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Morphological variation and the process of domestication of *Stenocereus stellatus* (Cactaceae) in Central Mexico[1]

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Morphological variation was analyzed in wild, managed in situ, and cultivated populations of the columnar cactus *Stenocereus stellatus* in central Mexico. The purpose was to evaluate whether morphological divergence between manipulated and wild populations has resulted from domestication processes. Variation of 23 morphological characters was analyzed among 324 individuals from 19 populations of the Tehuacán Valley and La Mixteca Baja. Multivariate statistical analyses were used to group individuals and populations according to their morphological similarity. Individuals grouped according to the way of management and fruit characteristics were the most relevant for grouping. Within each region, sweet fruits with pulp colors other than red were more frequent in cultivated populations, where fruits were also larger, contained more and bigger seeds, and had thinner peel and fewer spines than fruits from wild individuals. Phenotypes common in managed in situ and cultivated populations generally occur in the wild but in lower frequencies. Artificial selection has thus operated by enhancing and maintaining desirable rare phenotypes in managed in situ and cultivated populations, causing divergent patterns of morphological variation from wild populations. Cultivation has caused the strongest level of divergence, but divergence has also been significant with management of wild populations in situ.

Key words: Cactaceae; columnar cacti; domestication; Mixteca; morphological variation; *Stenocereus stellatus*; Tehuacán Valley.

Domestication is an evolutionary process through which domesticated plants and animals become morphophysiologically divergent from their wild ancestors (see Darwin, 1859, 1868; Schwanitz, 1966; Harlan, 1992). Such divergence is a result of artificial selection and other evolutionary forces determined by manipulation of plants and animals by humans. In plants, the process of domestication has been generally associated with cultivation in controlled environments out of their wild populations (Harlan, 1992; Zohary and Hopf, 1993). Although humans have also practiced different forms of manipulation of wild populations (Rindos, 1984; Harris, 1989; Casas et al., 1997a), the role of these forms of plant manipulation in domestication has not been evaluated.

Different forms of management of wild populations in situ have been reported in a number of plant species in Mexico (Alcorn, 1981; Bye, 1993; Caballero, 1994; Casas and Caballero, 1996; Casas et al., 1996), and they seem to be common ways of plant manipulation by people in Mesoamerica (Casas et al., 1997a). Casas and Caballero (1996) have suggested that domestication under forms of management in situ (in situ domestication) may be an attractive model for explaining domestication of some plant species, especially long-lived perennials. However, the demonstration and evaluation of this process are yet to be done.

In this study, the case of *Stenocereus stellatus* (Pfeiffer) Riccobono is analyzed. This is a columnar cactus species endemic to central Mexico, occurring in the wild as part of tropical deciduous and thorn-scrub forests. It is also cultivated in home gardens, and some wild populations are managed in situ since it is a useful species (Casas et al., 1997b). This situation offers the possibility of studying the evolution of this species under domestication processes and determining whether domestication has been significant under forms of management of wild populations in situ.

During August and September, the season when fruits of *S. stellatus* are ripe, it is possible to observe a significant morphological variation in fruit characteristics. This variation might be phenotypic expression influenced by natural environmental conditions since the range of *S. stellatus* covers altitudes from 600 to 2000 m, levels of

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precipitation between 300 and 800 mm/yr, annual mean temperatures from 17° to 24°C, and soils derived from limestones, sandstones, volcanic rocks or alluvial deposits. Conversely, this morphological variation may have a genetic basis and be favored by the self-incompatible sexual reproduction system, which, along with vegetative propagation, is characteristic of this species (Casas, 1997).

Nevertheless, the variation in fruits could be also the result of manipulation of this species by humans. According to archaeological information obtained in caves from the Tehuacán Valley, *S. stellatus* has apparently been used by people for more than 5000 yr (MacNeish, 1967; Smith, 1967); Currently, ten different indigenous groups inhabiting the area use and manage this species mainly because of its edible fruits. Casas et al. (1997b) reported that management of wild populations of *S. stellatus* in situ is carried out by sparing some desirable phenotypes, while removing others during clearance of vegetation and sometimes enhancing numbers of the spared desirable phenotypes by planting their branches. Cultivation of this species is practiced mainly in home gardens, where desirable phenotypes are vegetatively propagated and new variation is incorporated through tolerance of volunteer seedlings.

Pulp color, flavor, amount of edible matter, peel thickness, and spininess of the fruits are the most significant characteristics used by people in folk classification of variants, in assessing quality of products, and in selecting individuals of *S. stellatus* for preferential propagation (Casas et al., 1997b). Manipulation of this plant species by people thus appears to involve artificial selection. This seems to be particularly intense in home gardens, where manipulation of *S. stellatus* is by planting and replacing individuals continually. However, it could also be significant in managed in situ populations, where selection is mainly directed to increase frequencies of good phenotypes existing in wild populations (Casas et al., 1997b).

The main hypothesis of this study was that if artificial selection has been significant, both management in situ and cultivation of this species might have changed to some extent patterns of morphological variation (especially in those characters that are direct targets of human selection) from those occurring in wild and unmanaged populations. Accordingly, the purpose of this study was to analyze patterns of morphological variation in wild, managed in situ, and cultivated populations of *S. stellatus,* in order to examine whether human selection has modified the phenotypic structure of manipulated populations. This study also focused on comparing morphology of individuals from two regions (the Tehuacán Valley and La Mixteca Baja), in order to examine to what extent patterns of morphological variation in populations can be related to environmental factors.

MATERIALS AND METHODS

Regions studied—The study was carried out in the Tehuacán Valley and La Mixteca Baja regions, in Central Mexico. The Tehuacán Valley is located in the southeast of the state of Puebla and the northwest of the state of Oaxaca (Fig. 1). The climate is arid and semiarid with an annual mean precipitation of 300 mm. Tropical deciduous and thorn-scrub forests are present. La Mixteca Baja forms part of the Balsas river basin and, although it is located just south of Tehuacán, maintains important phytogeographic differences from that region (Villaseñor, Dávila, and Chiang, 1990). La Mixteca Baja includes the northwest of Oaxaca, the southeast of Puebla, and the northeast of Guerrero states. It is a mountainous region with altitudes ranging from 600 to 3000 m. Vegetation varies from thorn-scrub and tropical deciduous forests in the lower dry and warm settings to pine forests in the higher wet and temperate areas.

Populations studied—Three groups of populations of *S. stellatus* managed in different ways by people were selected in the two regions (Fig. 1). General information on these populations is summarized in Table 1. The first group is represented by six wild populations, three of them from Tehuacán (Zapotitlán-W, San Juan Raya-W, and Coxcatlán-W) and three from La Mixteca (Chinango-W, Tepexco-W, and Tequixtepec-W). The second group is formed by seven populations managed in situ, three of them from Tehuacán (Metzontla-M, San Lorenzo-M, and Coapan-M) and four from La Mixteca (Chinango-M, Tepexco-M, Camotlán-M, and Huajolotitlán-M). The third group is composed of six samples of cultivated individuals in home gardens from the villages of Los Reyes Metzontla (Metzontla-C), San Lorenzo (San Lorenzo-C), and Zapotitlán (Zapotitlán-C) in Tehuacán, and from the villages of Chinango (Chinango-C), San Juan Nochistlán (Nochistlán-C), and Lunatitlán (Lunatitlán-C) in La Mixteca.

Sampling of populations—Transects were used as the sampling method for wild and managed in situ populations. The area of wild populations was delimited by cleared areas (agricultural fields, roads, or human settlements) surrounding the populations, whereas the area of populations managed in situ included both recently cleared and fallow agricultural fields where individuals of *S. stellatus* were tolerated. The transects were traced along the longest dimension of each population in order to represent individuals from as different environmental conditions as possible within each population, and 5 m wide given that crown diameter of individual plants ranges from 0.5 to 4 m. Sampled area (i.e., length of transect given constant width) varied in each population according to density of the population (Table 1) in order to include at least ten and at most 50 individuals.

Home gardens were the sampling units in cultivated populations. Nearly 10% of the home gardens in a village were sampled at random. A number was given to each home garden in a village, and then a list of numbers was drawn from a table of random numbers. With a similar method, 10% of the total number of individuals within the home gardens selected were randomly sampled.

Due to the natural clonal propagation of *S. stellatus,* it was difficult to identify isolated individuals in the field. For purposes of sampling, an individual was considered in this study as a unit of branches emerging together from the ground. Because morphological comparisons included reproductive parts, only individuals at reproductive stage were sampled.

A total of 324 individuals were sampled, 89 of them from the wild populations, 90 from the populations managed in situ, and 145 from home gardens (Table 1).

Morphological characters analyzed—A total of 23 characters were analyzed (Table 2). According to ethnobotanical information (Casas et al., 1997b), characters such as pulp color and flavor, spininess and thickness of the peel, and amount of edible matter were considered to be direct targets of human selection. Other characteristics, which, according to local people, are not targets of selection, were also included in order to have a reference of general patterns of morphological variation independent of human influence. These included characters used by botanists for the taxonomy of columnar cacti (Bravo-Hollis, 1978; Gibson and Horak, 1978).

Qualitative characters analyzed included two forms of fruit (Table 2), two different peel colors, two pulp flavors, and two categories of pulp color (recorded as ''red,'' the predominant pulp color in wild popula-

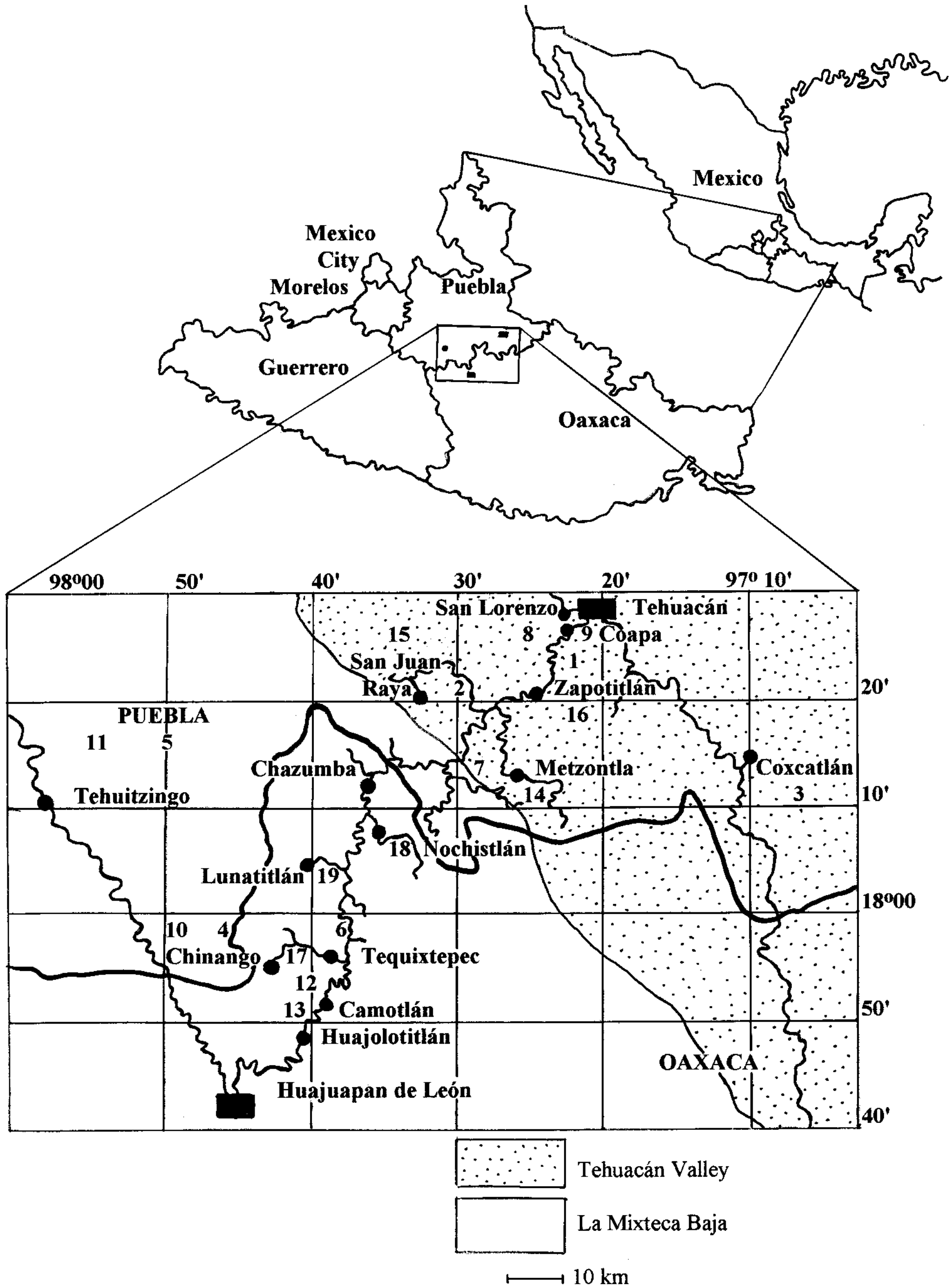

Fig. 1. The Tehuacán Valley and La Mixteca Baja. Location of the populations of *Stenocereus stellatus* studied. Wild populations: 1 = Zapotitlán-W; 2 = San Juan Raya-W; 3 = Coxcatlán-W; 4 = Chinango-W; 5 = Tepexco-W; 6 = Tequixtepec-W. Managed in situ populations: 7 = Metzontla-M; 8 = San Lorenzo-M; 9 = Coapa-M; 10 = Chinango-M; 11 = Tepexco-M; 12 = Camotlán-M; 13 = Huajolotitlán-M. Cultivated populations: 14 = Metzontla-C; 15 = San Lorenzo-C; 16 = Zapotitlán-C; 17 = Chinango-C; 18 = Nochistlán-C; 19 = Lunatitlán-C.

tions, and ''not red,'' including pink, purple, yellow, orange, and white) distinguished and used by people in the folk classification of variants of this species (Casas et al., 1997b). Alternative variants of each qualitative character were considered as discrete character states. For the remaining quantitative characters, three to five measurements for each character per individual were obtained to calculate a representative mean value.

Length and diameter of the highest branch of each individual sampled were measured by a measuring stick and a forestaff, respectively. Number of stem ribs was counted always at the middle part of the branches selected. Width and depth of stem ribs were measured by a caliper, also at the middle part of the branches selected. Number of spines per areole, longitudinal distance between areoles, and size of the central spine in areoles (estimated as the product of the maximum length of the spine and the diameter in the middle part of the spine) were recorded in randomly selected areoles.

Fruit size was estimated by measuring maximum diameter and length of fruits and then calculating the volume as the volume of oblate spheroids by the formula $v = (4/3)\pi a^2 b$, where a is half the transverse diameter of the fruit and b is half its length.

TABLE 1. General information on populations of *Stenocereus stellatus* sampled.

Population	Elevation (m)	Annual mean temp. (°C)	Annual rain fall (mm)	Origin of soils	Habitat	Sampled area (m²)	Density of pop. (indiv./ha)	No. of indiv. analyzed
Wild (Tehuacan)								
Zapotitlán-W	1550	21.2[a]	450[a]	sandstones	thorn-scrub forest	1500	273	24
Sn. Juan Raya-W	1800	20.9[a]	649.7[a]	limestones	thorn-scrub forest	8500	29	10
Coxcatlán-W	1000	23.8[a]	440.6[a]	volcanic rocks	tropical deciduous forest	6000	280	15
Wild (Mixteca)								
Chinango-W	1700	20.6[a]	720.5[a]	volcanic rocks	tropical deciduous forest	6000	35	20
Tepexco-W	1150	23.0[a]	763.7[a]	volcanic rocks	tropical deciduous forest	10500	14	10
Tequixtepec-W	1650	20.6[a]	720.5[a]	volcanic rocks	tropical deciduous forest	10000	9	10
Managed (Tehuacán)								
Metzontla-M	2000	17.2[b]	527.9[b]	limestones	agricultural field	1000	120	15
Sn. Lorenzo-M	1700	19.1[a]	590.0[a]	limestones	fallow agricultural fields	10000	34	20
Coapa-M	1650	18.6[a]	479.6[a]	limestones	fallow agricultural fields	3000	42	10
Managed (Mixteca)								
Chinango-M	1700	20.6[a]	720.5[a]	volcanic rocks	agricultural fields	7500	48	15
Tepexco-M	1100	23.0[a]	763.7[a]	volcanic rocks	fallow agricultural fields	3500	42	10
Camotlán-M	1600	20.6[a]	720.5[a]	volcanic rocks	fallow agricultural fields	4000	38	10
Huajolotitlán-M	1600	20.6[a]	720.5[a]	volcanic rocks	fallow agricultural fields	3000	28	10
Cultivated (Tehuacán)								
Metzontla-C	1900	17.2[b]	527.9[b]	alluvial	home gardens	2600	781	30
San Lorenzo-C	1700	19.1[a]	590.0[a]	limestones	home gardens	2000	172	15
Zapotitlán-C	1550	21.4[a]	450.0[a]	alluvial	home gardens	2000	158	10
Cultivated (Mixteca)								
Chinango-C	1600	20.6[a]	720.5[a]	alluvial	home gardens	3000	259	50
Nochistlán-C	1650	20.6[a]	720.5[a]	alluvial	home gardens	1500	181	20
Lunatitlán-C	1650	20.6[a]	720.5[a]	alluvial	home gardens	1500	176	20

[a] Information based on García (1988).
[b] Information based on Valiente (1991).

TABLE 2. Morphological characters analyzed.

Characters	Target of human selection	No. of parts measured per indiv.	Units
Number of branches	NO	variable	number
Length of the highest branch	NO	1	m
Diameter of the highest branch	NO	1	cm
Number of stem ribs	NO	5 branches	number
Stem rib width	NO	5 ribs	cm
Stem rib depth	NO	5 ribs	cm
Number of spines per areole	NO	5 areoles	number
Size of the central spines	NO	10 areoles	mm²
Distance between areoles	NO	5 pairs of areoles	cm
Fruit form	NO	Single	1 = spherical; 2 = elongated
Peel color	NO	Single	1 = red; 2 = green
Pulp color	YES	Single	1 = red; 2 = not red
Pulp flavor	YES	Single	1 = sour; 2 = sweet
Fruit size	YES	3–5 fruits	cm³
Number of areoles per fruit	YES	3–5 fruits	number
Number of areoles per cm²	YES	3–5 fruits	number
Peel thickness	YES	3–5 fruits	mm
% edible part of fruit mass	YES	3–5 fruits	%
% water of pulp mass	YES	3–5 fruits	%
Number of seeds per fruit	NO	3–5 fruits	number
Mean seed mass	NO	300–500 seeds	mg
Total seed mass per fruit	NO	3–5 fruits	g
% seed mass of pulp mass	NO	3–5 fruits	%

The total number of areoles per fruit was counted. The number of areoles per square centimeter was measured by using a card with 2-cm² holes always situated on the equatorial plane of the fruits. All complete or incomplete areoles included in the squared holes were counted and then divided by 2 to have a measure per square centimetre. Thickness of the peel was measured with a caliper always in the equatorial plane of the fruits.

Percentage of edible part of the fruit (pulp and seeds) was calculated as the ratio of the mass between the pulp and seeds and the total mass of the fruit, including the peel. The percent water of pulp mass was estimated as the ratio: (dry pulp mass/fresh pulp mass) $\times$ 100.

Total number of seeds per fruit was counted and their total mass measured. Mean seed mass was estimated by weighing a sample of 100 seeds per fruit and dividing by 100 to obtain the average seed mass. Percent of seed to pulp was estimated from the ratio of the total mass of seeds to the total mass of the edible portion per fruit.

Methods of data analysis—Patterns of morphological similarity/difference were analyzed by multivariate statistical methods, as in other studies such as Pickersgill, Heisser, and McNeill (1979), Casas and Caballero (1996), Colunga-García Marín, Estrada-Loera, and May-Pat (1996), and Mapes et al. (1996).

Principal Component (PCA) and Discriminant Function Analyses (DFA) were directed to analyze patterns of individuals within each region in order to visualize possible differences among populations according to their way of management. DFA was also aimed at evaluating the overlap between wild, managed in situ, and cultivated populations in their overall morphology, by looking at misassignment of individuals from their original groups. Evaluation of the discriminant functions derived from DFAs by one-way MANOVAs was directed to test the null hypothesis that there are no significant differences between wild, managed in situ, and cultivated populations. The eigenvectors resulting from

PCAs and the standardized discriminant function coefficients resulting from DFAs were used to identify the characteristics that most significantly contribute to classifying individuals (Sneath and Sokal, 1973; Krzanowski, 1990). Cluster Analysis (CA) was performed to examine the morphological similarity, at population level, between the populations studied of the two regions analyzed together. The purpose was to visualize possible differences between populations of the Tehuacán Valley and La Mixteca, which would be possibly related to the environmental differences existing among these regions. CA was also directed to visualize the morphological similarity/difference of populations under a similar management across the regions.

Basic data matrices were constructed with morphological characters considered as variables. PCAs were performed with the mean values per individual of each of the 19 quantitative characters and the character states of the qualitative characters. DFAs included only quantitative characters. CA included the mean values of the quantitative characters per population and the proportion of individuals per population producing fruits with spherical form, red peel, red pulp and sweet flavor. The individual plants from each region analyzed by PCAs and DFAs, as well as the 19 populations, in CA were considered as Operational Taxonomic Units (OTUs). Numerical values of characters of the basic data matrices were standardized by subtracting the mean value of the character per individual or population from the average for this character over all individuals or populations studied, and then dividing by the standard deviation for this character in the sample of individuals or populations.

PCAs were performed on correlation matrices between characters calculated by using the Pearson correlation coefficient (Sneath and Sokal, 1973). For DFAs, the individuals were arranged in three groups according to form of management (wild, managed in situ, and cultivated). One-way MANOVAs for evaluating population differences were performed using Wilks' Lambda as the test statistic. CA was performed by calculating a similarity matrix between populations using the Euclidean Distance coefficient and then processing this matrix by the UPGMA method (Sneath and Sokal, 1973). CA and PCAs were carried out using NTSYS-PC version 1.8 (Rohlf, 1993), while DFAs were performed by SYSTAT version 7.0 (SYSTAT, 1997).

Two-way analyses of variance tested statistical significance of differences for each quantitative morphological character among populations according to their region of provenance (Tehuacán and La Mixteca), and according to their management regime (wild, management in situ, and cultivation). Tukey's highest significant difference tests (HSD, 95%) were performed.

RESULTS

Patterns of variation among individuals—In PCAs, nearly 50% of the variation is explained by the first three principal components, mainly the first one (30% in Tehuacán and 21% in La Mixteca). Individuals of the two regions were distributed in continuous gradients rather than in discrete groups within the space of the first two principal components (Fig. 2). However, along Principal Component Axis 1, most of the wild individuals occupy the left side of the plots, whereas most of the cultivated ones are in the right side and those from managed in situ populations predominate in the middle part along with some cultivated individuals. Along Principal Component Axis 2, most wild individuals from La Mixteca (Fig. 2b) are in the upper part of the plot, whereas managed in situ and cultivated individuals predominate in the middle and lower part of the plot.

According to DFAs, a high percentage of the variation is explained by the first discriminant function and according to MANOVAs there are significant differences among the three groups of populations in both regions (Table 3). Most of the individuals were classified correctly, indicating that in each region the three groups are different. However, as in PCAs, some individuals of one group are morphologically similar to individuals of the other two groups (Table 4). Overlaps are more frequent among managed in situ and cultivated populations (Fig. 3).

Eigenvectors resulting from PCAs (Table 5) show that in both regions the most important characters in the first and second principal components are fruit size, density of spines on fruits, mean and total seed mass, and proportion of pulp and peel thickness. Pulp flavor, diameter of branches, and rib width are important in the ordination of individuals of Tehuacán, whereas pulp color, branch length, and rib depth are important in La Mixteca. According to standardized discriminant function coefficients (Table 5), mean seed mass and number of seeds are important characters for classifying groups in both regions. However, fruit size and peel thickness are the most important characters in Tehuacán, whereas density of spines in fruits is the most important in La Mixteca.

Patterns of variation among populations—CA grouped populations into two main clusters (Fig. 4). The first cluster includes all the populations from the Tehuacán Valley as well as two wild and one managed in situ populations from La Mixteca. On the other hand, the second cluster includes the remaining wild, managed in situ, and cultivated populations from La Mixteca. The first cluster is divided into two groups. The first group is formed by five of the six wild populations analyzed, with the wild populations from the Tehuacán Valley (Zapotitlán-W, San Juan Raya-W, and Coxcatlán-W) presenting higher similarity among themselves and forming a subgroup. The second group includes two subgroups, one of them represented by the managed in situ populations from Tehuacán (Metzontla-M, Coapa-M, and San Lorenzo-M), along with the managed in situ population Chinango-M from La Mixteca. The other subgroup is formed by the three cultivated populations of Tehuacán (Metzontla-C, San Lorenzo-C, and Zapotitlán-C). The second cluster is constituted by a single group (the third group), which includes three subgroups. The first one is composed of the wild and managed in situ populations of Tepexco from La Mixteca; the second contains two managed in situ populations from that region (Camotlán-M and Huajolotitlán-M), and the third includes the three cultivated populations from La Mixteca (Chinango-C, Nochistlán-C, and Lunatitlán-C). Thus, with the only exception of the wild and managed in situ populations of Tepexco, CA grouped the populations studied according to their way of management. But populations were classified also according to the region of provenance, with the exception of the wild populations Tequixtepec-W and Chinango-W, as well as the managed in situ population Chinango-M, which, being from La Mixteca, grouped with the wild and managed in situ populations of Tehuacán, respectively.

Differences among populations and trends of morphological change under domestication—Across regions, the populations studied were significantly different

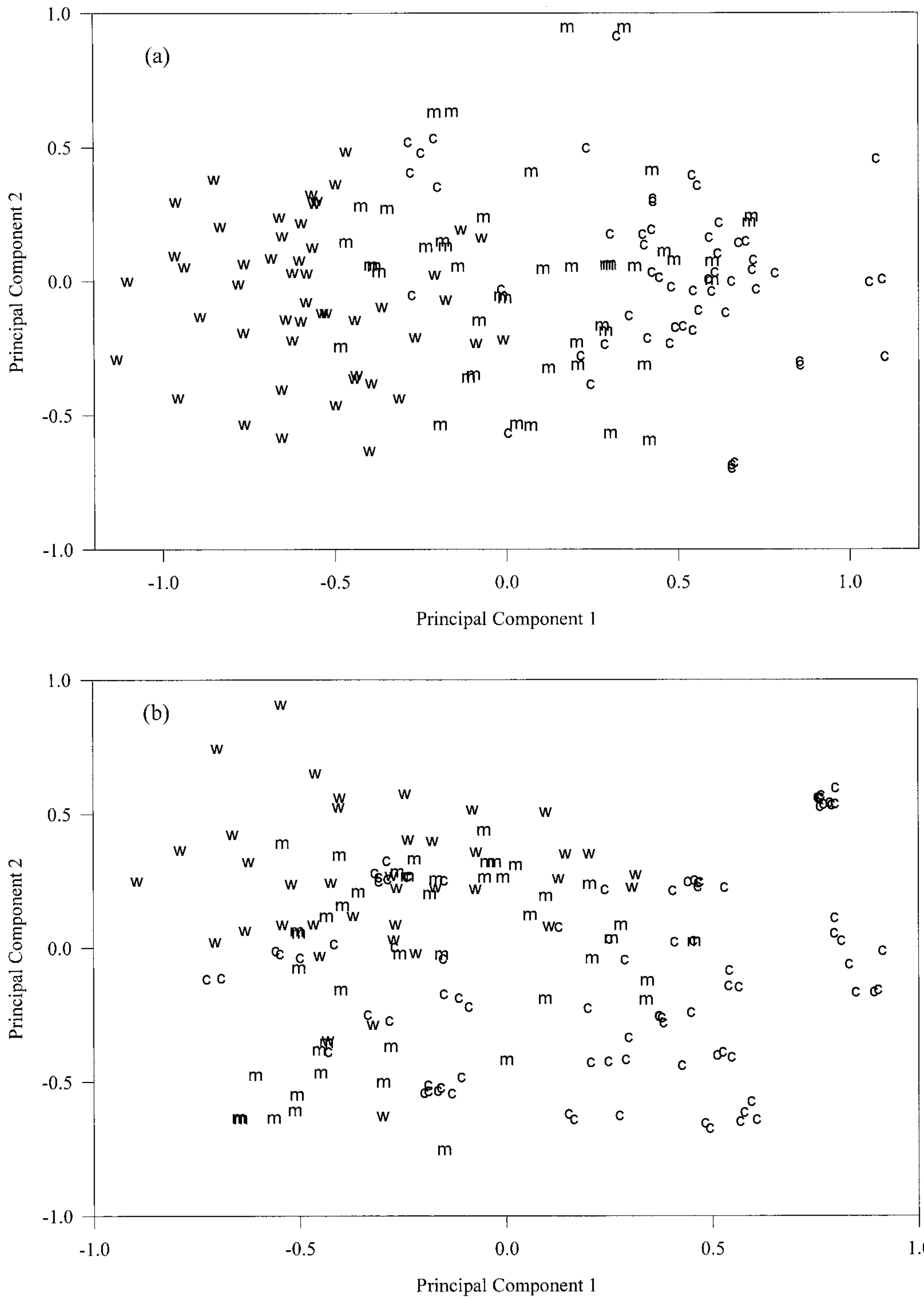

Fig. 2. Projection of individuals of *Stenocereus stellatus* in the space of the first and second principal components. (a) Populations of the Tehuacán Valley; (b) populations of La Mixteca Baja (w = wild; m = managed in situ; c = cultivated individuals).

TABLE 3. DFA and MANOVA scores comparing wild, managed in situ, and cultivated populations of *Stenocereus stellatus* from the Tehuacán Valley and La Mixteca Baja.

Discriminant function	Eigenvalue		Percentage variation		Wilks' Lambda		*F*		df		*P*	
	Tehuacán	Mixteca	Tehuacán	Mixteca	Tehuacán	Mixteca	Tehuacán	Mixteca	Tehuacán	Mixteca	Tehuacán	Mixteca
1	3.36	1.29	83.5	66.0	0.089	0.234	15.88	8.65	38, 256	38, 308	0.000	0.000
2	0.66	0.67	16.5	34.0								

TABLE 4. Classification of individuals of wild, managed in situ, and cultivated populations from the Tehuacán Valley and La Mixteca Baja according to DFA.

		Predicted group					
		Wild		managed in situ		Cultivated	
Region	Actual group	Count	%	Count	%	Count	%
Tehuacán Valley	Wild	47	95.9	2	4.1	0	0.0
	Managed in situ	1	2.2	40	88.9	4	8.9
	Cultivated	2	3.6	9	16.4	44	80.0
Mixteca Baja	Wild	29	72.5	5	12.5	6	15.0
	Managed in situ	5	11.1	36	80.0	4	8.9
	Cultivated	6	6.7	7	7.8	77	85.6

in all the characters analyzed, except in number of ribs and peel thickness (Table 6). In La Mixteca, plants of *Stenocereus stellatus* had significantly more, longer, and thicker branches with wider and deeper ribs, as well as fewer but bigger spines in more distanced areoles than plants in the Tehuacán Valley. Fruits of this species in La Mixteca were also significantly larger, with more areoles although fewer per area, more and heavier seeds, with a higher proportion of edible mass and water in the pulp, and a lower proportion of seeds with respect to pulp, compared with fruits of this species in Tehuacán.

When morphology was compared among populations according to their management regime, plants of all populations were similar in branch length, distance between areoles, and number of areoles per fruit, but significantly different in the rest of the characters (Table 6). Plants of cultivated populations presented significantly more branches with wider and deeper ribs than plants of wild and managed in situ populations. Wild populations presented smaller spines, thicker fruit peel, and a higher proportion of seed mass with respect to pulp mass than the other populations. The rest of the characters varied significantly from wild to managed in situ, to cultivated populations. Thus, as the management of plants was more intensive, they presented progressively thicker branches, with more ribs and more spines per areole, whereas fruits were larger, with fewer areoles per square centimetre, more and heavier seeds, and with a higher proportion of edible mass and water in the pulp.

Interactions between region and type of management were significant in branch diameter, rib dimensions, spine size, and percent water of pulp, which were significantly different only among populations of the Tehuacán Valley, as well as in number and density of areoles in fruit, and seed mass, which presented more pronounced differences among populations of the Tehuacán Valley.

The highest correlations between characters were those between peel thickness and percent of pulp in fruits ($r = -0.81$ in Tehuacán and $r = 0.72$ in La Mixteca), as well as between fruit size and density of spines in peel ($r = -0.77$ in Tehuacán and $r = -0.60$ in La Mixteca), fruit size and total seed mass ($r = 0.75$ in Tehuacán and $r = 0.69$ in La Mixteca).

In all the populations of Tehuacán, the proportion of individuals producing spherical fruits was higher than that producing the elongated ones (Table 7), whereas in La Mixteca, nearly one-half of the individuals sampled produced fruits of each form. Most of the individuals of the two regions produced fruits with red peel and pulp, but >40% of the cultivated individuals from La Mixteca produced fruits with green peel and pulp colors other than red. Most of the wild individuals produced sour fruits, whereas most individuals from the managed in situ and cultivated populations produced sweet fruits. However, the proportion of individuals producing sweet fruits was generally higher in La Mixteca than in Tehuacán.

DISCUSSION

Multivariate analyses generally grouped both individuals and populations of *S. stellatus* according to their form of management. In addition, from MANOVAs, the null hypothesis that there were no significant morphological differences between wild, managed in situ, and cultivated populations was rejected. These results appear to confirm the hypothesis by Casas (1997) and Casas et al. (1997b) that human management has significantly influenced morphological divergence of both managed in situ, and cultivated populations from wild populations of this species and that, therefore, domestication may be caused not only through cultivation but also through management of wild populations in situ. Casas and Caballero (1996) and Casas et al. (1997a) suggest that in situ domestication may be a model by which to investigate domestication in perennial plants, especially those with outbreeding reproductive systems, because of the difficulties for fixation of desirable characters by direct sowing of seeds from desirable phenotypes. The case of *S. stellatus*, therefore, appears to be an example for developing such a model.

The overlaps between the different types of populations, identified by both PCAs and DFAs (Figs. 2, 3; Table 4) reveal important information for analyzing the process of domestication of *S. stellatus.* These overlaps are explicable because, according to local people, the introduction of individuals from wild and managed in situ populations to home gardens is continually being carried out. These overlaps indicate that commonly cultivated phenotypes occur also in wild and, especially, in managed in situ populations, although in low frequencies, and that wild phenotypes have maintained their morphological characteristics in managed in situ populations and when they are brought to cultivation in home gardens. This observation, along with the fact that these characteristics are expressed differently in individuals of different origin cultivated within a same home garden, suggests that such characteristics have an important genetic component. This would indicate then that changes in morphological characters may be inherited and that artificial

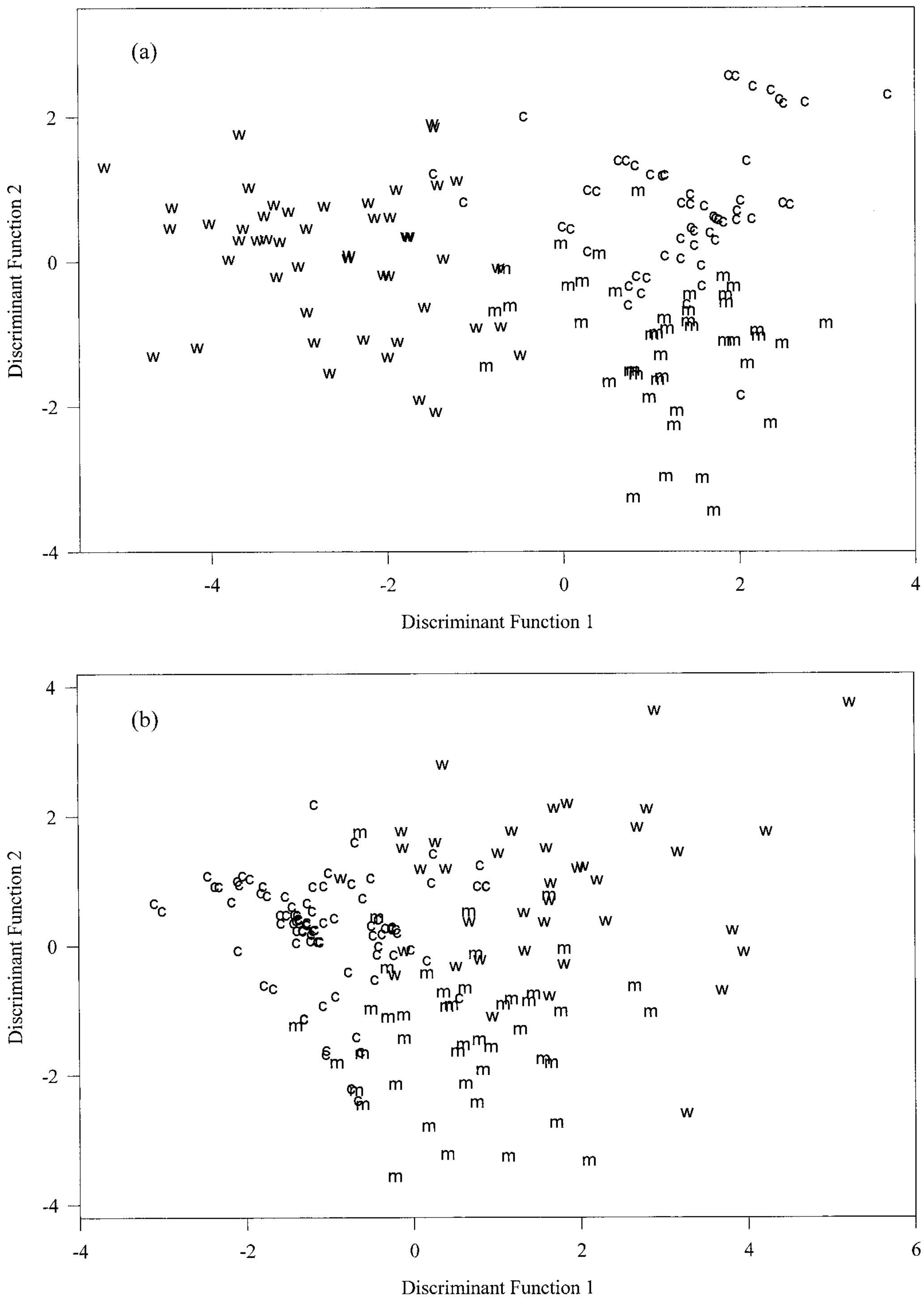

Fig. 3. Discriminant analysis. Classification of individuals of *Stenocereus stellatus* according to forms of management. (a) Populations of the Tehuacán Valley; (b) populations of La Mixteca Baja (w = wild; m = managed in situ; c = cultivated individuals)

selection on these characters is causing the morphological differences.

Overlaps between wild and managed in situ populations would be expected because managed in situ populations derived directly from wild populations. However, the overlaps are relatively small and these types of populations have diverged significantly, illustrating that artificial selection under management in situ has also been significant. Groups of managed in situ and cultivated individuals appear to be the most similar among themselves since overlaps between them were the most frequent. The information obtained thus indicates that morphological divergence is significant between wild and managed in situ populations but especially strong between wild and

TABLE 5. Eigenvectors in the first (PC1) and second (PC2) principal components from PCA. Standardized coefficients in the first (DF1) and second (DF2) discriminant functions from DFA.

	Tehuacán				Mixteca			
Character	PC1	PC2	DF1	DF2	PC1	PC2	DF1	DF2
Number of branches	0.53	0.14	0.41	−0.21	0.37	0.56	−0.31	0.38
Length of the highest branch	0.23	0.19	0.03	−0.21	0.30	0.66	0.04	0.19
Diameter of the highest branch	0.71	0.46	0.14	−0.12	0.34	−0.48	0.12	−0.09
Number of stem ribs	0.11	0.15	0.42	−0.38	−0.30	−0.26	−0.20	−0.01
Stem rib width	0.66	0.47	0.32	0.38	0.33	0.16	−0.28	0.35
Stem rib depth	0.53	0.57	0.42	−0.25	0.65	−0.05	−0.33	0.42
Number of spines per areole	0 23	−0.13	0.08	−0.41	−0.09	−0.71	−0.08	−0.72
Size of central spines	0.56	0.02	0.48	0.15	0.09	0.23	0.21	−0.56
Distance between areoles	0.20	0.15	−0.77	0.38	0.33	0.04	−0.10	0.23
Fruit form	0.03	−0.18	[a]	[a]	0.34	0.06	[a]	[a]
Peel color	0.29	−0.33	[a]	[a]	0.60	0.14	[a]	[a]
Pulp color	0.25	−0.24	[a]	[a]	0.71	0.12	[a]	[a]
Pulp flavor	0.64	−0 14	[a]	[a]	0.21	0.00	[a]	[a]
Fruit size	0.88	−0.11	0.07	0.60	0.87	−0.25	−0.01	0.18
Total number of areoles per fruit	−0.34	−0.16	0.09	0.05	0.20	−0.25	−0.49	0.30
Number of areoles per cm^2	−0.83	0.14	−0.35	0.19	−0.63	0.18	0.76	0.23
Peel thickness	−0.57	0.53	−0.50	0.23	0.15	0.65	0.36	0.34
% edible part of fruit mass	0.72	−0.50	−0.25	0.04	0.24	−0.71	0.10	0.42
% water of pulp mass	0.52	−0.65	0.03	0.22	0.52	0.22	0.17	−0.19
Number of seeds per fruit	0.55	0.43	0.71	−0.65	0.54	−0.28	0.06	−0.43
Mean seed mass	0.81	−0.01	0.70	0.13	0.65	0.19	−0.48	−0.04
Total seed mass per fruit	0.84	0.25	−0.40	0.42	0.75	−0.12	−0.01	−0.02
% seed mass of pulp mass	−0.57	0.04	0.01	0.52	−0.36	0.39	0.13	0.13

[a] Characters not analyzed in DFA.

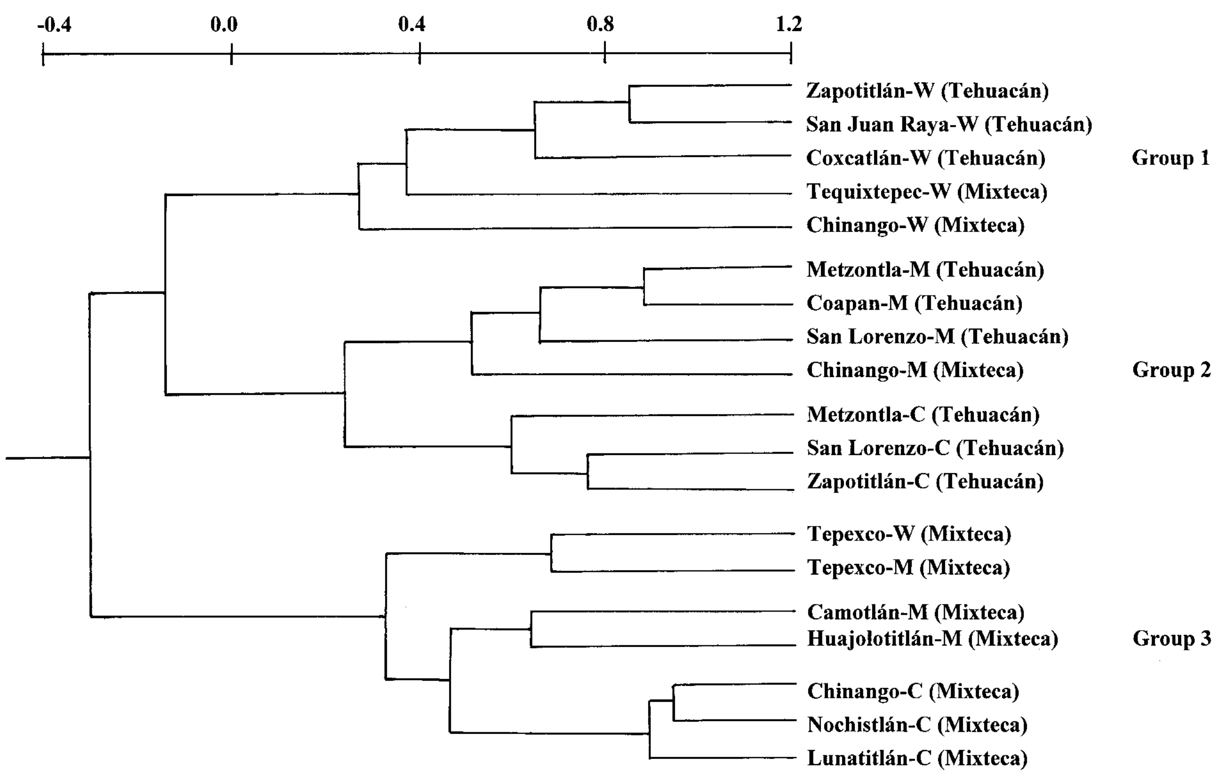

Fig. 4. Classification of populations of *Stenocereus stellatus* studied resulting from Cluster Analysis. Wild populations (a) from the Tehuacán Valley: Zapotitlán-W; San Juan Raya-W and Coxcatlán-W; (b) from La Mixteca: Chinango-W; Tepexco-W and Tequixtepec-W. Populations managed in situ (a) from the Tehuacán Valley: Metzontla-M; San Lorenzo-M and Coapan-M.; (b) from La Mixteca: Chinango-M; Tepexco-M; Camotlán-M and Huajolotitlán-M. Cultivated populations (a) from the Tehuacán Valley: Metzontla-C; San Lorenzo-C; Zapotitlán-C; (b) from La Mixteca: Chinango-C; Nochistlán-C and Lunatitlán-C.

TABLE 6. Mean values ± SE of morphological characters in wild, managed in situ, and cultivated populations from the Tehuacán Valley and La Mixteca Baja. F and P values according to two-way ANOVA. Mean values of populations with different type of management followed with the same letter did not differ at $P < 0.05$ after Tukey's HSD test.

Character	Regions (df = 1) Tehuacán	Mixteca	F	Management (df = 2) Wild	Managed	Cultivated	F	Region × Management (df = 2) F
Number of branches	16.6 ± 1.9	26.6 ± 1.8	14.75***	16.3 ± 2.4 (a)	20.3 ± 2.4 (a)	28.3 ± 1.9 (b)	8.09***	1.79
Length of the highest branch (m)	3.2 ± 0.07	3.7 ± 0.07	31.20***	3.6 ± 0.09 (a)	3.4 ± 0.09 (a)	3.6 ± 0.07 (a)	2.98	2.93
Diameter of the highest branch (cm)	13.2 ± 0.11	14.3 ± 0.11	42.33***	12.8 ± 0.15 (a)	13.9 ± 0.15 (b)	14.6 ± 0.12 (c)	45.79***	29.30***
Number of ribs	10.1 ± 0.08	9.9 ± 0.08	2.95	9.6 ± 0.11 (a)	9.9 ± 0.09 (b)	10.4 ± 0.10 (c)	14.75***	3.30*
Rib width (cm)	3.1 ± 0.04	3.5 ± 0.04	55.61***	3.1 ± 0.05 (a)	3.3 ± 0.05 (a)	3.5 ± 0.04 (b)	20.16***	36.22***
Rib depth (cm)	2.5 ± 0.03	2.9 ± 0.03	78.62***	2.6 ± 0.04 (a)	2.6 ± 0.04 (a)	2.9 ± 0.03 (b)	22.98***	8.50***
Number of spines per areole	14.4 ± 0.17	13.0 ± 0.17	33.85***	12.6 ± 0.22 (a)	13.7 ± 0.18 (b)	14.8 ± 0.22 (c)	24.43***	1.12
Size of the central spine (mm^2)	0.21 ± 0.01	0.29 ± 0.01	101.84***	0.22 ± 0.01 (a)	0.26 ± 0.01 (b)	0.26 ± 0.01 (b)	13.49***	23.96***
Distance between areoles (cm)	2.3 ± 0.03	2.6 ± 0.03	52.02***	2.5 ± 0.04 (a)	2.4 ± 0.04 (a)	2.5 ± 0.03 (a)	2.82	1.73
Fruit size (cm^3)	33.4 ± 1.51	53.6 ± 1.48	90.97***	31.4 ± 1.96 (a)	41.0 ± 1.94 (b)	58.2 ± 1.58 (c)	61.21***	2.77
Number of areoles per fruit	28.1 ± 0.48	31.3 ± 0.47	21.73***	30.4 ± 0.62 (a)	28.7 ± 0.61 (a)	30.0 ± 0.50 (a)	2.13	9.92***
Number of areoles per cm^2	2.6 ± 0.06	2.1 ± 0.05	38.88***	3.0 ± 0.07 (c)	2.2 ± 0.07 (b)	1.7 ± 0.06 (a)	102.31***	3.44*
Peel thickness (mm)	0.34 ± 0.007	0.33 ± 0.007	2.03	0.38 ± 0.009 (b)	0.31 ± 0.009 (a)	0.32 ± 0.007 (a)	22.58***	0.48
Number of seeds per fruit	1054.8 ± 25.5	1248.9 ± 25.0	29.52***	975.9 ± 33.1 (a)	1219.8 ± 32.7 (b)	1289.9 ± 26.6 (c)	24.07***	0.65
% water of pulp mass	82.4 ± 0.34	88.3 ± 0.34	149.38***	84.2 ± 0.45 (a)	85.7 ± 0.44 (b)	86.8 ± 0.36 (c)	7.70***	4.63**
% edible part of fruit mass	53.6 ± 0.72	63.0 ± 0.70	88.86***	53.0 ± 0.93 (a)	58.7 ± 0.92 (b)	63.2 ± 0.75 (c)	37.19***	2.29
Mean seed mass (mg)	1.12 ± 0.02	1.17 ± 0.02	5.08*	0.96 ± 0.02 (a)	1.13 ± 0.02 (b)	1.35 ± 0.02 (c)	89.45***	12.01***
Total seed mass (g)	1.18 ± 0.04	1.42 ± 0.04	21.81***	0.97 ± 0.05 (a)	1.32 ± 0.05 (b)	1.62 ± 0.04 (c)	58.04***	5.46**
% seed mass of pulp mass	7.8 ± 0.25	5.1 ± 0.25	62.16***	7.5 ± 0.32 (b)	6.2 ± 0.32 (a)	5.7 ± 0.26 (a)	9.47***	2.19

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

TABLE 7. Percentage of individuals exhibiting character states of qualitative characteristics of fruits in populations of *Stenocereus stellatus* from the Tehuacán Valley and La Mixteca Baja.

Character	Tehuacán Valley Wild	Managed in situ	Cultivated	La Mixteca Baja Wild	Managed in situ	Cultivated
Form						
Spherical	67.4	65.3	67.3	55.0	52.0	50.0
Elongated	32.6	34.7	32.7	45.0	48.0	50.0
Peel color						
Red	96.0	93.0	87.3	100.0	85.5	57.8
Green	4.0	7.0	12.7	0.0	15.5	42.2
Pulp color						
Red	100.0	100.0	89.0	95.0	86.7	56.7
Not red	0.0	0.0	11.0	5.0	13.3	43.3
Flavor						
Sour	100.0	47.0	29.0	72.5	11.0	16.7
Sweet	0.0	53.0	71.0	27.5	89.0	83.3

cultivated populations, probably because artificial selection is particularly intense under the continual planting and replacing of individuals cultivated in home gardens.

Although part of the phenotypes of managed in situ and cultivated populations originated from wild populations, some cultivated phenotypes were rare or not observed in the wild. This is particularly the case of individuals with large fruits and pulp colors other than red. Thus, only 2.3% of the individuals sampled in wild populations were found presenting pink and yellow pulp, whereas other pulp colors (purple, orange and white) were not observed in the wild. On the other hand, nearly 42% of individuals sampled in cultivated populations of La Mixteca were of these phenotypes. The questions are still open of whether these phenotypes originated in the wild and were carried to home gardens or if they originated in home gardens and escaped to the wild. But, regardless of these possible origins, it seems to be clear that success of such phenotypes is low in the wild and it only may be higher under human protection. In other words, domestication of *S. stellatus* appears to have been operating by protecting and enhancing individuals whose morphological characteristics are favorable to humans but that are scarce (some of them probably absent) in the wild.

The most important characters for explaining the patterns of variation in populations and the ordination of individuals in PCA and DFA are: (1) fruit size (larger among cultivated individuals); (2) density of spines in fruits (higher in fruits of wild individuals); (3) peel thickness (thicker in fruits of wild individuals); (4) total mass of seeds (higher in fruits of cultivated individuals); (5) mean seed mass (heavier in cultivated individuals); and (6) proportion of edible part in fruits (higher in cultivated individuals). Pulp color was relevant in the classification of groups only in La Mixteca, where individuals with ''not red'' pulp fruits were abundant in cultivated populations, whereas flavor of fruits was relevant in the Tehuacán Valley, where the proportion of individuals producing sweet fruits was markedly different between wild, managed in situ, and cultivated populations. Among the vegetative characters, only the dimensions of ribs and branches seemed relevant (larger dimensions in cultivated individuals).

Most of these characters are those that constitute direct targets of selection by people (Casas et al., 1997b), which reinforces the conclusion that artificial selection is the crucial factor for explaining the divergence between wild and manipulated populations. The only exceptions are amount and mass of seeds, which were significant characters even though people informed us that they are not targets of selection. Changes in these characteristics might be a consequence of selection for larger fruits because, since the pulp is formed by funiculus (Bravo-Hollis, 1978), both the amount of pulp and fruit size would be related with amount and size of funiculus. In fact, correlation between these characters presented relatively high values. However, a possible occurrence of human selection on this character in the past should not be discarded since consumption of seeds separately from pulp apparently has occurred since prehistoric times (Callen, 1967; Casas et al., 1997b).

Morphological variation of *S. stellatus* appeared to be influenced also by environmental conditions. Thus, CA clustered populations in part according to the region from which they originated and univariate analyses of variance found significant differences between populations of the two regions in most of the morphological characteristics analyzed. The populations sampled in the two regions present differences in annual mean temperatures, soils, and vegetation types (Table 1). However, the most clear environmental difference between the regions, and probably the most significant for explaining morphological variation, is annual precipitation, which is significantly higher in la Mixteca (720.5–763.7 mm) than in the Tehuacán Valley (440.6–590.0 mm).

Some of the morphological characters distinguishing populations of *S. stellatus* across the regions appear to be affected by differences in rainfall. This is the case of the dimensions of branches, which are related with the turgidity of branch tissue. In general, branches of this species presented greater length and diameter in La Mixteca than in Tehuacán. Differences in robustness of the branches were pronounced among wild and managed in situ populations, which are exposed to natural environmental conditions, but not among cultivated populations, which are exposed to environments that occasionally are watered by people. Fruit size would also be expected to be influenced by availability of water, since the bigger fruits from La Mixteca generally presented a higher proportion of water in pulp than the smaller fruits from Tehuacán. However, the correlation between fruit size and proportion of water in pulp is low (0.56 in Tehuacán and 0.44 in La Mixteca), indicating that fruit size is not simply determined by amount of water.

Qualitative morphological characters were also different across the regions. Thus, a higher proportion of individuals in populations from La Mixteca produced fruits with green peel, pulp color different than red and sweet flavor (Table 7). But, apart of human selection, factors influencing such characteristics in wild populations are unknown.

In conclusion, although populations of *S. stellatus* of the two regions differ morphologically, probably due to environmental differences, within each region wild and manipulated populations have diverged morphologically presumably due to artificial selection. Although the strongest level of divergence from wild populations was found to occur in cultivated populations, it is also significant in wild populations managed in situ. This strongly suggests that domestication in situ is an ongoing process in this plant species.

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