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Structure and woody species diversity of the *Dasylirion cedrosanum* (Nolinaceae) rosette scrub of central and southern Coahuila State, Mexico

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Abstract: The most prominent vegetation type in the state of Coahuila, in northern Mexico, is Chihuahuan Desert Scrub. This plant formation encompasses the little known *Dasylirion cedrosanum* (sotol) rosette scrub, a community that extends over more than one fourth of Coahuila and whose most distinctive species is subjected to intense extraction from its native communities for a variety of purposes. Based on a highly replicated sampling procedure that included 131 plots located in the state's central and southern portions, we analyzed vegetation structure, floristics, and species diversity of this plant community. A cluster analysis allowed us to differentiate five variants (associations) of the *Dasylirion cedrosanum* rosette scrub, which together host a richness of 97 species of vascular plants distributed in 61 genera and 28 families. These communities occurred across an elevational range of 850-2,550 m a.s.l. *Dasylirion cedrosanum* density varied between 193 and 705 ind./ha, with the highest value occurring in the *Quercus intricata-Dasylirion cedrosanum* association. Other prominent species in these scrublands were *Agave lecheguilla* and *Euphorbia antisyphilitica*. The *Agave lecheguilla-Dasylirion cedrosanum* association was the most broadly distributed and it hosted the highest richness species, while the largest Shannon diversity index value was recorded for the *Dasylirion cedrosanum-Viguiera greggii* association. The effects of human utilization of this species on the structure of those plant communities where it occurs are largely unknown; further studies are needed to better understand its dynamics and to be able to suggest more adequate regulations for its commercial harvesting.
Key words: Chihuahuan Desert, cluster analysis, elevation gradient, natural resources utilization, *sotol* production.

Resumen: La vegetación más prominente en el estado de Coahuila, en el norte de México, es el matorral desértico chihuahuense. Esta formación vegetal incluye el matorral rosetófilo de *Dasylirion cedrosanum*, comunidad poco conocida que cubre más de la cuarta parte del estado de Coahuila y cuya especie característica es sometida a una explotación intensa en sus comunidades nativas para distintos fines. Con base en un muestreo fuertemente replicado, que incluyó 131 unidades de muestreo ubicadas en el centro y sur del estado, se evaluó la estructura de la vegetación, su composición florística y la diversidad de especies de esta comunidad vegetal. Un análisis de clasificación numérica permitió diferenciar cinco variantes (asociaciones) del matorral rosetófilo de *Dasylirion cedrosanum*, que en conjunto albergan una riqueza de 97 especies agrupadas en 61 géneros y 28 familias. Estos matorrales se distribuyen en un intervalo altitudinal de 850-2,530 m s.n.m. La densidad de *Dasylirion cedrosanum* varió de 193 a 705 ind./ha; el valor más alto fue registrado en la asociación *Quercus intricata-Dasylirion cedrosanum*. Otras especies comunes en estos matorrales fueron *Agave lecheguilla* y *Euphorbia antisyphilitica*. La asociación *Agave lecheguilla-Dasylirion cedrosanum* tuvo la distribución espacial más amplia y la mayor riqueza de especies, mientras que el mayor valor del índice de diversidad de Shannon se obtuvo para la asociación *Dasylirion cedrosanum-Viguiera greggii*. Hay un gran desconocimiento en torno a los efectos del uso de esta especie por el ser humano sobre la estructura de las comunidades en las que ésta se presenta; por lo tanto, es necesario realizar nuevos estudios que permitan conocer su dinámica y establecer la normatividad más adecuada para su aprovechamiento comercial.
Palabras clave: análisis de clasificación, aprovechamiento de recursos vegetales; Desierto Chihuahuense; gradiente altitudinal; producción de sotol.

The most prominent vegetation type in the state of Coahuila, in northern Mexico, is Chihuahuan Desert Scrub. This plant formation is mostly represented by microphyllous scrub and rosette scrub (Henrickson and Johnston, 1986; Villarreal and Valdés, 1992-1993). Rosette scrub often referred to also as rosette-scrub forest, is a community dominated by evergreen, short and spiny shrubs, with rosette-forming leaves concentrated at the plant's base (Rzedowski, 1966; Box, 1981; Martorell and Ezcurra, 2002). In the Chihuahuan Desert, the rosette-dominated plant communities variously known as Lechuguilla scrub, *Yucca* woodland, *Dasylirion* scrub, or *Dasylirion* woodland, account together for approximately 12% (60,840 km^2) of the total area of this biogeographical region (Henrickson and Johnston, 1986), while in Coahuila, rosette scrub extends over an area of 40,579 km^2, which represents more than one fourth (26.8%) of the state territory (ICE, 2001). While at first glance, its floristic composition and structure do not appear to vary greatly across space, in fact four variants have been described for this community (Henrickson and Johnston, 1986; González-Elizondo *et al.*, 2007). One of them is the *Dasylirion* scrub, regarded as a physiognomically distinct plant community typical of the Chihuahuan Desert and of the entire North American Arid Region (Martorell and Ezcurra, 2002). This community is generally found in mountainous areas, at elevations between 1,000 and 2,000 m a.s.l., on lithosols and on areas with abundant limestone outcrops (Henrickson and Johnston, 1986).

The genus *Dasylirion* comprises 16 species, all of them distributed in mountainous arid and semi-arid regions of northern Mexico and southwestern USA (Bogler, 1995, 1998), with four of them occurring in Coahuila (Villarreal, 2001). *Dasylirion cedrosanum* Trel. is the most abundant species of this genus, and it is the physiognomically dominant component of the rosette scrub that occurs in south-central Coahuila and adjacent areas of the states of Durango and Zacatecas, Mexico (Henrickson and Johnston, 1997; Villarreal, 2001). This taxon represents one of the most important non-timber forest products in the state rural areas, as it is used for human and cattle nourishment, as well as a source of construction materials, handcraft making, and alcoholic distills (Marroquín *et al.*, 1981; Romahn de la Vega, 1992, Olhagaray *et al.*, 2004). Its relevance has increased recently as it is now being harvested for the commercial production of *sotol*, an alcoholic beverage obtained from the stems (Marroquín *et al.*, 1981; Sierra *et al.*, 2008). Regrettably, this activity lacks adequate management plans and there are no commercial plantations of this species; instead, the plants are extracted directly from their native ecosystems (Villavicencio *et al.*, 2007). Therefore, its populations are likely to undergo severe reductions in the near future. Such population decline would probably also affect other important accompanying species, since Coahuila's rosette scrub hosts the largest number of endemic plant taxa and species included in the Mexican Official List of Endangered Species for this State (Villarreal-Quintanilla and Encina-Domínguez, 2005; SEMARNAT, 2010).

The goals of this study were to describe vegetation structure and floristics of the *Dasylirion cedrosanum* scrub, and to provide ecological information for this community in Coahuila, including the associated shrub species, in order to contribute to the existing knowledge about this species and to provide a stronger basis for its management.

Materials and methods

Study area. The study was conducted in the central and southern portions of Coahuila state, over an area of approximately 20,779 km^2 (ICE, 2001) (Figure 1), i.e. 4.1% of the 507,000 km^2 corresponding to the Chihuahuan Desert Region (CDR) (MacMahon and Wagner, 1985). The study area includes several smaller *sierras* (mountain ranges) that form part of the Eastern Sierra Madre (*Sierra Madre Oriental*) and the Mexican Plateau (*Altiplanicie Mexicana*) physiographic provinces: Arteaga, Los Alamitos, La Concordia, Las Delicias, La Fragua, La Gavia, Jimulco, La Madera, Menchaca, La Paila, Parras, San Marcos, Zapalinamé. Elevation ranges from 900 m in central Coahuila to 2,500 m in the mountains of the state southeastern corner. The prevailing climates are of two types (García, 2004): very dry climates (BWhw) typical of the western portion of the study area, which is part of the Mexican Plateau, and semi-warm dry climates (BS_0hw), characteristic of the Eastern Sierra Madre, in the central and southeastern parts of the study area. Annual temperature oscillation is high; mean annual temperature ranges from 17 to 19 ºC, with maxima of 25 to 32 ºC from May through October, and minima of 1 to 7 ºC from November to April; on average there are 12 days with frost each year. Total annual precipitation ranges between 350 and 450 mm, with rainfall concentrating in summer months. Lower Cretaceous sedimentary rocks, mostly limestone and conglomerates, characterize parental material in the area. Soils are mostly lithosols, calcareous regosols, and haplic xerosols, and they are shallow with low organic matter content, loamy texture, and good drainage. Villarreal and Valdés (1992-1993) classified regional vegetation as rosette desert scrub (*matorral desértico rosetófilo*), and highlighted *Agave lecheguilla*, *Dasylirion cedrosanum*, *Euphorbia antisyphilitica*, and *Hechtia texensis* as the most frequent plant species. At some localities in the SE part of Coahuila transitional communities exist among this vegetation type, sub-montane scrub and pinyon pine forest, where the most representative species are *Quercus intricata* and *Pinus cembroides*.

Vegetation sampling and analysis. We selected a total of 131 sites across the sierras of central and southern Coahuila, within the known range of *Dasylirion cedrosanum* (Pinkava, 1984; Rodríguez *et al.*, 1994; Villarreal, 1994; 2001). At each site we sampled vegetation in a 500 m^2 circular plot, within which we tallied the number of individuals of this species and measured the diameters and heights of their rosettes, as well as the crown cover of all woody species present in the plot. At each site we recorded elevation and geographical coordinates (with a GPS), slope inclination (with a Haaga inclinometer), and aspect.

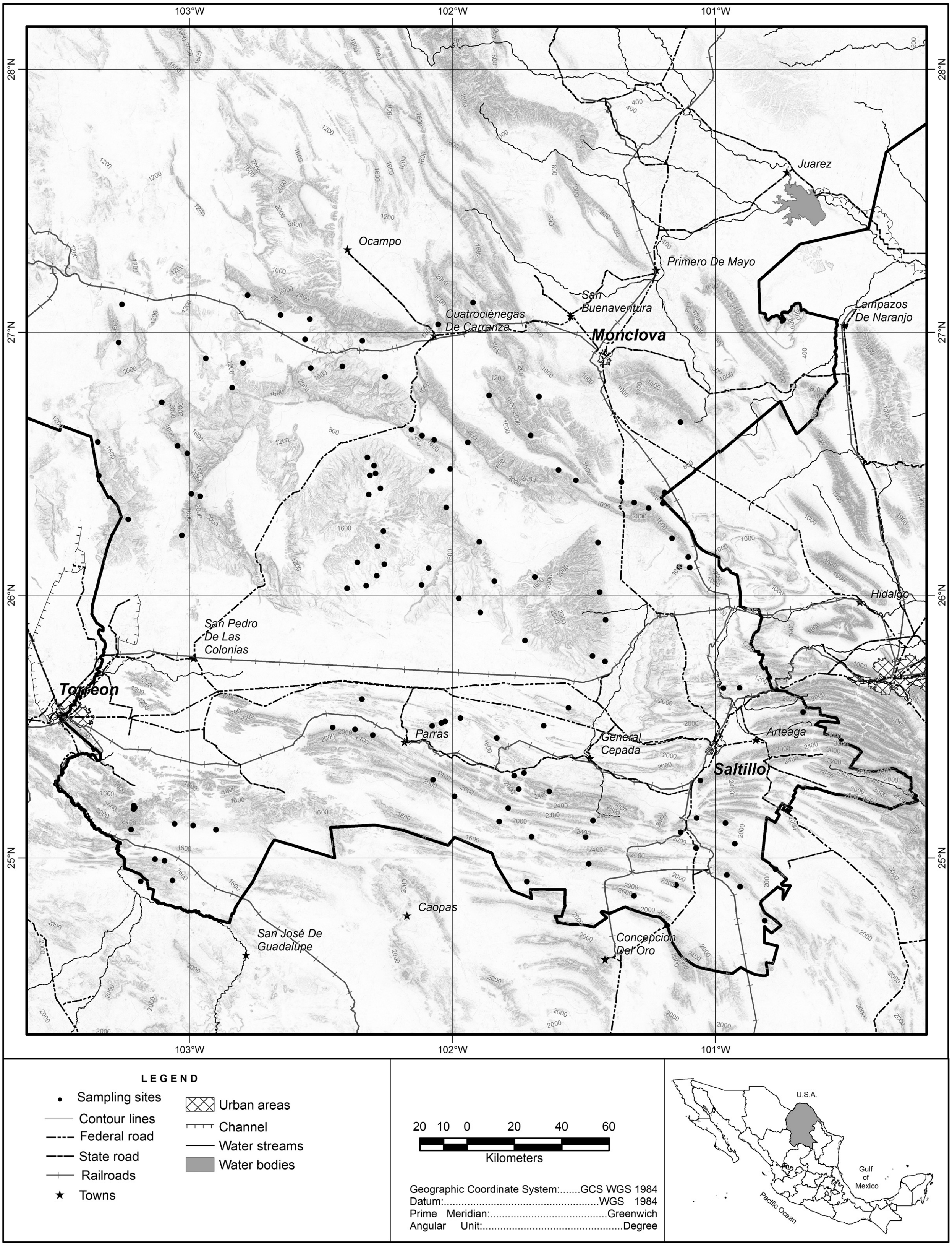

Figure 1. Distribution of sampling sites of the *Dasylirion cedrosarum* rosette scrub in central and southern Coahuila State, Mexico.

We constructed a matrix containing density values of 90 species occurring in all sampling sites, with which we performed a cluster analysis using Ward's method (Minimum Variance), an agglomerative, polythetic, and hierarchical classification procedure (Ward, 1963; Manly, 1986). The classification was performed with NTSYSpc ver. 2.0 (Rohlf, 1998). Between plot similarities were calculated with the Morisita Index. For each group of plots interpreted as a plant association, we calculated density, frequency, and crown cover for each species; relative values of these variables were summed in order to calculate Relative Importance Values (RIV; Mueller-Dombois and Ellenberg, 1974), according to the following formula:

$$\text{RIV} = \frac{\text{relative density} + \text{relative cover} + \text{relative frequency}}{3}$$

We chose this conventional way of estimating the structural contributions of the species occurring in the community as it integrates in a single calculation the three basic attributes of vegetation structure. We also calculated log2 Shannon-Wiener's (*H'*) diversity index (Magurran, 1988), and evenness (*E*) according to Pielou (1966); pairwise comparisons of diversity indices between associations was performed through Hutcheson (1970) modified *t*-test as described by Magurran (1988). Finally, we examined *Dasylirion cedrosanum* distribution along the altitudinal gradient by performing a simple linear regression (Zar, 1999) of this species densities on sampling site elevation.

Results

Floristic composition. In total, 97 species belonging to 61 genera, and 28 families were recorded (Appendix). The richest families were Cactaceae (30 species), Fabaceae and Asteraceae (12 each), and Agavaceae (9). In turn, the richest genera were *Opuntia* (7 species), *Acacia* (5), *Agave* (4), and *Viguiera*, *Leucophyllum*, *Quercus*, and *Yucca* (3 species each). Eight species were endemic to Coahuila and adjacent regions in neighboring states, and seven have official protection status according to the Mexican environmental legislation (SEMARNAT, 2010), with three species being part of both groups (Table 1). The large majority of species recorded (91, 93%) were shrubs, while the few remaining taxa were trees. In addition to *Dasylirion cedrosanum*, the most abundant species were *Agave lecheguilla*, *Euphorbia antisyphilitica*, *Hechtia texensis*, and *Viguiera greggii*. Some dominant species in neighboring plant communities were also common here, such as *Larrea tridentata*, *Lindleya mespiloides*, *Pinus cembroides*, *Quercus intricata*, and *Rhus virens*.

Site classification. The classification of the sampling sites allowed us to differentiate five vegetation variants at the cutoff level of 55%, which were interpreted as plant associations of the *Dasylirion cedrosanum* rosette scrub (Figure 2). In general, these associations occurred along an elevational gradient that increased from top to bottom in the dendrogram, from 850 to 2,530 m a.s.l. The first three associations comprised 105 sites (80% of the total); their mean elevation was lower than 1,600 m a.s.l., and they were characterized by the dominance of low, rosette-like shrubs, in addition to some succulent species. Conversely, the remaining two associations occurred above the 1,600 m contour and were dominated mostly by microphyllous and sclerophyllous shrubs and trees.

Vegetation structure in the associations of the Dasylirion cedrosanum *rosette scrub*. (1) *Hechtia texensis-Agave lecheguilla* association. This association occurred in the most arid section (central-west) of the study area. Most sites concentrated on the lower slopes (mean 1,300 m a.s.l.; range 856-

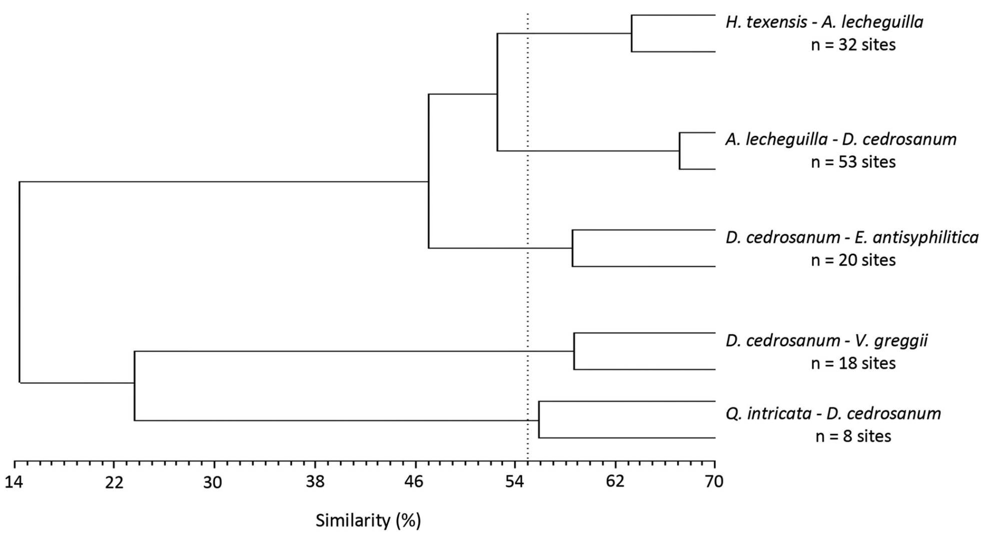

Figure 2. Classification of sampling plots in the *Dasylirion cedrosanum* rosette scrub in Coahuila, Mexico.

Table 1. Species occurring in the *Dasylirion cedrosanum* rosette scrub with geographical ranges restricted to the state of Coahuila, Mexico, or that have been listed under a protection or threat category according to Mexican environmental legislation (SEMARNAT, 2010).

Species	Distribution	Protection/threat status
Acacia glandulifera	Endemic to Coahuila	None
Agave victoriae-reginae	Endemic to Coahuila	In danger of becoming extinct
Ariocarpus fissuratus var. *lloydii*	Endemic to Coahuila	Noner
Ariocarpus retusus	Not endemic	Subjected to special protection
Astrophytum capricorne	Endemic to Coahuila	Threatened
Coryphantha lloydii	Endemic to Coahuila	None
Echinocactus platyacanthus	Not endemic	Subjected to special protection
Epithelantha micromeris	Not endemic	Subjected to special protection
Ferocactus pilosus	Not endemic	Subjected to special protection
Flourensia ilicifolia	Endemic to Coahuila	None
Flourensia retinophylla	Endemic to Coahuila	None
Glandulicactus uncinatus	Not endemic	Threatened
Grusonia bradtiana	Endemic to Coahuila	None
Lophophora williamsii	Not endemic	Subjected to special protection
Pinus pinceana	Not endemic	Subjected to special protection
Salvia chamaedryoides var. *coahuilensis*	Endemic to Coahuila	None
Thelocactus rinconensis var. *nidulans*	Endemic to Coahuila	Threatened
Viguiera brevifolia	Endemic to Coahuila	None

1,581 m a.s.l.) with southern aspect of the La Madera and El Fuste *sierras*. Vegetation consisted in desert scrub with an open canopy up to 0.5 m in height, and was dominated by *H. texensis* and *A. lecheguilla*; along with *Euphorbia antisyphilitica*, these species accounted for 55% of plant cover and 57% of total RIV. *Dasylirion cedrosanum* ranked fourth in RIV (11.52%), and its mean density and height (± 1 SD) in this association were 284 ± 6.24 ind./ha and 1.39 ± 0.23 m, respectively (Table 2). Individuals of this species were scattered in the vegetation and often they were the only prominent plants in the vegetation physiognomy. Because of the topographically low position of this association, some very common species of the microphyllous scrub typical of valley bottoms and flatter sites were abundant in it, such as *Grusonia bradtiana* and *Larrea tridentata*.

(2) *Agave lecheguilla-Dasylirion cedrosanum* association. This was the most widespread of all associations, as it occurred across much of the study area. However, it was particularly common in mid-slopes (mean 1,500 m a.s.l.; range 905 to 2,381 m a.s.l.) with northern aspect of the *sierras* of the central-eastern part of the study area (La Paila and La Gavia), and in those located in the southeast and southwest parts (Zapalinamé, Parras, and Jimulco). Vegetation of this association was dominated by *A. lecheguilla*, a colony-forming species that accounted for as much as 30% of total plant cover and of total RIV (Table 2). The co-dominant species was *D. cedrosanum*, with a RIV of 13.4% and a mean density (± 1 SD) of 492 ± 16.9 ind./ha; mean vegetation height (± 1 SD) in this association was 1.37 ± 0.16 m. Additional common species were *Fouquieria splendens* and *Euphorbia antisyphilitica* (RIVs of 5.8 and 5.1%, respectively). Although less abundant, barrel cacti were also present, represented mostly by *Ferocactus pilosus* and *Echinocactus platyacanthus* which, along with *D. cedrosanum* and *F. splendens*, were the physiognomic dominants of this association.

(3) *Dasylirion cedrosanum-Euphorbia antisyphilitica* association. The preferential habitat for this association consists of low hills and mountain tables of the Parras and La Paila *sierras*, with a mean elevation of *ca.* 1,400 m a.s.l. (range: 1,289-1,610 m a.s.l.). The most important physiognomic component was *D. cedrosanum* (43% of total plant cover; RIV of 22.2%, and mean density and height (± 1 SD) of 193 ± 3.47 ind./ha and 1.6 ± 0.12 m, respectively). Other abundant species with smaller RIVs were *E. antisyphilitica*, *Fouquieria splendens*, and *Agave lecheguilla*, with RIV values ranging from 10.3 to 12.5%. Similarly to the first association described above, this one showed a clear preference for sites with very gentle slopes near valley bottoms, where soil depth and the vicinity of microphyllous scrubs favor the establishment of species typical of that community, such as *Jatropha dioica*, *Larrea tridentata*, and *Lippia graveolens*.

(4) *Dasylirion cedrosanum-Viguiera greggii* association. This association occurs on mid- and high slopes with a northern aspect in the *sierras* of southern Coahuila (Zapalinamé, Parras and Jimulco), with a mean elevation of 1,919 m a.s.l. (range: 1,375 to 2,527 m a.s.l.). *Dasylirion cedrosanum* was the species with the largest structural contribution, accounting for almost one third of total plant cover (Table 2);

Table 2. Structural contribution of the species occurring in the five associations recognized for the *Dasylirion cedrosanum* rosette scrub in southern and central Coahuila. RIV = relative importance value.

Species	Mean Height (m)	Density (ind./ha)	Relative density (%)	Relative cover (%)	Relative frequency (%)	RIV (%)
Hechtia texensis-Agave lecheguilla (856-1581 m a.s.l.)						
Hechtia texensis	0.35	3976	34.73	18.15	11.07	21.32
Agave lecheguilla	0.40	3201	27.96	18.50	10.38	18.94
Euphorbia antisyphilitica	0.65	2625	22.92	18.73	10.38	17.34
Dasylirion cedrosanum	1.39	284	2.48	21.00	11.07	11.52
Fouquieria splendens	2.05	53	0.45	9.36	5.53	5.11
Other 40 species		1308	11.46	14.26	51.57	25.77
Agave lecheguilla-Dasylirion cedrosanum (905-2381 m a.s.l.)						
Agave lecheguilla	0.45	5648	60.65	26.74	9.46	32.28
Dasylirion cedrosanum	1.37	492	5.28	25.45	9.46	13.40
Fouquieria splendens	1.80	83	0.89	12.13	4.46	5.82
Euphorbia antisyphilitica	0.60	646	6.94	3.77	4.64	5.12
Other 66 species		2442	26.24	31.91	71.98	43.38
Dasylirion cedrosanum-Euphorbia antisyphilitica (1289-1610 m a.s.l.)						
Dasylirion cedrosanum	1.60	193	11.65	43.30	11.69	22.21
Euphorbia antisyphilitica	0.55	317	19.14	7.07	9.94	12.05
Fouquieria splendens	1.90	149	8.99	15.82	8.18	11.00
Agave lecheguilla	0.40	269	16.24	4.01	10.52	10.26
Larrea tridentata	1.02	132	7.97	8.78	9.35	8.70
Lippia graveolens	0.95	149	8.99	8.90	7.01	8.30
Jatropha dioica	0.32	162	9.78	1.54	5.26	5.53
Other 19 species		285	17.23	10.58	38.05	21.95
Dasylirion cedrosanum-Viguiera greggii (1375-2527 m a.s.l.)						
Dasylirion cedrosanum	1.25	704	13.84	29.84	4.26	15.98
Viguiera greggii	0.76	601	11.81	7.15	4.26	7.74
Agave scabra	0.94	640	12.58	4.50	4.26	7.11
Lindleya mespiloides	1.70	305	6.00	10.41	4.02	6.81
Agave striata	0.50	428	8.43	3.02	4.02	5.16
Other 50 species		2406	47.34	45.08	79.18	57.20
Quercus intricata-Dasylirion cedrosanum (2009-2130 m a.s.l.)						
Quercus intricata	1.50	3612	49.25	27.59	10.12	28.98
Dasylirion cedrosanum	1.70	705	9.61	12.59	10.12	10.77
Leucophyllum langmaniae	1.54	1140	15.54	5.37	6.32	9.08
Pinus cembroides	3.20	207	2.82	14.26	8.86	8.65
Rhus virens	2.50	287	3.91	14.51	6.32	8.25
Lindleya mespiloides	2.20	187	2.55	7.48	6.32	5.45
Other 11 species		1195	16.32	18.20	51.94	28.82

RIV of this species was 16.0%, and its mean density and height (± 1 SD) were 704 ± 17.92 ind./ha and 1.25 ± 0.28 m, respectively. Co-dominant species were *V. greggii*, *Agave scabra*, and *Lindleya mespiloides*, with RIVs between 6 and 8%. As a result of the elevational distribution of this association, often turns into an ecotone with the sub-montane scrub typical of higher elevations, which results in a considerable number of associated woody species; in fact, some low-statured individuals of *Juniperus*, *Pinus*, and *Quercus* were observed, whilst the number of succulent plants, in particular of cacti, was low relative to the former three associations.

(5) *Quercus intricata-Dasylirion cedrosanum* association. This association thrives on high slopes with northern aspect in the mountains located in southern Coahuila (Arteaga and Concordia *sierras*), with a mean elevation of 2,083 m a.s.l.

Table 3. Shannon-Wiener diversity indices (H'), Pielou evenness (E), and woody species richness, both total (Total S) and mean richness by sampling plot (Mean S) in five associations of the *Dasylirion cedrosanum* rosette scrub. Bold typeface indicates the largest value in each column.

Floristic association	H' (bits)	E (%)	Total S	Mean S
1. *Hechtia texensis-Agave lecheguilla*	2.472	45.017	45	1.40
2. *Agave lecheguilla-Dasylirion cedrosanum*	2.774	45.257	**70**	1.32
3. *Dasylirion cedrosanum-Euphorbia antisyphilitica*	3.547	75.465	26	1.30
4. *Dasylirion cedrosanum-Viguiera greggii*	**4.396**	**76.034**	55	**3.05**
5. *Quercus intricata-Dasylirion cedrosanum*	2.598	63.563	17	2.12

Note: There were significant differences in H' between associations 1 and 4 (t = 3.62, g.l. = 11,466, $P < 0.001$), and between associations 2 and 4 (t = 3.18, g.l. = 10,282, $P < 0.01$).

(range: 2,009 to 2,130 m a.s.l.). The rosette scrub representing this association was mostly composed of colonies or patches of short individuals of *Quercus intricata* (1.5 m in height), a shrub species with RIV of 29.0% (Table 2). The single co-dominant in this association was *D. cedrosanum* (RIV of 10.77 %), which here had a mean density (± 1 SD) of 705 ± 30.36 ind./ha, and a mean height of 1.70 ± 0.26 m. Other species making significant contributions to vegetation structure were *Leucophyllum langmaniae* and *Pinus cembroides*, with RIV between 8 and 10%. This is the most mesic association among all five floristic variants and represents the upper altitudinal limit of the *D. cedrosanum* rosette scrub. At higher elevations oak and pine forests occur and, in fact, the floristic composition and the physiognomy of this association are more suggestive of a less humid variant of those forests than of a typical *Dasylirion* community.

Diversity indices. The largest values of H' and E were obtained for the *Dasylirion cedrosanum-Viguiera greggii* association (4.396 bits and 76.0%, respectively; Table 3); at the opposite end, values calculated for the *Hechtia texensis-Agave lecheguilla* association (2.472 bits and 45.0%) reflected a much less diverse community. In analyzing total species richness by association, we recorded the largest number of species (70) in the *A. lecheguilla-D. cedrosanum* association. However, this figure conceals important differences in the concentration of species on an area basis: the *D. cedrosanum-V. greggii* association clearly had the highest species density (3.05 species 500 m^{-2} on average), followed distantly by the *Quercus intricata-D. cedrosanum* association, in which mean density was 2.12 species 500 m^{-2} (Table 3). According to the t-tests performed to statistically compare diversity values between pairs of associations, most comparisons did not yield significant differences, except for the comparison between associations 1 and 4 (t = 3.62, d.f. = 11,466, $P < 0.001$), and between associations 2 and 4 (t = 3.18, d.f. = 10,282, $P < 0.01$).

Density and distribution of Dasylirion cedrosanum. The elevational range displayed by *D. cedrosanum* in Coahuila is very broad (850-2,530 m a.s.l.). Along this gradient its density increases linearly at an approximate rate of 68 ind./ha for every 100 m increase in elevation (Figure 3). Mean density at elevations < 1,000 m was always < 200 ind./ha, whereas at higher elevations (2,000-2,500 m a.s.l.) densities ranged from 900 to 1,200 ind./ha. *Dasylirion cedrosanum* reached its highest abundance in the mountains located in southern Coahuila, on the Eastern Sierra Madre, whereas the lowest densities were recorded in the *sierras* of Central Coahuila, in the Mexican Plateau Physiographic Province.

Discussion

Floristic composition and diversity. The woody flora associated to the *Dasylirion cedrosanum* scrub comprises 97 species. This floristic richness is high considering that this is the least frequent variant of the rosette scrub (Henrickson and Johnston, 1986); furthermore, this figure is similar to the 90 shrub species reported for analogous xerophytic scrubs in the El Huizache area, state of San Luis Potosí, also in the Chihuahuan Desert (Huerta-Martínez and García-Moya, 2004).

The high floristic richness of this plant community may partially result from the occurrence of species typical of neighboring communities, such as the microphyllous scrub,

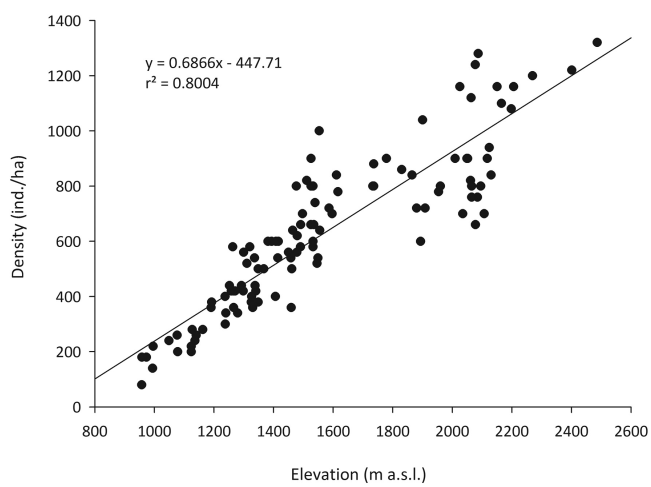

Figure 3. Altitudinal variation of *Dasylirion cedrosanum* density in Coahuila, Mexico.

the sub-montane scrub, and the pinyon pine forest, because its geographical distribution covers a wide elevational gradient. In fact, given its large richness, this community can be regarded as the most prominent variant of the rosette scrub in Coahuila. Overall, its flora matches that of the arid zones of Mexico regarding the richest families and genera (Rzedowski, 1978). Nonetheless, the exclusion from this study of herbaceous species of Asteraceae and Poaceae, both of which stand among the most prominent plant groups in these ecosystems (Rzedowski, 1978; Pinkava, 1984; Rodríguez *et al*., 1994; Villarreal, 1994), should not be overlooked as it implies a considerable underestimation of total floristic richness. In turn, the prevalence of Agavaceae, Cactaceae, and Fabaceae in the area is a shared feature with the woody flora typical of other xerophytic scrub communities of Mexico (Rzedowski, 1978; Marroquín *et al*., 1981). One of the most relevant aspects of this community composition is that 15% of all recorded species have narrowly restricted distributions or some protection status according to Mexican environmental legislation (SEMARNAT, 2010); furthermore, most of them are members of the Cactaceae family, in agreement with the intense diversification process undergone by this group in Coahuila and overall in the Chihuahuan Desert region (Godínez-Álvarez and Ortega-Baes, 2007).

Examples of species occurring in this area that are highly relevant for conservation are *Astrophytum capricorne*, *Thelocactus rinconensis* var. *nidulans*, and *Glandulicactus uncinatus*. All of them are at risk of extinction (SEMARNAT, 2010) and the former two are endemic to Coahuila and adjacent areas (Villarreal-Quintanilla and Encina-Domínguez, 2005). In addition, the conservation of *Ariocarpus retusus* and *Lophophora williamsii* is a reason for concern, as these two species are subjected to an intense extraction from its natural milieu (Robbins, 2003). This information is important because Godínez-Álvarez and Ortega-Baes (2007) reported that the state of Coahuila has the highest species richness (> 125 species) and hosts more than 50 endangered species of cacti. *Agave victoriae-reginae*, a species that was also present in the studied community, perhaps holds the highest conservation priority, as it is classified as endangered, in addition to being endemic to the state and surrounding areas, and whose largest populations occur in our study area (Martínez-Palacios *et al*., 1999). Diversity indices are high according to Margalef (1991), with Shannon-Wiener index ranging from 1.5 to 3.5 bits, with exceptional values of 4.5 bits. These values are consistent with the notion that plant diversity in Mexico's arid regions is high in hilly areas, where the prevalence of shallow, stony soils is associated to increased water availability, ultimately resulting in higher species richness (Rzedowski, 1978). Moreover, in such areas micro-relief is more heterogeneous, which creates a higher diversity of habitats (Pérez *et al*., 2008). Shannon-Wiener index had a sigmoid pattern along the altitudinal gradient where *Dasylirion cedrosanum* thrives; it peaked at a mean elevation of 1,920 m, at the transition from rosette scrub to more temperate plant communities like pinyon-pine forest, which results in an increased diversity caused by the concurrence of these two vegetation types. Marroquín *et al*. (1981) also pointed to this elevational transition as the cause of a high floristic diversity in Coahuila rosette scrub. Interestingly, the largest values of Shannon-Wiener index were obtained for the *Dasylirion cedrosanum*-dominated associations, which may be due to the fact that the most important species in the remaining associations (those dominated by *Hechtia texensis*, *Agave lecheguilla*, and *Quercus intricata*) have large biomass accumulations and a more intense occupation of space derived from the vegetative reproduction that characterizes them (Marroquín *et al*., 1981; Reyes-Agüero *et al*., 2000). Unlike communities dominated by *sotol*, which reproduces mostly through seeds (Bogler, 1995), the dominance of clonal plants results in lower diversity and evenness in their associations (Margalef, 1991). *Dasylirion cedrosanum*-dominated stands are not only more diverse, but they also host more cacti species, some of which have a distinct conservation status.

Distribution and structure of the Dasylirion cedrosanum rosette scrub. The cluster analysis showed that *D. cedrosanum* does not form highly discrete units within its range, but rather that this species is variously mixed with those more typical of other rosette scrub associations, such as the sub-montane scrub and the pinyon pine forest, and with those from the microphyllous scrub, with which it alternates its dominance depending on elevation and water availability. Similar patterns were reported for the Catorce Range of San Luis Potosí (Granados-Sánchez and Sánchez-González, 2003). The distribution patterns observed in our area both for the associations and their most important species do not differ from those described elsewhere for several mountainous regions of Mexico deserts (Pavón *et al*., 2000; Martorell and Ezcurra, 2002). These patterns are closely related to elevation, a physical variable that serves as a surrogate of humidity and temperature (Daubenmire, 1982; Reynolds *et al*., 2000), and whose effect is most evident on the vegetation of arid and semi-arid zones (Montaña and Valiente-Banuet, 1998; Huerta-Martínez *et al*., 2004). The high densities of *Agave lecheguilla*, *Euphorbia antisyphilitica*, and *Hechtia texensis*, as well as of cacti and other xerophytic floristic elements of associations dominated by these three species, have been attributed to the scarce rainfall and higher temperatures that prevail at lower elevations (Marroquín *et al*., 1981; Pavón *et al*., 2000; Reyes-Agüero *et al*., 2000), whereas the groups containing more woody species, both shrubs and trees, at the highest reaches of the gradient concur with the prevalence of more humid and temperate conditions at those sites (Granados-Sánchez and Sánchez-González, 2003). However, *Dasylirion cedrosanum*-dominated associations occur at intermediate elevations, according to the findings of Martorell and Ezcurra (2007), who reported that species of *Dasylirion*, *Nolina*, and *Yucca* are abundant at mid-elevations of mountains within arid and semi-arid regions of Mexico where fog is a recurring phenomenon. Their abundance could be linked to the morphology of their leaves and their heights, both of which provide plants access to an increased water supply through fog interception. Though fog incidence has not been investigated in our study region, this phenomenon is frequent in the rainy season and occasional in the winter, with the incursion of cold fronts (pers. obs.), suggesting that this factor may have a significant influence on *Dasylirion cedrosanum* distribution and abundance.

Vegetation structure of the studied communities is similar to that described for the rosette scrub (*sensu lato*) regarding the most important species (Rzedowski, 1978; Marroquín *et al*., 1981; Henrickson and Johnston, 1986; Villarreal and Valdés, 1992-1993; González-Elizondo *et al*., 2007). A structural feature that we observed, which is common within the vegetation typical of many arid regions, particularly in mountainous areas, is that a few species with clonal growth make the largest contribution to plant cover (Rzedowski, 1978; Pérez-García and Meave, 2004). This was the case of *Agave lecheguilla*, *Hechtia texensis*, and *Quercus intricata*. Although *Dasylirion cedrosanum* is the most frequent species in all associations, its low density results in its low RIV ranking relative to clonal species. Therefore, localities where *D. cedrosanum* had the highest RIV were uncommon: only two associations, accounting for almost one third (29%) of the sampled surface, were both physiognomically and structurally dominated by this species. This result supports Henrickson and Johnston conclusions (1986), who reported that *sotolares* (*Dasylirion*-dominated scrub communities) are rare in the Chihuahuan Desert. This result also suggests that our study species is a poor competitor and that it could face regeneration problems should its populations continue to be impacted by human activity, considering its dependence on sexual reproduction, low growth rates, and long life cycle (Palma-Estrada, 2000; Sierra *et al*., 2008). This information, together with the structure of its populations across its geographical range, should be given thoughtful consideration in preparing management plans for this species.

Dasylirion cedrosanum density and ecological relations. In Coahuila *D. cedrosanum* occurs on mountains and hilly terrain, at elevations between 850 and 2,600 m a.s.l., on stony, shallow, calcareous soils and dry continental or dry, semi-hot climates. These environmental conditions are common in the Chihuahuan Desert (Henrickson and Johnston, 1997), where most species of this genus are present (Bogler, 1995). Although, *D. cedrosanum* is considered a typical element of the rosette scrub (Marroquín *et al*., 1981), in these communities it has a low density and in fact, its density increases considerably at higher elevations, in transitional areas with sub-montane scrub and pinyon pine forest, where it becomes one of the most common vegetation components (Henrickson and Johnston, 1986; Granados-Sánchez and Sánchez-González, 2003). The fact that the highest densities of this species were recorded in north-facing slopes and in xerophytic scrub communities of the Eastern Sierra Madre suggests that it responds positively to increasing humidity levels and decreasing temperatures, a possibility that future studies may confirm. Despite the considerable variation of *D. cedrosanum* density between the associations characterized by the presence of this species, in our study region its mean density (475 ind./ha) is almost 40% larger than the value reported (341 ind./ha) for the northeastern part of the state of Zacatecas (Robles *et al*., 2008). Comparable differences exist for density between these two regions across elevations (at 1,900 m a.s.l. in Coahuila density was estimated at 855 ind./ha *versus* 574 ind./ha in Zacatecas). However, further research is needed to determine the underlying causes of the differences in density between these two regions, considering that in the subregion of Cedros and Mazapil, northern Zacatecas, the harvesting of *sotol* individuals for preparing alcoholic beverages has been going on for over two decades already (Robles *et al*., 2008), while harvesting in Coahuila is still incipient.

To-date, the effects of the harvesting of this species for different purposes on the structure of its populations and the associated species are unknown; the same is true for the disturbance caused on the plant communities where this species thrives. Undoubtedly, there is an urgent need to design management plans in order to minimize the impacts of human disturbance on this community, as well as to prevent a potential shrinkage of *Dasylirion cedrosanum* range; ultimately, these actions may be critical for the conservation of this species. In this regard, the use of micro-propagation techniques for this species is cause for some optimism, as it could increase its regeneration rates (Villavicencio *et al*., 2007). Also, we need to study the dynamics of its populations in all associations where this species occurs in order to ensure the most adequate regulation for its potential commercial extraction. Considering the lack of protected areas in this region, the conservation of the *D. cedrosanum* rosette scrub, as well as of all the endemic and threatened taxa associated to this community remains in peril under current land use practices. In order to be successful, the size and status of these areas should acknowledge the compromise between the needs of development and those of conservation (Riemann and Ezcurra, 2005).

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Appendix. Checklist of vascular plant species in the *Dasylirion cedrosanum* rosette scrub of central and southern Coahuila State, Mexico.

AGAVACEAE
- *Agave lecheguilla* Torr.
- *A. scabra* Ortega
- *A. striata* Zucc.
- *A. victoriae-reginae* DT.Moore.
- *Yucca carnerosana* (Trel.) McKelvey
- *Y. rigida* (Engelm.) Trel.
- *Y. treculeana* Carriére

ANACARDIACEAE
- *Bonetiella anomala* (I.M.Johnst.) Rzed.
- *Rhus virens* Lindh. ex A.Gray

ASTERACEAE
- *Ageratina calophylla* (B.L.Rob.) R.M.King. et H.Rob.
- *Chrysactinia mexicana* A.Gray
- *Flourensia ilicifolia* Brandegee
- *F. retinophylla* S.F.Blake ex B.L.Rob.
- *Gochnatia hypoleuca* (DC.) A.Gray
- *Gymnosperma glutinosum* (Spreng.) Less.
- *Jefea brevifolia* (A.Gray) Strother
- *Parthenium argentatum* A.Gray
- *P. incanum* Kunth
- *Viguiera brevifolia* Greenm.
- *V. greggii* (A.Gray) S.F.Blake
- *V. stenoloba* S.F.Blake

BERBERIDACEAE
- *Berberis trifoliolata* Moric.

BORAGINACEAE
- *Tiquilia greggii* (Torr. et A.Gray) A.T.Richardson

BROMELIACEAE
- *Hechtia texensis* S.Watson

BUDDLEJACEAE
- *Buddleja marrubiifolia* Benth.

CACTACEAE
- *Ariocarpus retusus* Scheidw.
- *A. fissuratus* (Engelm.) K.Schum. var. *lloydii* (Rose) W.T.Marshall
- *Astrophytum capricorne* (A.Dietr.) Britton et Rose
- *Coryphantha lloydii* (Britton et Rose) Fosberg
- *C. palmeri* Britton et Rose
- *Cylindropuntia imbricata* (Haw.) F.M.Knuth
- *C. leptocaulis* (D.C.) F.M.Knuth
- *Echinocactus horizonthalonius* Lem.
- *E. platyacanthus* Link et Otto
- *Echinocereus pectinatus* (Scheidw.) Engelm.
- *E. stramineus* (Engelm.) Rümpler
- *Epithelantha micromeris* (Engelm.) F.A.C.Weber ex Britton et Rose
- *Escobaria chaffeyi* Britton et Rose
- *E. strobiliformis* (Poselger) Scheer ex Boed.
- *Ferocactus hamatacanthus* (Muhlenpf.) Britton et Rose
- *F. pilosus* (Galeotti ex Salm-Dyck) Werderm.
- *Grusonia bradtiana* (J.M.Coult.) Britton et Rose
- *Glandulicactus uncinatus* (Galeotti ex Pfeiff.) Backeb.
- *Lophophora williamsii* (Lem. ex Salm-Dyck) J.M.Coult.
- *Mammillaria chionocephala* J.A.Purpus.
- *M. pottsii* Scheer ex Salm-Dyck
- *Neolloydia conoidea* (DC.) Britton et Rose
- *N. smithii* (Muehlenpf.) Kladiwa et Fittkau
- *Opuntia lindheimeri* Engelm.
- *O. microdasys* (Lehm.) Pfeiff.
- *O. phaeacantha* Engelm.
- *O. rastrera* F.A.C.Weber
- *O. stenopetala* Engelm.
- *Stenocactus multicostatus* (Hildm.) A.Berger ex A.W.Hill
- *Thelocactus rinconensis* (Poselger) Britton et Rose var. *nidulans* (Quehl) Glass et R.A.Foster

CAPPARACEAE
- *Koeberlinia spinosa* Zucc.

CELASTRACEAE
- *Mortonia palmeri* Hemsl.

CUPRESSACEAE
- *Juniperus flaccida* Schltdl.
- *J. saltillensis* M.T.Hall

EPHEDRACEAE
- *Ephedra aspera* Engelm. ex S.Watson
- *E. compacta* Rose

ERICACEAE
- *Arbutus xalapensis* Kunth

EUPHORBIACEAE
- *Euphorbia antisyphilitica* Zucc.
- *Jatropha dioica* Cerv.

FABACEAE
- *Acacia berlandieri* Benth.
- *A. crassifolia* A. Gray
- *A. glandulifera* S. Watson

Appendix. Continuation

A. neovernicosa Isely
A. rigidula Benth.
Bauhinia lunarioides A.Gray ex S.Watson
B. uniflora S.Watson
Calia secundiflora (Ortega) Yakovlev
Calliandra conferta Benth.
Dalea bicolor Humb. et Bonpl. ex Willd.
Mimosa biuncifera Benth.
Prosopis glandulosa Torr.

FAGACEAE
Quercus greggii (A.DC.) Trel.
Q. intricata Trel.
Q. pringlei Seemen

FOUQUIERIACEAE
Fouquieria splendens Engelm.

KRAMERIACEAE
Krameria cytisoides Cav.

LAMIACEAE
Salvia ballotiflora Benth.
S. chamaedryoides Cav. var. *coahuilensis* (Fernald) K.M.Peterson

MALPIGHIACEAE
Mascagnia sericea Nied.

NOLINACEAE
Dasylirion cedrosanum Trel.
Nolina cespitifera Trel.

OLEACEAE
Fraxinus greggii A.Gray

PINACEAE
Pinus cembroides Zucc.
P. pinceana Gordon et Glend.

RHAMNACEAE
Ceanothus greggii A.Gray

ROSACEAE
Lindleya mespiloides Kunth

RUBIACEAE
Bouvardia ternifolia (Cav.) Schltdl.

SCROPHULARIACEAE
Leucophyllum candidum I.M. Johnst.
L. frutescens (Berland.) I.M. Johnst.
L. langmaniae Flyr

VERBENACEAE
Lippia graveolens Kunth

ZYGOPHYLLACEAE
Larrea tridentata (Sessé et Moc. ex DC.) Coville