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Population genetics and process of domestication of *Stenocereus pruinosus* (Cactaceae) in the Tehuacán Valley, México

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ABSTRACT

Population genetics of wild, managed in situ and cultivated populations of *Stenocereus pruinosus* coexisting in Central Mexico were studied. We hypothesized that artificial selection decreases genetic diversity in managed populations and influences differentiation of populations depending on the amount of gene flow. Nine wild, managed in situ and cultivated populations (264 individual plants) were studied through isozyme analysis (10 loci). Genetic variation of *S. pruinosus* is the highest reported in columnar cacti species (e.g. $H_T = 0.592$). Genetic variation in cultivated populations (Ho = 0.611, He = 0.588) was slightly higher than in wild (Ho = 0.556, He = 0.583) and managed in situ populations (Ho = 0.536, He = 0.578), but differences were not significant. Most of the genetic variation occurred within populations, with low differentiation and high gene flow among all populations ($F_{ST} = 0.064$, $Nm_{FST} = 3.659$ and $Nm_{GST} = 3.803$ in average) associated to bat pollination, seed dispersal by birds and transportation of vegetative propagules by people. Genetic distances were not correlated with geographic distances and in most cases are lower between similarly managed populations. Managed in situ and cultivated populations are important reservoirs of genetic diversity of this species to be considered in conservation programs.

1. Introduction

Domestication is an evolutionary process of plants and animals guided by humans mainly through artificial selection (Darwin, 1859). It is a continuous process, which derives in morphological, physiological, behavioral, and genetic divergences between populations of managed organisms and their wild relatives (Casas et al., 2007). The cultural area known as Mesoamerica, comprising the territory from southern Mexico to northern Costa Rica is one of the main centers of domestication of plants in the World (Harlan, 1975; Hawkes, 1983; Vavilov, 1951). In Mesoamerica, it is possible to study the ongoing processes of artificial selection of plant species currently under domestication (Casas et al., 2007). For some of these species, wild, semidomesticated, and domesticated populations coexist with continuous genetic interactions, thus influencing the evolution of both crops and wild relatives. Therefore, this region is particularly interesting for studying the natural and cultural factors influencing domestication. Ethnobotanical and evolutionary studies in Mesoamerica have documented a broad spectrum of incipient processes of domestication that are particularly interesting, as they allow the study of early phases of domestication which could in turn unveil how agriculture originated (Casas et al., 2007;

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Colunga-GarcíaMarín and Zizumbo-Villarreal, 2007; Colunga-GarcíaMarín et al., 1986, 1996; Hughes et al., 2007; Zárate et al., 2005). In this study, we analyze the genetics of wild and managed populations of the columnar cactus *Stenocereus pruinosus*, a species of high cultural value under incipient process of domestication.

Columnar cacti have been used by peoples since the earliest phases of human occupation of the arid and semiarid portions of Mesoamerica (Flannery, 1986; MacNeish, 1967). The highest diversity of these plants occurs in Mexico (nearly 75 species), particularly in the Balsas river basin and the Tehuacán Valley in Central Mexico where 43 species have been recorded (Valiente-Banuet et al., 1996). In these regions, columnar cacti are used as food, building material, fodder, living fences, and fuel (Casas et al., 1999a). Some of these uses date back to nearly 10,000 years (MacNeish, 1967). Useful products of all of these species are gathered mainly in the wild, but for 22 species of columnar cacti managed individuals with favorable phenotypes to humans are let standing or intentionally propagated in areas where vegetation is cleared. Twelve of these species are also cultivated in home gardens (Casas et al., 1999a). Therefore, these are also important areas of domestication of columnar cacti.

According to Arias et al. (1997), *S. pruinosus* is an arborescent cactus up to 8 m in height. Branches are green with pruinosus apexes and 5–8 ribs. Flowers are infundibuliform 7–10 cm in length growing in the branch apexes, with green brownish external tepals and white internal tepals. Cortés-Díaz (1996) reported that flowers have nocturnal anthesis with self-incompatible breeding system being pollinated by bats. The ellipsoid fruits locally called "pitayas de mayo" may have white, yellow, purple, orange and more commonly red pulp with black seeds. Vegetative propagation is common in both natural and artificial environments, and individual plants derived from branches approximately 1.2 m in length produce flowers 2 or 3 years after being planted (Casas et al., 1999a). This species is widely distributed in sem-iarid areas of the states of Oaxaca, Puebla, Chiapas, Tamaulipas, Veracruz, and Yucatán (Bravo-Hollis, 1978).

S. pruinosus (Otto) Buxb. is one of the cactus species more intensely managed in Central Mexico (Casas et al., 1999a; González-Insuasti and Caballero, 2007), as its fruits have the highest economic value of all columnar cacti species of that region (Casas et al., 1999a). Fruits of this species are gathered in wild populations. There are also silvicultural managed in situ populations constituted by individuals that were left standing, and sometimes propagated when forests were cleared for establishing corn fields. This type of management commonly involves selection favoring individual plants with larger and sweeter fruits, peel with lower density of spines, and pulp with various colors. Finally, in the semiarid Central Mexico there are also cultivated populations of *S. pruinosus*, derived from plantations of branches from wild or in situ managed individuals with desirable phenotypes according to the attributes mentioned above. Cultivated populations are established mainly in home gardens. Thus, *S. pruinosus* can be considered as a plant under incipient domestication, with individuals belonging to three categories of management: wild, managed in situ, and cultivated populations.

Artificial selection has caused significant divergence in these morphological characters between wild and managed populations as it has been documented for species of columnar cacti (Arellano and Casas, 2003; Carmona and Casas, 2005; Casas et al., 1999b; Cruz and Casas, 2002). Also, effects of artificial selection on population genetics of columnar cacti have been documented in *Polaskia chichipe* (Gosselin) Backeberg (Otero-Arnaiz et al., 2005a, b), *Escontria chiotilla* (F.A.C. Weber) Rose (Tinoco et al., 2005), *Stenocereus stellatus* (Pfeiffer) Riccob. (Casas et al., 2006), and *Polaskia chende* (Gosselin) Backeberg (Ruíz-Durán, 2007). These studies have generally found that managed in situ and cultivated populations have slightly lower genetic variation than wild populations, but in the case of *S. stellatus* both managed in situ and cultivated populations have more genetic diversity than wild populations. This last pattern appears to be due to traditional management involving a continual replacement of individual plants within the plantations and the introduction of plants from other areas. Population genetics studies have also documented high gene flow occurring among all populations and therefore low genetic differentiation and structure of populations (Casas et al., 2007). In the case of *Stenocereus* species, gene flow is greatly determined by pollinators, mainly the bats *Leptonycteris curasoae* and *Choeronycteris mexicana* (Casas et al., 1999c), as well as several bird and bat species acting as seed dispersers.

According to Hawkes (1983) and Doebley (1992), domestication generally determines a decrease of genetic diversity in managed populations of organisms compared with wild populations since domesticated stands commonly include a selected fraction of the diversity existing in the wild. However, since the traditional management pattern has determined high levels of genetic variation in *S. stellatus*, and *S. pruinosus* is more intensely managed than that species, in this study we expected to find high levels of genetic diversity in managed in situ and cultivated populations. Also because of the management intensity, we expected to find higher genetic differentiation between wild and managed populations than that reported for *S. stellatus*, even when we expected to find high levels of gene flow because of the coexistence of populations in distances within the range of movement of pollinators and seed dispersers. This study analyzes whether the traditional management and incipient domestication of *S. pruinosus* has had consequences on the genetic diversity and structure of wild, managed in situ and cultivated populations, and documents gene flow among these coexisting population types.

2. Methods

2.1. Study area

The study was conducted in the Tehuacán Valley, located at the southeast of the state of Puebla and the northeast of the state of Oaxaca in Central Mexico (Appendix A electronic version only). It is a semiarid region with annual mean