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Agave salmiana Plant Communities in Central Mexico as Affected by Commercial Use

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Abstract *Agave salmiana* is a native plant species harvested for the commercial production of mezcal (*Agave* spirits) in the highlands of central Mexico. The objective of this study was to identify vegetation changes in natural communities where *A. salmiana* has been differentially harvested for commercial purposes. Three plant community categories were identified in the state of Zacatecas based on their history of *A. salmiana* utilization: short (less than 10 years of use), moderate (about 25 years), and long (60 or more years). Species cover, composition, and density were evaluated in field surveys by use category. A gradient of vegetation structure of the communities parallels the duration of *A. salmiana* use. *A. salmiana* density was greatest (3,125 plants ha^{-1}) in the short-use areas and less (892 plants ha^{-1}) in the moderate-use areas, associated with markedly greater density of shrubs (200%) and *Opuntia* spp. (50%) in moderate-use areas. The main shrubs were *Larrea tridentata*, *Mimosa biuncifera, Jatropha dioica* and *Buddleia scordioides* while the main *Opuntia* species were *Opuntia leucotricha* and *Opuntia robusta*. *A. salmiana* density was least (652 plants ha^{-1}) in the long-use areas where shrubs were less abundant but *Opuntia* spp. density was 25% higher than in moderate-use areas. We suggest that shrubs may increase with moderate use creating an intermediate successional stage that facilitates the establishment of *Opuntia* spp. Long-term *Agave* use is generating new plant communities dominated by *Opuntia* spp. (nopaleras) as a replacement of the original communities dominated by *A. salmiana* (magueyeras).

Keywords Magueyera · Mezcal · Nopalera · *Opuntia* · Shrub replacement

Introduction

Native flora in Mexico, as in other arid areas of the world, has traditionally suffered from overexploitation derived from lack of ecological knowledge of key species (Hernandez Xolocotzi 1970; Mata-González and Melendez-González 2005; Vilela and others 2009; Jimenez-Valdes and others 2010). *Agave* species are economically, and socially important in central and northern Mexico, but their populations have been severely over-used (Tello-Balderas and García-Moya 1985; García-Herrera and others 2010; García-Moya and others 2011). *Agave* species have a long history of use in North America; prior to corn domestication they were an important source of carbohydrates for native people in Mexico (Parsons and Darling 2000; Zizumbo-Villarreal and Colunga-GarcíaMarin 2008).

Fermentation of *Agave* for commercial production of spirits was initiated in the 16th century and became economically significant in the 17th and 18th centuries in association with population growth following the advent of successful mining operations in central and northern Mexico (Colunga-GarcíaMarin and Zizumbo-Villarreal 2007;

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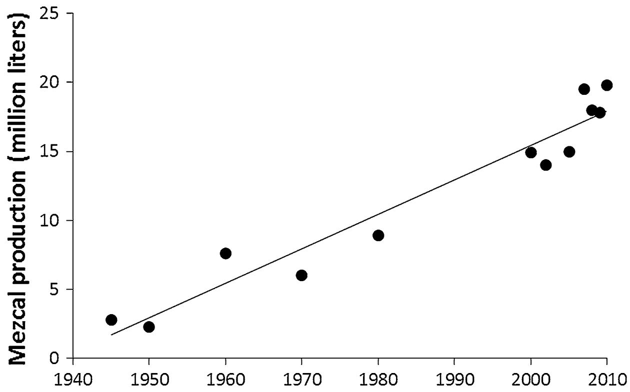

Fig. 1 Mezcal production in Mexico (million liters) from 1945 to 2010. Data fits a linear trend with $y = 0.2499x - 484.33$; $P < 0.01$; $R^2 = 0.94$. Data compiled and adapted from Hernandez Xolocotzi (1970), Salvatierra García (2003), SAGARPA (2006), Morales Carrillo and others (2007), COMERCAM (2010)

Zizumbo-Villarreal and Colunga-GarcíaMarin 2008). More recently, commercial production of mezcal (*Agave* spirit) increased from about 2.5 million liters in 1945–1950 to about 20 million liters in 2010 (Fig. 1). The high mezcal production puts enormous pressure on native *Agave* communities because the industry depends heavily on wildland harvesting (SAGARPA 2006) and plantations with little or no management.

Plant communities dominated by *Agave* species are regionally referred to as magueyeras. In semiarid ecosystems of southeast Zacatecas, Mexico, magueyeras are dominated by *Agave salmiana* Otto Salm Dick ssp. *crassispina* (Trel.) Gentry (maguey verde), which is a highly productive CAM species, reaching fresh weights at maturity up to 250 kg per plant (Tello-Balderas and García-Moya 1985). In fact, *A. salmiana* growing in mesic environments can produce up to 44 Mg of biomass ha^{-1} $year^{-1}$, which is comparable to other highly productive agricultural and forest C_3 and C_4 species (García-Moya and others 2011). Its high productivity and the growth potential of this species in a global scenario of higher temperatures make *A. salmiana* especially well positioned to face the challenges of climate change (García-Moya and others 2011). *A. salmiana* is also important for soil and water retention, typically occurring in shallow soils with low organic matter content (Granados 1999). In addition, magueyeras are an important food source and habitat for birds and other wildlife species in semiarid areas of Mexico (Martinez del Rio and Eguiarte 1987; Aguirre and others 2001).

A. salmiana has been used in the mezcal industry of the Altiplano Potosino-Zacatecano since colonial times (Tello-Balderas and García-Moya 1985). Recently, *A. salmiana* has also been used to complement tequila production as the demand for *Agave* raw material has increased and the production of *Agave tequilana* Weber var. azul, the main species for tequila production, has not satisfied the demand (Martínez Salvador and others 2005a). Typical land users contract with mezcal factories to harvest *Agave* and provide them with raw material (Tello-Balderas and García-Moya 1985). *A. salmiana* is processed for mezcal production by (1) removing the inflorescence bud to favor carbohydrate accumulation in the central body (piña) of the plant (appearance of the inflorescence bud in *A. salmiana* takes 8–20 years and indicates the beginning of its reproductive maturity and the end of its life cycle), (2) removing the leaves, and (3) harvesting the piña which contains the carbohydrates that are necessary for the fermentation process (Tello-Balderas and García-Moya 1985). The process results in the total elimination of individual plants. In periods of high demand *Agave* plants can be harvested during the pre-reproductive stage, which adversely affects asexual reproduction since pre-reproductive plants tend to produce high amounts of vegetative suckers (Martínez Salvador and others 2005a). Adding pressure to the exploitation of this resource, *A. salmiana* is commonly used by local ranchers to feed livestock when better forages are scarce (Pinos-Rodriguez and others 2009).

We have previously reported the density and distribution of *A. salmiana* populations (Martínez Salvador and others 2005a) as well as population structure and morphological characteristics of this species (Martínez Salvador and others 2005b) in central Mexico. However, despite their economic and ecological importance, we lack understanding of vegetation dynamics in *A. salmiana* communities subjected to intensive harvest. Studies have shown that selective elimination of keystone species might result in increase or decrease of associated plant populations mediated by competition or facilitation processes (See Whitford 2002 for a review). Given its prevalence in the study area we hypothesized the intense commercial use of *A. salmiana* would eliminate competition and enhance the presence of associated species. In general, we expected quantitative changes in the plant communities associated with the different levels of *A. salmiana* utilization.

Materials and Methods

Study Area

This study was conducted in 2002 and 2003 in the counties (municipios) of Pinos, Villa Hidalgo, and Noria de Angeles in the southeast part of the state of Zacatecas, Mexico (Fig. 2). Most of the area is ejido (a type of communal land in Mexico) that is mainly used for native flora (*Agave*) harvesting and livestock grazing. In this region the climate is semiarid with annual precipitation of 450 mm, mainly distributed from June to October, and mean annual

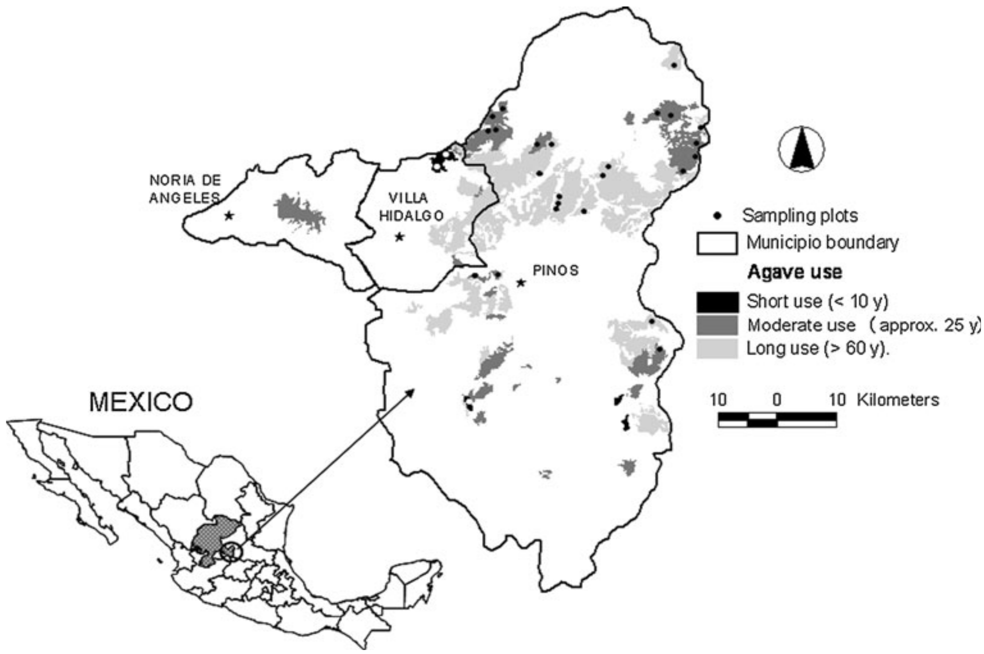

Fig. 2 Location of study area, sampling units, and distribution of plant communities with different history of *A. salmiana* use in southeast Zacatecas, Mexico. The study area is zoomed and includes three municipios: Noria de Angeles (west), Villa Hidalgo (center), and Pinos (east)

temperature ranging between 12 and 18°C. This area belongs to the Saladan Subdivision of the southern Chihuahuan Desert which remains poorly studied relative to the northern Chihuahuan Desert (MacMahon and Wagner 1985; Mata-González and others 2007).

The dominant soils in the area are Eutric Lithosols and Haplic Xerosols based on FAO soil classification modified for Mexico's local conditions (CETENAL 1972). Vegetation in southeast Zacatecas can be grouped into two broad categories: (1) xerophytic and (2) grassland. The xerophytic category, a combination of rosetophyllous and microphyllous communities, was the subject of this study and is characterized by plant communities where *A. salmiana* is abundant and commercially harvested for mezcal production. Other characteristic plants are cacti such as *Opuntia* spp. (nopal) and microphyllous shrubs including *Larrea tridentata* (gobernadora, creosetebush) and *Jatropha dioica* (sangregado, leatherstem) (Rzedowski 1978).

Methods

A. salmiana communities were initially identified from information obtained in direct interviews to local land users with emphasis on concrete knowledge, following methods in Tello-Balderas and García-Moya (1985). With this preliminary information we traveled through the study area identifying and obtaining coordinates and boundaries of areas that according to the users had long (60 years or more), moderate (about 25 years), and short (less than 10 years) history of *A. salmiana* harvest. The communities in these areas are henceforth identified as long-use, moderate-use, and short-use communities, respectively. The short-use communities included some areas with minimal commercial utilization mainly because of their remote locations or access difficulty. These categories of use were selected for two reasons (1) they were well defined by local accounts and (2) they appeared to have a differential effect on vegetation that was detectable on the ground by aerial photography (see below). Harvesting levels by use category through time are unknown but were assumed similar because, reportedly, they mostly depend on *Agave* maturity rate and commercial demand. Historical harvesting levels have been in correspondence with the variation in mezcal production, which has raised steadily (Fig. 1), implying a cumulative effect on plant communities.

Local accounts and the similar characteristics of climate, soil, and terrain support the assertion that the areas selected for their history of use originally sustained typical magueyera communities. Soils in the three use categories were very comparable: Eutric Lithosols and Haplic Xerosols occupied 70–85% of each area (Martínez Salvador and others 2005b) (Table 1). Eutric Lithosols are medium textured and shallow soils sometimes with coarse gravel in the soil profile. Haplic Xerosols are typical of areas with high calcium carbonate content and with presence of duripans and fragipans (CETENAL 1972). Both Lithosols and Xerosols are shallow, have a thin organic layer, and a calcareous phase. *A. salmiana* populations are mostly restricted to these shallow and calcareous soils, where they can successfully compete due to their shallow and highly specialized root systems (García-Herrera and others 2010; García-Moya and others 2011). In our sampling units soils ranged in depth from 25 to 34 cm (Table 1), while according to other reports in the area, deeper soils

Table 1 Terrain and soil attributes of three *A. salmiana* communities with different history of *A. salmiana* use in Zacatecas, Mexico

Attributes	Use categories		
	Average ± standard error		
	Short use (<10 years)	Moderate use (≈25 years)	Long use (>60 years)
Predominant soil types (%)	Eutric Lithosol-Haplic Xerosol 75	Eutric Lithosol-Haplic Xerosol 70	Eutric Lithosol-Haplic Xerosol 85
Texture of predominant soils 0–15 cm	Sandy loam	Sandy loam	Sandy loam
Soil depth (cm)	34 ± 5.6	25 ± 6.1	30 ± 5.8
Indurated layer	Yes	Yes	Yes
Calcareous	Yes	Yes	Yes
Surface litter (%)	34 ± 9.9	23 ± 10.8	46 ± 12.8
Rockiness (%)	16 ± 9.8	25 ± 7.1	39 ± 16.3
Elevation (m)	2,217 ± 89	2,146 ± 68	2,229 ± 75
Slope (%)	19 ± 7	28 ± 7	18 ± 6

(≥50 cm) tend to support grasslands (Aguado-Santacruz and others 2002; Mata-González and others 2007). Other soil and terrain variables (texture, presence of indurated layer, high calcium carbonate content, rockiness, surface litter cover, elevation, and slope) were also similar among the sites within the three use categories.

ArcGIS 9.1 was used to identify and digitize these areas using black and white aerial photographs taken in 2001 by INEGI (Mexico's Instituto Nacional de Estadística, Geografía e Informática). We conducted photogrammetric analyses and rapid field surveys and found that in general areas with long use had <20% canopy cover (the projected aerial plant parts onto the ground), areas with moderate use had 20–40% canopy cover and areas with short use had >40% canopy cover. The correspondence between vegetation cover and degree of *A. salmiana* utilization was corroborated by multiple field visits and additional interviews with users. An additional goal was to ensure that other possible factors such as grazing pressure or fire were not differentially affecting the different vegetation groups of our study. Some areas were eliminated from our analysis for not having adequate records, but in general grazing pressure was similar and there were no accounts of wildfires perhaps for the lack of fine fuel. At the time of our sampling *A. salmiana* communities extended over 59,900 ha in the study area, of which 2, 86, and 12% was occupied by communities in the short-use, moderate-use, and long-use categories, respectively (Fig. 2).

The appropriate field sample size was determined from the standard error of the density of all species in a preliminary survey (McCune and Grace 2002). We randomly established 12 circular plots of 250 m^2 in each use category to sample plant community characteristics during the summer. All field observations were obtained by the same personnel to reduce risk of individual observer bias. Within these plots we documented (1) number of live individuals by plant species and (2) canopy diameter, base diameter, and height of all live shrubs and succulents (the main community components). We did not record grasses because they were rarely present. With this information we calculated density by species, species richness (total number of species), and the Shannon-Wiener diversity index. Canopy and basal areas per plant (m^2) and species cover (as percentage of ground cover) were calculated using the canopy and trunk diameters. We also calculated the dry biomass production of *A. salmiana* in each use category using plant dimensions and the biomass equation presented in Martinez-Morales and Meyer (1985).

Data Analysis

A principal component analysis (PCA) was performed to graphically explore and differentiate the use categories based on the influence of multiple variables of vegetation and terrain (Olsson and Staaf 1995; McCune and Grace 2002). We also used analyses of variance to more specifically compare the use categories with respect to vegetation variables: canopy cover, basal cover, canopy area and basal area per plant, plant height, plant density, *A. salmiana* dry matter production, species diversity, and richness. Furthermore, species density was also compared among use categories. Significant differences were declared at $P < 0.05$ and mean separation was performed using the Duncan test. All analyses were performed with SAS software, version 9.2 (SAS Institute Inc., Cary, NC).

Results

The PCA results separated the three use categories into two groups: one group consisting of the communities with short use and another group consisting of the communities with

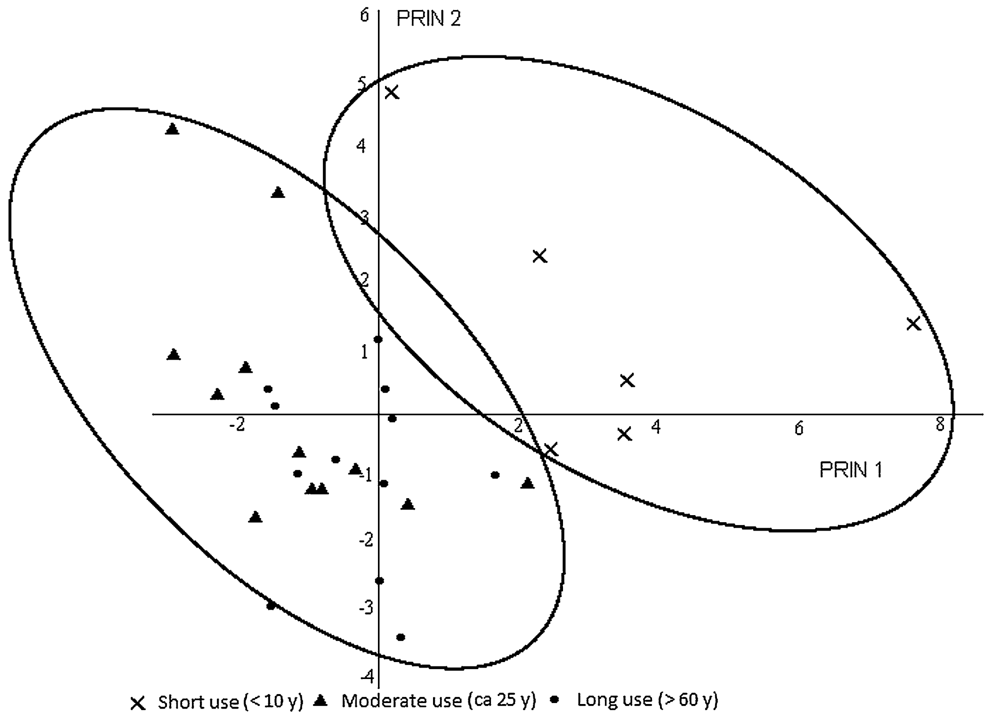

Fig. 3 PCA of the association among *A. salmiana* communities with different history of *A. salmiana* use in Zacatecas, Mexico. PC-1 explained 33% of the variability and PC-2 explained 22% of the variability

both moderate and long use (Fig. 3). 32% of the variance was explained by PC1 (*Agave* density) and 22% by PC2 (canopy cover). The ANOVA results showed that all vegetation variables differed among the three categories of use (Table 2). Areas with short use had higher ($P < 0.05$) canopy and basal cover as well as higher canopy and basal area per plant than those with moderate and long use. Plant height, species richness, and *A. salmiana* biomass production were also greater ($P < 0.05$) in short-use communities than in the other two communities. Plant density was higher ($P < 0.05$) in moderate-use communities than in short-use and long-use communities, and species diversity (Shannon-Wiener) was lower in short-use communities than in the other two use categories.

Further testing for differences among use categories, individual species densities were compared (Table 3). In the short-use areas, *A. salmiana* was by far the dominant species with 3,125 plants ha^{-1} representing 53% of the individuals in the community. Nineteen other species provided the other 47% of individuals, but the most abundant were *J. dioica* (14%), *L. tridentata* (4%), and *Opuntia cochinera* (4%). In moderate-use areas, *A. salmiana* had 892 plants ha^{-1} representing only 12% of the plant community while microphyllous shrubs were more dominant: *Buddleia scordioides* (16%), *J. dioica* (14%), *Mimosa biuncifera* (13%), and *L. tridentata* (11%). In areas of long use *A. salmiana* was least dense (652 plants ha^{-1}) representing 11% of the community. Although in moderate-use and long-use communities the proportion of *A. salmiana* was similar, this was attributable to the decrease in total plant density observed in long use communities (Table 2). In long-use communities, plants that co-dominated with *A. salmiana* were *J. dioica* 13%, *Opuntia leucotricha* 11%, and *Opuntia robusta* 9%. The microphyllous shrubs that were abundant in the moderate-use communities were much less dominant in the long-use communities: *B. scordioides* 16 versus 2%, *M. biuncifera* 13 versus 7%, and *L. tridentata* 11 versus 7%.

Higher degrees of magueyera use resulted in expected lower proportions of *A. salmiana* accompanied by higher proportions of *Opuntia* spp. in the communities (Fig. 4). The proportion of microphyllous shrubs in the moderate-use communities was 2.5 times greater than in short-use communities. However, the proportion of microphyllous shrubs in the long-use communities was only 1.5 times higher than in short-use communities and 35% lower than the proportion in moderate-use communities.

Discussion

Initial analysis of vegetation indicated that plant communities could be grouped into (1) those with short history of *A. salmiana* use and (2) those with moderate and long history of *A. salmiana* use. The communities with short use of *A. salmiana* seem to represent an established community in which this species dominates with more than 50% of the vegetation cover and density. Decades of commercial utilization and lack of adequate management plans (Martínez Salvador and others 2005a) have resulted in *A salmiana* dominance of only 11–12%. However, plant communities

Table 2 Vegetation and terrain attributes of three *Agave salmiana* communities with different history of *A. salmiana* use in Zacatecas, Mexico

Attributes	Use categories		
	Average ± standard error		
	Short use (<10 years)	Moderate use (≈25 years)	Long use (>60 years)
Canopy cover (%)	52 ± 11	29 ± 5	21 ± 4
Basal cover (%)	9 ± 2	4 ± 1	3 ± 1
Canopy area per plant (m^2)	0.88 ± 0.2	0.39 ± 0.1	0.37 ± 0.1
Basal area per plant (m^2)	0.15 ± 0.04	0.06 ± 0.02	0.06 ± 0.01
Plant height (m)	0.82 ± 0.1	0.58 ± 0.1	0.54 ± 0.1
Plant density (no. ha^{-1})	5,908 ± 256	7,465 ± 315	5,647 ± 189
Diversity index (Shannon-Wiener)	1.46 ± 0.2	1.99 ± 0.3	2.21 ± 0.4
Species richness (number of species)	12.3 ± 2	8.3 ± 1	7.7 ± 1
A. salmiana production (dry kg m^{-2})	1.6 ± 0.4	0.3 ± 0.1	0.2 ± 0.1

have been modified in multiple manners and further analyses indicated that there are clear differences that distinguish the three categories of use that were initially explored.

The void left by selective harvest of *A. salmiana* plants has triggered substitutions in plant communities where *A. salmiana* lost dominance mainly to microphyllous shrubs in moderate-use areas and to both microphyllous shrubs and *Opuntia* species in long-use areas. Long-use areas have been exploited for decades longer than those with moderate use and there is little recovery over time in these areas because the commercial utilization scheme does not include an effective plant regeneration strategy and because in recent years *A. salmiana* plants have been utilized even before reaching complete maturity (Martínez Salvador and others 2005a). We suggest that moderate-use communities in which microphyllous shrubs are highly prevalent may be a transitional stage between the short-use communities and the long-use communities that are increasingly dominated by *Opuntia* species. Such increase in dominance was observed in different *Opuntia* species, from those highly adapted to disturbance such as *Opuntia imbricata* to those less adapted to disturbance and more dominant climax species such as *O. robusta* (Gonzalez-Espinosa and Quintana-Ascencio 1986; Allen and others 1991).

We suggest the reduction in *A. salmiana* dominance caused by commercial harvest was first capitalized upon by microphyllous shrubs. In desert environments, parallel examples demonstrated that shrubs can dominate and replace grasses following heavy grazing, drought, or fire suppression (Grover and Musick 1990; Milchunas and Lauenroth 1993; Valone and Sauter 2005; Mata-González and others 2007). With low competition, shrubs are capable of establishment in open ground because they are highly tolerant to extremes in temperature and low moisture (López and others 2007). The subsequent dominance of *Opuntia* species in areas where *A. salmiana* is least abundant is attributable to *Opuntia* competitiveness causing of shrub replacement. It is well established that shrubs serve as nurse plants to cacti, substantially improving their chance for survival by providing protection from excessive heat, frost, wind, and predation as well as improved soil conditions (Yeaton 1978; Yeaton and Romero-Manzanares 1986; Valiente-Banuet and Ezcurra 1991; Flores and Yeaton 2000; Reyes-Olivas and others 2002; Flores and Jurado 2003). *Larrea* spp. have been reported as nurse plants for cacti in both North America and South America (Yeaton 1978; Méndez and others 2004).

It is possible that *Opuntia* spp. is outgrowing and outcompeting the nurse shrubs in the long-use areas causing vigor loss and mortality. Previous studies indicate that in the southern Chihuahuan desert the replacement of *L. tridentata*, *M. biuncifera* and *Acacia schaffneri* by *Opuntia* spp. was attributable to (1) mechanical damage imposed by taller and more robust cacti on the shrub, and (2) a rain shadow caused by the shallow *Opuntia* roots producing rain interception and preventing light rainfall events to benefit the deeper-rooted shrubs (Yeaton 1978; Yeaton and Romero-Manzanares 1986; Flores and Yeaton 2000). Similar replacement of nurse shrubs by large cacti has also been observed in the Sonoran desert (McAuliffe 1984) and the Tehuacan valley of central Mexico (Flores-Martínez and others 1994). However, we do not have data on the specific interactions between cacti and shrubs and thus our nurse-protégé hypothesis remains speculative. Yet, it was clear that *Opuntia* gained dominance over time in areas previously dominated by *Agave* or shrubs. *A. salmiana* can also grow under established nurse shrubs to subsequently become dominant (Yeaton and Romero-Manzanares 1986). In our study area, *Agave* recruitment was low probably because the species is used before reaching maturity (Martínez Salvador and others 2005a).

Table 3 Average density of species found in three *Agave salmiana* communities with different level of *A. salmiana* use in Zacatecas, Mexico

Species	Use categories		
	Short use (<10 years)	Moderate use (≈25 years)	Heavy use (>60 years)
Agaves	Number of plants ha^{-1} ± standard error		
Agave salmiana Otto Salm Dick ssp. *crassispina* (Trel.) Gentry	3,125 ± 15.6	892 ± 16.2	652 ± 16.7
Microphyllous shrubs			
Acacia farnesiana (L.) Willd.	74 ± 5.2	38 ± 0.3	0
Acacia schaffneri (S. Watson) F. J. Herm.	0	0	213 ± 13.3
Acacia vernicosa Standley	48 ± 2.6	0	228 ± 28.9
Berberis trifoliata Moric.	85 ± 7.5	53 ± 0.6	100 ± 5.8
Buddleia scordioides Kanth.	0	1,216 ± 126.2	101 ± 0.3
Dalea bicolor Humb. and Bonpl. ex Willd.	0	0	196 ± 0.3
Fluorensia cernua DC	0	0	295 ± 17.0
Jatropha dioica Sease ex Cerv.	813 ± 90.9	1,063 ± 108.3	727 ± 77.9
Larrea tridentata [DC] Cov.	260 ± 19.6	827 ± 109.7	424 ± 64.1
Condalia ericoides (A. Gray) M.C. Johnst.	0	480 ± 65.2	81 ± 0.3
Mimosa biuncifera Benth.	117 ± 9.8	954 ± 115.2	400 ± 44.5
Prosopis velutina Woot.	64 ± 3.2	0	0
Cacti			
Echinocereus stramineus (Engelm.) F. Seitz	36 ± 1.4	427 ± 35.2	80 ± 8.1
Ferocactus histrix (DC) Lindsay	173 ± 28.6	0	67 ± 6.6
Ferocactus latispinus (Haw.) Br. and R.	60 ± 4.0	0	19 ± 0.3
Mammillaria lasiacantha Engelm.	0	0	160 ± 2.9
Opuntia cantabrigensis Lynch	76 ± 10.1	87 ± 0.3	89 ± 0.3
Opuntia cochinera Griffiths	220 ± 36.7	0	0
Opuntia imbricata (Haw) D C.	98 ± 7.5	164 ± 5.5	240 ± 23.1
Opuntia leptocaulis DC.	0	0	133 ± 6.6
Opuntia leucotricha DC.	100 ± 6.9	267 ± 11.8	613 ± 85.2
Opuntia microdasys (Lehm) Pffeifer	120 ± 4.6	158 ± 6.6	113 ± 9.2
Opuntia rastrera Weber	157 ± 16.7	360 ± 22.2	120 ± 10.7
Opuntia robusta Wendl.	200 ± 22.5	267 ± 26.6	485 ± 71.0
Opuntia streptacantha Lemaire	0	213 ± 13.3	100 ± 12.1
Opuntia tunicata (Lehm.) Link and Otto	40 ± 1.2	0	0
Others			
Dasylirion spp. Zucc.	42 ± 2	0	0
Yuca filifera Chab.	0	0	11 ± 0.3

The presence of well-developed *A. salmiana* populations was determinant in separating (PCA) the lightly-use communities from the other two communities with higher use. Such separation is compatible with the more developed canopies and vegetation uniformity that was observed in lightly-used communities with respect to the more heavily used communities. *A. salmiana* dominance was more important in separating the PCA groups than the dominance of shrubs or *Opuntia* spp. This is congruent with our proposal that high density magueyeras are stable communities that are transitioning towards plant communities dominated by *Opuntia* spp. (nopaleras) as a result of the current commercial utilization of *A. salmiana*.

The short-use communities were highly dominated by *A. salmiana* but they had a high number of low-density, secondary species. As *A. salmiana* lost dominance in the moderate-use and long-use areas, species richness decreased but the diversity index increased. This suggests that in dense stands of *A. salmiana* many species can survive but are maintained in check by the intense resource competition. *Agave*'s competitive ability can be attributable to a combination of traits including high water use

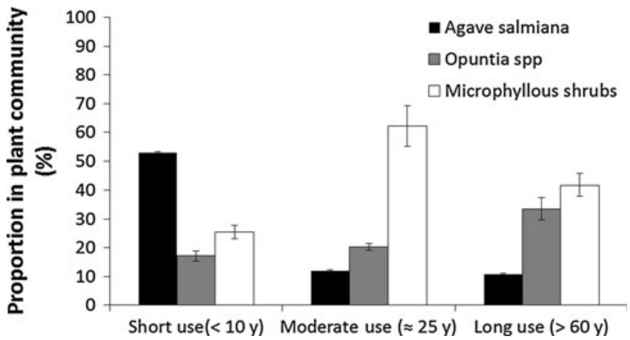

Fig. 4 Proportion (%) of *A. salmiana*, *Opuntia* spp., and microphyllous shrubs in three communities with different history of *A. salmiana* use in Zacatecas, Mexico. *Error bars* indicate standard error of the mean

efficiency (CAM photosynthesis), more continuous water uptake and water storage than other non-succulents, and rapid water uptake and soil water depletion during small rain events by shallow roots even at high temperatures (Nobel 1997). Only when *A. salmiana* dominance decreased could other species thrive and form well represented populations. The community then was functionally more diverse without the dominance of a single species. The disturbance caused by elimination of *A. salmiana* removed the barriers for a more diverse community, preventing competitively dominant species from suppressing others in the community. Low diversity would be anticipated in relatively undisturbed *A. salmiana* communities and in communities dominated by *Opuntia* spp. after severe commercial exploitation.

To summarize, the current intense commercial harvest of *A. salmiana* has profound impacts on the remaining plant communities. Decrease in *Agave* can shift communities to ones dominated by woody microphyllous. Continued harvest of immature *Agave* in these woody communities hinders its recovery and eventually favor a replacement of microphyllous shrubs by *Opuntia* species. Although the mechanism for this transition remains unclear, such replacement phenomenon has been well documented in similar areas (Yeaton and Romero-Manzanares 1986). Our results suggest the original dense magueyeras of the area are transitioning towards nopaleras. Changes associated with this transition include a more diverse plant community where *A. salmiana*, is no longer dominant. However, it is foreseeable that as long as *A. salmiana* is intensively used in the area without a viable regeneration plan, *Opuntia* spp. will become denser and more dominant in the area, excluding other species and similarly reducing plant diversity.

In terms of the commercial viability of the mezcal industry, part of which is still based on the exploitation of wildland vegetation, the current rates of utilization of *A. salmiana* on examined lands within the study area appear unsustainable and detrimental to magueyera community function. The commercial use of native *A. salmiana* communities must be accompanied by a conservation plan to ensure that this species can continue providing its important ecological functions. It is particularly important that management centers on avoiding the harvest of pre-reproductive plants because these represent the highest potential for producing new individuals (Martínez Salvador and others 2005a).

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