

Maintenance of phenotypic and genotypic diversity in managed populations of *Stenocereus stellatus* (Cactaceae) by indigenous peoples in Central Mexico

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Abstract. The columnar cactus *Stenocereus stellatus* is used in Central Mexico for its edible fruits which are harvested in wild, managed *in situ* and cultivated populations. Management *in situ* of wild populations is conducted by selectively sparing and enhancing the abundance of plants with desirable phenotypes when fields are cleared for agricultural use. Cultivation of desirable phenotypes is carried out by vegetative propagation in homegardens. Effects of human management on morphological and genetic variation of *S. stellatus* were analyzed by comparing morphological diversity indices (MD, based on Simpson's index) and expected (H_e) heterozygosity indices from allozyme analysis, in wild, managed *in situ*, and cultivated populations from La Mixteca and the Tehuacán Valley regions. Morphological diversity was similar among regions, but populations from the wetter La Mixteca region averaged higher genetic variation ($H_e = 0.279$) than populations from Tehuacán ($H_e = 0.265$). On average, populations manipulated by people had higher levels of variation (MD = 0.479 ± 0.012 , $H_e = 0.289$ in cultivated populations; MD = 0.461 ± 0.014 , $H_e = 0.270$ in managed *in situ* populations) than wild populations (MD = 0.408 ± 0.017 , $H_e = 0.253$), which is apparently due to a continual introduction and replacement of plant materials in the manipulated populations. The results illustrate that human management may not only maintain but also increase both morphological and genetic diversity of manipulated plant populations in relation to that existing in the wild. Managed *in situ* and cultivated populations of *S. stellatus* are important reservoirs of variation, and are crucial for the general maintenance of diversity in wild populations. These populations may play a principal role in designing strategies for the conservation of variation of this cactus.

Introduction

Human manipulation and transformation of environments and organisms are generally thought to cause a reduction of biological diversity at either community or population levels (Wilson 1988). However, exceptions to such

destructive impact have been documented by studies among indigenous peoples throughout the world. Indigenous peoples are the inhabitants, users, and stewards of the areas with the highest biodiversity on Earth (Brush and Stabinsky 1996; Toledo 2001), and they commonly manage the local environment in a way that maintains or even increases the diversity of living forms (Nabhan et al. 1982; Posey 1985; Gadgil et al. 1993; Haverkort and Millar 1994; Reichhardt et al. 1994; Toledo et al. 1994). Maintenance of biodiversity is influenced by human cultural processes (Bellón and Brush 1994; Bellón 1996) and, therefore, cultural survival has increasingly been considered a keystone for conservation of biological diversity (Gadgil et al. 1993). Consequently, understanding indigenous technology and ecosystem management can significantly contribute to development of conservation strategies.

Indigenous peoples commonly use and manage at the same time different species, landraces, and varieties of crop plants. This is indicative of an active manipulation of considerable plant diversity (see examples in Zizumbo and Colunga 1982; Alcorn 1984; Alvarez-Buylla et al. 1989; Caballero 1991; Oldfield and Alcorn 1991; Casas et al. 1994; Bellón 1996; Brush and Stabinsky 1996; Nazarea 1998; Amorozo 2000; Brush 2004). However, comparisons of the variation existing in manipulated populations with variation in wild or weedy populations of relatives of crop species are rarely documented. Our research, therefore, was focused on analyzing the effects of human management on the biological diversity within sympatric wild and managed populations of a single plant species.

Mexico has been recognized as one of the areas with the highest biological and cultural diversity (Toledo and Ordóñez 1993; Toledo 2001), as well as one of the main centers of domestication of plants of the world (Harlan 1975; Hawkes 1983). Mexican indigenous peoples have interacted with a broad spectrum of plants since prehistory (Smith 1967; MacNeish 1992), including some of the crops currently cultivated worldwide, and numerous plant species used at regional level. Columnar cacti are important plant resources since they are dominant components of arid and semiarid areas covering nearly half the Mexican territory (Casas and Barbera 2002), and they have been used by people for thousands of years (MacNeish 1967; Smith 1967). At present, these plants are widely used by indigenous peoples as food (fruit, flower buds, young stems, seeds), fodder (fruit, branches), medicine (branches), fuel (wood), construction (wood), and soil protection (barriers and fences constructed with entire individuals) (Casas et al. 1999; Casas and Barbera 2002; Casas et al. 2002). Products of most columnar cacti are gathered in the wild, but 20 species are under silvicultural management, and 12 species are also cultivated, wild and managed populations commonly being sympatric (Casas et al. 1999; Casas and Barbera 2002).

This study analyzed the case of *Stenocereus stellatus* (Pfeiffer) Riccobono, a columnar cactus endemic to Central Mexico. Fruits, flowers, and seeds of *S. stellatus* (common name 'xoconochtlí') are used as food, branches are

used as fodder and fuel, and individual plants are used as barriers to protect soil erosion (Casas et al. 1997). Wild populations of this cactus species occur as part of thorn-scrub and tropical deciduous forests in the Tehuacán Valley and the portion of the Balsas river basin in the intersection of the states of Morelos, Puebla, Guerrero, and Oaxaca (Figure 1). Local people, especially those belonging to the Nahuatl, Popoloca, and Mixtec indigenous ethnic groups, may obtain useful products of xococonchli by gathering them in wild populations. Additionally, people harvest products from populations managed *in situ* as well as from cultivated populations in homegardens (Casas et al. 1997). Populations managed *in situ* result from selective sparing and enhancing the abundance of particularly desirable individuals through vegetative propagation, while also eliminating others during land clearing. Because management *in situ* involves the manipulation of wild populations, this form of management has been considered as silviculture (Casas et al. 1997). Cultivation in homegardens is carried out by vegetative propagation of branches of desirable wild or previously cultivated phenotypes, and also by sparing desirable individuals spontaneously established from seeds dispersed by birds, bats and humans in their feces (Casas et al. 1997).

Casas et al. (1997, 1999a) found that morphological features such as fruit color, flavor, amount of edible matter, peel thickness, and spine number are distinguished by people to characterize products. These fruit characters are the basis for selectively favoring certain *S. stellatus* individuals. The selective sparing and enhancing of desirable phenotypes constitute mechanisms of artificial selection, which have had significant effects on the composition of phenotypes in managed *in situ*, and cultivated populations. According to Casas et al. (1997; 1999a), phenotypes which produce fruit with desirable attributes are more abundant in managed *in situ* populations than in the wild, and more so in cultivated populations, where unique phenotypes absent from the wild are common.

In this study, we tested the hypothesis that if artificial selection is significant in managed *in situ* and cultivated populations, favoring only a portion of the existing variation in wild populations, a reduction of biological diversity compared to wild populations should be expected. Also, we tested the hypothesis that higher diversity might be expected in homegardens compared with that in populations managed *in situ*. This last hypothesis is based on the observation by Casas et al. (1997, 1999a, 1999b) that management *in situ* involves the sparing and enhancing of a subsample of wild phenotypes, whereas cultivation involves continual replacement of individual plants, introduction of plant material from different homegardens and villages, and the establishment of seedlings derived from sexual reproduction. These hypotheses are consistent with a pattern generally documented in crop plants, in which cultivated varieties may show a higher morphological variation than their wild relatives (Hawkes 1983) but, because crop plants generally involve a small fraction of the gene pool of the species, wild populations generally have

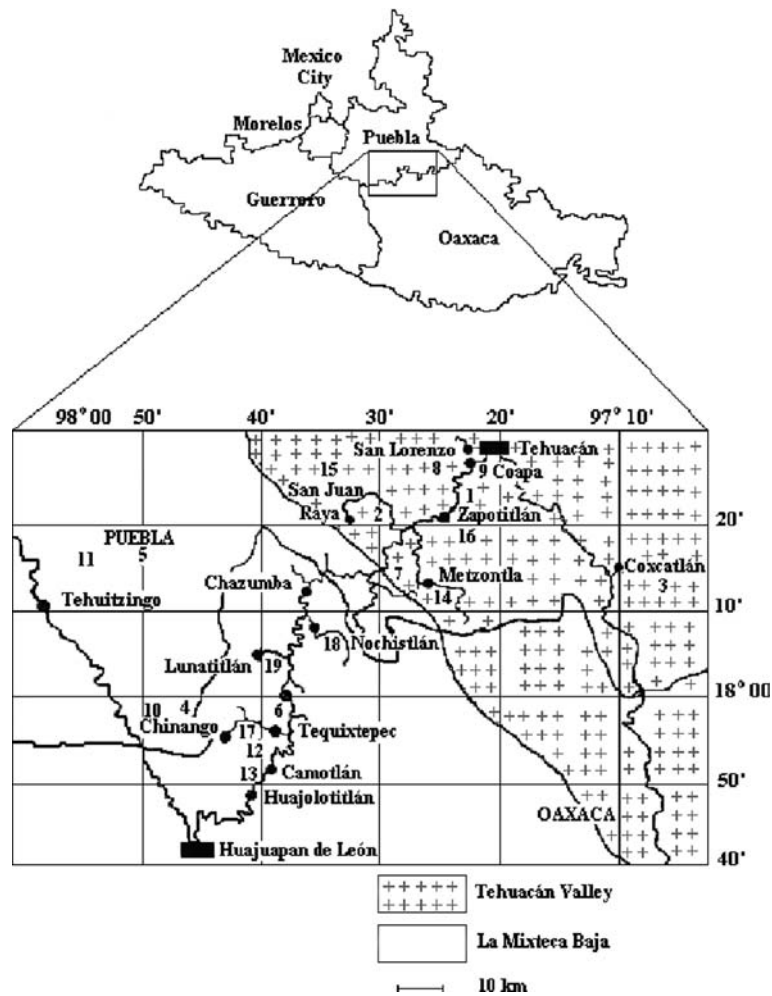


Figure 1. Range of distribution of *S. stellatus* and populations studied in the Tehuacán Valley and La Mixteca regions.

higher genetic diversity than cultivated ones (Harlan 1975; Hawkes 1983; Doebley 1992).

In this study, patterns of both morphological and genetic variation in populations of *S. stellatus* were examined in environments under different forms of management in order to test the hypotheses that manipulated populations are less diverse than wild ones, and that cultivated populations are more diverse than those under silvicultural management. The purpose was to determine how artificial selection has altered the patterns of variation existing in the species, and to examine the role of manipulated populations in the maintenance of diversity.

Methods

Study site

The study was conducted in the Tehuacán Valley and La Mixteca Baja regions, in central Mexico. The Tehuacán Valley is an area of nearly 10,000 km², located in the southeast of the state of Puebla and the northwest of the state of Oaxaca (Figure 1), which forms part of the Papaloapan river basin. It is a complex physiographic mosaic with internal valleys separated by mountain chains, in which 29 types of plant associations have been described (Valiente-Banuet et al. 2000). The climate is semiarid, with an annual mean precipitation of 400 mm and an annual mean temperature of 21 °C (Dávila et al. 2002). Columnar cacti are distributed in thorn-scrub and tropical deciduous forests. La Mixteca Baja covers an area of approximately 50,000 km², located in the northwest of the state of Oaxaca, the northeast of the state of Guerrero and the southwest of the state of Puebla, forming part of the Balsas river basin (Casas et al. 1994). It is a complex mountainous region with elevations ranging from 600 to 3000 m, with thorn-scrub and tropical deciduous forests in the lower dry and warm settings to pine and fir forests in the higher wet and temperate areas. Columnar cacti occur in the lower settings, where annual mean temperature is 22 °C and annual mean precipitation is 760 mm (Casas et al. 1994). A total of 19 populations of *S. stellatus* were studied in both regions (Figure 1), including six wild populations, seven populations managed *in situ* in areas recurrently cleared for agriculture, where desirable *S. stellatus* were left, and six homegardens from the same number of villages. Table 1 shows general information on particular habitats of the populations studied. Populations within the Tehuacán Valley are separated up to 61 km (the most distant populations were those from San Lorenzo and Coxcatlán), whereas populations within La Mixteca are separated up to 40 km (the most distant populations are those from Lunatitlán and Huajolotitlán) (see Figure 1). The most distant populations studied are those from Coxcatlán and Huajolotitlán, which are separated by a distance of 98 km.

Study system

Stenocereus stellatus is an arborescent, succulent, columnar cactus that may be 2–6 m in height when mature, characteristically branching at base, stems of pale bluish green or dark green color and red or pink flowers forming crowns in the top of the branches. Fruits are spherical or ellipsoid, spiny, green or red peeled berries 20–75 cm³ in size, size strongly varying according to amount of rainfall and management type (Casas et al. 1997, 1999a; Casas et al. 2002). Fruit pulp may be red, white, pink, purple, yellow or orange, the red color being predominant in wild populations (nearly 95% of individuals), whereas in cultivated populations pulp colors other than red may be present in more than

Table 1. Location and habitat description for sampled populations of *Stenocercus stellatus*. Capital letters at the end of population names indicate management type (W = wild subject to gathering, M = managed *in situ*, and C = cultivated).

| Population | Elevation (m) | Annual mean temp. (°C) | Annual rainfall (mm) | Habitat | Density of population (plants ha ⁻¹) | Indiv. analyzed (morphology) | Indiv. analyzed (genetic variation) |
|-------------------|---------------|------------------------|----------------------|---------|--|------------------------------|-------------------------------------|
| <i>Tehuacan</i> | | | | | | | |
| Zapotitlán-W | 1550 | 21.2 ^d | 450.0 ^a | Tsf | 273 | 24 | 48 |
| S.J. Raya-W | 1800 | 20.9 ^a | 649.7 ^a | Tsf | 29 | 20 | 48 |
| Coxcatlán-W | 1000 | 23.8 ^a | 440.6 ^a | Tsf | 280 | 20 | 48 |
| Metzontla-M | 2000 | 17.2 ^b | 527.9 ^b | Af | 120 | 20 | 48 |
| S. Lorenzo-M | 1700 | 19.1 ^a | 590.0 ^a | Faf | 34 | 20 | 48 |
| Coapan-M | 1650 | 18.6 ^a | 479.6 ^a | Faf | 42 | 20 | — |
| Metzontla-C | 1900 | 17.2 ^b | 527.9 ^b | H | 781 | 30 | 48 |
| S. Lorenzo-C | 1700 | 19.1 ^a | 590.0 ^a | H | 172 | 20 | — |
| Zapotitlán-C | 1550 | 21.4 ^a | 450.0 ^a | H | 158 | 20 | — |
| <i>La Mixteca</i> | | | | | | | |
| Chinango-W | 1700 | 20.6 ^a | 720.5 ^a | Tdf | 35 | 20 | 48 |
| Tepeaco-W | 1150 | 23.0 ^a | 763.7 ^a | Tdf | 14 | 20 | — |
| Tequixtepec-W | 1650 | 20.6 ^a | 720.5 ^a | Tdf | 9 | 20 | — |
| Chinango-M | 1700 | 20.6 ^a | 720.5 ^a | Af | 48 | 20 | 48 |
| Tepeaco-M | 1100 | 23.0 ^a | 763.7 ^a | Faf | 42 | 20 | — |
| Camotlán-M | 1600 | 20.6 ^a | 720.5 ^a | Faf | 38 | 20 | — |
| Huajolotitlán-M | 1600 | 20.6 | 720.5 | Faf | 28 | 20 | — |
| Chinango-C | 1600 | 20.6 ^a | 720.5 ^a | H | 259 | 50 | 48 |
| Lunatitlán-C | 1650 | 20.6 ^a | 720.5 ^a | H | 176 | 20 | — |
| Nochistlán-C | 1650 | 20.6 ^a | 720.5 ^a | H | 181 | 20 | — |

In the column of Habitat, Tsf = thorn-scrub forest, Tdf = tropical deciduous forest, Af = agricultural fields, Faf = fallow agricultural fields, H = homegardens. ^aInformation based on García (1988); ^bInformation based on Valiente (1991).

40% of individuals (Casas et al. 1999a). *S. stellatus* has vegetative propagation which naturally occurs from branches that fall down, and people take advantage of this characteristic for cultivation and management *in situ* (Casas et al. 1997). Casas et al. (1999b) reported that this species has also sexual reproduction with a marked self-incompatible breeding system. According with these authors, flowers have nocturnal anthesis and are pollinated by nectarivorous bats, with no significant differences in flower morphology and behavior, blooming season, pollination biology, and breeding system between wild and manipulated populations. Seed dispersal is carried out by frugivorous bats and birds, as well as by humans (Casas et al. 1997). According to Casas et al. (1999b), spatial barriers to pollen or seed flow among wild and manipulated populations are unlikely because of the intervention of bats and birds in these processes. For instance, bats of the genus *Leptonycteris*, the most important bats pollinating *S. stellatus* (Casas et al. 1999b), have been reported by Horner et al. (1998) to fly in a single night as much as 100 km from their roosts to feed at cactus flowers and fruit in the Sonoran Desert. Temporal barriers are also unlikely since blooming season overlaps in wild and manipulated populations from both La Mixteca and the Tehuacán Valley.

Sampling of populations

Samples of 20–50 individuals were analyzed from all 19 populations studied (Table 1). Vegetative characters were measured in the field in the individuals sampled, and samples of five fruits produced by those individuals were collected for morphological analyses. Samples of 48 individuals from ten of the above populations were collected for the allozyme survey.

Since *S. stellatus* propagates vegetatively, an individual of this species was considered to be a unit of branches emerging together from the ground. Because morphological comparisons included fruits, only individuals of reproductive stage were sampled for that purpose. For allozyme analysis reproductive and not reproductive individuals were sampled. Sampled individuals were permanently marked with metal tags and numbers drawn in waterproof ink to identify them during successive years.

Wild and managed *in situ* populations were sampled with transects to facilitate collection from different environmental conditions and to encompass the size and density of the population. Transects 10 m wide were used (sometimes placed side by side in the population) to map the spatial position of all plants in the population for population genetics studies. Transect length was at least 50 m but it was defined according to the size of the population, the environmental heterogeneity, and the density of the population, in order to include at least 20 reproductive plants within the maximum longitudinal distance covered by the populations.

In cultivated populations the sampling units were homegardens. Approximately 10% of homegardens in a village were sampled at random, and nearly

20% of all the individuals present at a homegarden were chosen for the study, and the selection of these plants was at random.

Morphometric analysis

A total of 23 morphological characters were analyzed, including 19 quantitative characters of both vegetative and reproductive parts, as well as 4 qualitative characters of fruits (Table 2). Individual plants were considered a unit. Mean values per plant were calculated for quantitative characters by measuring three to five parts (branches, ribs, areoles, spines or fruits) and 300–500 seeds per plant. Qualitative characters included fruit form (spherical or elongated), peel color (red or green), pulp color (red or not red), and pulp flavor (sour or sweet).

Simpson's index was used for estimating morphological diversity in the populations studied. This index is defined as $D = 1 - \sum_{i=1}^s (p_i)^2$, where p_i is the proportion of the total number of individuals sampled in a population representing the i th morphological character state, and s is the number of morphological character states.

For the morphological diversity index, frequencies of qualitative characters were calculated directly, whereas quantitative characters were transformed into multistate qualitative variables from which character state frequencies were calculated. Quantitative character ranges were converted into discrete classes based upon one-way analyses of variance performed for each quantitative character among the 19 populations studied. Intervals significantly different, calculated through Tukey's highest significant difference range tests, were used to determine categorical values of continuous variables. Qualitative states were defined by the lowest limit of a given interval and the lowest limit of the next significantly different interval (Table 2). The total number of character states per population was then defined and the frequency of each character state calculated per population. The average of diversity indices of all characters per population was calculated and considered as the Morphological Diversity index (MD) per population. Significance of differences in MD among populations, groups of populations pooled by region, and by management type was tested with non parametric Wilcoxon tests (JMP, SAS Institute 1996). Comparisons among pairs of populations or groups of populations (per region and per management type) were tested with t tests.

Allozyme analysis

A total of 48 individuals per population were sampled in ten of the 19 populations of *S. stellatus* studied, including three wild, four managed *in situ*, and three cultivated populations from both regions. Stem tissue and/or immature flower buds were collected from each cactus, snap frozen in liquid nitrogen and

Table 2. Morphological characters analyzed in *Stenocercus stellatus*. Intervals are ranges of quantitative characters significantly different according to Tukey HSD tests, which correspond to one categorical state.

| Character | Units | Interval | State | Interval | State | Interval | State | Interval | State |
|-----------------------------------|-----------------|-------------|-------|-------------|-------|-------------|-------|-------------|-------|
| Number of branches | number | 1.00–18.50 | 1 | 18.60–52.00 | 2 | | | | |
| Branch length | m | 2.10–3.15 | 1 | 3.16–4.15 | 2 | 4.16–5.40 | 3 | | |
| Branch diameter | cm | 9.70–11.50 | 1 | 11.60–13.50 | 2 | 13.60–16.00 | 3 | | |
| Number of ribs | number | 7.80–8.95 | 1 | 8.96–10.65 | 2 | 10.66–11.70 | 3 | | |
| Rib width | cm | 2.21–2.70 | 1 | 2.71–3.21 | 2 | 3.22–3.46 | 3 | 3.47–4.10 | 4 |
| Rib depth | cm | 2.05–2.40 | 1 | 2.41–2.85 | 2 | 2.86–3.30 | 3 | | |
| Spines per areole | number | 9.60–12.60 | 1 | 12.70–15.40 | 2 | 15.50–18.10 | 3 | | |
| Central spine size | mm ² | 0.080–0.190 | 1 | 0.191–0.280 | 2 | 0.281–0.370 | 3 | 0.371–0.470 | 4 |
| Distance between areoles | cm | 1.80–2.19 | 1 | 2.20–2.60 | 2 | 2.61–3.20 | 3 | | |
| Areoles per fruit | number | 20.5–29.1 | 1 | 29.2–38.0 | 2 | | | | |
| Areoles/cm ² in fruits | number | 1.10–1.84 | 1 | 1.85–2.61 | 2 | 2.62–3.30 | 3 | 3.31–4.11 | 4 |
| Peel thickness | mm | 0.190–0.291 | 1 | 0.292–0.391 | 2 | 0.392–0.530 | 3 | | |
| Fruit size | cm ³ | 5.00–32.00 | 1 | 32.10–55.80 | 2 | 55.90–90.00 | 3 | | |
| Amount of water in pulp | % | 75.00–81.90 | 1 | 82.00–87.20 | 2 | 87.30–94.00 | 3 | | |
| Amount of pulp in fruits | % | 36.00–49.80 | 1 | 49.90–63.00 | 2 | 63.10–74.00 | 3 | | |
| Number of seeds per fruit | number | 500–990 | 1 | 991–1250 | 2 | 1251–1700 | 3 | | |
| Mean seed mass | mg | 0.55–0.82 | 1 | 0.83–1.08 | 2 | 1.09–1.37 | 3 | 1.38–1.68 | 4 |
| Total seed mass per fruit | g | 0.40–0.96 | 1 | 0.97–1.49 | 2 | 1.50–2.10 | 3 | | |
| Ratio of seed mass of pulp | % | 0.020–0.051 | 1 | 0.052–0.090 | 2 | 0.091–0.123 | 3 | | |
| Fruit form | category | spherical | 1 | elongated | 2 | | | | |
| Peel color | category | red | 1 | green | 2 | | | | |
| Pulp color | category | red | 1 | not red | 2 | | | | |
| Pulp flavor | category | sour | 1 | sweet | 2 | | | | |

stored at $-70\text{ }^{\circ}\text{C}$ for genetic analysis. Frozen samples for allozyme analysis were ground to a fine powder with a mortar and pestle with liquid nitrogen and a polyvinylpyrrolidone-phosphate buffer (Mitton et al. 1979) to stabilize the proteins. The extract was absorbed onto filter paper wicks and stored at $-70\text{ }^{\circ}\text{C}$ until run on starch gels. For the allozyme analysis 4 buffer systems and 11 enzyme stains were used to resolve 15 putative allozyme loci: aspartate aminotransferase (AAT1, AAT2), alcohol dehydrogenase (ADH1), diaphorase (DIA1), fluorescent esterase (FE1), isocitrate dehydrogenase (IDH1), 6-phosphogluconate dehydrogenase (6-PGD2), phosphoglucose isomerase (PGI1, PGI2), phosphoglucomutase (PGM1, PGM2), shikimic dehydrogenase (SKDH1), triosephosphate isomerase (TPI1, TPI2), and UTP-glucose-1-diphosphate (UGPP1). Two to four alleles were found at each of the ten polymorphic loci.

Genetic diversity parameters were estimated using an unpublished computer program developed by M. D. Loveless and A. F. Schnabel and by POPGENE (Yeh et al. 1997). Gene and genotype frequencies were estimated for each population, as well as standard genetic diversity statistics at the population, region, type of management and species (pooled) levels (Hedrick 1983; Hamrick and Godt 1989). These statistics included: percent of polymorphic loci (P), mean number of alleles per locus (A), and expected heterozygosity (H_e). Differences in the mean value for P , A and H_e were compared between management types (wild, managed *in situ* and cultivated) and between pooled regional values (Tehuacán and Mixteca). Significant differences in P were determined with non-parametric Kruskal-Wallis H tests (SAS Institute 2000). Similarly, a non-parametric Kruskal-Wallis H test for significant differences in expected heterozygosity (H_e) between the different harvest types was performed on jackknifed values (Weir and Cockerham 1984). Significant differences in A were tested with ANOVA (JMP, SAS Institute 1996).

Results

Details of the morphological diversity indices per population are available by request to the first author. The highest values of morphological diversity were recorded in the cultivated population of Metzontla, in Tehuacán (MD = 0.546 ± 0.024 , average \pm S.E), the wild population of Chinango, in La Mixteca (MD = 0.515 ± 0.033), and the managed *in situ* populations of Tehuacán (MD = 0.519 ± 0.032 in Coapan, MD = 0.507 ± 0.030 in Metzontla, and MD = 0.488 ± 0.033 in San Lorenzo), whereas the lowest values were recorded in the wild population of San Juan Raya, in Tehuacán (MD = 0.278 ± 0.045) and the managed *in situ* population of Chinango, in La Mixteca (MD = 0.368 ± 0.042) (Table 3). On average, the highest levels of morphological diversity occurred in the managed *in situ* populations of Tehuacán (MD = 0.505 ± 0.018) and the cultivated populations of both regions (MD = 0.489 ± 0.017 in Tehuacán and MD = 0.468 ± 0.017 in

La Mixteca) (Table 3). The lowest levels were recorded in the wild populations of Tehuacán (average MD = 0.364 ± 0.025), especially San Juan Raya, followed by those of the managed *in situ* populations of La Mixteca (average MD = 0.428 ± 0.019), especially those of Chinango and Tepexco. In the Tehuacán Valley, average morphological diversity in managed *in situ* and cultivated populations was significantly higher than in wild populations ($\chi^2 = 21.06$, $df = 2$, $p < 0.0001$), whereas in La Mixteca there were no significant differences in morphological diversity among populations under different management types ($\chi^2 = 2.10$, $df = 2$, $p = 0.349$).

Average morphological diversity in populations between regions was similar (0.453 ± 0.012 in Tehuacán and 0.447 ± 0.012 in La Mixteca, $\chi^2 = 0.25$, $df = 1$, $p = 0.617$). However, comparison of average indices by type of management across regions indicates that morphological diversity in wild populations of La Mixteca was significantly higher (MD = 0.453 ± 0.023) than in wild populations of Tehuacán (MD = 0.364 ± 0.025 ; $\chi^2 = 7.25$, $df = 1$, $p < 0.007$). In contrast, managed *in situ* populations of Tehuacán had higher average diversity (MD = 0.505 ± 0.018) than managed *in situ* populations of La Mixteca (MD = 0.428 ± 0.019 ; $\chi^2 = 9.21$, $df = 1$, $p = 0.002$). Morphological diversity in cultivated populations of both regions was similar (0.489 ± 0.017 in Tehuacán and 0.468 ± 0.017 in La Mixteca, $\chi^2 = 0.465$, $df = 1$, $p = 0.497$) (Table 3).

Cultivated and managed *in situ* populations from both regions had significantly higher average variation (MD = 0.479 ± 0.012 in cultivated populations, MD = 0.461 ± 0.014 in managed *in situ* populations) than wild populations (MD = 0.408 ± 0.017 ; $\chi^2 = 6.96$, $df = 2$, $p < 0.031$) (Table 3).

The highest levels of genetic variation (Table 3) were recorded in the cultivated population of Chinango, in La Mixteca ($p = 92.86$, $A = 2.50$, $H_e = 0.333$) and in the managed *in situ* populations of San Lorenzo and Metzontla, in Tehuacán (in average $p = 89.29$, $A = 2.40$, $H_e = 0.288$). In contrast, the lowest variation was recorded in the wild populations of Coxcatlán and Zapotitlán, in Tehuacán (average $p = 82.14$, $A = 2.29$, $H_e = 0.241$), followed by the managed *in situ* population of Chinango and Camotlán, in La Mixteca (average $p = 78.57$, $A = 2.25$, $H_e = 0.253$). Cultivated populations had higher average of H_e than managed *in situ* populations, and these last in turn higher than wild populations ($H_e = 0.289$, $H_e = 0.270$, and $H_e = 0.253$, respectively). However, in other parameters wild populations had higher average diversity than managed *in situ* and cultivated population ($p = 85.71$, $p = 83.93$, $p = 78.57$, respectively; and $A = 2.38$, $A = 2.32$, $A = 2.36$, respectively). Comparisons of average diversity measures between populations under different management types yielded significant differences in expected heterozygosity (H_e , $p < 0.05$) but not percent polymorphic loci (P , $p = 0.28$) or mean number of alleles per locus (A , $p = 0.94$).

Average genetic variation in La Mixteca was higher ($p = 92.86$, $A = 2.50$, $H_e = 0.279$) than in Tehuacán ($p = 80.95$, $A = 2.32$, $H_e = 0.265$). This

Table 3. Measures of genetic variation and morphological diversity in populations of *Stenocereus stellatus* from the Tehuacán Valley and La Mixteca region.

| Region | Management type | Population | $P(\%)$ | A | H_e | MD |
|--------------------------------|--------------------------------|--------------------------------|---------|---------------|---------------|---------------|
| Tehuacán | Wild | Coxcatlán | 78.57 | 2.07 | 0.244 ± 0.060 | 0.410 ± 0.040 |
| | | Zapotitlán | 85.71 | 2.50 | 0.237 ± 0.061 | 0.404 ± 0.043 |
| | Management <i>in situ</i> | S.J. Raya | | | | 0.278 ± 0.045 |
| | | Average Wild | 82.14 | 2.29 | 0.241 | 0.364 ± 0.025 |
| | | San Lorenzo | 92.86 | 2.36 | 0.282 ± 0.056 | 0.488 ± 0.033 |
| | | Metzonlla | 85.71 | 2.43 | 0.293 ± 0.066 | 0.507 ± 0.030 |
| | | Coapan | | | | 0.519 ± 0.032 |
| | | Average managed <i>in situ</i> | 89.29 | 2.40 | 0.288 | 0.505 ± 0.018 |
| | Cultivated | Metzonlla | 85.71 | 2.57 | 0.311 ± 0.064 | 0.546 ± 0.024 |
| | | Zapotitlán | 57.14 | 2.00 | 0.222 ± 0.067 | 0.478 ± 0.030 |
| San Lorenzo | | | | | 0.443 ± 0.028 | |
| Average cultivated populations | | 71.43 | 2.29 | 0.267 | 0.489 ± 0.017 | |
| Mixteca | Wild | Regional average | 80.95 | 2.32 | 0.265 | 0.453 ± 0.012 |
| | | Chinango | 92.86 | 2.57 | 0.278 ± 0.064 | 0.515 ± 0.033 |
| | Tepexco | | | | 0.391 ± 0.045 | |
| | Tequixtepec | | | | 0.451 ± 0.037 | |
| | Managed <i>in situ</i> | Average wild | 92.86 | 2.57 | 0.278 | 0.453 ± 0.023 |
| | | Camotlán | 78.57 | 2.29 | 0.241 ± 0.062 | 0.461 ± 0.037 |
| | | Chinango | 78.57 | 2.21 | 0.265 ± 0.069 | 0.368 ± 0.042 |
| | | Tepexco | | | | 0.397 ± 0.036 |
| | Cultivated | Huajolotlán | | | | 0.485 ± 0.035 |
| | | Average managed <i>in situ</i> | 78.57 | 2.25 | 0.253 | 0.428 ± 0.019 |
| Chinango | | 92.86 | 2.50 | 0.333 ± 0.063 | 0.477 ± 0.033 | |
| Lumatitlán | | | | | 0.479 ± 0.027 | |
| Nochistlán | | | | | 0.448 ± 0.030 | |
| Average cultivated | | 2.86 | 2.50 | 0.333 | 0.468 ± 0.017 | |
| Both regions | Regional average | 85.72 | 2.39 | 0.279 | 0.447 ± 0.012 | |
| | Average wild | 85.71 | 2.38 | 0.253 | 0.408 ± 0.017 | |
| | Average managed <i>in situ</i> | 83.93 | 2.32 | 0.270 | 0.461 ± 0.014 | |
| | Average Cultivated | 78.57 | 2.36 | 0.289 | 0.479 ± 0.012 | |
| General | All populations | 82.86 | 2.35 | 0.264 | 0.450 ± 0.015 | |

Diversity parameters include: Percent polymorphic loci (P), mean number of alleles per locus (A), expected heterozygosity (H_e) and morphological diversity index (MD).

trend was consistent when comparing both wild and cultivated populations from the two regions, but was reversed in the case of the managed *in situ* populations, which were more diverse in Tehuacán (compare the regional averages of P , A , and H_e of wild, managed *in situ* and cultivated populations in Table 3). In the Tehuacán Valley, the highest variation was found in managed *in situ* populations, followed by cultivated populations, and the lowest variation was recorded in the wild (compare average values of P , A , and H_e per management type in that region in Table 3). In La Mixteca, the highest variation was found in the cultivated population, followed by the wild population, and the lowest variation was recorded in the managed *in situ* populations studied (compare average values of P , A , and H_e per management type in that region in Table 3). Comparisons of average diversity measures among populations within the Tehuacán Valley and La Mixteca indicated a significant difference in H_e ($p < 0.05$) but not in P ($p = 0.66$) or A ($p = 0.62$).

Correlation between morphological diversity and expected heterozygosity was not significant ($r = 0.515$, $p = 0.128$).

Discussion

Our study revealed that (1) populations of *S. stellatus* generally contain high levels of morphological and genetic diversity, (2) genetic diversity was higher in La Mixteca than in the Tehuacán Valley, (3) contrary to our expectations, both morphological and allozyme variation was generally higher in populations manipulated by people than in wild populations, and (4) traditional management of this cactus species appears to be important to design conservation strategies.

Morphological and genetic variation of S. stellatus

The average value of the morphological diversity index for the species studied was $MD = 0.450 \pm 0.015$ (Table 3) but, because the method developed here to estimate morphological diversity has not been used in other species, comparisons are not possible for the moment. This method and the index used could be useful to analyze the status of phenotypic variation of accessions in germplasm banks and populations of plant resources targeted for conservation and for other purposes.

Genetic diversity of *S. stellatus* was in average $p = 82.86\%$, $A = 2.35$ and $H_e = 0.264$, information that is consistent with the general pattern of high genetic diversity documented for columnar cacti (see Hamrick et al. 2002). The average value of A found in this study is the highest reported for columnar cacti by allozyme analysis, and the value of H_e estimated for the species is only lower than that reported for *Pilosocereus lanuginosus* ($H_e = 0.274$) through

allozyme analysis by Nassar et al. (2003), and than that reported for *Polaskia chichi* ($H_e = 0.658$) through microsatellite analysis by Otero-Arnaiz et al. (in press). Values of A and H_e of *S. stellatus* are higher than those reported for *Pachycereus schottii* ($A = 1.39$, $H_e = 0.214$) by Parker and Hamrick (1992), also higher than those reported for *Carnegiea gigantea* ($A = 1.20$, $H_e = 0.129$) and *S. thurberi* ($A = 1.33$, $H_e = 0.201$) by Hamrick et al. (2002), for *Cereus repandus* ($A = 1.47$, $H_e = 0.242$) and *S. griseus* ($A = 1.35$, $H_e = 0.218$) by Nassar et al. (2003), for *Pachycereus pringlei* ($A = 1.38$, $H_e = 0.212$) by Fleming et al. (1998), and for *Escontria chiotilla* ($A = 1.5$, $H_e = 0.122$) by Tinoco et al. (in press).

Status of diversity of S. stellatus in La Mixteca Baja and the Tehuacán Valley

Our study revealed that although morphological variation was generally similar among regions, it was significantly higher in the wild populations of La Mixteca, compared with wild populations from Tehuacán, whereas allozyme variation in La Mixteca was generally higher than in the Tehuacán Valley. As documented in other plants with clonal and sexual reproduction, differences in levels of genetic diversity could be associated with differences in proportions of sexual and clonal recruitments (Chung and Epperson 2000; Chung et al. 2000), historical factors (Hamrick and Godt 1996; Nason et al. 2002), landscape changes (Young 1995; Sork et al. 1999), and or differential actions of evolutionary forces (Hamrick et al. 1992; Hamrick and Godt 1996).

Seed germination and survival of seedlings of columnar cacti are strongly limited by humidity (Rojas-Aréchiga et al. 1997; Rojas-Aréchiga and Vázquez-Yanes 2000; Rojas-Aréchiga et al. 2001), therefore, proportions of sexual and clonal recruitments could be influenced by differences in soil humidity, caused by either differences in rainfall or soil capacity to retain water (Cornejo 2004). The higher rainfall in La Mixteca, compared with Tehuacán, could determine higher success of sexual reproduction and recruitment and, therefore, higher levels of genetic diversity. However, this hypothesis is yet to be tested, and information on historical climatic differences between regions would be necessary to analyze the possible effect of this process in a long-lived perennial plant such as *S. stellatus*.

Differences in genetic diversity suggest also the hypothesis that populations of La Mixteca Baja are ancestral to the Tehuacán Valley populations. This interpretation, difficult to verify based only on genetic diversity measures, considers the historical relationships between the flora of the Tehuacán Valley and the Balsas river basin, demonstrated by the fact that both regions share a high proportion of plant taxa (Villaseñor et al. 1990). A hypothetical human influence in dissemination of *S. stellatus* from the Balsas river basin to Tehuacán could also be considered, since the oldest remains of this plant species in caves of the Tehuacán Valley are nearly 5500 years of antiquity (MacNeish

1967; Smith 1967), a substantial time later than first human occupation of the area, which has been estimated that occurred more than 10,000 years ago (MacNeish 1967, 1992).

Morphological and genetic diversity associated to management

Contrary to our expectations, patterns of both morphological and allozyme variation among populations within each region consistently indicate that diversity in populations manipulated by people was higher than in wild populations, with the exception of only two managed *in situ* populations of La Mixteca (from Chinango and Tepexco, see Table 3). Not only does this information illustrate that human management of plant populations may not reduce morphological and genetic diversity, but that diversity may be maintained and even enhanced by traditional agricultural practices.

High level of variation in manipulated populations could be due in part to the occurrence of high levels of gene flow between all populations, which is favored by the intervention of bats in pollination and bats, birds and humans in seed dispersal (Casas et al. 1999b). However, high diversity of *S. stellatus* in managed *in situ* and cultivated populations is apparently also caused by the interest of people in maintaining variants with different special attributes offering differential advantages, which involves a continual introduction and replacement of plant materials in the manipulated populations as documented by Casas et al. (1997).

Regarding the low diversity in managed *in situ* populations, previous ethnobotanical information (Casas et al. 1997) indicated that wild populations of *S. stellatus* are scarcer in the Tehuacán Valley. Therefore, management *in situ* of wild populations in this region involves more care than in La Mixteca, where wild populations are more common. In La Mixteca, people leave some individual plants from the original wild populations in cleared areas, whereas in Tehuacán, people not only leave cactus individuals but also propagate branches of the desirable phenotypes in the cleared areas and introduce branches from homegardens. In populations with low diversity, loss of diversity is apparently associated with a particular type of management in which the original population is only thinned when clearing land. Unfortunately, this type of management is gaining popularity. At present, the traditional agricultural systems give way to agricultural systems that include incomes from other activities (goat raising, seasonal migration for employment in urban areas, among others).

Traditional management and conservation

The traditional technology of management *in situ* of columnar cacti within fields (such as maize plantings) as well as cultivation are important strategies

for supporting agriculture and biodiversity in the region. Such traditional methods have benefits for production of staple crops and soil protection, but also appears to be relevant for maintaining important reservoirs of genetic diversity for *S. stellatus* and potentially other columnar cacti, *Opuntia*, agaves and perennial plant species managed in a similar manner (Casas et al. 1999; Casas et al. 2001; González-Soberanis and Casas 2004).

Subsistence patterns among indigenous peoples commonly involve obtaining essential resources from primary production practices in limited areas. This has historically led to landscape manipulation for agricultural, pastoral or forestry activities to ensure adequate yields and diverse resources for the various needs of the social group. Formerly, this was recognized as conserving and enhancing biodiversity at a landscape level but also, as discussed here, it can occur at a species level. Indigenous people appear then to apply the same principles to assure diversity at both landscape and species level. Thus, as proposed by Gadgil (1987), there is evidence of incentives for indigenous people to nurture and sustain diversity in their immediate environs.

Traditional management of maize fields associated with maintenance of *S. stellatus* could have important consequences for the conservation of genetic variation in this species. Currently, it is possible to increase both number of cactus individuals and levels of genetic variation of this species within maize fields. Increased genetic variation is important for increased fruit production because, as mentioned, *S. stellatus* is self-incompatible (Casas et al. 1999b). Information from this study allows us to identify sources of genetic variation among the populations studied in each region, and to design agro-silvicultural plots containing high levels of genetic diversity of this cactus species. Other columnar cacti species are managed in similar ways in the area (Casas et al. 1999; Cruz and Casas 2002; Arellano and Casas 2003; Carmona and Casas 2005), as are tree species, such as *Sideroxylon palmeri* (González-Soberanis and Casas 2004). Therefore, maintenance and enhancement of the traditional silvicultural practices associated with agriculture of maize could help the conservation of genetic diversity of a number of plant species in the Tehuacán Valley.

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