Endangered Cacti in the Chihuahuan Desert: I. Distribution Patterns

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Abstract: *We mapped the geographical distributions of 93 endangered species of cacti from the Chihuahuan Desert Region. We divided the region into grids of 30 minutes latitude by 30 minutes longitude and calculated species frequencies for each grid. The grids with the highest species richness values are aggregated in areas of moderate elevation, particularly towards the southeastern and, to a lesser extent, the eastern margins of the Chihuahuan Desert Region, in northern San Luis Potosí and the southern portions of Coahuila, Nuevo León, and Tamaulipas. This vast area constitutes the most important nucleus of cactus species concentration in the continent. Species richness decreases toward the western segment of the Chihuahuan Desert Region and from the Cuatro Ciénegas region to the north and northwest. Another important area is the Queretaroan-Hidalgoan Arid Zone, where several grids containing an important assemblage of endangered species occur. Climatic factors, such as minimum temperatures and mean annual precipitation, explain the current distribution patterns of these plants, and the recent Pleistocene climatic episodes appear to have played a determinant role in the existence of areas of high species concentration and in the proliferation of narrow endemics. Special actions are urgently needed to conserve the endangered Cactaceae of this region. We propose that a carefully selected network of small areas would be an appropriate approach for the conservation of these plants. But species richness cannot be taken as the sole criterion in the determination of protected areas. Additional criteria, such as degree of endemicity, degree of threat to species and areas, habitat diversity, and biogeographic congruence with other plant and animal groups, should be analyzed before these areas are selected. Propagation in botanical gardens using scientific criteria and commercial propagation would be additional methods of conservation.*

Cactáceas Amenazadas en el Desierto Chihuahuense: I. Patrones de Distribución

Resumen: *Se integraron las distribuciones geográficas de 93 especies de cactáceas amenzadas de la Región del Desierto Chihuahuense. Esta región se subdividió en cuadros de 30 minutos de latitud por 30 minutos de longitud y se calcularon las frecuencias de especies para cada uno de los cuadros. Los cuadros con los mayores valores de riqueza de especies están agregados en áreas de altitud moderada, ubicados particularmente hacia los márgenes sureste, y en menor medida, este de la Región del Desierto Chihuahuense, en el norte de San Luis Potosí, y en el sur de Coahuila, Nuevo León y Tamaulipas. Esta vasta área constituye el núcleo de concentración de especies de cactáceas amenazadas más importante del continente. A partir de esta área, la riqueza de especies decrece hacia el segmento oeste de la Región del Desierto Chihuahuense y de la región de Cuatro Ciénegas hacia el norte y noroeste. Además, en la Zona Arida Queretano-Hidalguense, la cual es considerada como una disyunción del Desierto Chihuahuense, se localizan varios cuadros con un importante contingente de especies amenazadas. Algunos factores climáticos, tales como temperaturas mínimas y precipitación promedio anual, explican los patrones de distribución actuales de estas plantas, y los eventos climáticos del Pleistoceno parecen haber jugado un papel determinante en la existencia de áreas de alta concen-*

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tración de especies y en la proliferación de endemismos restringidos. Se requieren acciones especiales para proteger a las cactáceas amenazadas de la Región del Desierto Chihuahuense. Se propone que un enfoque apropiado para la conservación de estas plantas podría ser la selección cuidadosa de una red de pequeñas áreas. Sin embargo, la riqueza de especies no es el único criterio en la determinación de áreas protegidas. Existen criterios adicionales tales como la frecuencia de endemismos, el grado de amenaza de áreas y especies en particular, la diversidad de hábitats y la congruencia biogeográfica con otros grupos de plantas y animales, los que deberán ser analizados antes de que estas áreas sean seleccionadas. La propagación en jardines botánicos con criterios científicos, así como la propagación comercial, podrían ser métodos adicionales de conservación.

Introduction

Conservation biologists assign great value to sites with high species richness such as tropical forests and coral reefs, but it has also been widely accepted that habitats and geographical regions rich in narrowly endemic or endangered taxa should have priority when conservation actions are taken (Usher 1986; Vermeij 1993). This affirmation rests on the assumption that rare species (Ravinowitz 1981), especially those with small geographical ranges, are unusually vulnerable to extinction.

The Cactaceae are a morphologically heterogeneous yet taxonomically natural plant group comprising 100 genera and about 1500 species (Barthlott & Hunt 1993). With the exception of *Rhipsalis baccifera*, which is widespread, members of this family are entirely confined to the American continent. With 48 genera and some 563 species, Mexico is the most important center of diversity of the family. Most Mexican cacti occur in the arid and semiarid regions of the country, and the most significant proportion of these are distributed in the Chihuahuan Desert (Hernández & Godínez 1994), primarily in the states of Coahuila, Nuevo León, Tamaulipas, and San Luis Potosí. One of the most striking features of cactus biogeography is the frequent existence of endemic, sometimes narrowly endemic, taxa. In fact, 73% of the genera and 78% of the species in Mexico are essentially restricted to the country, and many species and varieties are found in only one or a few localities (Hernández & Godínez 1994).

Cacti are a highly endangered group. The entire family is included in Appendix II of the Convention of International Trade in Endangered Species (Convention on International Trade in Endangered Species 1990), and several genera and species are listed in Appendix I. It has been estimated (Hernández & Godínez 1994) that 35% (197 species) of the species of Mexican cacti are endangered. Of these, 115 (58.4%) occur within the confines of the Chihuahuan Desert Region (CDR) and marginal areas.

Although little information has been published (Jarvis 1979; Sánchez-Mejorada 1982; Fuller & Fitzgerald 1987), natural populations of many Mexican species of cacti have been considerably affected by the collection of plants for use as ornamentals and as collectors' items. In addition, arid and semiarid lands have been dramatically modified by agriculture, goat raising, mining, and other productive activities. These forms of disturbance have had a tremendous impact on cactus populations because cacti usually have slow growth rates, long life cycles, and low recruitment rates via seed germination, which makes them extremely vulnerable to disturbance (Hernández & Godínez 1994).

A prerequisite for the conservation of any group of organisms is an adequate knowledge of its biogeography. Unfortunately, the precise distribution patterns of cactus species have not been studied. We sought to detect the areas of highest concentration of endangered cacti in the CDR through the integrated mapping of their known geographical distributions.

The CDR is the largest and least-studied desert in North America. It is located in a physiographically diverse plateau in north-central Mexico, bordered by the Sierra Madre Occidental and the Sierra Madre Oriental, and extends into parts of Arizona, New Mexico, and Texas. The region's boundaries are disputed, particularly its southern and northern limits (Shreve 1942; Contreras 1955; Johnston 1977; Morafka 1977; Schmidt 1979; Medellín-Leal 1982). According to Henrickson and Straw (1976), the region extends from southern San Luis Potosí, at about 21°40′N latitude, into a small portion of Arizona and into the Río Grande and Pecos River Basins in New Mexico and Texas, at about 34°30′N latitude. The estimated area of this region approximates 507,000 km^2 (Henrickson & Straw 1976), and about 80% of it occurs in Mexico.

A significant number of the cactus considered in this study (Appendix 1) grow outside the CDR margins. For instance, a number of species occur in disjunct intermontane valleys and canyons within the Sierra Madre Oriental, as for example the Jaumave and Aramberri valleys, where the typical CDR floristic elements intermix with nondesert vegetation types (pinyon-oak, pine, and oak forests). Several other species occur in what has been called the Queretaroan-Hidalgoan Arid Zone and in some portions of Guanajuato. The Queretaroan-Hidalgoan Arid Zone, which consists primarily of two discontinuous arid depressions surrounded by mountains, is geographically and climatically separated from the main CDR and includes well-known localities such as the Barranca de Metztitlán, the Valle del Mezquital, the Valle de Actopan in Hidalgo, and the Extóraz River Basin. There is general agreement that this zone is a disjunct fragment of the CDR (Medellín-Leal 1982).

Methods

The CDR was divided into grid squares of 30 minutes latitude by 30 minutes longitude. The area of the squares diminishes from south to north, ranging from 2964 km^2 in the southern limit of the desert (20°N) to 2719 km^2 in the north (34°N). This difference was ignored, however, because variation was small and because the species were aggregated in specific portions of the study area. To obtain an estimate of the species frequencies per area unit (species richness), we counted the number of species per grid square. The base map in Figs. 2 and 3 was taken from Medellín-Leal (1982), because the limits of the CDR proposed by this author more naturally fit the distribution of the species studied here.

Hernández and Godínez (1994) listed a total of 115 species of endangered cacti occurring in the Mexican portion of the CDR and marginal areas. Based on the availability and reliability of information, 93 species were selected for this study (Appendix 1). Latitude and longitude of the known locality or localities of every species were obtained. Data were exclusively obtained from a database of cactus herbarium collections from North and Central America (Hernández et al. 1993), which currently comprises 8500 records from 32 herbaria. Of these, we used 1151 records corresponding to the endangered species for which accurate geographical information was available. A considerable amount of information in the database was a product of 15 field expeditions to the CDR from October 1989 to July 1993.

Results

Of the approximately 255 grid squares considered in the CDR, only 122 (47.8%) contained at least 1 species of endangered cacti, 37 (14.5%) had a minimum of 4 species, 19 (7.5%) had 7 or more species, and the richest square had 14 species (Fig. 1). The following results consider only those grid squares containing at least seven species (Figs. 2 and 3). Appendix 2 is a list of the grid squares having four or more species, their particular position, and the cactus species present in each one. The squares have been arbitrarily named after well-known localities (Fig. 2).

At the southern end of the CDR three separate

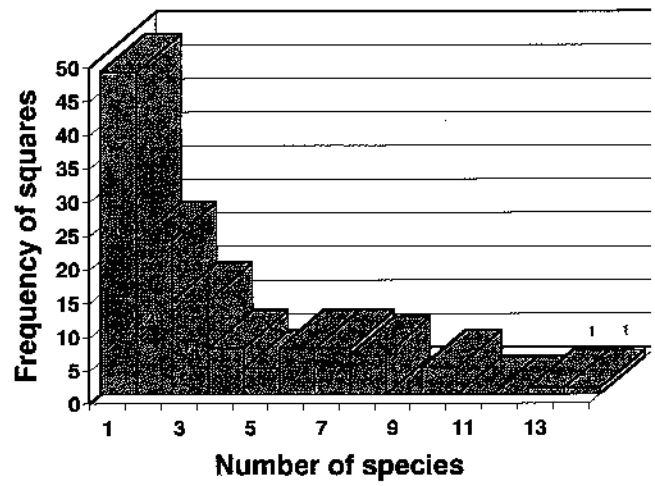
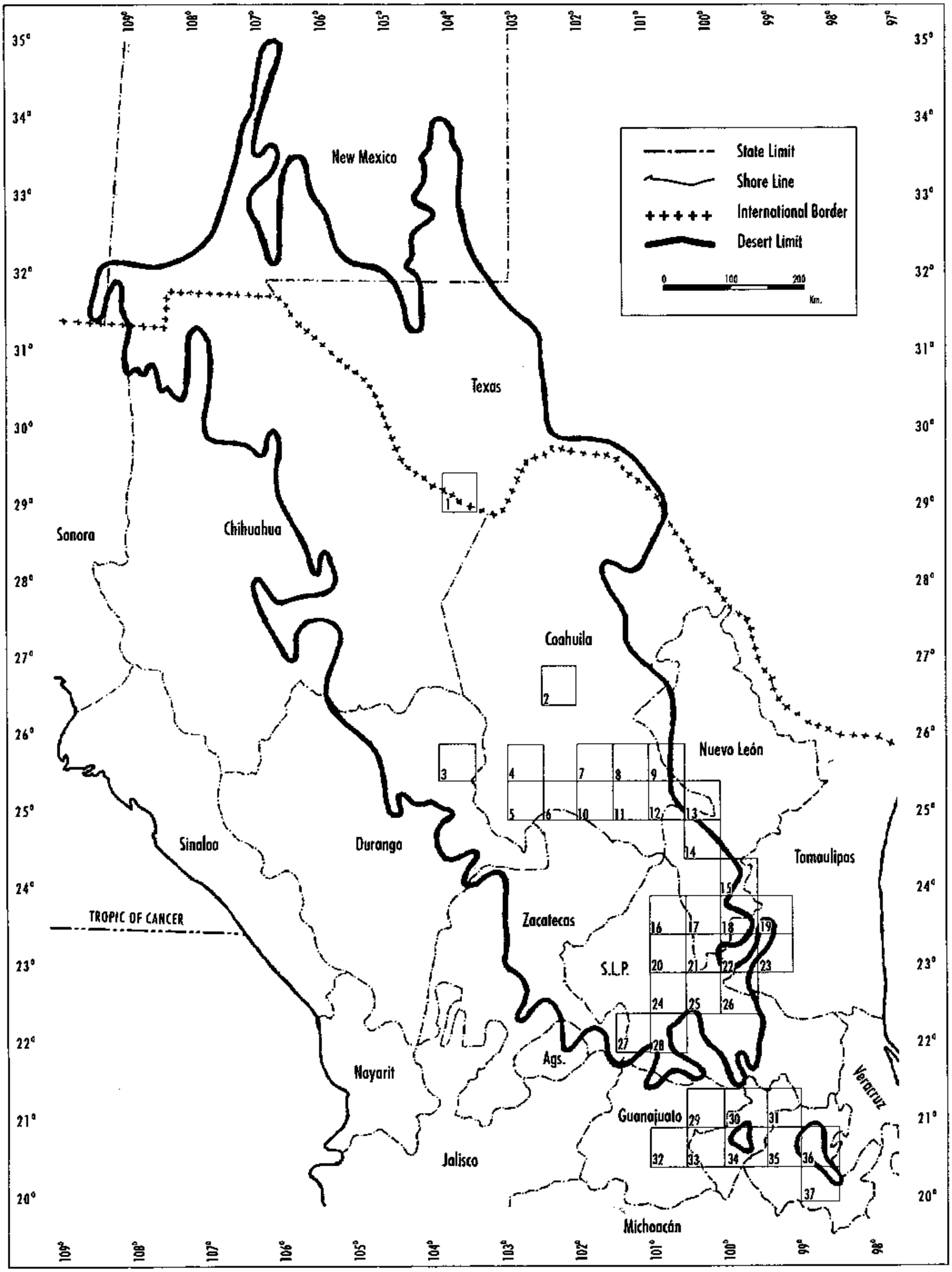


Figure 1. Frequency distribution of grid squares containing different numbers of species.

squares, the Tolimán, Metztitlán, and Xichú squares, contained 13, eight, and seven species respectively (Figs. 2 and 3). These correspond to the Queretaroan-Hildalgoan Arid Zone, which is separated by the main body of the Chihuahuan Desert by an extensive area with a more mesic climate. The species at the Tolimán square were mostly found in the dry to semidry valleys west of the Moctezuma River, particularly in the southern portion of the Extóraz River basin. Those of the Metztitlán square occurred mostly within a complex of slender, climatically dry canyons formed by effluents of the Moctezuma River (for example, Río Grande Tulancingo and Río Tizahuapan). The species at the Xichú square grew in semidry areas of Guanajuato, mainly in the vicinities of San Luis de la Paz, Pozos, and Xichú.

The San Luis Potosí square (7 spp.) is situated in the southern edge of the main body of the CDR (Figs. 2 and 3) and is separated from the Tolimán and Metztitlán squares. Adjacent to it, towards its northeast, lies the Huizache square, which had the highest number of endangered species (14 spp.). This square is rivaled only by the Tolimán square (13 spp.). Adjacent to the Huizache square, toward the north, there are three other important squares possessing significant numbers of species: the Mier y Noriega, the Doctor Arroyo, and the Matehuala each had 10 species. These squares are contiguous toward the east with the Tula (7 spp.), Miquihuana (7 spp.), and Aramberri (8 spp.) squares, which in turn are connected with the Ciudad Victoria (8 spp.) and Jaumave (7 spp.) squares. The Huizache, San Luis Potosí, Mier y Noriega, Doctor Arroyo, Matehuala, Tula, Miquihuana, Aramberri, Ciudad Victoria, and Jaumave squares represent the most important assemblage of endangered species of cacti in the CDR and the entire continent (Figs. 2 and 3).

Most of the San Luis Potosí, Huizache, Mier y Noriega, Doctor Arroyo, Matehuala, and Tula squares are situated


State Limit
Shore Line
International Border
Desert Limit
0 100 200
Km.
New Mexico
Texas
Sonora
Chihuahua
Coahuila
Nuevo León
Tamaulipas
Sinaloa
Durango
Zacatecas
S.L.P.
Ags.
Nayarit
Jalisco
Guanajuato
Michoacán
Veracruz
TROPIC OF CANCER
35° 34° 33° 32° 31° 30° 29° 28° 27° 26° 25° 24° 23° 22° 21° 20°
109° 108° 107° 106° 105° 104° 103° 102° 101° 100° 99° 98° 97°

within the traditional boundaries of the CDR (Figs. 2 and 3). Conversely, the Miquihuana, Aramberri, Ciudad Victoria, and Jaumave squares are located outside the eastern margin of the southeastern segment of the CDR, within the Sierra Madre Oriental, where the cactus species usually occur in relatively narrow valleys that are geographically isolated from the CDR (Figs. 2 and 3). The most important of these is the Valley of Jaumave, which is known for its wealth of narrowly endemic species and varieties of cacti, including the genus *Obregonia*, which is restricted to the valley.

The northwest set of highly diverse grid squares is connected to another area with a significant number of species. The area is located in southeastern Coahuila and to a lesser extent in western Nuevo León and corresponds to the grid squares Galeana (7 spp.), Saltillo (8 spp.), Ramos Arizpe (7 spp.), General Cepeda (8 spp.), and Marte (8 spp.). This area is topographically complex because it includes considerable portions of the Sierra Madre Oriental and large extensions of lower-altitude, relatively flat valleys. Here the Chihuahuan Desert vegetation penetrates the mountain ranges along valleys and canyons and intergrades with mesic, nondesert vegetation types. In addition, the internal slopes of the mountain ranges contain numerous isolated, dry valleys and canyons.

The Cuatro Ciénegas square (10 spp.) is separate from the remaining high-diversity squares in Coahuila and is part of the Bolsón of Cuatro Ciénegas Region, which lies near the eastern limit of the CDR in central Coahuila. The bolsón is an intermontane valley approximately 40 by 25 km. It is recognized for its high degree of floristic and faunistic endemism and its varied aquatic features and associated gypsum dunes (Pinkava 1984). The Cuatro Ciénegas square is the northernmost area in the CDR, with a significant number of endangered cacti.

Those grid squares containing from 7 to 14 species constitute the most important area of species concentration of endangered cacti. From these areas, species richness decreases gradually or in some cases abruptly (Figs. 2 and 3). Thus, adjacent to the Tolimán, Metztitlán, and Xichú squares there are six more squares of lesser importance (Figs. 2 and 3) that are located in semidry areas of Guanajuato, Querétaro, and Hidalgo: San Miguel de Allende (5 spp.), Querétaro (5 spp.), Peñamiller (4 spp.), Landa de Matamoros (4 spp.), Zimapán (4 spp.), and Pachuca (6 spp.). Strictly speaking, most of these areas contain little of the typical Chihuahuan Desert vegetation, but we decided not to exclude them from this analysis because they share many species in common with the Tolimán, Metztitlán, and Xichú core areas.

There are several secondary grid squares contiguous to the grouping starting in the San Luis Potosí grid square in the south and concluding in the Marte square in the north (Figs. 2 and 3). The Mexquitic square contained five species and is located just west of the San Luis Potosí square. In addition, the species-rich Huizache square is bordered by the El Tepeyac (5 spp.), Arista (6 spp.), and Villa de Guadalupe (5 spp.) grid squares, which are situated toward its east, west, and northwest, respectively. The most significant of these, however, are a conglomerate of secondary squares in southern Coahuila and northeastern Durango that are located west of the Marte and General Cepeda squares. These are the Cinco de Mayo (6 spp.), Parras (6 spp.) and Gómez Palacio (4 spp.) squares. This area also contains two additional squares, the Hipólito (6 spp.) and Rayones (4 spp.) squares, that are associated with the Marte and Saltillo squares.

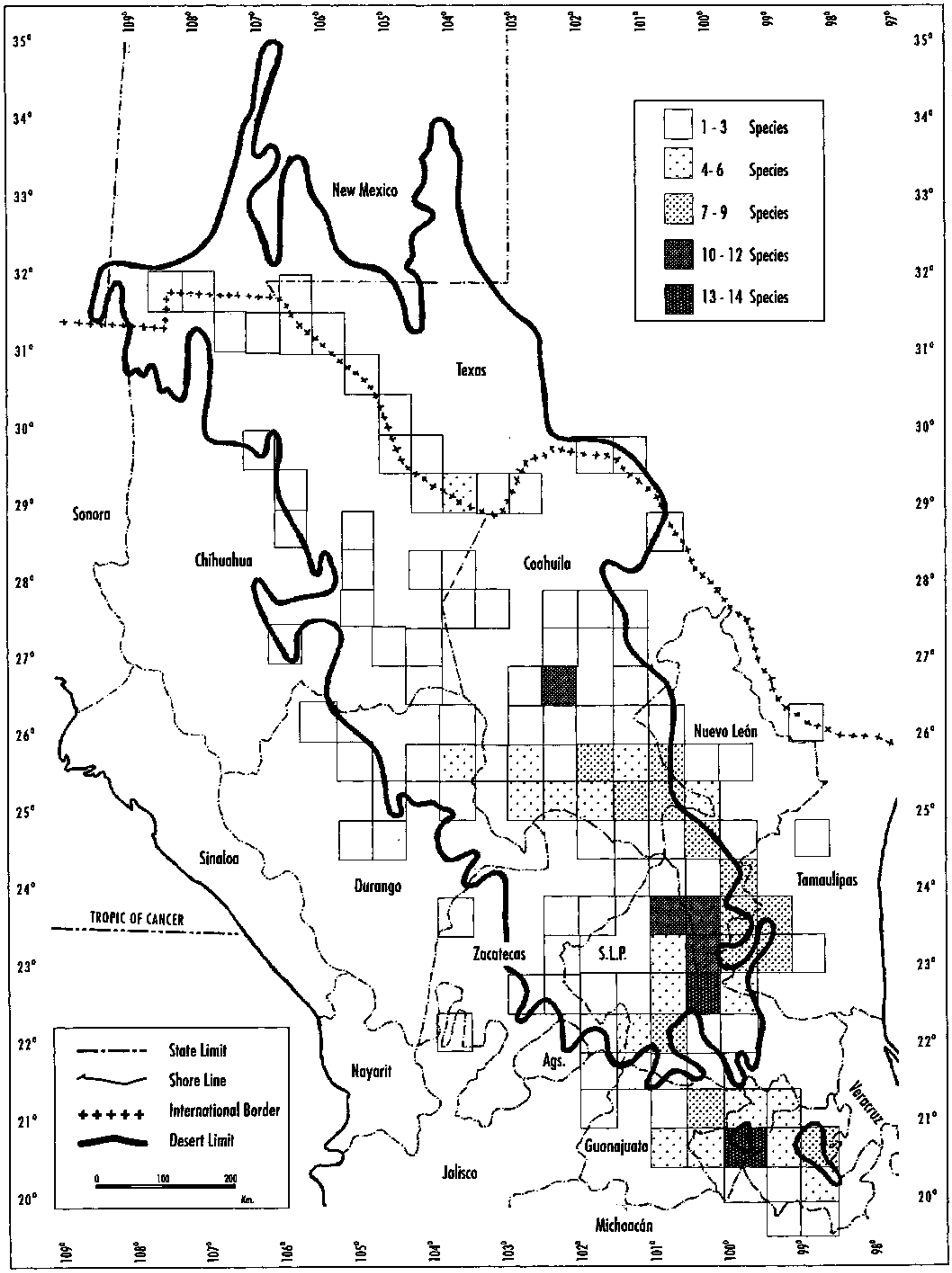
Several hundred kilometers north of this area is an isolate square, the Big Bend square, with four species, that is divided by the Mexico–United States border. The Big Bend Region is well known for its unusual array of succulent plants, many of which reach their northern limit of distribution in this area.

Discussion

Biogeographical Considerations

Endangered species of cacti are concentrated toward the southeastern segment of the CDR (Fig. 3). Most of the grid squares with more than seven species aggregate to form a narrow belt that runs from San Luis Potosí City along the southeastern border of the desert into southern Coahuila, south of 26° north parallel. In addition, four species-rich squares are disjunct from this area: Three of them correspond to the Queretaroan-Hidalgoan Arid Zone and the fourth to the Bolsón of Cuatro Ciénegas (Figs. 2 and 3). An indication of the highly aggregate distribution of the Chihuahuan Desert endangered cacti is the fact that 72.8% (67 spp.) of the species included in this study were found in the 19 richest squares. Moreover, an additional set of 14 species occurred apart from

Figure 2. Localization of the grid squares containing four or more species of endangered cacti in the Chihuahuan Desert Region: 1 = Big Bend, 2 = Cuatro Ciénegas, 3 = Gómez Palacio, 4 = San Pedro, 5 = Viesca, 6 = Parras, 7 = Marte, 8 = Hipólito, 9 = Ramos Arizpe, 10 = Cinco de Mayo, 11 = General Cepeda, 12 = Saltillo, 13 = Rayones, 14 = Galeana, 15 = Aramberri, 16 = Matehuala, 17 = Doctor Arroyo, 18 = Miquihuana, 19 = Ciudad Victoria, 20 = Villa de Guadalupe, 21 = Mier y Noriega, 22 = Tula, 23 = Jaumave, 24 = Arista, 25 = Huizache, 26 = El Tepeyac, 27 = Mexquitic, 28 = San Luis Potosí, 29 = Xichú, 30 = Peñamiller, 31 = Landa, 32 = San Miguel, 33 = Querétaro, 34 = Tolimán, 35 = Zimapán, 36 = Metztitlán, 37 = Pachuca.


1 - 3 Species
4 - 6 Species
7 - 9 Species
10 - 12 Species
13 - 14 Species
New Mexico
Texas
Sonora
Chihuahua
Coahuila
Nuevo León
Tamaulipas
Sinaloa
Durango
Zacatecas
S.L.P.
TROPIC OF CANCER
Nayarit
Ags.
Guanajuato
Jalisco
Michoacán
Veracruz
State Limit
Shore Line
International Border
Desert Limit
0
100
200
Km.

these 19 squares but were distributed in the 18 squares that contained 4–6 species. This means that 88% (81 spp.) of the endangered cacti considered in this study are distributed, although not exclusively, in 37 spatially agglomerate squares within the CDR and marginal areas. Outside these areas species richness declines considerably, to the extreme that 85 squares have only from one to three species. In the remaining squares within the CDR, representing approximately 52.2% of the whole area, no endangered species have been documented.

In addition to the highly concentrated distribution pattern of the endangered cacti, most of the species occur at moderate elevations in or near valley bottoms where desert scrub communities are present. In fact, most of the areas of the species-rich squares lie at elevations ranging from 1200 to 1700 m, although some areas (such as the Valley of Jaumave, Cuatro Ciénegas) occur at lower elevations.

The geographical distribution of most cacti is strongly limited by climatic factors, particularly by exposure to freezing temperatures for periods longer than 24 hours and by low precipitation (Steenbergh & Lowe 1976; Yeaton & Cody 1979; Gibson & Nobel 1986; Nobel 1988). The northernmost area of the CDR receives some snowfall during the winter months, and there is a trend toward highest annual and monthly temperatures and longest frost-free seasons toward lower elevation and latitudinal locations (Schmidt 1979). The hottest, driest, and lowest areas in the CDR are in the Río Grande and the Trans-Pecos (600–1675 m elevation), the Bolsón de Cuatro Ciénegas (740 m at the valley bottom), and the Bolsón de Mapimí (1075 m). As elevation rises from these areas to the south and east, there is increased precipitation (Anonymous 1981).

It has been suggested (Van Devender 1986) that species richness, including the importance of the frost-sensitive succulents, increases from north to south, and the distribution patterns shown here support this affirmation. Our results contradict the popular idea that cacti are common in the driest, hottest deserts. In fact, most of the cactus-rich squares within the CDR correspond to areas with relatively mild climates, outside regions where precipitation is exceedingly low or where temperature variations throughout the year are extreme. Examination of climatic charts (Anonymous 1981) shows that the ranges of most of the cactus species coincide surprisingly well with the areas with dry, semi-hot climates (subtype BS_0 in Köppen's climatic classification, as modified by García 1964), and to a lesser extent with semidry climates (subtypes BS_1h and BS_1k). These areas, receiving mean annual precipitations of 300 to 600 mm, are different from the northern and northwestern fragments of the CDR, where very dry climates (subtype BW) prevail and where precipitation usually does not exceed 300 mm per year. The only exception to this pattern is in the Cuatro Ciénegas square and in parts of the secondary squares in southern Coahuila and Durango (Viesca, San Pedro de las Colonias, and Gómez Palacio), where several endangered species occur in areas dominated by very dry (BW) climates.

Climatic patterns explain why the endangered cacti are concentrated mostly toward the eastern and particularly southeastern edges of the CDR. But current climate does not account for the proliferation of narrow endemics and the high frequency of disjunct distributions. The answer to this problem probably is in the recent climatic history of the region.

Recent studies of plant megafossils found in packrat (*Neotoma* spp.) middens (see reviews in Betancourt et al. 1990) provide evidence of vegetational changes that occurred in the North American deserts as a result of Pleistocene climatic changes. Middens from different ages and localities in the northern and central portions of the CDR have documented cooler and wetter climates and the consequent widespread expansion of woodland and forest communities into areas currently occupied by desert communities (Van Devender 1986, 1990). Thus there is no question that the pleistocene glacial-interglacial cycles, particularly the last glacial maximum (Wisconsin, 11,000 years ago), have shaped current plant distributions in the CDR.

The packrat-midden fossil record shows that during the late Wisconsin the entire area occupied by the Chihuahuan Desert in the United States was covered by montane communities such as pinyon-juniper-oak woodland (Van Devender 1990). Southward and in the lower elevation areas, however, where the magnitude of this climatic impact was more moderate, the predominance of pure woodland communities decreased. In the Bolsón de Mapimí of the Chihuahuan Desert, for instance, elements, including many cactus species, were found intermixed with woodland species in middens from three sites dated at 11,700–13,600 years (Van Devender & Burgess 1985). Similarly, during the same period, several diagnostic Chihuahuan Desert plants grew along with woodland species in the lowest-elevation site of the Big Bend area (Rio Grande Village, 610 m altitude). Consequently, Van Devender and Burgess (1985) and Van Devender (1986) have suggested that both the Bolsón de Mapimí and Big Bend areas acted as refugia for Chihuahuan Desert elements during the Wisconsin glacial maximum. Afterward, during the Holocene, desert scrub communities began to expand as woodlands retreated and the Chihuahuan Desert reached its greatest extent in the late Holocene (Van Devender 1990).

The late Wisconsin precipitation gradients paralleled

Figure 3. Patterns of geographical distribution of endangered cacti in the Chihuahuan Desert Region.

those of today, with moisture decreasing at lower latitudes and elevations (Van Devender 1990). At that time the biota of the southern fragment of the CDR, including the Queretaroan-Hidalgoan Arid Zone and the disjunct arid valleys in the Sierra Madre Oriental, probably experienced reduced extinction rates relative to those in the extreme north. Thus, it is likely that mild, equable climates in this portion of the CDR allowed many of the desert taxa to coexist with woodland and even tropical elements. We hypothesize that most of the lowland portions of the 19 most cactus-rich squares in the CDR acted as refuge areas for an important assemblage of cactus species during the last glacial episode. Later, during the transition to more-modern climatic regimes during the Holocene, many cactus species, particularly those with adequate dispersal abilities, expanded to reach their current ranges. Conversely, the numerous relict narrow endemics, which are remarkably common in these refuge areas, did not colonize further territory, presumably because their dispersal abilities are exceedingly limited.

In addition to the effect of climatic factors, it is highly probable that soil differentiation accounts for the existence of a substantial number of narrow endemics in the CDR (Johnston 1977; Powell & Turner 1977). Several geographically restricted cactus species are known as strict edaphic specialists (for example, *Ariocarpus kotschoubeyanus*, *Aztekium hintonii*, *A. ritteri*, *Geohintonia mexicana*, *Strombocactus disciformis*, *Turbinicarpus subterraneus*), and there are numerous, less-obvious cases of edaphic specialization. We cannot reach definite conclusions, however, because knowledge of plant-soil relationships in the CDR, particularly regarding the Cactaceae, is limited. It is likely that edaphic factors, acting in conjunction with climatic variables, have greatly stimulated speciation within the Chihuahuan Desert flora.

Conservation Considerations

The determination of the geographical patterns of the Cactaceae family is an essential requirement for its conservation. Each 1 of the 93 species of cacti included in this study falls somewhere between two extremes of rarity, from those with very narrow distributions to those with wide ranges but low-density populations.

Ideally, these plants should be protected through the establishment of in situ protected areas. Conservation measures should be particularly centered on the quadrants containing the highest numbers of species. But conservation of the richest 19 quadrants, which would mean the overall conservation of 72.8% of the endangered species, seems improbable given the magnitude of the area. One single square (such as Huizache) is more than twice as large as the area of the entire Mapimí Biosphere Reserve (120,000 ha). Thus, perhaps an appropriate approach would be the careful selection of a network of relatively small areas within the CDR. The selection of these areas should be based on a thorough analysis of variables such as species richness, degree of endemicity or taxonomic uniqueness, and habitat diversity. A more-detailed analysis of the cactus-rich areas incorporating these variables is in preparation. Cacti are poorly represented in herbarium collections, and further collections would improve the fidelity of our results. It is unlikely, however, that the general distribution would differ from the scheme presented here.

A supplementary means of conserving endangered cacti in the CDR could be the propagation of genetically representative samples of the species in regional botanical gardens. Commercial propagation in certified nurseries, in and outside Mexico, could also relieve pressure on natural populations by minimizing collecting.

It is unfortunate that the arid and semiarid zones are poorly represented within Mexico's National System of Natural Protected Areas; none of the critical, species-rich quadrants revealed in this study are included in a protected area. The only representative protected area within the Mexican portion of the CDR is the Mapimí Biosphere Reserve. (In addition, there is the Big Bend National Park.) Unfortunately, none of these areas is particularly rich in endangered Cactaceae (Ruiz de Esparza 1988), and none of the species occurring in them is restricted to their limits.

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Literature Cited

Anonymous. 1981. Atlas nacional del medio físico. Estados Unidos Mexicanos. Secretaría de Programación y Presupuesto, México, D.F.

Barthlott, W. and D. Hunt. 1993. Cactaceae. Pages 161-197 in K. Kubitzki, J. Rohwer, and V. Bittrich, editors. The families and genera

of vascular plants. II. Dicotyledons. Springer-Verlag, Berlin.
Betancourt, J., T. Van Devender, and P. Martin, editors. 1990. Packrat middens. The last 40,000 years of biotic change. The University of Arizona Press, Tucson.
Convention on International Trade in Endangered Species. 1990. Appendices I, II and III to the Convention. U.S. Fish and Wildlife Service, Washington, D.C.
Contreras, A. 1955. Definición de las zonas áridas y su delimitación en la República Mexicana. Pages 3–40 in E. Beltrán, editor. Problemas de las zonas áridas de México. Instituto Mexicano de Recursos Naturales Renovables, Mexico, D.F.
Fuller, D., and S. Fitzgerald. 1987. Conservation and commerce of cacti and other succulents. World Wildlife Fund, Washington, D.C.
García, E. 1964. Modificaciones al sistema de clasificación climática de Koppen. Published by the author, México, D.F.
Gibson, A., and P. Nobel. 1986. The cactus primer. Harvard University Press, Cambridge, Massachusetts.
Henrickson, J., and R. Straw. 1976. A gazetteer of the Chihuahuan Desert Region. A supplement to the Chihuahuan Desert flora. California State University, Los Angeles.
Hernández, H. M., V. Alvarado, and R. Ibarra. 1993. Base de datos de colecciones de cactáceas de Norte y Centroamérica. Anales del Instituto de Biología, Universidad Nacional Autónoma de México, Serie Botánica 64:87–94.
Hernández, H. M., and H. Godínez. 1994. Contribución al conocimiento de las cactáceas mexicanas amenazadas. Acta Botánica Mexicana 26:33–52.
Hunt, D. 1992. Cactaceae checklist of the Convention on Trade in Endangered Species. Royal Botanic Gardens, Surrey, England.
Jarvis, C. E. 1979. Trade in cacti and other succulent plants in the United Kingdom. Cactus and Succulent Journal of Great Britain 41: 113–118.
Johnston, M. C. 1977. Brief resume of botanical, including vegetational, features of the Chihuahuan Desert Region with special emphasis on their uniqueness. Pages 335–359 in R. H. Wauer and D. H. Riskind, editors. Transactions of the symposium on the biological resources of the Chihuahuan Desert Region, United States and Mexico. National Park Service, Washington, D.C.
Medellín-Leal, F. 1982. The Chihuahuan Desert. Pages 321–372 in G. L. Bender, editor. Reference handbook on the deserts of North America. Greenwood Press, Westport, Connecticut.
Morafka, D. J. 1977. A biogeographical analysis of the Chihuahuan Desert through its herpetofauna. Biogeographica 9:1–313.
Nobel, P. 1988. Environmental biology of agaves and cacti. Cambridge University Press, New York.
Pinkava, D. 1984. Vegetation and flora of the Bolsón of Cuatro Ciénegas Region, Coahuila, Mexico. IV. Summary, endemism and corrected catalogue. Journal of the Arizona-Nevada Academy of Science 19:23–47.
Powell, A. M., and B. L. Turner. 1977. Aspects of the plant biology of the gypsum outcrops of the Chihuahuan Desert. Pages 315–325 in R. H. Wauer and D. H. Riskind, editors. Transactions of the symposium on the biological resources of the Chihuahuan Desert Region, United States and Mexico. National Park Service, Washington, D.C.
Rabinowitz, D. 1981. Seven forms of rarity. Pages 205–217 in H. Synge, editor. The biological aspects of rare plant conservation. John Wiley and Sons, Chichester, England.
Ruiz de Esparza, R. 1988. Lista de especies vasculares. Pages 225–239 in C. Montaña, editor. Estudio integrado de los recursos vegetación, suelo y agua en la Reserva de la Biósfera de Mapimí. Instituto de Ecología A.C., México, D.F.
Sánchez-Mejorada, H. 1982. Mexico's problems and programmes monitoring trade in common and endangered cacti. Cactus and Succulent Journal of Great Britain 44:36–38.
Schmidt, R. H., Jr. 1979. A climatic delineation of the "real" Chihuahuan Desert. Journal of Arid Environments 2:243–250.
Shreve, F. 1942. The desert vegetation of North America. Botanical Review 8:195–246.
Steenbergh, W., and C. Lowe. 1976. Ecology of the saguaro. I. The role of freezing weather on a warm-desert plant population. Pages 49–92 in Research in the parks. National Park Service symposium series no. 1. U.S. Government Printing Office, Washington, D.C.
Usher, M. B. 1986. Wildlife conservation evaluation: attributes, criteria and values. Pages 3–44 in M. B. Usher, editor. Wildlife conservation evaluation. Chapman and Hall, London.
Van Devender, T. 1986. Pleistocene climates and endemism in the Chihuahuan Desert flora. Pages 1–19 in J. Barlow, A. M. Powell, and B. Timmermann, editors. Second symposium on the resources of the Chihuahuan Desert Region. Chihuahuan Desert Research Institute, Alpine, Texas.
Van Devender, T. 1990. Late quaternary vegetation and climate of the Chihuahuan Desert, United States and Mexico. Pages 104–133 in J. Betancourt, T. Van Devender, and P. Martin, editors. Packrat middens. The last 40,000 years of biotic Change. The University of Arizona Press, Tucson.
Van Devender, T., and T. Burgess. 1985. Late pleistocene woodlands in the Bolsón de Mapimí: A refugium for the Chihuahuan Desert biota? Quaternary Research 24:346–353.
Vermeij, G. J. 1993. Biogeography of recent extinct marine species: implications for conservation. Conservation Biology 7:391–397.
Yeaton, R., and M. Cody. 1979. The distribution of cacti along environmental gradients in the Sonoran and Mohave Deserts. Journal of Ecology 67:529–541.

Appendix 1.

List of endangered species of cacti from the Chihuahuan Desert and marginal areas included in this study.[a]

Taxon	*General Distribution*[b]
Ariocarpus agavoides	Tam
A. bravoanus	SLP
A. fissuratus	
var. *fissuratus*	Coah, Tex
var. *hintonii*	SLP
var. *lloydyi*	Coah, Dgo, Zac
A. kotschoubeyanus	Coah, NL, Qro, SLP, Tam, Zac
A. retusus	Coah, NL, SLP, Tam, Zac
A. scaphirostris	NL
A. trigonus	NL, Tam
Astrophytum asterias	Tam, Tex
A. capricorne	Coah, NL
A. myriostigma	Coah, SLP, Tam
A. ornatum	Gto, Hgo, Qro, SLP
Aztekium hintonii	NL
A. ritteri	NL
Cephalocereus senilis	Hgo, Ver
Coryphantha odorata	SLP, Tam
C. poselgeriana	Coah, Dgo, SLP
C. pseudoechinus	Coah, NL
C. werdermannii	Coah, Chih
Echinocactus grusonii	Qro
E. parryi	Chih
E. platyacanthus	Coah, Gto, Hgo, NL, Oax, Pue, Qro, SLP, Tam, Zac
Echinocereus delaetii	Coah
E. knippelianus	Coah, NL
E. longisetus	Coah, NL
E. nivosus	Coah
E. palmeri	Chih
E. pulchellus	Ags, Hgo, Jal, NL, Oax, Pue, Qro, SLP, Zac

Appendix 1. Continued

Taxon	*General Distribution*[b]
E. schmollii	Qro
Escobaria aguirreana	Coah
E. laredoi	Coah
E. roseana	Coah
Ferocactus latispinus	
var. *latispinus*	Ags, Dgo, EM, Gto, Hgo, Jal, Qro, Pue, SLP, Zac
F. macrodiscus	
var. *septentrionalis*	Gto
F. pilosus	Coah, Dgo, NL, SLP, Tam, Zac
Geohintonia mexicana	NL
Hamatocactus crassihamatus	Gto
Leuchtenbergia principis	Coah, Dgo, NL, SLP, Tam
Lophophora diffusa	Qro
Mammillaria albicoma	Tam
M. aureilanata	SLP
M. aurihamata	SLP
M. baumii	Tam
M. carmenae	Tam
M. grusonii	Coah
M. hahniana	Qro
M. herrerae	Gto, Qro
M. humboldtii	Hgo
M. klissingiana	Tam
M. lenta	Coah
M. longimamma	Hgo, Qro, Ver
M. mathildae	Qro
M. melaleuca	Tam
M. moelleriana	Dgo, Zac
M. nana	Gto, Qro, SLP
M. painteri	Qro
M. parkinsonii	Hgo, Qro
M. pennispinosa	
var. *nazarensis*	Dgo
var. *pennispinosa*	Coah, Dgo
M. pilispina	NL, SLP
M. plumosa	Coah, NL
M. rettigiana	Gto
M. schiedeana	Hgo
M. surculosa	SLP, Tam
M. theresae	Dur
M. weingartiana	NL
M. zephyranthoides	EM, Gto, Hgo, Oax, Pue, Qro
Neobuxbaumia euphorbioides	Tam, Ver
N. polylopha	Hgo, Qro
Obregonia denegrii	Tam
Opuntia rufida	Chih, Coah, Dgo, Tex
Pelecyphora aselliformis	SLP
P. strobiliformis	NL, Tam
Peniocereus greggii	
var. *greggii*	Ari, Chih, Coah, Dgo, NM, Tex
Sclerocactus intertextus	Ari, Chih, NM, Tex
S. mariposensis	Coah, Tex
S. uncinatus	Chih, Coah, Dgo, NL, NM, Qro, SLP, Son, Tam, Tex, Zac
S. unguispinus	Chih, Coah, Dur, SLP, Zac
Stenocactus coptonogonus	Gto, Hgo, SLP, Zac
Strombocactus disciformis	Hgo, Qro
Thelocactus hastifer	Qro
T. macdowellii	Coah, NL
T. tulensis	
var. *tulensis*	SLP, Tam
var. *buekii*	NL
var. *matudae*	NL
Turbinicarpus gautii	Coah, NL
T. gielsdorfianus	Tam
T. horripilus	Hgo
T. knuthianus	SLP
T. laui	SLP
T. pseudomacrochele	Qro
T. pseudopectinatus	NL, SLP, Tam
T. saueri	Tam
T. schmiedickeanus	
var. *dickisoniae*	NL
var. *flaviflorus*	SLP
var. *gracilis*	NL
var. *klinkerianus*	SLP
var. *macrochele*	SLP
var. *schmiedickeanus*	Tam
var. *schwarzii*	SLP
T. subterraneus	
var. *subterraneus*	NL
var. *zaragozae*	NL
T. valdezianus	Coah, NL
T. viereckii	
var. *major*	NL
var. *viereckii*	Tam

[a] *Modified from Hernández & Godínez 1994. Nomenclature follows Hunt (1992).*

[b] *Ags = Aguascalientes, Ari = Arizona, Chih = Chihuahua, Coah = Coahuila, Dgo = Durango, EM = Estado de México, Gto = Guanajuato, Hgo = Hidalgo, Jal = Jalisco, NL = Nuevo León, NM = New Mexico, Oax = Oaxaca, Pue = Puebla, Qro = Querétaro, SLP = San Luis Potosí, Son = Sonora, Tam = Tamaulipas, Tex = Texas, Ver = Veracruz, Zac = Zacatecas.*

Appendix 2.

Localization and lists of species of the grid squares containing at least four species of endangered cacti in the Chihuahuan Desert Region.

Big Bend Square (29°00′–29°30′ N, 103°30′–104°00′ W)

Ariocarpus fissuratus
Opuntia rufida
Sclerocactus mariposensis
S. uncinatus

Cuatro Ciénegas Square (26°30′–27°00′ N, 102°00′–102°30′ W)

Ariocarpus fissuratus
Astrophytum capricorne
Coryphantha poselgeriana
C. werdermannii
Escobaria aguirreana
Ferocactus pilosus
Mammillaria grusonii
Opuntia rufida
Sclerocactus mariposensis
S. uncinatus

Gómez Palacio Square (25°30′–26°00′ N, 103°30′–104°00′ W)

Ariocarpus fissuratus
Leuchtenbergia principis
Sclerocactus uncinatus

Appendix 2. Continued

S. unguispinus

San Pedro de las Colonias Square (25°30′–26°00′ N, 102°30′–103°00′ W)
Astrophytum capricorne
A. myriostigma
Coryphantha poselgeriana
Mammillaria grusonii
Opuntia rufida
Sclerocactus uncinatus

Marte Square (25°30′–26°00′ N, 101°30′–102°00′ W)
Ariocarpus fissuratus
Astrophytum capricorne
Coryphantha poselgeriana
C. pseudoechinus
Echinocereus delaetii
Sclerocactus mariposensis
S. uncinatus
Turbinicarpus gautii

Hipólito Square (25°30′–26°00′ N, 101°00′–101°30′ W)
Ariocarpus kotschoubeyanus
Astrophytum capricorne
Coryphantha poselgeriana
C. werdermannii
Escobaria roseana
Leuchtenbergia principis

Ramos Arizpe Square (25°30′–26°00′ N, 100°30′–101°00′ W)
Ariocarpus retusus
Astrophytum capricorne
Coryphantha pseudoechinus
Mammillaria plumosa
Thelocactus mcdowellii
Turbinicarpus gautii
T. valdezianus

Viesca Square (25°00′–25°30′ N, 102°30′–103°00′ W)
Ariocarpus fissuratus
A. kotschoubeyanus
Astrophytum myriostigma
Echinocereus knippelianus
Mammillaria lenta
Sclerocactus uncinatus

Parras Square (25°00′–25°30′ N, 102°00′–102°30′ W)
Ariocarpus fissuratus
Astrophytum capricorne
Coryphantha poselgeriana
Echinocereus knippelianus
Leuchtenbergia principis
Turbinicarpus gautii

Cinco de Mayo Square (25°00′–25°30′ N, 101°30′–102°00′ W)
Ariocarpus fissuratus
A. retusus
Coryphantha poselgeriana
Echinocereus nivosus
Escobaria laredoi
Turbinicarpus gautii

General Cepeda Square (25°00′–25°30′ N, 101°00′–101°30′ W)
Ariocarpus kotschoubeyanus
A. retusus
Astrophytum capricorne
Coryphantha poselgeriana
Echinocactus platycanthus
Escobaria roseana
Ferocatus pilosus

Appendix 2. Continued

Turbinicarpus gautii

Saltillo Square (25°00′–25°30′ N, 100°30′–101°00′ W)
Ariocarpus retusus
Echinocactus platyacanthus
Echinocereus knippelianus
Ferocactus pilosus
Mammillaria pilispina
Sclerocactus uncinatus
S. unguispinus
Turbinicarpus gautii

Rayones Square (25°00′–25°30′ N, 100°00′–100°30′ W)
Ariocarpus scaphirostris
Aztekium ritteri
Mammillaria pilispina
Thelocactus tulensis

Galeana Square (24°30′–25°00′ N, 100°00′–100°30′ W)
Ariocarpus retusus
Aztekium ritteri
Echinocactus platyacanthus
Ferocactus pilosus
Sclerocactus uncinatus
Thelocactus tulensis
Turbinicarpus gautii

Aramberri Square (24°00′–24°30′ N, 99°30′–100°00′ W)
Ariocarpus kotschoubeyanus
Echinocactus platyacanthus
Ferocactus pilosus
Mammillaria weingartiana
Pelecyphora strobiliformis
Thelocactus tulensis
Turbinicarpus pseudopectinatus
T. schmiedickeanus

Matehuala Square (23°30′–24°00′ N, 100°30′–101°00′ W)
Ariocarpus fissuratus
A. retusus
Astrophytum myriostigma
Echinocactus platyacanthus
Ferocactus pilosus
Mammillaria aurihamata
Sclerocactus uncinatus
Thelocactus tulensis
Turbinicarpus schmiedickeanus
T. valdezianus

Doctor Arroyo Square (23°30′–24°00′ N, 100°00′–100°30′ W)
Ariocarpus kotschoubeyanus
A. retusus
Echinocactus platyacanthus
Ferocactus pilosus
Leuchtenbergia principis
Pelecyphora strobiliformis
Sclerocactus uncinatus
Turbinicarpus schmiedickeanus
T. pseudopectinatus
T. valdezianus

Miquihuana Square (23°30′–24°00′ N, 99°30′–100°00′ W)
Ariocarpus retusus
Ferocactus pilosus
Pelecyphora strobiliformis
Thelocactus tulensis
Turbinicarpus schmiedickeanus
T. subterraneus
T. pseudopectinatus

Appendix 2. Continued

Ciudad Victoria Square (23°30′–24°00′ N, 99°00′–99°30′ W)
Ariocarpus trigonus
Astrophytum myriostigma
Leuchtenbergia principis
Mammillaria albicoma
M. baumii
M. carmenae
M. klissingiana
Obregonia denegrii

Villa de Guadalupe Square (23°00′–23°30′ N, 100°30′–101°00′ W)
Ariocarpus fissuratus
Echinocactus platyacanthus
Ferocactus pilosus
Sclerocactus uncinatus
Turbinicarpus schmiedickeanus

Mier y Noriega Square (23°00′–23°30′ N, 100°00′–100°30′ W)
Ariocarpus retusus
Astrophytum myriostigma
Echinocactus platyacanthus
Ferocactus pilosus
Leuchtenbergia principis
Sclerocactus uncinatus
Thelocactus tulensis
Turbinicarpus pseudopectinatus
T. schmiedickeanus
T. viereckii

Tula Square (23°00′–23°30′ N, 99°30′–100°00′ W)
Ariocarpus kotschoubeyanus
A. retusus
Echinocactus platyacanthus
Ferocactus pilosus
Mammillaria melaleuca
Thelocactus tulensis
Turbinicarpus pseudopectinatus

Jaumave Square (23°00′–23°30′ N, 99°00′–99°30′ W)
Ariocarpus trigonus
Echinocactus platyacanthus
Neobuxbaumia euphorbioides
Obregonia denegrii
Turbinicarpus gielsdorfianus
T. saueri
T. viereckii

Arista Square (22°30′–23°00′ N, 100°30′–101°00′ W)
Ariocarpus retusus
Astrophytum myriostigma
Echinocactus platyacanthus
Ferocactus pilosus
Leuchtenbergia principis
Sclerocactus uncinatus

Huizache Square (22°30′–23°00′ N, 100°00′–100°30′ W)
Ariocarpus bravoanus
A. kotschoubeyanus
A. retusus
Astrophytum myriostigma
Coryphantha odorata
Echinocactus platyacanthus
Ferocactus pilosus
Leuchtenbergia principis
Mammillaria pilispina
M. surculosa
Sclerocactus uncinatus
Thelocactus tulensis

Appendix 2. Continued

Turbinicarpus knuthianus
T. schmiedickeanus

El Tepeyac Square (22°30′–23°00′ N, 99°30′–100°00′ W)
Ariocarpus agavoides
A. kotschoubeyanus
A. retusus
Astrophytum myriostigma
Thelocactus tulensis

Mexquitic Square (22°00′–22°30′ N, 101°00′–101°30′ W)
Ariocarpus retusus
Echinocactus platyacanthus
Echinocereus pulchellus
Mammillaria nana
Stenocactus coptonogonus

San Luís Potosí Square (22°00′–22°30′ N, 100°30′–101°00′ W)
Ariocarpus retusus
Echinocactus platyacanthus
Ferocactus latispinus
Leuchtenbergia principis
Mammillaria aureilanata
Pelecyphora aselliformis
Stenocactus coptonogonus

Xichú Square (21°00′–21°30′ N, 100°00′–100°30′ W)
Astrophytum ornatum
Ferocactus latispinus
F. macrodiscus
Hamatocactus crassihamatus
Mammillaria herrerae
M. nana
M. zephyranthoides

Peñamiller Square (21°00′–21°30′ N, 99°30′–100°00′ W)
Astrophytum ornatum
Lophophora difussa
Mammillaria hahniana
M. parkinsonii

Landa Square (21°00′–21°30′ N, 99°00′–99°30′ W)
Astrophytum ornatum
Mammillaria hahniana
M. longimamma
Neobuxbaumia polylopha

San Miguel Square (20°30′–21°00′ N, 100°30′–101°00′ W)
Ferocactus latispinus
F. macrodiscus
Mammillaria nana
M. rettigiana
M. zephyranthoides

Querétaro Square (20°30′–21°00′ N, 100°00′–100°30′ W)
Ferocactus latispinus
Mammillaria longimamma
M. mathildae
M. nana
M. painteri

Tolimán Square (20°30′–21°00′ N, 99°30′–100°00′ W)
Ariocarpus kotschoubeyanus
Astrophytum ornatum
Echinocactus grusonii
E. platyacanthus
Echinocereus schmollii
Ferocactus latispinus
Lophophora diffusa
Mammillaria herrerae
M. longimamma
M. parkinsonii
Strombocactus disciformis

Appendix 2. Continued

Thelocactus hastifer
Turbinicarpus pseudomacrochele
Zimapán Square (20°30′–21°00′ N, 99°00′–99°30′ W)
Echinocactus platyacanthus
Echinocereus pulchellus
Neobuxbaumia polylopha
Strombocactus disciformis
Metztitlán Square (20°30′–21°00′ N, 98°30′–99°00′ W)
Astrophytum ornatum
Cephalocereus senilis
Echinocactus platyacanthus
Mammillaria humboldtii
M. longimamma
M. schiedeana
Neobuxbaumia polylopha
Turbinicarpus horripilus
Pachuca Square (20°00′–20°30′ N, 98°30′–99°00′ W)
Cephalocereus senilis
Echinocactus platyacanthus
Echinocereus pulchellus
Ferocactus latispinus
Mammillaria longimamma
Stenocactus coptonogonus