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David Bravo-Aviles

Universidad Autonoma Metropolitana Iztapalapa

José Alejandro Zavala-Hurtado

Universidad Autonoma Metropolitana Iztapalapa

Beatriz Rendón (✉ bra@xanum.uam.mx)

Universidad Autonoma Metropolitana Iztapalapa <https://orcid.org/0000-0003-0750-2081>

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Evolution under domestication of correlated attributes in two edible columnar cacti in Mexico

David Bravo-Aviles^a, José Alejandro Zavala-Hurtado^b, Beatriz Rendón-Aguilar^{b*}

^a Doctorado en Ciencias Biológicas y de la Salud. Departamento de Biología, Universidad Autónoma Metropolitana. Av. San Rafael Atlixco 186, Col. Vicentina, Delegación Iztapalapa, 09340 México, D. F., México.

^b Departamento de Biología, Universidad Autónoma Metropolitana, Ciudad de México, México.

*Corresponding Author: Beatriz Rendón-Aguilar. Departamento de Biología, Universidad Autónoma Metropolitana, Avenida San Rafael Atlixco No. 186, Colonia Vicentina, C.P. 09360, Delegación Iztapalapa, Ciudad de México, México.

Email: bra@xanum.uam.mx; telephone: 58046449

Evolution under domestication of correlated attributes: damage levels, defense mechanisms, and fitness components in two edible columnar cacti in Mexico

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Abstract

Stenocereus pruinosus and *S. stellatus* are columnar cacti from central Mexico, distributed in the Valle de Tehuacán and the Mixteca Baja regions. Both species have populations subject to three different forms of human management: wild, *in situ* and cultivated, growing in sympatry. The objectives of the present study were to compare variation in damage levels, defense mechanisms and fitness components between 1) both species due to differences in the intensity of management; 2) populations of both species subject to different forms of management; 3) two regions with different management practices and physical conditions, in these two columnar cacti. We estimated the percentage of damage, abundance of spines as resistance, and branching rate as a tolerance component, number of fruits produced in one year, number of seeds per fruit and percentage of seed germination as fitness components. The differences between species, forms of management and regions were estimated with ANOVA tests. A paired correlation with the measured variables within each form of management was used to observe the correlated attributes in both species. We found differences between species, forms of management and regions, mostly concordant with the domestication syndromes. More managed populations, present more damage and less resistance, without compromising fitness, which is the target attribute. Correlated attributes exhibited significant correlations in both species and forms of management. Some of them were concordant with domestication syndrome: More damage/less resistance, or more damage/more branching rate. Our results show that human management can influence the evolution of the interaction of correlated attributes like defense mechanisms, damage and fitness in these columnar cacti.

Introduction

Domestication is an evolutionary process mediated by human selection; its main purpose is to modify the morphophysiological attributes of species with which it is concerned. Through this conscious selection, which has taken place over thousands of years, organisms have been modified to obtain desirable attributes, or *domestication syndromes* (Heiser 1988; Rendón and Núñez-Farfan 1998). Such domestication syndromes—including increased size, variations in shapes and colors, boosted self-pollination systems and / or vegetative reproduction that is associated with sterility (Schwanitz 1966; Harlan 1975; Rindos 1984; Heiser 1988; Gepts and Papa 2002) —comprise attributes that have been subject to direct human selection.

Nevertheless, a phenotypic integration exists (Pigliucci 2003) and—because there are groups of functional attributes that are more integrated in organisms—it is expected that changes in target attributes will also produce changes in other characteristics, which are not directly desirable or favored by humans. These are considered *correlated attributes* (Murren 2002).

Some attributes proposed as domestication syndromes are clearly the consequence of correlated responses. This is true in the case of a decrease in chemical compounds, related to defense mechanisms, or in the case of a decrease in levels of genetic diversity (Huot et al. 2014; Poulicard et al. 2016)—unless these are subject to direct human selection (Moreira et al. 2018). Thus, the classification of target or correlated attribute, depends on the human selection, and must be analyzed in terms of the purposes for which the organism has been domesticated.

The evolution of plants' defense strategies under domestication, in particular, has not been analyzed—whether under the concept of phenotypic integration or as a correlated attribute. Various examples in the literature mention a decrease in resistance. Yet this is measured as a single attribute, isolated from the others (e.g., high levels vs. small levels of secondary metabolites; more spines vs. few spines) (Oliveira and da Machado 2003; El-Seedi et al. 2005; Silva et al. 2010; Falcão et al. 2012). In evolutionary ecology, it is well recognized that plant species have two defensive strategies against natural enemies: resistance and tolerance. Resistance reduces the level of attack, damage or infection by herbivores and pathogens through secondary compounds or structures (Kennedy and Barbour 1992) and enhances fitness. Tolerance does not avoid damage, but reduces the fitness loss caused by a certain damage level (Strauss and Agrawal 1999; Roy and Kirchner 2000; Heil 2010). Some models, developed to explain the evolution of defensive strategies in wild species, assume a trade-off between defense and growth. This is because plants have many constraints that limit them, in terms of allocating resources to both strategies (Stearns 1989; Herms and Mattson 1992; Simms and Triplett 1994). Evidence around the evolution of defense mechanisms has also resulted in two explanations; one suggests a trade-off between resistance and tolerance, while the other proposes a joint evolution of both mechanisms (Pilson 2000; Medel 2001; Fornoni et al. 2003, 2004; Núñez-Farfán et al. 2007). Thus, we have a complex scenario: growth vs. defense—but in which way does the defense take place (resistance or tolerance)? Plants can evolve a trade-off response: growth versus resistance; growth versus tolerance; but also growth versus defense mechanisms (when a joint evolution exists). Fitness costs are an important consequence of the trade-off between growth and resistance (Huot et al. 2014), but not in a trade-off between growth and tolerance.

According to trade-off models, plants should allocate a higher proportion of resources for growth and reproduction in the domestication process, and a minimal proportion to defense mechanisms (Herms and Mattson 1992). This is confirmed by the patterns seen in the most important domesticated species. Grasses exhibit a considerable increase in reproductive structures, which are the most important food source (Schwanitz 1966; Heiser 1988; Doebley 1992). A similar pattern is observed in legumes (beans, lentils, peas) (Zangerl and Bazzaz 1992). The question is: what are the effects of allocating energy from these useful structures to correlated attributes, such as defense strategies? Based on the theory, this trade-off should increase damage levels in domesticated plants, as compared to their wild relatives (Rosenthal and Dirzo 1997; Massei and Hartley 2000).

Although defensive strategies have been studied from an evolutionary perspective in some domesticated plants, only some components have been analyzed. These are mostly associated with resistance (Rosenthal and Kotanen 1994; Rosenthal and Dirzo 1997; Massei and Hartley 2000; Chaudhary 2013). These components have also been analyzed mainly in annual species that are of global importance. Many perennial species—as well as species used at a regional or local level—have thus been poorly studied.

Columnar cacti are an important group of plants, including species that humans have used for at least 8000 years (Callen 1967; Smith 1967) and that were probably subjected to domestication not long after that. They are currently considered to be undergoing a domestication process, because different forms of management coexist in the same geographic area in a sympatric form. Wild populations grow in their natural habitat, but are gathered by local inhabitants. *In situ* managed populations are comprised of individual

plants left standing after clearing a field for maize cultivation, which implies agroforestry management. Cultivated populations are established in cultivated fields or in backyard orchards (Casas et al. 1997, 2006; Parra et al. 2008, 2010).

This gradient in forms of management has produced a differential effect on plant populations, due to differential human selection pressures. Various morphological and genetic changes have thus been documented (Rojas-Aréchiga et al. 2001; Otero-Arnaiz et al. 2005; Tinoco et al. 2005; Blancas et al. 2006; Casas et al. 2006; Parra et al. 2008, 2010; Guillén et al. 2009; Cruse-Sanders et al. 2013). Yet none of these studies has attempted to analyze the evolution of defense strategies as correlated attributes, in the domestication process.

In columnar cacti, some studies have demonstrated that damage has a negative effect on fitness (Silva and Martínez 1996; Pimienta et al. 1999; Medel 2001; Mueller et al. 2005; Campos et al. 2006; Goheen et al. 2007; Peco et al. 2011). Others have analyzed resistance mechanisms. These include the abundance of spines and its effect on fitness components—along with the thickness of the cuticle and its relationship with levels of damage (Medel 2001; Silva et al. 2010). A compensatory response after damage has also been reported. This consists of an increase in shoots on branches after being damaged, without a drastic decrease in fitness (Medel 2001).

Columnar cacti have great cultural, economic and ecological importance in México and, in the recent decades, different reports have indicated the presence of some damage types (Bravo-Avilez et al. 2014, 2019a, b). Individuals of different cactus species have been observed under different conditions, from those that can produce healthy new branches to those that die altogether. Cactus species have been subject to varied levels of intensity of management (González-Insuasti and Caballero 2007). Thus, we wonder whether there is

correlated response between damage levels, defense mechanisms and some fitness components—between and within species—according to the different levels of intensity of management.

We selected two species for this study, which comprise populations that are subject to different forms of management and exhibit different damage levels. They thus represent an appropriate system within which to study correlated changes between damage levels, defense mechanisms and fitness components. We consider the first two to be correlated attributes—rather than target attributes, as they have been described in previous studies, which recognize only the fruit (fitness component) as the target attribute (Casas et al. 1997; Luna-Morales and Aguirre, 2001)

Both species—*Stenocereus pruinosus* (Otto) Buxbaum. and *S. stellatus* (Pfeiff.) Riccob.—are distributed in the Mixteca Baja and the Valle de Tehuacán regions (see Table 1 for details of each species and region). Yet differences in management have been reported, between the two species and in both regions (Casas et al. 1997). *S. pruinosus* is currently subject to a higher intensity of management (González-Insuasti and Caballero 2007), while *S. stellatus* seems to have been used more intensively in the distant past—maybe thousands of years ago (Smith 1967).

At the species level, it is expected that *S. pruinosus* will show the characteristics of a more intensively managed species, related to *S. stellatus*: higher damage levels, lower resistance levels, higher tolerance levels and higher levels in some fitness components.

At the regional level, the populations of the Valle de Tehuacán are expected to present less resistance, more levels of damage and an increase in some fitness components than those of the Mixteca Baja region. This is as a result of historical management, at least for *S. stellatus*; there is evidence of its older use in the Valle de Tehuacán, going back at least 5,400 years (Smith 1967).

Between the forms of management of both species, an increase in some fitness components, like fruit production, is expected in cultivated populations, because this is the target attribute. Since a trade-off between resistance vs. growth and reproduction is expected, populations with higher fitness values (cultivated populations) will exhibit a decrease in resistance and higher damage levels. They will also show a higher branching rate (tolerance), related to wild populations.

The objectives of the present study were to analyze the correlated response between damage levels, defense mechanisms and some fitness components in these two columnar species: 1) at the species level, due to differences in the intensity of management; 2) between populations of both species subject to different forms of management; and 3) between two regions with different management practices and physical conditions.

Materials and methods

Study system

The study includes two species of columnar cacti, belonging to the genus *Stenocereus* and recognized in Mexico as *pitayas*:

Stenocereus pruinosus (Otto) Buxbaum. and *S. stellatus* (Pfeiff.) Riccob. (see Table 1). The study was carried out in six localities in

the Valle de Tehuacán, and in six localities in the Mixteca Baja. Each population corresponds to a species and to a different form of management (Figure 1, Table 1). In 2012, a total of 167 individuals of *S. pruinosus* and 180 individuals of *S. stellatus* were sampled, ranging from 121 to 760 cm in height (average 355.6 ± 125.3 cm). Attributes related to architecture, phenology and damage were recorded.

Variation in damage levels

Damage was recorded via a subsample of branches from each individual; more than 50% of the branches from the middle part and periphery of each individual were chosen for this subsample. In all, 1048 branches of 167 individuals were sampled for *S. pruinosus* and 1043 branches of 180 individuals for *S. stellatus*. A percentage of damage was subjectively estimated for each branch. Damage included all physical and biological damage types present in each branch (for more details on the damage types found, see: Bravo-Aviles et al. 2014; Bravo-Aviles et al. 2019a, b; Bravo-Aviles and Rendón-Aguilar in process).

Variation in defense mechanisms

To evaluate the phenotypic characteristics related to defense mechanisms, the resistance and branching rates were estimated in the sampled branches.

Resistance. From each individual, two to four branches were randomly chosen from the middle part and periphery. Half of them were considered healthy (when they were completely healthy or with little damage [less than 10% of damage]) and half with a high damage level (over 80%). For *S. pruinosus*, 487 branches were sampled; 459 were sampled for *S. stellatus*. Resistance was estimated as the length of the central spines (*lcs*) in all areoles (*a*) present at 150 cm² (30 cm long x 5 cm wide) at breast height on the branch. We also counted the number of ribs (*r*) present at breast height, in the branches sampled. The formula used is:

$$\text{Resistance} = r * a * lcs$$

Where a higher resistance value indicates higher levels of resistance.

Branching rate (BR). Because tolerance implies a redistribution of energy allocated to different attributes of plants (e.g., root, branches, leaves) as a response to damage, BR was considered a component of tolerance in this study. The same branches used for the resistance analysis (N = 487 for *S. pruinosus* and 459 for *S. stellatus*) were used for the BR analysis. New branching shoots emerging between 2012 and 2013 were recorded. The BR considered the number of branches at the start of sampling (*t1*) and the new branches produced at the end of sampling (*t2*). Thus, the BR value corresponds to:

$$\text{BR} = (t2 - t1) / t1$$

Variation in fitness components

The fitness components considered in this study corresponded to female reproductive success. We counted the number of fruits produced in 2012, from late April to early June for *S. pruinosus* (N = 167 individuals) and from mid-July to the end of September for *S. stellatus* (N = 180 individuals). We estimated an average number of seeds per fruit, which was obtained from the count of seeds present in a sample of fruits of both species (145 fruits of *S. pruinosus* and 217 of *S. stellatus*). The total number of seeds was weighed from each fruit, and a sample of 200 seeds was taken and weighed. With these data, an extrapolation was made to estimate the number of seeds per fruit: c) percentage of seed germination, based on germination tests carried out in a LUZEREN germination chamber at 25 °C, 60% humidity and a photoperiod of 12 hours. Seeds from a subsample of fruits were used for germination tests (N = 38 fruits for *S. stellatus* and N = 21 for *S. pruinosus*). In these tests, 30 seeds from each species in each management form in each region were located in petri dishes, with five repetitions of each. Germinated seeds were counted every 24 hours, and germination was considered to occur when the radicle was visible to the naked eye.

Statistical analysis

Variation in damage levels, defense mechanisms and fitness components between species. An ANOVA was performed to estimate the differences in damage levels, defense mechanisms (resistance and BR) and fitness components between species. The data were transformed to follow the assumptions of normality: damage, using the arcsine of the square root of the damage / 100; BR and fitness components, using a logarithm with base 10. The analyses were carried out using JMP® software (Sall et al. 2017).

Variations in damage levels, defense mechanisms and fitness components between forms of management and regions. To estimate possible differences in the variables analyzed, a factorial ANOVA was performed for each species, considering the factors: form of management (M = wild, *in situ* and cultivation); region (R = Mixteca Baja, Valle de Tehuacán); and the interaction form of management x region (M * R). The data were then transformed, as previously mentioned. Subsequently, a Tukey test was applied to determine which interactions were statistically different. All analyses were carried out using JMP® software (Sall et al. 2017).

Multiple correlations as evidence of correlated responses between damage levels, defense mechanisms and fitness, due to domestication. To analyze the relationship between the variables analyzed and to infer possible correlated responses associated with domestication, according to the forms of management, Spearman correlation matrices (ρ) were developed using JMP® software (Sall et al. 2017). The variables included damage levels, resistance, BR and number of fruits; the number of branches on the plant was a covariable. These correlations were analyzed for each species and each form of management. The statistical significance between paired regressions was obtained using the Pairwise correlations test. Both analyses were carried out using the JMP® software (Sall et al. 2017).

Results

Variation between species in correlated responses. Evidence of differences in the intensity of management

Significant differences were found between the species in nearly all analyzed variables, with the exception of the branching rate (Table 2, 4). These differences did not completely agree with the hypothesis. The highest damage levels were found in *S. stellatus*, but also a higher resistance level. Fitness components also showed differences between the two species: *S. stellatus* produced the greatest number of fruits, but *S. pruinosus* produced fruits with the highest number of seeds and its percentage of germination was also higher (Table 2, 4).

Variation between regions and forms of management

Variation in damage levels

A factorial ANOVA indicated that *Stenocereus pruinosus* exhibited statistical differences only between regions, whereas higher damage levels occurred in the Mixteca Baja region (Tables 3, 4).

Stenocereus stellatus exhibited significant differences in the main factors, and in the M * R interaction. Cultivated populations had higher damage levels, compared with *in situ* and wild management, and the Valle de Tehuacán region presented higher damage levels. The M * R interaction indicated that all populations from the Valle de Tehuacán presented more damage, as did the cultivated population of the Mixteca Baja; the other populations of this region presented smaller damage levels.

It is worth noting the higher damage level, and the higher branch mortality, recorded for the wild population of *S. stellatus* from the Valle de Tehuacán (Ajalpan) and for the cultivated population from the Mixteca Baja (Chinango) during the sampling period (Figure 2). These populations presented the smallest resistance values and the smallest number of fruits produced. However, the percentage of germination of their seeds was relatively high (40.33% and 43.25%, respectively).

Variation in defense mechanisms

Resistance. For *S. pruinosus*, the presence of spines as a component of resistance differed significantly between forms of management and M * R interaction, but not between regions (Tables 3, 4). Differences between the forms of management indicated that the wild population was more resistant. The M * R interaction indicated that the wild and the cultivated populations of the Valle de Tehuacán presented the highest and the lowest resistance levels, respectively.

Stenocereus stellatus exhibited significant differences in the main factors and M * R interaction. The *in situ* managed population presented the highest resistance, while the cultivated population presented the lowest resistance. Between regions, the populations of the Mixteca Baja presented higher resistance. The M * R interaction indicated that the wild population of the Mixteca Baja presented the highest resistance, while the wild population of the Valle de Tehuacán was the least resistant.

Branching rate (BR). *Stenocereus pruinosus* exhibited significant differences only in the M * R interaction, where the cultivated and the managed *in situ* populations of the Mixteca Baja presented the highest and the smallest branching rates, respectively.

A similar pattern was found for *S. stellatus*, where statistical differences were found only in the M * R interaction. The wild population of the Valle de Tehuacán and the managed *in situ* population of the Mixteca Baja presented the highest branching rates, while the managed *in situ* population of the Valle de Tehuacán and wild population of the Mixteca Baja exhibited the lowest branching rates.

Variation in fitness components

Stenocereus pruinosus showed significant differences in fitness components between forms of management, regions and M * R interaction (Tables 3, 4). In relation to the number of fruits, the managed *in situ* and cultivated populations produced higher numbers of fruits, but a smaller number of seeds—and the percentage of germination was smaller in the managed *in situ* populations. Between regions, in the Valle de Tehuacán the plants produced a greater number of fruits but fewer seeds/fruit, and had a higher percentage of germination. The M * R interaction indicated that the populations of the Mixteca Baja did not differ significantly in the production of fruit between forms of management. Meanwhile, the managed *in situ* and cultivated populations of the Valle de Tehuacán produced more fruit than did the wild population. In relation to the number of seeds/fruit, the cultivated population of the Mixteca Baja presented the higher number of seeds; opposite, the cultivated population of the Valle de Tehuacán presented the smaller number of seeds/fruit. Finally, the percentage of germination was higher in the cultivated population of the Valle de Tehuacán, but the managed *in situ* and cultivated populations of the Mixteca Baja had the smallest percentage of germination.

In *S. stellatus*, all fitness components also showed significant differences. The number of fruits differed only in the M * R interaction. The cultivated population in the Valle de Tehuacán produced the highest number of fruits, as did the wild and managed *in situ* populations of the Mixteca Baja. The number of seeds per fruit differed, according to the forms of management and the M * R interaction. In relation to the form of management, the cultivated and managed *in situ* populations presented higher numbers of seeds/fruit. The interaction showed the fruits of the managed *in situ* and cultivated populations, in both regions, to present higher numbers of seeds/fruit. Finally, the percentage of germination differed between regions and according to the M * R interaction. In the Mixteca Baja, a higher percentage of germination was recorded. Meanwhile, the interaction showed that the seeds of managed *in situ* and cultivated populations in the Mixteca Baja, as well as the seeds of the wild and managed *in situ* populations of the Valle de Tehuacán (Tables 3, 4) had the highest percentage of germination.

Multiple correlations as evidence of a correlated response of damage levels, defense mechanisms and fitness, due to domestication

Between species

The general multiple correlation between the estimated variables showed different patterns, in both species (Table 5).

In the case of *S. pruinosus*, damage was positively correlated with BR and the number of branches—and negatively correlated with resistance and fitness. Therefore, the less resistance the plants had, the more they were damaged and the fewer fruits they produced.

The more damaged the plants, the more BR was favored. Resistance was negatively correlated with BR and the number of branches, suggesting the existence of a trade-off between resistance and BR. In addition, plants with more branches exhibited less resistance. For *S. stellatus*, damage was negatively correlated with resistance and fitness. Plants with higher numbers of branches also increased fruit production, and resistance was positively correlated with fitness.

Between forms of management, within each species

The analysis of the correlations by forms of management, within each species, showed that there were also differences.

In *S. pruinosus*, there were significant correlations between forms of management, which differed from those shown at the species level (Table 6). In wild populations, damage was negatively correlated with resistance and positively with the number of branches; resistance was negatively correlated with the number of branches. The managed *in situ* populations exhibited different patterns.

Resistance was negatively correlated with damage and number of branches, and fitness was positively correlated with number of branches. Even when the number of branches is not a direct measure of tolerance, it is related to the production of vegetative tissue, which could favor some farmer's practices. The cultivated populations exhibited more similitudes with the general pattern observed at the species level, except that a negative correlation between the number of branches and fitness was detected.

In *S. stellatus*, the correlations between the variables analyzed in the three forms of management maintained the general pattern obtained at the species level, it means that damage was negatively correlated with resistance and fitness. Also, the plants with the

higher number of branches increased fruit production, and resistance was positively correlated with fitness. The exception was the cultivated population, which exhibited a significant positive correlation between the BR and the number of branches.

DISCUSSION

González-Insuasti and Caballero (2007) proposed a gradual intensity scale for the management scheme, for some cacti in the Valle of Tehuacán region. This was based on the number of people carrying out species management, the complexity of each form of management and the number of different management practices they realized. *S. pruinosus* was considered the most intensively managed cactus, followed by *S. stellatus*. Based on this, we expected that correlated attributes would exhibit changes according to this management: higher levels of damage, lower resistance levels, higher levels of BR and higher fitness values in *S. pruinosus*. Yet we found that this pattern agreed only in terms of resistance and fitness attributes, such as a higher number of seeds and percentage of germination. Based on current management and historical evidence of the use of both species, we propose that this intensive management in *S. pruinosus* is recent, while there is an ancient history of management of *S. stellatus* that stretches back to around 5,400 years ago (Smith 1967). This historical management of *S. stellatus* is reflected in a higher susceptibility to damage—but, at the same time, in a higher resistance level. Yet even though the two species are close species—which belong to the same genus, are genetically located in very close clades (Bárcenas et al. 2011) and are subject to the same forms of management—morphological differences are evident (e.g., number of branches, number and distribution of fruits in the branches) and these could represent obstacles

(e.g., evolutionary constraints) for human selection. The intensity of management, as proposed by González-Insuasti and Caballero, thus does not necessarily correspond to a direct effect of the domestication process.

Respect to differences between regions, in *S. pruinosis*, the higher damage level recorded in the Mixteca Baja was the opposite of what was expected. It is possible that a greater dissemination with clones in this region could explain this damage, however for this species there is no evidence in this way. Historically, there is no evidence of ancestral use of this species, as in the case of *S. stellatus*. More comparative studies between regions should be carried out.

In *S. stellatus*, the highest damage level and the least resistance supported the hypothesis of ancestral management in the Valle de Tehuacán. The greatest clonal propagation of this species in the Mixteca Baja reported by Casas et al. (1997), apparently has not decrease resistance levels as well as the presence of more damage for this region. Efforts to disseminate the importance of sexual reproduction to obtain good quality raw material in the long term, which would enrich the populations of managed plants, should be transmitted to the farmers in charge of managing these species. Casas et al. (1997, 1999) reported that the plants in the Mixteca Baja region were generally more vigorous and produced more fruits—which were heavier and had a higher number of seeds—than those of the Valle de Tehuacán. We did not find differences neither in fruit production or number of seeds/fruit, but only in seed germination, which was lower in the Valle de Tehuacán. In this sense, there is no evidence of an increase in fitness for the Valle de Tehuacán, the management practices in each region do not differ in the results of fruit production. It is possible that previous studies considered only health plants and this could modify mean values for fruit production.

Related to the differences between forms of management, in the present study, significant differences in most attributes were associated with damage levels, resistance mechanisms and fitness components. These were recorded in populations with different forms of management—some concordant with the hypotheses, based on the general model of domestication syndromes, and others due to evolutionary processes associated with their own natural history.

Variations in defense mechanisms—in particular, resistance—agreed with the theory of domestication since a decrease in resistance response was detected in the cultivated populations of both species. Our data also agreed with those reported for *S. stellatus* (Casas et al. 1999), in terms of a decrease in the number of spines in cultivated populations. This characteristic could facilitate fruit harvest, or manipulate branches during transplant because farmers need to get closer to the plants in order to cut the fruits. Yet more studies are needed, to understand how human selection and environmental factors interact in the number, distribution and size of spines, and in their role as a defensive attribute. Other resistance mechanisms, not considered in this work, would surely provide physical resistance to both *Stenocereus* species. These include thickness of the cuticle (Silva et al. 2010) or physiological traits, such as the production of secondary metabolites (Kircher et al. 1967; Bruhn and Sánchez-Mejorada, 1977; Oliveira and Da Machado 2003; El-Seedi et al. 2005; Ennouri et al. 2014).

Spines provide resistance to several plant species, including cacti (Milewski et al. 1991; Medel 2001; Gómez and Zamora 2002). They are also easily measurable structures, so phenotypic changes in populations can be easily estimated; we thus decided to include this

resistance component in our study. It would be interesting, however, to incorporate the other attributes in future studies, assessing their variation in relation to the domestication process.

We found that, in *S. pruinosa*, the branching rate was negatively correlated with resistance. This suggests the presence of a trade-off between resistance and growth, for this species. *S. stellatus*, on the other hand, does not present a significant correlation between these attributes. Resistance is also positively correlated with fitness, reflecting the fact that resistance is the main defense mechanism in this species.

Defense mechanisms, like secondary compounds assigned to defense against herbivores, have been compared in studies of populations of cultivated and wild relatives of species of agronomic interest—mainly herbs and / or shrubs (Chaudhary 2013, citations within). Rosenthal and Dirzo (1997) and Massei and Hartley (2000). The presence of spines has been considered a resistance mechanism for various groups of plants, including cacti (Milewski et al. 1991; Medel 2001; Gómez and Zamora 2002). Medel (2001) reported the coexistence of resistance and tolerance in a columnar cactus. Tolerance has been documented in wild and domesticated plants of *Zea* spp. and *Lycopersicon* spp. (Welter and Steggall 1993; Rosenthal and Kotanen 1994). Changes in defense strategies must be considered, in future studies of domestication in columnar cacti—attempting to elucidate whether they are target attributes or correlated ones, depending on the purposes of farmers.

Certainly, the target attribute for human selection in both species is the fruit. We found that fruit production, in managed populations of both species, is favored by human selection. Casas et al. (1997) reported the same pattern in *S. stellatus*. Regarding the number of

seeds per fruit, the cultivated populations of *S. stellatus* produced a higher number than did the wild populations. These data agree with Casas et al. (1997) and Luna-Morales (2004). Our results for *S. pruinosus* showed a smaller number of seeds in the cultivated populations, which is coherent with the domestication syndromes (Schwanitz 1966). However, it is opposite to the results previously reported by Luna-Morales (2004),

The percentage of seed germination, in managed *in situ* populations of *S. pruinosus*, presented the smallest value compared with the wild and cultivated populations. This was consistent with Guillen et al. (2009). However, in *S. stellatus* we found that management did not generate changes in the percentage of germination. Our results were different to those previously reported, where wild and cultivated populations showed the highest levels of seed germination (Rojas-Aréchiga et al. 2001; Guillén et al 2009; Rodríguez-Morales et al. 2013; Guillén et al. 2015). It is possible that there were differences, in some physical and biological aspects of the populations from which the samples were taken (e.g., maternal effects, in the case of fruits and seeds coming from damaged plants).

Domestication syndromes would imply that plants with higher resistance would present higher levels of fitness (Núñez-Farfán et al. 2007). Thus, damage negatively affects fitness (Mueller et al. 2005; Campos et al. 2006; Goheen et al. 2007). Some studies in wild cacti indicate that damage negatively affects the production of flowers and fruits (Hoffman et al. 1993; Silva and Martínez 1996; Peco et al. 2011).

Our results indicated that, in both species, fitness components increased their response and resistance decreased as management intensity increased. This can be attributed to human selection (Casas et al. 1997, 1999; Luna-Morales 2004), through two possible

explanations. One is that decreased resistance is an unconsciously selected trait, but has not reached levels that can promote higher levels of damage in cultivated populations. The second is that—if we assume that both attributes have been favored by human selection—the intensity of selection towards some of the fitness components is likely higher than that towards resistance.

It is also possible that damage is more frequent due to changes in the management conditions of places where the plants grow—such as in the case of overgrazing by goats. Malo et al. (2011) have shown introduced species of cattle to cause more damage than native species, in the columnar cactus *Echinopsis terscheckii*. Rosas-García (unpublished data) also found that damage levels, in *S. pruinosus* and *S. stellatus*, are related to the surrounding vegetation structure. Damage levels can also be associated with the current management of the orchards where these species are growing. A lack of renewal of the plants in orchards; a high density of old plants; urban growth; the abandonment of orchards, due to migrating human populations; and a lack of interest amongst the younger generations (Obs per.) are all topics that could be incorporated to analyze damage. The relationship between these characteristics and the damage should be analyzed later.

An analysis that directly associates the structure that provides resistance with a certain type of damage is not within the scope of our research but could be carried out later.

Changes in correlated attributes have been poorly addressed, in research around perennial domesticated species. Most studies involve domesticated species and their wild relatives (Turcotte et al. 2014), rather than populations of the same species that are subject to

different forms of management—as is the case for many Mesoamerican species like cacti. These changes in correlated attributes can be expressed positively (as synergies) or negatively (as antagonisms or trade-offs) (Schwanitz 1966; Harlan 1975; Gepts and Papa 2002). In the present study, we found differences in correlated attributes between nearly all attributes analyzed, between species and between populations within each species.

In terms of defense mechanisms, we found a trade-off between resistance and branching rate in *S. pruinosus*, while in *S. stellatus* it was not found. This indicates that—even in species that are evolutionarily close (Bárcenas et al. 2011)—there are variations in defense mechanisms. These results also contribute to the different scopes related to the controversy over the expression of defense mechanisms, in which some authors confirm a trade-off between both resistance and tolerance (Stearns 1989; Simms and Triplett 1994) while others show evidence of a joint response (Pilson 2000; Medel 2001; Núñez-Farfán et al. 2007).

In both species, a smaller resistance was correlated with higher damage levels and a decrease in fitness (number of fruits). However, damage levels were higher only in the cultivated plants of *S. stellatus*. Although a negative correlation was found between damage and resistance in both species, it is not possible to affirm that this damage was due to the reduction in the number of spines—nor, in contrast, whether the damaged plants were losing their spines after suffering the damage. A clear and profound explanation is needed. It is also important to note that, in the present study, we considered spines as a component of resistance. It is possible that this attribute functions in the presence of some damage types, so it would be necessary to incorporate other resistance components for a clearer picture (Medel 2001; Silva et al. 2010).

The differences in correlated attributes between forms of management, within each species, also suggest that farmers' cultural practices have enhanced these correlated attributes. For example, cultivated populations of *S. pruinosa* exhibited a significant correlation between the number of branches and fitness. This suggests that pruning may be playing an important role in fruit production, since—if plants have many branches—they tend to have more damage and produce fewer fruits, while pruning regulates both branch and fruit production. In *S. stellatus*, the positive correlation between resistance and fitness has not been modified by management, but it has been important to ensure the local farmers to obtain the fruit production they need. Finally, we must emphasize the vital importance of understanding the effects of human selection on different attributes; how phenotypic integration has been modified by its actions; and how attributes that are not of direct human interest, nor target attributes, can also be modified during this process. Yet it is also necessary to incorporate ecological, cultural and historical elements to interpret these correlated responses as a dynamic process—one that can change over just a few generations.

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Figures

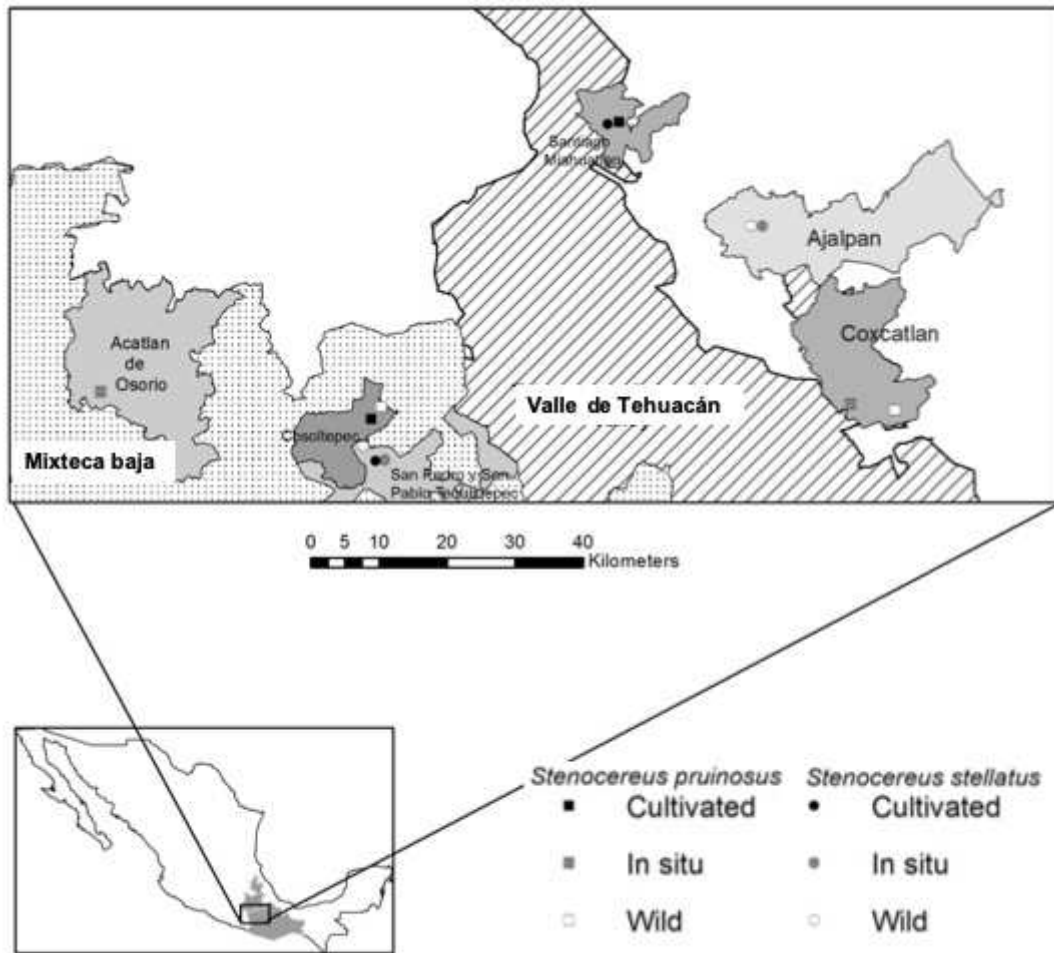


Figure 1

Each population corresponds to a species and to a different form of management (Figure 1) Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

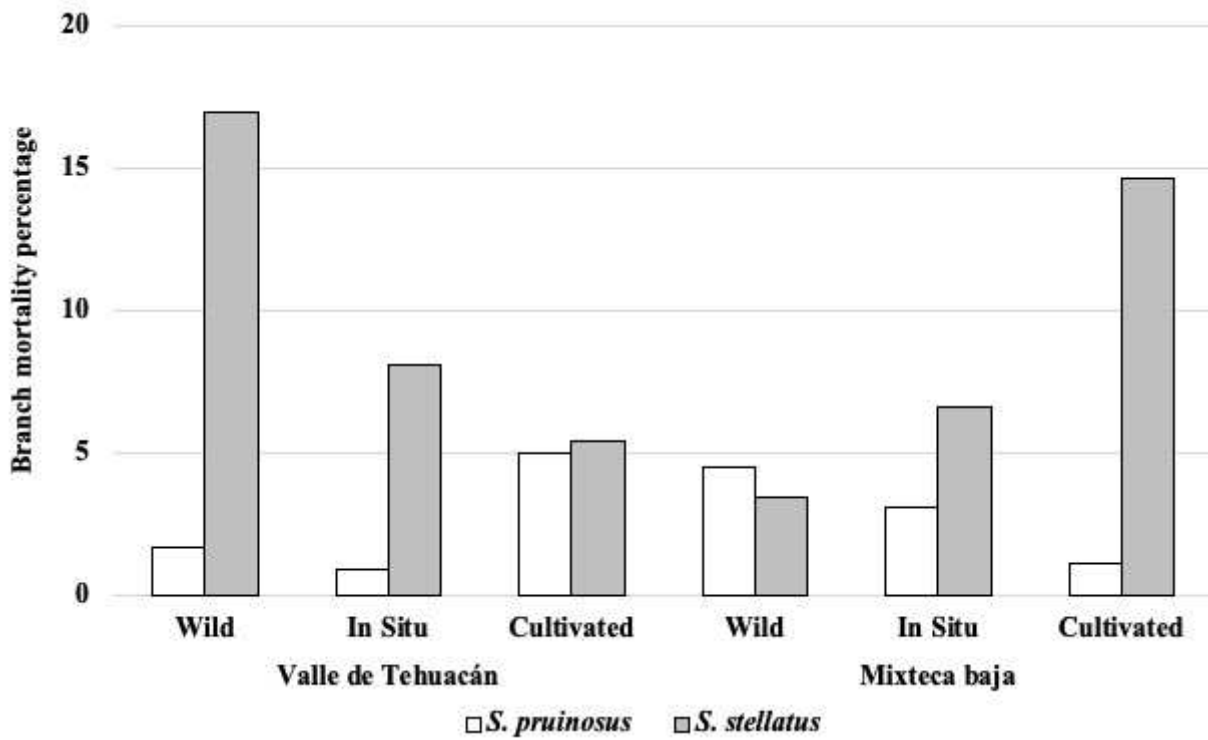


Figure 2

It is worth noting the higher damage level, and the higher branch mortality, recorded for the wild population of *S. stellatus* from the Valle de Tehuacán (Ajalpan) and for the cultivated population from the Mixteca Baja (Chinango) during the sampling period (Figure 2).