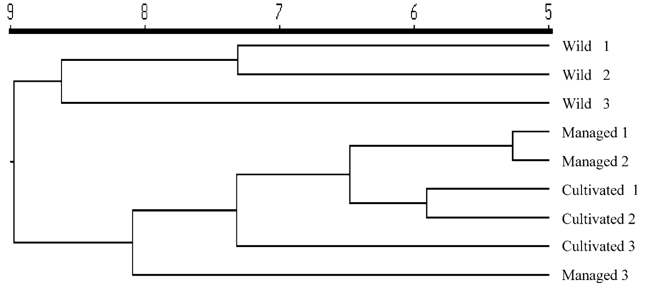

Fig. 2. Classification of populations of *Polaskia chichipe* studied according to cluster analysis of morphological variation.

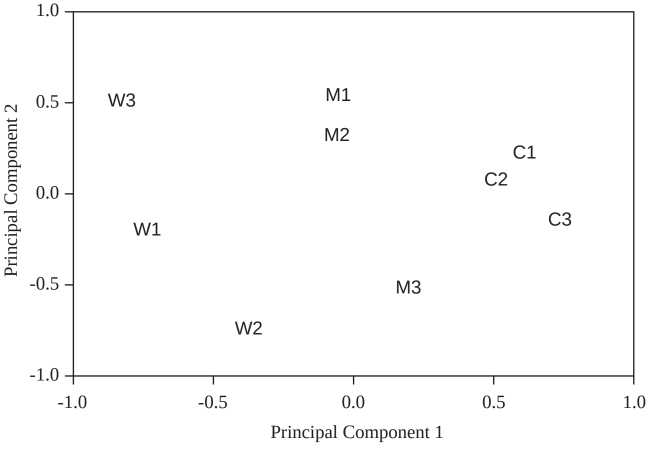

Fig. 3. PCA ordination of the first two principal components describing the morphological variation in nine populations of *Polaskia chichipe* collected from three wild (W), three managed in situ (M) and three cultivated (C) populations at three sites in central Mexico.

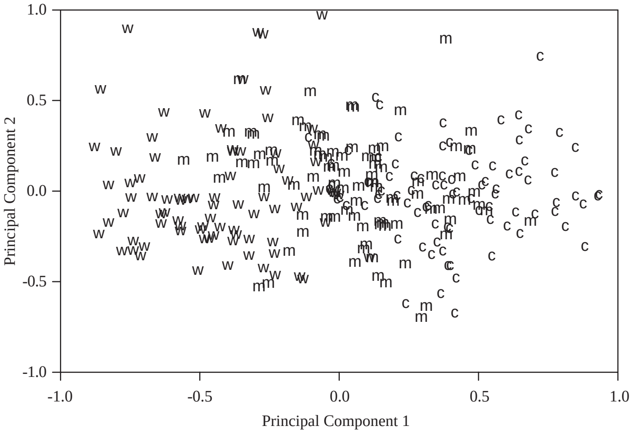

Fig. 4. PCA ordination of the first two principal components describing the morphological variation in 270 *Polaskia chichipe* individuals collected from three wild (W), three managed in situ (M) and three cultivated (C) populations at three sites in central Mexico.

and shows that the same characters explain the majority of the variation in both this PCA and the one described above for populations.

3.4. Discriminant function analysis

DFA and MANOVA scores indicate that there are significant differences between the wild, the managed in situ and the cultivated pre-established groups (Table 2).

Table 2
DFA and MANOVA scores comparing morphological variation of wild, managed in situ and cultivated populations of *P. chichipe*

Discriminant function	Eigenvalue	% variation	Canonic correlation	Wilks' Lambda	*F*	df	*P*
1	2.558	92.06	0.85	0.234	17.964	30,506	0.000
2	0.2206	7.94	0.43				

Table 3
Classification of wild, managed in situ and cultivated individuals of *P. chichipe* according to DFA

Actual group	Predicted group							
	Wild		Managed in situ		Cultivated		Total	
	Num	%	Num	%	Num	%	Num	%
Wild	81	90.00	9	10.00	0	0.00	90	100.00
Managed in situ	9	10.00	70	77.78	11	12.22	90	100.00
Cultivated	1	1.11	21	23.33	68	75.56	90	100.00

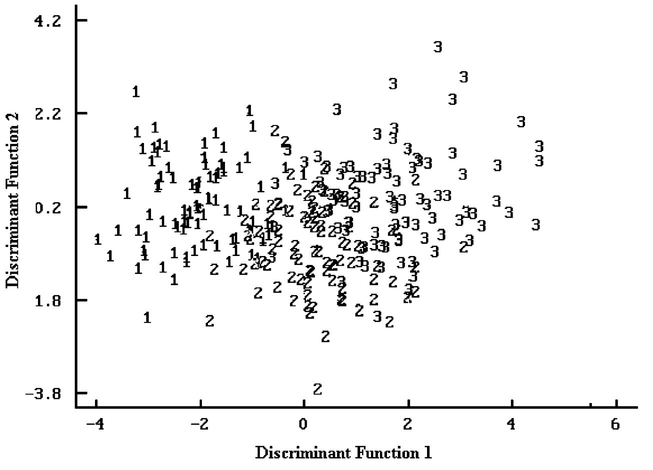

Fig. 5. Classification of individuals of *Polaskia chichipe* according to discriminant function analysis. 1 = wild individuals, 2 = managed in situ individuals, 3 = cultivated individuals.

Nearly 90% of the actual wild individuals are included within the predicted wild group, along with 10% of the actual managed in situ individuals and only 1% of the actual cultivated individuals (Table 3). The predicted managed in situ group is composed of 78% of the actual managed in situ individuals, as well as 10% and 23% of the actual wild and cultivated individuals, respectively. The predicted cultivated group is conformed by 76% of the actual cultivated individuals, as well as 12% of the managed in situ individuals (Table 3). Fig. 5 shows the classification of the individuals of *P. chichipe* resulting from this analysis, indicating a continuous gradient of individuals similar to that resulting from PCA.

3.5. One-way ANOVA

These analyses indicate that there are significant differences in 25 characters (Table 4). However, only 8 show clear differentiation according to the type of population management (fruit length and diameter, weight of fruit, pulp, and peel, seed number and weight, and length of the central spine). There were no significant differences in density of areoles on fruits, length of pistils and anthers, diameter of anthers and stem, number and dimensions of ribs, and distance between areoles.

4. Discussion

At present, *Polaskia chichipe* is a plant resource of economic importance for the local people of the Tehuacán Valley. The archaeological information available (Byers, 1967; MacNeish, 1967; Smith, 1967; Callen, 1967) does not allow for inferences regarding when this plant species was first used and managed by people. However, new reviews of the archaeological material first collected by MacNeish could allow for interesting reinterpretations of the information, as it has occurred with other groups of plants, such as legume trees (Zárate, 2000).

The use and management of *P. chichipe* for its edible fruits by local people led to the development of traditional knowledge on the variation of morphological characters in this species. People used this knowledge for the differential appropriation of the useful products and for the manipulation of natural populations and increased both the quantity and quality of the resources. People perceived variation in fruit size, flavour and thorniness as well as fruit yield among individuals, and they preferred to gather fruits from more productive individuals (see Otero-Arnaiz et al., 2003), with larger fruits, sweet flavour, and less thorniness. Other characters, such as pulp colour other than red and peel thickness, that have been reported as indicators of the quality of the resource in other columnar cacti species (Casas et al., 1997, 1999b, c; Luna and Aguirre, 2001) were not relevant in the case of *P. chichipe*. In different ways people not only gathered but also managed the better phenotypes, in order to increase their numbers in areas where they have a significant impact. These included areas such as those cleared for establishing corn fields, and home gardens. In the cleared areas (the populations managed in situ), current people spared individuals of chichipe, and $\sim$30% of them did it selectively, preferring to maintain the better phenotypes. This appeared not to be a new custom but rather an old cultural practice inherited from previous generations. Some people suggested that the young plants should be spared since they were the most productive and produced the largest fruits. However, it was not possible to conclude that size and productivity were solely a function of age. In contrast, we observed young plants which produced few and small fruits and old plants which produced more and larger fruits. Future studies could test this observation, but the important

Table 4
Mean values ± standard error of morphological characters in wild, managed in situ, and cultivated populations of *Polaskia chichipe*. Results of one-way ANOVA

Character	Wild 1	Wild 2	Wild 3	Man. 1	Man. 2	Man. 3	Cult. 1	Cult. 2	Cult. 3	df.	*F*	*P*
Fruit length	16.35 ± 0.47 A	17.00 ± 0.30 A	17.61 ± 0.47 A	21.56 ± 0.40 B	20.81 ± 0.30 B	21.50 ± 0.36 B	23.93 ± 0.41 C	23.86 ± 0.36 C	22.39 ± 0.31 BC	8 245	57.51	0.000
Fruit diameter	17.22 ± 0.49 A	17.81 ± 0.36 A	18.83 ± 0.41 A	21.62 ± 0.44 B	21.11 ± 0.36 B	21.62 ± 0.35 B	22.99 ± 0.30 BC	23.65 ± 0.32 C	22.34 ± 0.36 BC	8 245	37.11	0.000
Number of areoles	18.25 ± 0.61 AB	18.28 ± 0.49 AB	17.70 ± 0.45 A	17.27 ± 0.54 A	16.59 ± 0.46 A	20.26 ± 0.49 B	18.05 ± 0.54 AB	17.95 ± 0.38 A	18.65 ± 0.58 AB	8 245	3.99	0.000
Fruit weight	2.39 ± 0.20 A	2.94 ± 0.17 A	3.44 ± 0.21 A	6.15 ± 0.28 B	5.65 ± 0.19 B	6.07 ± 0.25 B	7.07 ± 0.21 C	7.73 ± 0.21 C	7.20 ± 0.16 C	8 245	89.03	0.000
Weight of fruit peel	1.33 ± 0.11 A	1.78 ± 0.09 A	2.35 ± 0.18 AB	2.84 ± 0.13 AB	2.64 ± 0.10 AB	2.91 ± 0.11 C	3.45 ± 0.15 C	3.68 ± 0.15 C	3.37 ± 0.08 C	8 243	37.84	0.000
Thickness of fruit peel	1.39 ± 0.07 A	1.18 ± 0.08 B	1.66 ± 0.09 A	1.52 ± 0.08 B	1.46 ± 0.08 AB	1.43 ± 0.07 AB	1.48 ± 0.07 AB	1.42 ± 0.08 AB	1.37 ± 0.09 AB	8 243	2.59	0.009
Weight of fruit pulp	1.10 ± 0.10 A	1.39 ± 0.12 A	1.28 ± 0.09 A	3.27 ± 0.17 B	2.98 ± 0.12 B	3.15 ± 0.15 B	3.62 ± 0.13 C	3.95 ± 0.11 C	3.83 ± 0.11 C	8 243	81.60	0.000
Seed weight	0.22 ± 0.01 A	0.22 ± 0.01 A	0.22 ± 0.01 A	0.31 ± 0.01 B	0.26 ± 0.01 B	0.27 ± 0.01 B	0.37 ± 0.01 C	0.35 ± 0.01 C	0.33 ± 0.01 C	8 240	36.79	0.000
Number of seeds	308.75 ± 11.64 A	317.13 ± 13.09 A	306.18 ± 11.89 A	363.99 ± 16.59 A	349.16 ± 11.18 A	366.02 ± 10.36 A	474.20 ± 11.99 C	448.56 ± 16.50 C	430.83 ± 16.29 C	8 240	21.74	0.000
Pericarpel length	13.47 ± 0.20 A	12.62 ± 0.20 A	13.04 ± 0.25 A	13.05 ± 0.29 A	13.29 ± 0.25 A	14.45 ± 0.21 B	13.40 ± 0.17 A	13.40 ± 0.19 A	13.84 ± 0.19 AB	8 261	5.78	0.000
Pericarpel diameter	10.50 ± 0.10 AB	11.17 ± 0.26 B	10.13 ± 0.15 A	10.82 ± 0.14 AB	10.68 ± 0.11 AB	10.86 ± 0.11 AB	11.14 ± 0.20 B	10.77 ± 0.10 AB	10.62 ± 0.22 AB	8 261	3.80	0.000
Tepals length	16.73 ± 0.28 AB	17.48 ± 0.40 AB	17.65 ± 0.50 AB	17.70 ± 0.43 AB	16.45 ± 0.33 A	17.87 ± 0.32 AB	18.21 ± 0.35 B	16.79 ± 0.30 AB	16.08 ± 0.33 AB	8 261	2.79	0.006
Perianth diameter	19.97 ± 0.53 AB	21.67 ± 0.44 B	18.65 ± 1.08 A	21.65 ± 0.42 B	22.25 ± 0.71 B	21.43 ± 0.57 B	21.96 ± 0.52 B	21.63 ± 0.41 B	25.56 ± 0.57 C	8 261	12.01	0.000
Ovary length	2.58 ± 0.08 A	2.79 ± 0.07 AB	3.12 ± 0.12 B	2.73 ± 0.08 AB	2.62 ± 0.07 A	2.82 ± 0.07 AB	2.80 ± 0.08 AB	2.72 ± 0.07 AB	3.33 ± 0.13 B	8 261	7.22	0.000
Ovary diameter	3.49 ± 0.09 AB	3.91 ± 0.09 B	3.90 ± 0.11 B	3.91 ± 0.26 B	3.77 ± 0.07 AB	3.35 ± 0.06 A	3.77 ± 0.06 AB	3.64 ± 0.08 AB	3.95 ± 0.10 B	8 261	3.19	0.002
Nectarous chamber length	2.65 ± 0.07 AB	2.50 ± 0.04 A	3.36 ± 0.05 C	2.77 ± 0.15 AB	2.74 ± 0.07 AB	2.99 ± 0.08 B	2.60 ± 0.08 AB	2.89 ± 0.07 AB	2.57 ± 0.70 A	8 261	8.04	0.000

Table 4 (*continued*)

Character	Wild 1	Wild 2	Wild 3	Man. 1	Man. 2	Man. 3	Cult. 1	Cult. 2	Cult. 3	df.	*F*	*P*
Nectarous chamber	3.60 ± 0.09	3.91 ± 0.08	3.45 ± 0.14	3.40 ± 0.02	3.65 ± 0.06	3.84 ± 0.06	3.67 ± 0.09	3.72 ± 0.07	3.96 ± 0.09	8	4.67	0.000
	AB	B	AC	A	AB	B	AB	AB	B	261		
Pistil diameter	1.56 ± 0.03	1.79 ± 0.03	1.39 ± 0.04	1.70 ± 0.04	1.68 ± 0.03	1.66 ± 0.03	1.83 ± 0.04	1.68 ± 0.03	1.78 ± 0.04	8	14.89	0.000
	B	C	A	BC	BC	BC	C	BC	C	261		
Stigma lobes	8.60 ± 0.10	8.77 ± 0.12	8.62 ± 0.19	8.30 ± 0.13	8.54 ± 0.11	8.69 ± 0.11	9.02 ± 0.09	8.64 ± 0.15	8.96 ± 0.10	8	3.02	0.003
Number	AB	AB	AB	A	AB	AB	B	AB	B	261		
Stigma lobes length	5.16 ± 0.11	5.12 ± 0.11	4.43 ± 0.14	5.37 ± 0.11	5.25 ± 0.12	9.00 ± 0.13	5.14 ± 0.10	5.13 ± 0.11	4.30 ± 0.10	8	7.25	0.000
	B	B	B	B	B	B	B	B	A	261		
Stamens length	16.03 ± 0.23	16.05 ± 0.24	14.42 ± 0.35	15.31 ± 0.31	15.25 ± 0.30	16.86 ± 0.26	16.00 ± 0.27	16.07 ± 0.23	15.87 ± 0.25	8	6.35	0.000
	BC	BC	A	AB	AB	C	BC	BC	BC	261		
Height	3.18 ± 0.13	3.68 ± 0.14	3.44 ± 0.14	3.12 ± 0.11	3.16 ± 0.12	3.09 ± 0.10	3.36 ± 0.12	3.46 ± 0.15	3.22 ± 0.12	8	2.44	0.015
	AB	B	AB	AB	AB	A	AB	AB	AB	257		
Rib width	23.49 ± 0.90	24.57 ± 0.77	23.43 ± 0.83	21.95 ± 0.69	21.42 ± 0.90	24.63 ± 0.87	21.98 ± 0.88	22.07 ± 0.49	23.08 ± 0.82	8	2.28	0.023
	A	A	A	A	A	A	A	A	A	257		
Rib depth	19.92 ± 0.46	20.71 ± 0.37	19.89 ± 0.44	19.73 ± 0.427	19.82 ± 0.48	21.28 ± 0.48	19.30 ± 0.44	20.00 ± 0.51	20.96 ± 0.60	8	1.91	0.058
	A	A	A	A	A	A	A	A	A	257		
Number of spines	8.51 ± 0.14	8.97 ± 0.10	8.81 ± 0.13	8.78 ± 0.15	8.61 ± 0.14	9.05 ± 0.11	8.81 ± 0.10	8.85 ± 0.10	9.23 ± 0.11	8	3.30	0.001
per areole	A	AB	AB	AB	AB	AB	AB	AB	B	257		
Central spine length	11.88 ±	12.08 ±	13.83 ±	12.29 ±	14.21 ±	14.82 ±	16.05 ±	15.33 ±	16.15 ±	8	6.62	0.000
	A	A	AB	A	AB	AB	B	B	B	257		
Central spine	0.65 ± 0.04	0.57 ± 0.02	0.60 ± 0.02	0.74 ± 0.07	0.69 ± 0.04	0.65 ± 0.03	0.76 ± 0.04	0.63 ± 0.03	0.77 ± 0.04	8	3.69	0.000
Diameter	AB	A	A	AB	AB	AB	B	AB	B	257		

Different capital letters indicate significant differences according to Tukey multiple range tests ($\alpha = 0.05$).

outcome from this study is the observation of artificial selection favouring individuals producing better fruits for humans.

Sparing plants with better phenotypes appears to be the simplest way to increase their abundance. This is a common form of management for perennial plants throughout Mesoamerica (Casas and Caballero, 1996; Casas et al., 1996, 1997; Zárate, 2000), including cacti (Colunga-García et al., 1984; Casas et al., 1997, 1999a; Luna and Aguirre, 2001; Cruz and Casas, 2002; Arellano and Casas, 2003). Additionally, in disturbed habitats, people propagate in situ this plant species by planting branches and transplanting seedlings and young plants. Often the original intent is to relocate individuals to areas where they will not interfere with agricultural activities, but this practice also serves to increase the abundance of the cactus resource. Ultimately, propagation in situ induces the abundance of the better phenotypes in these managed areas. In contrast, propagation of *Polaskia chichipe* in homegardens is not as intense as with other species such as *Stenocereus stellatus* (Casas et al., 1997, 1999b) and *S. pruinosus* (Luna and Aguirre, 2001), which are intensively cultivated by vegetative propagation for commercialization of their fruits. In home gardens, people occasionally propagate branches or young plants of especially good phenotypes of *Polaskia chichipe* found in the field or in other home gardens. Otherwise, young plants are established from seeds dispersed by birds and humans by chance, because garden space for chichipe plants is limited. Casas et al. (1997) documented that individuals of *S. stellatus* are continually replaced within home gardens. In the case of chichipe this does not occur frequently, since it takes longer to replace productive individuals of this species, instead people prefer to replace only old or dead plants. It is possible that in the past cultivation of chichipe was more active, but now, it is restricted to a few spaces available in homegardens.

The morphometric analyses suggested that artificial selection favouring better phenotypes for humans played a significant role in modifying patterns of morphological variation in manipulated populations. Analyses of variance indicated that, although most of the characters differed significantly among populations, only 8 varied according to the management status. Primarily these were fruit characters, the plant part directly subject to artificial selection, with mean values that ranged from smallest in wild populations, intermediate in managed in situ populations and largest in the cultivated populations. These results are similar to findings for other species of columnar cacti (Casas et al., 1999b; Luna and Aguirre, 2001; Cruz and Casas, 2002; Arellano and Casas, 2003) and *Opuntia* spp. (Colunga-García et al., 1984). Measurements of flowers from managed populations, such as dimensions of pericarpel and floral tube, were significantly larger than in wild populations. It is possible that these characters are an indirect result of artificial selection for increased fruit size.

Other characters of *Polaskia chichipe* which vary significantly (Table 4) differ not in relation to the form of management, but could be related to environmental differences. It is clear that those characters without significant effect were related to dimensions of branches, these are expected to be variable since these are exceptionally plastic characters influenced by the environment, and perhaps not by artificial selection.

All multivariate analyses (Figs. 2–5) classified populations and individuals according to the type of management to which they were subject. This reinforces the suggestion that management and human selection favouring abundance of better phenotypes influence the patterns of morphological variation. Principal component and discriminant function analyses (Table 3, Figs. 4 and 5) classified the individuals of *P. chichipe* within a continuous gradient of differentiation with wild and cultivated individuals in the extremes, and DFA and MANOVA (Table 2) resulted in rejection of the null hypothesis that there are no differences among the populations studied according to their management regime. There were overlaps in morphological similarity, mainly among the wild and managed in situ individuals, since the managed in situ individuals derive from wild populations; and among the managed in situ and the cultivated ones, since it is more common that people bring to home gardens plants from the managed in situ populations than from the wild. Overlaps among wild and cultivated individuals were scarce, which indicates that the greatest difference were among these groups.

Overlaps among groups indicate that within a given location it is possible to find individuals with different phenotypes, but also individuals that are morphologically similar to those occurring in other populations. In turn, this information suggests that the morphological variation analyzed is determined not only by environmental differences but apparently also by genetic factors. This is a hypothesis yet to be tested by quantitative genetics approaches. Reciprocal transplantation and common garden experiments would be necessary to evaluate the heritability of the characters. Such information is crucial to analyse the process of domestication of this plant species since domestication is an evolutionary process and in real evolutionary processes only those heritable characters are relevant. Within managed in situ populations, people enhanced the abundance of some phenotypes that occurred naturally in wild populations. This effect was more intense within home gardens. If selection acts on heritable characters, as present information suggests, it would indicate that *P. chichipe* is under the evolutionary process of domestication. Studies on the genetic structure of populations using molecular markers, as well as studies on quantitative genetics could give more information on the genetic aspects of the evolutionary process of domestication of these plants.

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