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Morphological variation and domestication of *Escontria chiotilla* (Cactaceae) under silvicultural management in the Tehuacán Valley, Central Mexico

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Abstract

People of the Tehuacán Valley, Central Mexico utilise the columnar cactus *Escontria chiotilla* for their edible fruits, gathering them in the wild and in silviculturally managed populations. Silvicultural management consists in sparing and enhancing selectively, in disturbed areas, individual trees producing fruits of the better quality for consumption and commercialisation. Fruits of trees in silviculturally managed populations are generally larger (27.23 ± 0.39 cm) and heavier (11.10 ± 0.44 g), with a higher amount of pulp (4.84 ± 0.27 g), and more (532.72 ± 15.60) and heavier (0.78 ± 0.013 mg) seeds than in wild non-manipulated populations (22.62 ± 0.31 cm, 6.44 ± 0.22 g, 2.33 ± 0.11 g, 407.63 ± 20.67, and 0.62 ± 0.015 mg, respectively). Phenotypes of trees producing better fruits were significantly more abundant in manipulated populations than in the non-manipulated ones. Artificial selection appears to be the cause of such differences among populations and, therefore, domestication process of this plant species is seemingly occurring under silvicultural management.

Introduction

Domestication is an evolutionary process in which human selection is the crucial force causing genetic changes in populations of organisms. The resulting domesticated populations generally diverge from their parental wild populations in morphological, physiological and behavioural features favoured by humans (see Harlan (1975), Hawkes (1983), Casas et al. (1997a), Casas and Barbera (in press)). The human cultural area comprised between southern Mexico and northern Central America, known as Mesoamérica (Matos 1994), has been recognized as one of the main centres of domestication of plants in the world (Harlan 1975; Hawkes 1983). The extraordinary diversity of plants and cultures existing in the area, as well as the long history of interactions between indigenous peoples and environments of the region (~12,000 years, according to MacNeish (1992)), determine an ideal scenario for studying how processes of domestication are currently taking place and how they could have operated in the past.

Cacti are native of the New World, and their main distribution area are arid and semiarid zones (Bravo-Hollis 1978; Rzedowski 1993; Casas and Barbera (in press)). In Mexico such zones conform nearly two thirds of the territory (Toledo and Ordñez 1993). Since prehistory, ancient indigenous peoples of the Mexican Mesoamérica as well as those occupying the northern territory of Mexico, the cultural area known as Aridoamérica (see Nárez (1994)), utilised cacti as food, medicines, tools, and for religious and magic practices ((MacNeish 1967; Smith 1967; Bravo-Hollis 1978; Casas and Barbera (in press))). Currently, subsistence of indigenous peoples in these areas is based on seasonal agriculture, raising of goats, and gathering of a broad spectrum of plant resources, among them cacti (Felger and Moser 1976; Casas et al. 2001; Casas and Barbera (in press); Hammer 2001). Casas and Barbera (in press) recently recorded that 118 from a total of 420 species of cacti are utilized by peoples in the Mexican Mesoamérica. Among them, the most important are species of the genus *Opuntia* and columnar cacti of the tribes Pachycereeae and Cereeae.

Fruits of all these species are edible, and their stems and fruits are also used as fodder. Their wood is utilized for house and fence construction and, in the case of *Stenocereus stellatus* (Pfeiffer) Riccobono and *Polaskia* spp., wood is also a good fuel for pottery. Some species are also cultivated as living fences and for protection of soil erosion (Casas et al. 1999a; Hammer 2001).

Gathering of useful products is a common practice in wild populations of *Opuntia* and columnar cacti species, but wild populations of some species are also managed in situ under silvicultural methods (Casas et al. 1999a). Through this form of management, people spare individuals of useful plant species when clearing the land for agriculture and for other purposes (Casas et al. 1999a). In some species selection is even more specific, and people select for sparing only those phenotypes, within a given plant population, presenting the best qualities for utilisation. In the case of columnar cacti, people commonly select phenotypes producing more, larger and sweeter fruits, with thinner peel presenting fewer spines (see examples in Casas et al. (1997b, 1999a, 1999b)). People not only spare the favourable plants but they also may enhance their numbers through vegetative propagation within the same cleared area (Casas et al. 1997b, 1997a).

In the Tehuacán-Cuicatlán Valley, Central Mexico, our study area, there are 20 wild species of columnar cacti, 12 of them are managed in situ under silvicultural methods, whereas 8 species are cultivated in home gardens, plantations, and living fences (Casas et al. 1999a). For cultivating these plants, people generally select those individuals showing desirable characteristics from wild populations or other cultivated stands. Then, people obtain vegetative parts for propagating the selected plants in their home gardens in order to make easier the access to their products. Individual plants in home gardens may also derive from seedlings tolerated by people, and those that became established in the plot from seeds dispersed through bird, bat, or human faeces. Since people do not recognise the fruit quality of these plants based only on their vegetative characteristics, they decide to leave or remove the established individuals of columnar cacti after the plants produce fruits for the first time (see Casas et al. (1997b, 1999a, 1999b)).

Escontria chiotilla (F. A. C. Weber) Rose is a columnar cactus distributed in arid and semiarid regions of Central Mexico, particularly in parts of the Balsas river basin of the states of Guerrero, Michoacán, Oaxaca, Morelos, and Puebla. It is also distributed in the Papaloapan river basin, particularly in the Tehuacán-Cuicatlán Valley, in the states of Puebla and Oaxaca (Bravo-Hollis 1978). According to Bravo-Hollis (1978), Arias et al. (1997), these plants are 7 m height, with a short defined stem derived in straight branches which become twisted when old. The branches have 7–8 ribs with elliptic areoles placed very close from each other, with 10–15 radial short spines (the longest spines are the central ones which are 7 cm long in average). Flowers are 3 cm long, generally growing close to the top of the branches, having distinct light yellow tepals, with a scaly (spine-less) pericarpel. Fruits are 5 cm in diameter, with a red peel, but due to the presence of scales they are grey-reddish in appearance. Their pulp is red, edible, with numerous small black seeds. According to Oaxaca and Casas (unpublished data), blooming is particularly intense from April to June, but production of flowers is continuous throughout the whole year in all populations. Production of flowers and fruits, according to local people, starts nearly 10 years after seed germination.

This species grows better in plain terrains or slightly pronounced slopes, and is particularly abundant in perturbed areas. It is naturally associated with other giant columnar cacti such as *Pachycereus weberi* (J. Coulter) Backeb. and *Neobuxbaumia tetetzo* (F. A. C. Weber) Backeb., as well as other trees characteristic of thorn-scrub and tropical deciduous forests of the area (Valiente-Banuet et al. 2000). Vegetation where *E. chiotilla* is dominant is called ''jiotillal'' (Rzedowski 1978; Valiente-Banuet et al. 2000). In the Tehuacán-Cuicatlán Valley, *E. chiotilla* is one of the dominant species in the tropical deciduous forests located at the southeast of the region, between Coxcatlán, Puebla and Cuicatlán, Oaxaca. In this area, the species can be found in the wild but also in managed in situ populations which are recurrently perturbed and manipulated under silvicultural techniques. Hammer (2001) reports that *E. chiotilla* is occasionally cultivated in Mexico, although this was not the case in the Tehuacán Valley.

E.chiotilla has been utilized by local people for several thousands of years. MacNeish (1967), Smith (1967) reported archaeological remains of this plant species within caves occupied by humans in strata of approximately 7,000 years old, according to these authors. But through archaeological remains it is not possible to know whether *E. chiotilla* was managed by people. However, Casas et al. (1997a, 1999a) have reported that current peoples practise silvicultural management of wild populations in situ in order to increase both quality and quantity of fruits, and that some of these practices could have started centuries ago. At present, fruits are directly consumed by gatherers or commercialised at regional level (Casas et al. 1999a).

Recent studies with other columnar cacti species in the area have demonstrated that artificial selection has determined significant changes in patterns of morphological variation in populations under silvicultural management as well as in cultivated populations compared with non-manipulated wild populations. Relevant examples of such effect have been documented by Casas et al. (1998, 1999a) with *Stenocereus stellatus*, and Luna (1999) with *S. pruinosus* (Otto) F. Buxb. These authors demonstrated that in both cases phenotypes producing larger and sweeter fruits, with thinner peel presenting fewer spines, more and larger seeds, and with pulp colour other than red (the characteristic fruit colour in wild populations) were predominant in silviculturally managed and cultivated populations, whereas these phenotypes were scarce in wild populations.

Considering that *E. chiotilla* is being manipulated under silvicultural management, we hypothesised that local people of the Tehuacán Valley are practicing artificial selection on this plant species under silvicultural management in situ of wild populations, favouring an increase in numbers of individuals with desirable characteristics, such as those mentioned above. The purpose of this study therefore was to test such hypothesis, by documenting forms of use, management, and perception of morphological variation of *E. chiotilla* by local people; by identifying the plant parts that are targets of artificial selection, the direction of such selection and the mechanisms through which the artificial selection operates; and by comparing patterns of morphological variation of wild and silviculturally managed populations.

Materials and methods

Study area

The Tehuacán-Cuicatlán Valley is located at the southeast of the state of Puebla and the northwest of the state of Oaxaca in Central Mexico (Figure 1), having a total area of approximately 10000 km^2. This region has arid and semiarid zones, covering a range between 1220 to 3000 m, with 300 to 900 mm of rain per year, and mean temperatures of 14 to 26°C (García 1988).

This region constitutes a reservoir of a high biological diversity. It has been reported that in the Valley occur nearly 3000 plant species, 30% of them being endemic to the region (Dávila et al. 1993) 29 types of plant associations (Valiente-Banuet et al. 2000); more than 100 species of birds (Arizmendi and Monteros 1996); and 34 species of bats (Rojas-Martínez and Valiente-Banuet 1996; Valiente-Banuet et al. 1996). The human cultural richness is also high. It has been reported that 7 indigenous ethnic groups, as well as Black and Mestizo peoples occupy the territory of the region (Casas et al. 2001). Because of this situation, in 1998 the Mexican Government decreed the area as the Biosphere Reserve Tehuacán-Cuicatlán.

Populations studied

A total of 3 wild and 3 silviculturally managed populations of *E. chiotilla* were studied. Wild populations are located approximately 10 km at the southeast of the village of Coxcatlán, within communal lands of the villages of San Rafael and Guadalupe Victoria, municipality of Coxcatlán (Figure 1). This area covers nearly 150,000 m^2, mainly constituted by alluvial soils. Vegetation occurs as patches of different dimensions separated by perturbed areas. It is conformed by tropical deciduous forest with a significant presence of plant species characteristic of thorn-scrub forest, and one of the main constituents is *E. chiotilla*. Other common species in the area are: *Acacia cochliacantha* Humb. & Bonp. ex Willd., *A. constricta* Benth., *Agave macrocantha Zucc*., *Bursera morelensis* Ramírez, *B. arida* (Rose) Standley, *B. aloexylon* Engelm., *Ceiba parvifolia* Rose, *Cyrtocarpa procera* Kunth, *Gyrocarpus mocinnoi* Espejo, *Ipomoea arborescens* G. Don, *Mimosa luisana* Brandegee, *Myrtillocactus geometrizans* (C. Martius) Console, *Neobuxbaumia tetetzo*, *Pachycereus weberi*, *P. hollianus* (F. A. C. Weber) F. Buxb., *Stenocereus stellatus*, *S. pruinosus*, and *Zizyphus amole* (Sessé & Mociño) M. C. Johnston. The wild population I is located in the patch of vegetation just in front of the Coxcatlán cave explored by MacNeish (1967) (Figure 1). The wild population II is located approximately 2 km apart from the wild population I, following the

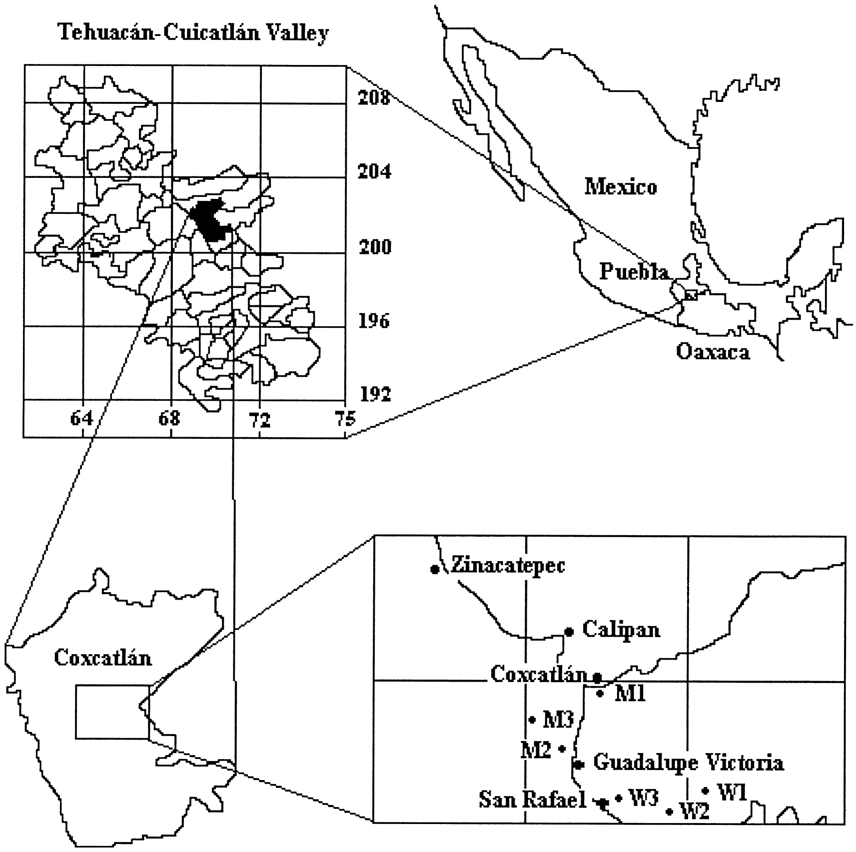

Figure 1. The study area. The Tehuacán-Cuicatlán Valley and the populations of *Escontria chiotilla* studied

river in direction to the village of San Rafael, whereas the wild population III is 2 km apart from the wild population II, close to the village of San Rafael.

Silviculturally managed populations are located close to the alluvial valley of the Río Salado. This area in some places is destined to cultivation of sugar cane, maize, and beans, but in the area between Coxcatlán and San Rafael is occupied by communities of tropical deciduous forests perturbed by recurrent cycles of cultivation of maize, abandoning, and re-clearing of vegetation. Plant communities in this area are characterized by extraordinary high densities of *Escontria chiotilla*, *Myrtillocactus geometrizans*, and *Stenocereus stellatus*, which are seasonally gathered for consumption by local people or for commercialisation in regional markets. The reason of the abundance of these species is that, according to local people, individuals of these species are spared and sometimes enhanced when terrains are cleared. These are the silviculturally managed populations. Managed population I is 3 km apart from the village of Coxcatlán near the road to San Rafael (Figure 1); managed population II is 7 km apart from Coxcatlán, close to the village of Guadalupe Victoria; and managed population III is 2 km apart from the managed population I and nearly 3 km apart from the managed population II. These populations are patches of secondary vegetation separated from each other by roads and completely cleared fields for cultivation of sugar cane.

Ethnobotanical studies

Ethnobotanical studies on forms of use and management of *Escontria chiotilla* were conducted among people of the villages of San Rafael and Coxcatlán. A survey of structured interviews was conducted among people of 20 households of the village of San Rafael (nearly 20% of the total number of households), which were randomly chosen, as well as 8 interviews conducted among people commercialising *E. chiotilla* in the market of the village of Coxcatlán. Interviews included questions on perception and human cultural meaning of morphological variation, forms of use and management of variants, and data on commercialisation, in order to identify and document processes of artificial selection, their targets and operation mechanisms.

Morphometric studies

Transects of 10 m wide and 50 or more m long were conducted in order to sample at least 20 reproductive individuals of *E. chiotilla* per population. Individuals sampled were labelled in order to easily identify them in later visits. A total of 3 to 5 flowers and fruits were collected per individual sampled. Flowers were preserved in 70% ethanol whereas fruits were transported in plastic bags within a portable cooler. Measuring of flower and fruit parts (Table 1) was conducted in the laboratory by a calliper, whereas weight of complete fruits, peel and pulp were weighed by a precision balance. Vegetative parts were measured in the field. Plant height was measured by a metric extensible stick, the main trunk diameter (just below the first branches), and branch diameter (of 5 branches) were measured by a forestaff. Number of ribs was counted in the middle part of 5 branches per individual. Width and depth of 5 ribs, distance between 5 pairs of areoles, and length of 5 central spines in areoles were measured with a calliper, always at the middle part of branches, and, also at this position, the number of spines in 5 areoles was counted.

A total of 29 morphological characters of flowers, fruits and vegetative parts were analysed (Table 1). Fruit characters were chosen to analyse possible phenotypic differences in features directly subject to artificial selection, whereas characters of flowers and vegetative parts were included to compare general patterns of morphological variation and to analyse their correlation with plant parts directly subject to artificial selection. Comparison of variation in these characters was expected to give information about variation associated to human manipulation and that related with environmental differences between populations.

Table 1. Morphological characters of *Escontria chiotilla* analysed.

Character	Units of measure
Fruit length	mm
Fruit diameter	mm
Fruit weight	g
Weight of fruit peel	g
Weight of fruit pulp	g
Total weight of seeds	g
Thickness of fruit peel	mm
Mean weight per seed	mg
Total number of seeds in fruits	number
Length of flower pericarpel	mm
Diameter of flower pericarpel	mm
Perianth length	mm
Ovary length	mm
Ovary diameter	mm
Style length	mm
Number of stigma lobes	number
Length of stigma lobes	mm
Length of nectar chamber	mm
Diameter of nectar chamber	mm
Anther length	mm
Anther width	mm
Height	m
Stem diameter	cm
Number of ribs	number
Rib width	cm
Rib depth	cm
Number of spines per areole	number
Spine size	cm
Distance between areoles	cm

Data analyses

Data analyses comprised multivariate statistical methods, including cluster analysis (CA), principal component analysis (PCA), and discriminant function analysis (DFA), in order to classify both individuals and populations studied according to their general morphological similarity. The purpose was to explore whether both individuals and populations silviculturally managed and the non-manipulated wild ones were morphologically different and which characters determine such differences. The three approaches were performed in order to corroborate consistency of the patterns. PCA was also directed to identify the variables with a higher contribution to explain the patterns of variation, whereas DFA tested the significance of multivariate morphological differences. These analyses were performed through the Numerical Taxonomy System (NTSYS) 8.0 (Rohlf 1993). One-way analyses of variance (ANOVA) were conducted in order to test the null hypothesis that there are not differences in morphological characters between the populations studied. These tests also aimed at evaluating trends of variation and degrees of differentiation in the characters analysed and were conducted by SYSTAT 7.0 (Smith 1967).

Except for the individual plant heights, a total of 3 to 5 measures were recorded per character per individual, and their average was considered per individual when variation was analysed among individuals (data matrix of 29 variables per 186 individuals), and per population when variation was analysed among populations (data matrix of 29 variables per 6 populations). Since the analysis included variables of different type and scale of measure, the resulting data matrices were standardized by the function $\mathbf{Y}' = \mathbf{Y}' - \mathbf{a}/\mathbf{b}$, where $\mathbf{Y}'$ is the standardised value of a given morphological character, $\mathbf{Y}$ is the real value of such character, $\mathbf{a}$ is the mean value of the character, and $\mathbf{b}$ is the standard deviation. For performing PCA, correlation matrices among variables were calculated by the Pearson correlation coefficient (Sneath and Sokal 1973), and from these matrices the Eigen-vectors were in turn computed. Eigen-vectors of the first two principal components were projected and plotted. DFA was performed from a matrix composed by all the wild individuals grouped on one hand, and all the managed individuals grouped on the other, as well as the most meaningful variables for explaining the variation resulting from the PCA (fruit length, diameter and weight; peel, pulp, and mean weight per seed; number of seeds, ovary length and diameter, nectar chamber length and diameter, anther width, and spine size). CA was performed by calculating a dissimilarity matrix between populations through the Euclidean Distance coefficient, which was then analysed by the UPGMA method (Sneath and Sokal 1973).

One-way ANOVAs were performed with non-standardised data, testing significance (95% of confidence) among the populations studied. Multiple range tests were conducted by Tukey's method (95% of confidence).

Results

Ethnobotany

According to the survey conducted, all the families interviewed utilize *E. chiotilla* for their edible fruits, which are consumed fresh, but also are used for preparing flavoured water and ice cream, jellies and sweets, products that are regionally commercialised between April and July, having a great demand. Fruits are obtained by gathering in both wild and silviculturally managed populations throughout the whole year, but especially between April and July, when fruit production is higher. Also, all people interviewed indicated that neither flower buds nor stems and seeds are consumed, as it occurs with other columnar cacti such as the ''tetecho'', *Neobuxbaumia tetetzo* and the ''xoconostle'', *Stenocereus stellatus*, as reported by Casas et al. (1997b, 1999a). Nearly 25% of the families interviewed utilize the dry branches of *E. chiotilla* as fuel wood, and it is considered as ''fuel of good quality'', utilized exclusively for cooking food. Approximately 6% of the total of households interviewed utilize fresh branches for feeding domestic animals (mainly goats and cows). They first remove the spines with a machete, and sometimes they also cut the branches in pieces. They do not bring the branches to their houses, but feed the animals in this form in the field.

People generally indicated that for gathering fruits they take into account their size, preferring to gather the largest ones. They indicated localities where it is possible to find a higher abundance of phenotypes with larger fruits, among them the Río Salado alluvial Valley, which was studied in this research. These sites are recognised as places where gathering of fruits of *E. chiotilla* is particularly intense. Some persons (6% of people interviewed) said to have observed that young trees produce larger fruits than the older ones, but most people disagreed with this opinion.

Most people (nearly 80% of people interviewed) informed that they have observed different colours of fruit pulp. They mentioned that the predominant pulp colour is red in both wild and silviculturally managed populations. This was the only colour recorded in this study. However 30% of the people interviewed said to have observed fruits with pink and orange pulp, whereas 18% said to have consumed fruits with white and yellow pulp, and 12% declared to have consumed fruits with purple pulp. According to people, pulp colours different than red occur in low numbers in general, but they are more common in areas where *E. chiotilla* is more abundant and produce larger fruits (the silviculturally managed populations). Fruits with pulp white, yellow and orange show a light green peel when mature, whereas fruits with pulp red, purple and pink show a red peel when mature. Although 6% of people interviewed considered that small fruits are the sweetest ones, most of the people opined on the contrary. People distinguish between sweet (''dulces'') and soar (''aciditos'') fruits, and both types commonly occur within a same area. Nearly 12% of people interviewed considered that red fruits are the sweetest ones, but the rest considered that the colour of the pulp is independent from the flavour of the fruit. All people interviewed said not to have observed differences in peel thickness, and this character, therefore, appears not to be relevant in the perception of quality of fruits by local people.

In the municipal market of Coxcatlán, fruits of *E. chiotilla* are commercialised between April and July. In July, 2000, 1 kg of fruits of this species had a value of ~2 U. S. dollars.

Most of the people interviewed (~90%) indicated that *E. chiotilla* reproduces exclusively by seeds, but ~10% of the people interviewed informed that they have propagated vegetatively this plant by planting their young branches (50–70 cm long, cut in the branching point) in erect position in the managed populations. None of the persons interviewed had planted *E. chiotilla* in their home gardens since, as they said, ''there are many plants near their homes, and the plant grows very slowly''. They prefer to utilize plants already established in wild and managed in situ populations.

In relation to management in situ of *E. chiotilla*, nearly 12% of people interviewed said that they cut all the trees of this species when they clear vegetation for establishing an agricultural field. However, 28% of people said that they spare all the trees of this species, whereas 60% of people said that they selectively spare those trees producing the best fruits (the largest, the sweetest, and, when found, pulp colours different than red).

Morphological variation: cluster analysis

In the phenogram of Figure 2, wild populations appear grouped in the upper part, whereas all the silviculturally managed populations are grouped in the lower part. The only exception is the managed population I which, according with the analysis, appears as morphologically intermediate with respect to the wild and managed groups.

Morphological variation: principal component analysis

Figures 3 and 4 respectively show the projection of individuals and populations of *E. chiotilla* analysed in the space of the two first principal components. In Figure 3, individuals are grouped within a continuous gradient, but it can be observed that most of the wild individuals are in the left part of the plot, whereas most of the silviculturally managed individuals are in the right one. There is a group of individuals composed by both wild and managed trees at the central part of the plot. These groups of individuals are clearly classified by the principal component 1 which, according to the resulting eigenvalues, accounts 37% of the variation. The characters with the highest contribution in the classification at component 1 are dimensions and weight of fruits, peel, pulp, and seeds, as well as number of seeds and dimensions of the ovaries, all of them with positive values (Table 2). In the principal component 2 (16% of the variation), the dimensions of the nectar chambers and ovaries were the most relevant characters (Table 2). Figure 4 shows the classification of the populations studied. The wild populations are clearly grouped at the left of the plot, whereas the silviculturally managed populations are grouped at the right. As in the cluster analysis, the managed population I occupies an intermediate position between wild and managed groups, and its position is influenced by the second principal component. Table 3 indicates that when morphological variation is analysed among populations, in the principal component 1 (accounting for the 41% of the variation) the same characters as in the analysis of the individuals are relevant. But in addition style length, perianth length and stem diameter have significant contribution. In the principal component 2 (accounting for the 14% of the variation) the most relevant characters were rib dimensions, spine size and mean weight per seed.

Morphological variation: discriminant function analysis

As indicated in Table 4 differences between wild and managed groups of individuals are highly significant. Table 5 shows that most of the real wild individuals (81%) were classified within the predicted wild group, whereas 19% of them were morphologically similar to those of the predicted managed group. Similarly, most of the real individuals of the managed populations (78%) were grouped within the predicted managed group, whereas 22% of them were morphologically similar to those of the predicted wild group.

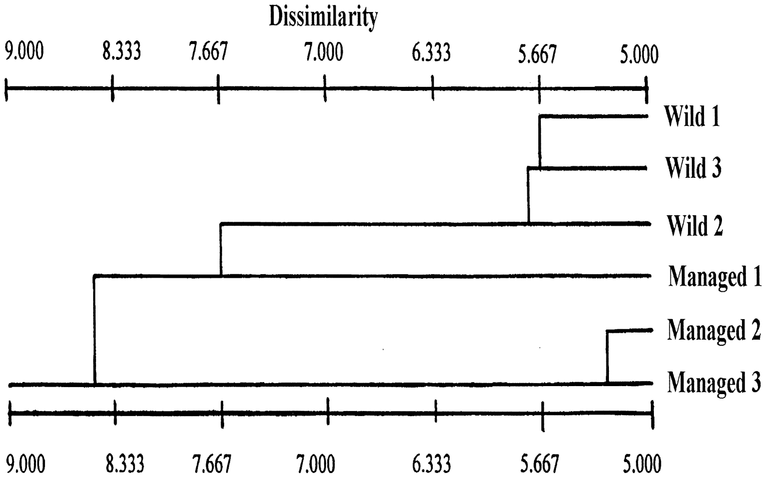

Figure 2. Phenogram resulting from the cluster analysis of morphological variation among wild and silviculturally managed populations of *Escontria chiotilla*

Correlation analysis

Table 6 shows that the highest correlation occurs among all the fruit characters analysed with the only exception of peel thickness, which had low correlation with the rest of the characters of the plant studied.

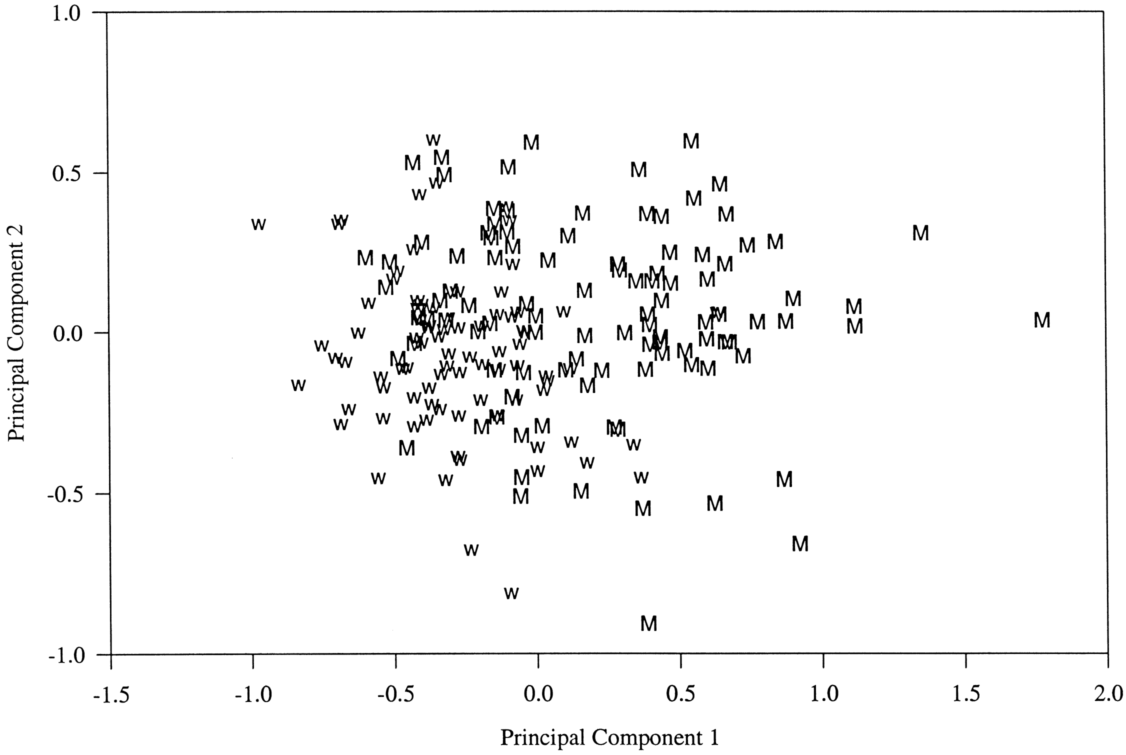

Figure 3. Principal component analysis. Classification of wild (W) and silviculturally managed individuals (M) of *Escontria chiotilla* according to their morphological similarity

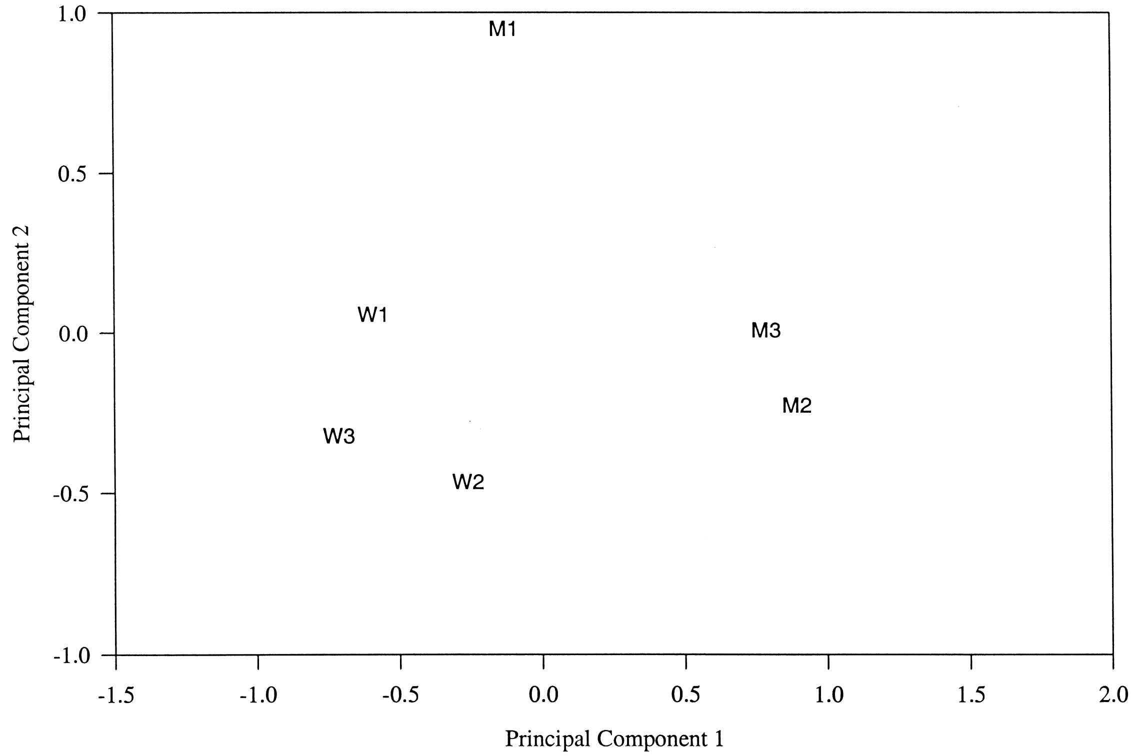

Figure 4. Principal component analysis. Classification of wild (W) and silviculturally managed (M) populations of *Escontria chiotilla* according to their morphological similarity

Correlation was also high among size of ovary, pericarpel and fruits, as well as among the dimensions of ribs. It is notorious the general low correlation between plant size (height and diameter of the trunk) and all the morphological characters analysed.

Morphological variation: one-way analyses of variance

Table 7 shows that dimensions of fruits, peel thickness, and number, dimensions and mean weight per seed in the managed populations were significantly higher than in wild populations. Also, the managed populations have significantly larger pericarpel and ovary, as well as more robust stem and branches than the wild oneas.

Discussion

Escontria chiotilla is a plant resource that has been utilized by humans of the Tehuacán Valley since prehistoric times (MacNeish 1967; Smith 1967) and continues being utilized by current people, who make direct use of their useful products and commercialise them to obtain monetary incomes. Fruits are at present the main useful parts and, consequently, the main targets of artificial selection. People distinguish differences in fruit size, flavour, and pulp colour within a single population, and among different populations. They recognise that larger fruits are more common in the ''jiotillales'', where individuals of *E. chiotilla* are particularly dense because of a history of silvicultural management by people. For consumption people prefer the larger and sweeter fruits, and these are the main criteria for selective sparing of individuals during clearing of land. In addition, people prefer to spare individuals producing pulp colour different than red, a character that, although apparently is not related with fruit size or flavour, is scarce and represents a cultural value related with its rareness. These criteria in general coincide with those documented with other cacti species subject to processes of domestication such as

Table 2. Eigen-vectors resulting from PCA of morphological variation among wild and silviculturally managed individuals of *Escontria chiotilla*.

Character	PC1	PC2	PC3
Fruit length	0.91631	0.16886	0.00905
Fruit diameter	0.92148	0.03111	0.01481
Fruit weight	0.94841	0.12442	0.02797
Weight of fruit peel	0.92604	0.05469	0.06709
Weight of fruit pulp	0.88679	0.16740	−0.00323
Total weight of seeds	0.77909	−0.08227	−0.10604
Thickness of fruit peel	0.00174	0.30112	0.42267
Mean weight per seed	0.52005	0.21141	−0.13271
Total number of seeds	0.70363	−0.12412	−0.09865
Length of flower pericarpel	0.45743	0.06859	0.17795
Diameter of flower pericarpel	0.20995	−0.23958	0.49239
Perianth length	0.28482	−0.09833	0.42074
Ovary length	0.60000	−0.08149	0.24715
Ovary diameter	0.17892	6.00000	0.39181
Style length	0.17946	0.10641	−0.13606
Number of stigma lobes	0.14825	−0.16802	−0.28469
Length of stigma lobes	0.12287	−0.43942	0.18817
Length of nectar chamber	−0.00701	−0.65667	0.10622
Diameter of nectar chamber	0.07296	−0.65947	0.18454
Anther length	0.15106	−0.58173	0.10892
Anther width	−0.19803	−0.67728	−0.07808
Height	0.06502	0.11524	0.34704
Stem diameter	0.16061	0.16543	−0.00230
Number of ribs	0.00561	0.03425	0.04549
Rib width	0.44787	−0.11725	−0.38329
Rib depth	0.39143	−0.28986	−0.46479
Number of spines per areole	−0.13546	−0.08747	−0.43067
Spine size	0.04964	−0.27139	−0.63704
Distance between areoles	0.29448	−0.24108	−0.35203

Stenocereus stellatus (Casas et al. 1998, 1999b), *S. queretaroensis* (Pimienta-Barrios and Nobel 1994), *S. pruinosus* (Luna 1999), and *Opuntia* spp. (Colunga et al. 1986).

Both gathering of fruits in wild populations and silvicultural management are currently important interactions between people and *E. chiotilla*. Silvicultural management occurs when people clear vegetation for cultivation of crop plants or for establishing home gardens. Most of the people spare the individuals producing better fruits by sparing only the good phenotypes and eliminating the undesirable ones. Such practise involves, therefore, artificial selection. People do not cultivate *E. chiotilla* at present and there is no evidence that this plant had been cultivated within home gardens or in plantations as in the case of other columnar cacti, such as *Stenocereus*, *Pachycereus*, *Myrtillocactus*, and *Polaskia* species occurring in the area (Casas et al. 1997b, 1999a; Luna 1999). According to local people, the restricted cultivation of this plant is due to the difficulties for vegetative propagation and because of the slow growth characterising this species. Given these characteristics, silvicultural management of wild populations is particularly important in *E. chiotilla*, because it substitutes the need of cultivating this plant to increase both the quantity and quality of fruits. In this sense, the silviculturally managed populations play a role similar to home gardens and plantations.

Statistical analyses consistently demonstrate that wild and silviculturally managed populations are morphologically different. In managed populations, individuals producing larger and heavier fruits, with a higher amount of pulp, and more and heavier seeds are more abundant. These characters were determinant to group both individuals and populations according to their form of management. The multivariate classification analyses showed a clear tendency to group wild individuals separated from the managed individuals. DFA demonstrated that these

Table 3. Eigen-vectors resulting from PCA of the morphological variation among wild and silviculturally managed populations of *Escontria chiotilla*.

Characters	PC1	PC2	PC3
Fruit length	0.92280	0.31819	0.17576
Fruit diameter	0.92999	0.32825	0.04168
Fruit weight	0.95428	0.23059	0.15451
Weight of fruit peel	0.95615	0.21385	0.13624
Weight of fruit pulp	0.94680	0.25536	0.16505
Total weight of seeds	0.51631	0.82140	−0.21575
Thickness of fruit peel	0.94483	−0.06393	0.03764
Mean weight per seed	0.61649	0.71441	0.24058
Total number of seeds	0.62798	0.58643	−0.49159
Length of flower pericarpel	0.77654	0.09127	−0.42721
Diameter of flower pericarpel	0.63172	−0.31982	0.03798
Perianth length	0.86354	−0.40598	0.09691
Ovary length	0.80590	−0.07410	0.50227
Ovary diameter	−0.21319	0.14579	0.39504
Style length	0.89526	−0.35976	−0.11100
Number of stigma lobes	−0.28833	0.68245	−0.62310
Length of stigma lobes	−0.57896	0.35827	0.14733
Length of nectar chamber	−0.72600	0.15455	−0.60754
Diameter of nectar chamber	−0.62036	0.49304	0.43990
Anther length	−0.09690	0.65401	−0.04454
Anther width	−0.93540	0.19736	0.05352
Height	0.22322	−0.79612	−0.29192
Stem diameter	0.87859	−0.08239	−0.19426
Number of ribs	0.23861	−0.14966	−0.83581
Rib width	0.55896	0.80770	−0.07713
Rib depth	0.01842	0.97184	−0.20893
Number of spines per areole	−0.70480	0.42941	0.16497
Spine size	−0.38569	0.90134	0.02959
Distance between areoles	−0.00871	0.68927	0.30762

Table 4. Scores of DFA among wild and silviculturally managed populations of *Escontria chiotilla*, based upon 13 morphological characters.

Discriminant function	Eigen-value	Relative percentage	Canonical correlation	
1	0.6626	100.00	0.6313	
Derived function	Wilks Lambda	X^2	d. f	Significance
0	0.6015	68.8825	13	0.0000

groups of individuals are significantly different. This analysis also showed that some wild individuals (~19%) have a similar phenotype to that predominant in the silviculturally managed populations, and that some individuals of the managed populations (~22%) have a similar phenotype to that predominant in the

Table 5. Classification of wild and silviculturally managed individuals of *Escontria chiotilla* based upon their morphological characters according to DFA.

Actual group	Predicted group					
	Wild Num.	%	Managed Num.	%	Total Num.	%
Wild	47	81.03	11	18.97	58	100.00
Managed	19	22.09	67	77.91	86	100.00

Table 6. The highest correlations among the morphological characters of *Escontria chiotilla* analyzed.

Character												
1	2	3	4	5	6	9	10	13	22	23	25	26
1.00												
0.86	1.00											
0.91	0.95	1.00										
0.88	0.92	0.95	1.00									
0.85	0.88	0.96	0.83	1.00								
0.69	0.62	0.65	0.64	0.60	1.00							
0.59	0.59	0.58	0.60	0.49	0.81	1.00						
0.43	0.27	0.32	0.37	0.25	0.34	0.32	1.00					
0.57	0.40	0.49	0.50	0.43	0.46	0.41	0.58	1.00				
0.03	0.08	0.06	0.08	0.06	−0.08	−0.02	0.08	0.09	1.00			
0.10	0.19	0.16	0.12	0.16	−0.03	−0.02	−0.04	0.01	0.35	1.00		
0.30	0.34	0.34	0.33	0.33	0.26	0.29	0.12	0.18	0.07	0.30	1.00	
0.23	0.29	0.26	0.28	0.23	0.28	0.32	0.14	0.16	0.01	0.18	0.66	1.00

1 = Fruit length; 2 = Fruit diameter; 3 = Fruit weight; 4 = Weight of fruit peel; 5 = Weight of fruit pulp; 6 = Total weight of seeds; 9 = Total number of seeds; 10 = Length of flower pericarpel; 13 = Ovary length; 22 = Height; 23 = Stem diameter; 25 = Rib width; 26 = Rib depth.

wild populations. This pattern, in the first case, indicates that phenotypes desirable for people can be found within wild populations although at low frequency, and that apparently artificial selection has increased their frequency in the managed populations. In the second case, the results indicate that wild phenotypes are not completely eliminated in the managed populations. The PCA identified an intermediate group composed by both wild and managed individuals, which is consistent with this interpretation.

Domestication as a real evolutionary process requires artificial selection acting on heritable characteristics, that is, genetically influenced, not only phenotypic expressions determined by the environment. Otherwise the effect of artificial selection would be lost in the subsequent generations. In this study, the genetic bases of morphological variations are not evaluated, it would require studies of quantitative genetics based on long term experiments of common garden and reciprocal transplantations, and this information, therefore, remains uncertain. However, the results indicating that within a single population it is possible to find phenotypes of both large and short fruits as well as large and short seeds and ovaries, strongly suggest that the variation analysed is not only determined by environmental factors. As mentioned, fruit characteristics are the main targets of artificial selection and the differences in such characteristics found among populations could be in part the result of this process, as similarly found Casas et al. (1998, 1999a, 1999b) in *Stenocereus stellatus*, Luna (1999) in *S. pruinosus*, and Cruz (2000) in *Polaskia chende*. But apart from fruit characters, populations also differed in some characteristics of flowers and vegetative parts. It is particularly important to mention that ovaries and pericarpels in the managed populations were larger than in wild populations. These characters are strongly correlated with the higher amount of seeds recorded in fruits from the managed populations (Table 6). Thus, selection for larger fruits and higher amount of pulp could have had consequences in the amount of seeds, since the volume of pulp is directly related with the amount of funiculus. In turn, a higher amount of seeds could have had consequences in the dimensions of the ovary and pericarpel. The correlation in size of these characters reinforce the hypothesis that fruit size is not only determined by environmental differences. Individuals in the silviculturally managed populations are more robust (taller, with a thicker trunk, and larger ribs) than individuals of the wild populations. These characteristics may be strongly influenced by environmental factors, mainly water in soils, but also may be determined by age. A deeper analysis of the influence of both age and environmental differences on the morphology of plants of *E. chiotilla* is yet to be done. Meanwhile, the present evidence suggests that artificial selection has been acting under silvicultural management, determining a process of domestication of this plant species *in situ*.

Casas et al. (1996, 1997a, 1999a) have been constructing the hypothesis that domestication of plants

Table 7. Mean values ± standard errors of morphological characters among wild (W) and managed (M) populations of *Escontria chiotilla* studied. F and significance scores according to one-way ANOVA. Capital black letters indicate significant differences according to Tukey's 95% multiple range tests (5 and 171 degrees of freedom).

Character	W1	W2	W3	M1	M2	M3	F	Significance
Fruit length	22.347 ± 0.572 A	23.280 ± 0.535 A	22.379 ± 0.483 A	26.438 ± 0.600 B	28.365 ± 0.830 B	27.046 ± 0.592 B	16.963	0.000
Fruit diameter	21.695 ± 0.648 A	22.009 ± 0.308 A	20.296 ± 0.456 A	24.540 ± 0.509 B	26.526 ± 0.837 B	25.339 ± 0.494 B	17.932	0.000
Fruit weight	6.484 ± 0.478 A	7.007 ± 0.313 A	6.047 ± 0.344 A	9.742 ± 0.552 B	12.700 ± 1.106 C	11.093 ± 0.556 BC	17.745	0.0000
Weigth of fruit peel	4.149 ± 0.265 A	4.418 ± 0.191 A	3.870 ± 0.217 A	5.511 ± 0.273 B	6.893 ± 0.450 C	6.098 ± 0.256 BC	16.196	0.000
Weight of fruit pulp	2.438 ± 0.258 A	2.496 ± 0.163 A	2.142 ± 0.170 A	4.119 ± 0.305 B	5.673 ± 0.712 B	4.850 ± 0.339 B	13.852	0.000
Total weight of seeds	0.229 ± 0.029 A	0.237 ± 0.015 A	0.209 ± 0.015 A	0.380 ± 0.026 B	0.306 ± 0.024 B	0.328 ± 0.014 B	8.264	0.000
Thickness of fruit peel	0.239 ± 0.017 AB	0.235 ± 0.016 AB	0.224 ± 0.012 A	0.238 ± 0.009 AB	0.280 ± 0.011 B	0.263 ± 0.008 AB	3.447	0.005
Mean weight per seed	0.630 ± 0.028 A	0.582 ± 0.026 A	0.647 ± 0.023 A	0.813 ± 0.011 B	0.740 ± 0.025 B	0.782 ± 0.026 B	14.985	0.000
Total number of seeds	421.26 ± 47.55 A	432.17 ± 29.53 A	346.28 ± 27.97 A	547.98 ± 28.37 B	472.65 ± 30.86 B	566.27 ± 20.42 B	8.069	0.000
Length of pericarpel	14.529 ± 0.542 A	14.564 ± 0.226 A	14.438 ± 0.248 A	14.832 ± 0.204 AB	15.088 ± 0.264 B	15.859 ± 0.246 B	3.619	0.004
Diameter of pericarpel	11.281 ± 0.170 A	11.045 ± 0.124 A	10.955 ± 0.124 A	10.915 ± 0.124 A	11.590 ± 0.121 A	11.192 ± 0.260 A	1.879	0.101
Perianth length	23.404 ± 0.609 A	24.247 ± 0.345 AB	23.657 ± 0.514 AB	23.475 ± 0.335 AB	25.530 ± 0.459 B	24.533 ± 0.301 AB	3.534	0.004
Ovary length	3.977 ± 0.188 A	4.171 ± 0.118 A	4.355 ± 0.126 A	4.299 ± 0.133 A	4.599 ± 0.203 A	4.537 ± 0.125 A	2.021	0.079
Ovary diameter	3.617 ± 0.134 A	3.578 ± 0.121 A	3.574 ± 0.074 A	3.912 ± 0.076 B	3.985 ± 0.098 B	3.950 ± 0.065 B	2.726	0.021
Style length	18.166 ± 0.410 A	18.684 ± 0.345 A	18.083 ± 0.358 A	18.181 ± 0.257 A	19.170 ± 0.320 A	18.859 ± 0.278 A	1.909	0.096
Number of stigma lobes	7.525 ± 0.252 A	7.226 ± 0.167 A	7.008 ± 0.100 A	7.507 ± 0.123 A	7.021 ± 0.146 A	7.232 ± 0.134 A	2.281	0.050
Length of stigma lobes	5.913 ± 0.245 A	6.161 ± 0.267 A	5.964 ± 0.370 A	6.228 ± 0.165 A	5.857 ± 0.163 A	5.545 ± 0.136 A	1.321	0.259
Length of nectar chamber	3.049 ± 0.114 B	2.967 ± 0.140 B	2.970 ± 0.067 B	2.798 ± 0.070 AB	2.330 ± 0.084 A	2.399 ± 0.067 A	9.238	0.000
Diameter of nectar chamber	3.851 ± 0.124 A	3.685 ± 0.083 A	3.834 ± 0.070 A	3.880 ± 0.080 A	3.754 ± 0.078 A	3.613 ± 0.077 A	1.767	0.123
Anther length	1.571 ± 0.045 A	1.604 ± 0.042 A	1.552 ± 0.040 A	1.654 ± 0.028 A	1.585 ± 0.022 A	1.545 ± 0.027 A	1.743	0.128
Anther width	0.737 ± 0.013 B	0.746 ± 0.022 B	0.769 ± 0.018 B	0.759 ± 0.012 B	0.652 ± 0.015 B	0.664 ± 0.010 B	12.045	0.000
Height	4.448 ± 0.158 B	4.519 ± 0.180 B	4.440 ± 0.144 B	3.793 ± 0.090 A	4.553 ± 0.088 B	4.451 ± 0.099 B	5.351	0.000
Stem diameter	14.948 ± 0.665 A	18.638 ± 0.974 AB	15.297 ± 0.925 A	17.503 ± 0.704 AB	19.257 ± 1.035 B	20.242 ± 0.967 B	5.889	0.000
Number of ribs	7.378 ± 0.080 B	7.305 ± 0.082 AB	7.076 ± 0.069 A	7.167 ± 0.065 AB	7.253 ± 0.068 AB	7.303 ± 0.070 AB	2.362	0.041
Rib width	3.451 ± 0.084 A	3.341 ± 0.110 A	3.303 ± 0.096 A	3.929 ± 0.133 B	3.596 ± 0.098 AB	3.816 ± 0.069 B	6.767	0.000
Rib depth	2.724 ± 0.057 AB	2.614 ± 0.066 A	2.554 ± 0.047 A	2.943 ± 0.053 B	2.622 ± 0.066 A	2.696 ± 0.045 A	6.730	0.000
Number of spines per areole	13.532 ± 0.468 A	12.733 ± 0.442 A	13.349 ± 0.313 A	13.582 ± 0.302 A	12.787 ± 0.205 A	12.881 ± 0.217 A	1.402	0.226

Table 7. (*continued*)

Character	W1	W2	W3	M1	M2	M3	F	Significance
Spine size	2.803 ± 0.157 A	2.367 ± 0.229 A	2.739 ± 0.137 A	3.399 ± 0.144 B	2.306 ± 0.114 A	2.667 ± 0.109 A	7.659	0.000
Distance between areoles	1.467 ± 0.037 A	1.357 ± 0.033 A	1.398 ± 0.029 A	1.471 ± 0.030 A	1.412 ± 0.033 A	1.396 ± 0.027 A	4.737	0.06

in Mesoamerica has occurred not only under cultivation but also under silvicultural management, and that such route of domestication could imply that domestication of plants could start before agriculture arose in the area. As mentioned, *E. chiotilla*, is not cultivated at present by local people (although it has been reported occasionally cultivated in other areas, see Hammer (2001), and silvicultural management seems to play an important role in increasing both quality and quantity of this resource. It constitutes, therefore, an ideal case for analysing processes of domestication in non cultivated plants but silviculturally managed. The results of our study suggest that artificial selection is operating under silvicultural management of this plant species, and that it has had notorious consequences altering the phenotypic structure of the managed populations, and that such phenotypic alteration apparently involves also genetic changes, and, therefore, support the hypothesis that domestication may occur under silvicultural management.

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References

Arias S., Gama S. and Guzmán U. 1997. Flora del Valle de Tehuacán-Cuicatlán. Fascículo 14 Cactaceae. Instituto de Biología, Universidad Nacional Autónoma de México, México.

Arizmendi M.C. and Monteros A.E. 1996. Avifauna de los bosques de Cactáceas columnares del Valle de Tehuacán, Puebla. Acta Zoológica Mexicana (nueva serie) 67: 25–46.

Bravo-Hollis H. 1978. Las Cactáceas de México. Universidad Nacional Autónoma de México, México. I.

Casas A., Vázquez M.C., Viveros J.L. and Caballero J. 1996. Plant management among the Nahua and the Mixtec from the Balsas River Basin: an ethnobotanical approach to the study of plant domestication. Human Ecology 24: 455–478.

Casas A., Caballero J., Mapes C. and Zárate S. 1997a. Manejo de la vegetación, domesticación de plantas y origen de la agricultura en Mesoamérica. Boletín de la Sociedad Botánica de México 61: 31–47.

Casas A., Pickersgill B., Caballero J. and Valiente-Banuet A. 1997b. Ethnobotany and domestication in xoconochtli, *Stenocereus stellatus* (Cactaceae), in the Tehuacán Valley and la Mixteca Baja, México. Economic Botany 51: 279–292.

Casas A., Valiente-Banuet A. and Caballero J. 1998. La domesticación de *Stenocereus stellatus* (Pfeiffer) Riccobono (Cactaceae). Boletín de la Sociedad Botánica de México 62: 129–140.

Casas A., Caballero J. and Valiente-Banuet A. 1999a. Use, management and domestication of columnar cacti in south-central Mexico: a historical perspective. Journal of Ethnobiology 19: 71–95.

Casas A., Valiente-Banuet A., Rojas-Martínez A. and Dávila P. 1999b. Morphological variation and the process of domestication of the columnar cactus *Stenocereus stellatus* in Central Mexico. American Journal of Botony 86: 522–533.

Casas A., Valiente-Banuet A., Viveros J.L., Caballero J., Cortés L., Dávila P. et al. 2001. Plant resources of the Tehuacán-Cuicatlán Valley, Mexico. Economic Botany 55: 129–166.

Casas A. and Barbera G. Mesoamerican domestication and diffusion. In: Nobel P.S. (ed.), Cacti: Biology and Uses. The University of California Press, Los Angeles, CA (in press).

Colunga P., Hernández-Xolocotzi E. and Castillo A. 1986. Variación morfológica, manejo agrícola tradicional y grado de domesticación de *Opuntia* spp. en El Bajío Guanajuatense. Agrociencia 7: 7–44.

Cruz M. 2000. Aspectos de la biología reproductiva de Polaskia chende (Gosselin) A. C. Gibson & Horak (Cactaceae) en el Valle de Tehuacán, Puebla, México, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán, México.

Dávila P., Villaseñor J.L., Medina R., Ramírez A., Salinas A., Sánchez-Ken J. et al. 1993. Listados Florísticos de México. X. Flora del Valle de Tehuacán Cuicatlán. Instituto de Biología Universidad Nacional Autónoma de México, México.

Felger R.S. and Moser M.B. 1976. Seri Indian food plants. Desert subsistence without agriculture. Ecology of Food and Nutrition 5: 13–27.

García E. 1988. Modificaciones al sistema de clasificación climática de Köpen (para adaptarlo a las condiciones de la República Mexicana). Instituto de Geografía, Universidad Nacional Autónoma de México, México.

Hammer K. 2001. Cactaceae. In: Hanelt P. (ed.), Institute of Plant Genetics and Crop Plant Research, Mansfeld's Encyclopedia of

Agricultural and Horticultural Crops. Springer-Verlag, Berlin, pp. 198–222.

Harlan J. 1975. Crops and man. Foundation for modern crop science series. American Society of Agronomy, Madison, Wisconsin.

Hawkes J.G. 1983. The diversity of crop plants. Harvard University Press, London.

Luna C. 1999. Etnobotánica de la Pitaya Mixteca (Pachycereeae), PhD, Colegio de Postgraduados, México.

MacNeish R.S. 1967. A summary of the subsistence. In: Byers D.S. (ed.), The Prehistory of the Tehuacán Valley. Volume I: Environment and Subsistence. University of Texas Press, Austin, TX, pp. 290–331.

MacNeish R.S. 1992. The origins of agriculture and settled life. University of Oklahoma Press, London.

Matos E. 1994. Mesoamérica. In: Manzanilla L. and López-Luján L. (eds), Historia Antigua de México. El México Antiguo, sus Areas Culturales, los Orígenes y el Horizonte Preclásic Vol. I. Porrúa, México, pp. 49–73.

Nárez J. 1994. Aridoamérica y Oasisamérica. In: Manzanilla L. and López-Luján L. (eds), Historia Antigua de México. El México Antiguo, Sus Áreas Culturales, Los Orígenes y el Horizonte Preclásic Vol. I. Porrúa, México, pp. 75–111.

Pimienta-Barrios E. and Nobel P.S. 1994. Pitaya (*Stenocereus* spp., Cactaceae). An ancient and modern fruit crop of México. Economic Botany 48: 76–83.

Rohlf J. 1993. Numerical Taxonomy and Multivariate Analysis System for the IBM PC Microcomputer (and compatibles). version 1.8. Applied Biostatistics Inc., New York.

Rojas-Martínez A. and Valiente-Banuet A. 1996. Análisis comparativo de la quiropterofauna del Valle de Tehuacán-Cuicatlán, Puebla-Oaxaca. Acta Zoológica Mexicana 67: 1–23.

Rzedowski J. 1978. La Vegetación de México. Limusa, Mexico.

Rzedowski J. 1993. Diversity and origins of the phanerogamic flora of Mexico. In: Ramamoorty T.P., Bye R., Lot A A. and Fa J. (eds), Biologycal Diversity of Mexico. Oxford University Press, Oxford, pp. 129–144.

Smith C.E. 1967. Plant remains. In: Byers D.S. (ed.), The Prehistory of the Tehuacan Valley. Vol. I: Environment and Subsistence. University of Texas Press, Austin, TX, pp. 220–225.

Sneath P.H.A. and Sokal R.R. 1973. Numerical Taxonomy. The Principles and Practice of Numerical Classification. Freeman, San Francisco, CA.

1997. SYSTAT, version 7.0. SPSS Inc., Chicago, IL.

Toledo V.M. and Ordñez M.J. 1993. The biodiversity scenario of Mexico: a review of terrestrial habitats. In: Ramamoorty T.P., Bye R., Lot A. and Fa J. (eds), Biological Diversity of Mexico. Oxford University Press, Oxford, pp. 757–777.

Valiente-Banuet A., Arizmendi M.C., Rojas-Martinez A. and Dominguez-Canseco L. 1996. Ecological relationship between columnar cacti and nectar-feeding bats in Mexico. Journal of Tropical Ecology 12: 103–119.

Valiente-Banuet A., Casas A., Dávila P., Arizmendi M.C., Godínez H., Alcántara A. et al. 2000. La vegetación del Valle de Tehuacán-Cuicatlán. Boletín de la Sociedad Botánica de México 67: 25–74.

Valiente-Banuet A., Casas A., Alcantara A., Dávila P., Flores-Hernández N., Arizmendi M.C. et al. 2000. La vegetaciór del valle de Tehuacá-Cuicatián. Boletin de la Sociedad Botánica de México 67: 25–75.