PLEISTOCENE CLIMATES AND ENDEMISM IN THE CHIHUAHUAN DESERT FLORA

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ABSTRACT

Chronological series of radiocarbon dated plant macrofossil assemblages from small geographic areas are providing excellent developmental sequences of vegetation for the last 35,000 years in the northern Chihuahuan Desert. Midden vegetation chronologies have been completed along a latitudinal gradient from the San Andres (33°11'N) and Sacramento mountains, New Mexico, and the Jueco Mountains (32°N), and the Rio Grande Village area (29°30'N) and Maravillas Canyon (29°33'N) in the Big Bend of Texas. Although the chronologies demonstrate some differences in composition and the timing of vegetation changes, they agree in a stepwise progression with the most mesic pinyon-juniper-oak vegetation in the Late Wisconsin and the most xeric in the last 4000 years. The Middle Holocene (about 8000-4500 years ago) was apparently very warm with strongly developed summer monsoons and a maximum expansion of grasslands. About 4500 years ago, a creosote-desertscrub corridor between the Chihuahuan and Sonoran deserts was established for the first time since the last interglacial. Deserts are probably at their maximum expansion today with the harshest climates of the present interglacial.

The majority of the endemic Chihuahuan Desert plants have affinities with the grasslands, thornscrub, or woodlands of the Sierra Madre Oriental to the east and south. Isolation during glacial/interglacial fluctuations has provided many opportunities for speciation in both desert and woodland plants. In the Bolson de Mapimi, pluvial lakes alternated with dry playas with exposed halophytic and gypsum substrates. A number of east-west vicariant species pairs whose disjunctions are probably pre-Pleistocene are discussed.

The latitudinal gradient in increasing numbers of species at lower latitudes can be explained in terms of latitudinal differences in extinction rates. The probability of extinction of isolated populations at the end of a glacial or an interglacial is greatest in the north and decreases to the south as the probability of speciation increases. Coupled with 15–20 glacial/interglacial cycles in the last 1.8 million years and a mild, equable climate where extremes in cold, heat, or drought have never been great enough to cause wholesale extinctions, the numbers of newly evolved and old relict species have gradually increased in the central and southern Chihuahuan Desert.

RESUMEN

Una serie cronológica de colecciones de macrofósiles de plantas fechadas por radiocarbón en pequeñas regiones geográficas ofrecen excelentes sucesiones que muestran el desarrollo de la vegetación para los últimos 35,000 años en el Desierto de Chihuahua norteño. Se han terminado de estudiar las cronologías de vegetación basural a lo largo de un gradiente latitudinal desde la Sierra de San Andrés (33°11'N) y la Sierra Sacramento, New Mexico, y la Sierra Hueco (32°N), y la región del Río Grande Village (29°30'N) y la Barranca Maravillas (29°33'N) en el Big Bend de Texas. Aunque las cronologías muestran diferencias en composición y tiempo de los cambios vegetales, están, sin embargo, de acuerdo con una progre-
El gradiente latitudinal en el creciente número de especies en latitudes más bajas puede explicarse en términos de diferencias latitudinales en porcentajes de extinción. La probabilidad de extinción de poblaciones aisladas a fines de un período glacial/interglacial ha ofrecido muchas oportunidades para la evolución de especies de plantas de desierto y de bosque. En el Bosón de Mapimi, lagunas pluviales alternaron con playas secas descubiertas con substratos halofíticos y de yeso. Se discuten un número de pares de especies vicarias del este y oeste cuyas separaciones son probablemente del pre-Pleistoceno.

El gradiente latitudinal en el creciente número de especies en latitudes más bajas puede explicarse en términos de diferencias latitudinales en porcentajes de extinción. La probabilidad de extinción de poblaciones aisladas a fines de un período glacial/interglacial ha ofrecido muchas oportunidades para la evolución de especies. Junto con los 15 a 20 ciclos glacial/interglacial en los últimos 1.8 millones de años y un clima benigno y uniforme donde los extremos de frío, calor, o sequía han sido bastante fuertes como para causar grandes extinciones, los números de especies recientemente evolucionadas y las vestigiales poco a poco han crecido en el Desierto de Chihuahua central y sureño.

Beginning in the 1960's, the analyses of well-preserved plant macrofossil assemblages from radiocarbon dated packrat (Neotoma spp.) middens have provided a wealth of information on the history of vegetation and climate in the arid areas of North America (Van Devender et al. 1979, Spaulding et al. 1983). Well-preserved plant macrofossil assemblages have documented widespread expansion of woodland and forest communities into most of the deserts of North America during the last glacial period, the Wisconsin. In this paper, I summarize the packrat midden record for the Chihuahuan desert and discuss its significance for the distribution and evolution of endemic species.

PACKRAT ECOLOGY

Packrats, or wood rats, are medium-sized rodents comprising about 20 species found from sea level up to 3350 m elevation in many habitats from British Columbia to Guatemala. Packrats carry various objects to their houses for use as construction materials or food (Finley 1958). Their waste piles or middens usually contain rich assemblages of plant fragments collected within 30–50 m of the house. When packrats live in rock shelters, houses are not well-developed but the middens often serve as urination perches and become very hard, dark, and shiny. These indurated middens can be preserved as long as they are dry. The oldest packrat midden discovered to date is more than 50,000 years old (Spaulding et al. 1983). The plant remains in the midden samples are well preserved and give reasonable reflections of the local vegetation near the sites. The plant remains or packrat fecal pellets are excellent for radiocarbon dating, allowing the assemblages to be placed in a time framework. Sequential series of packrat midden assemblages from a single area provide excellent records of the development of the local vegetation for the last 11,000 years or more. Packrat midden chronologies are providing remarkable paleoecological insights from within the deserts themselves.

GEOGRAPHICAL SETTING

The Chihuahuan Desert is unique among the deserts of the American Southwest because it is an interior continental desert in the rainshadows of the Sierra Madre Occidental to the west, the Sierra Madre Oriental to the east, the highlands of the Mexican Plateau to the south, and the Rocky Mountains to the north (Johnston 1977). Portions of the Chihuahuan Desert occur in the states of Arizona, New Mexico, Texas, Chihuahua, Durango, Coahuila, Zacatecas, Nuevo Leon, and San Luis Potosí along its 1600 km southeast to northwest axis (22°–33°N latitude). Morafka (1977) and Henrickson and Straw (1976) have mapped the major biotic provinces of the Chihuahuan Desert. Morafka divided the area from north to south into Trans-Pecos, Mapimian, and Saladan subprovinces based on biotic distributions (mostly of amphibians and reptiles).

The topography of the Chihuahuan Desert is a complex mosaic of mountains and valleys that generally decrease in elevation from the Continental Divide to the Gulf of Mexico in the north and that increase in elevation onto the Mexican Plateau to the south. The climate of the Chihuahuan Desert reflects the topographic complexity in a number of environmental gradients (Schmidt 1979). The hottest, driest, and lowest areas in the Chihuahuan Desert are on the Rio Grande on the United States-Mexican border in the Trans-Pecos (600–1675 m elevation), and in the mutual corners of Chihuahua, Durango, and Coahuila in the Bolson de Mapimi (1075–2000 m elevation). As elevations rise from these central lowlands precipitation increases and temperature decreases. The entire Chihuahuan Desert is dominated by a summer monsoonal rainfall pattern, although most areas have winter precipitation as well. The western half of the Chihuahuan Desert has greater percentages of summer precipitation than more easterly areas. Beyond the Chihuahuan Desert to the east both the percentage of winter precipitation and the total annual precipitation increase as elevation decreases toward the Gulf of Mexico. To the south the percentages of summer precipitation increase with elevation. However, occasional heavy Pacific fronts with winter precipitation reach the
central Chihuahuan Desert, resulting in an exceptional growth of spring plants (as in the winter-spring of 1978–79). This corresponds to anomaly pattern A of LaMarche and Fritts (1971) where the entire Southwest and northern Mexico have greater tree ring growth than eastern regions due to exceptional winter precipitation. To the east and south in the central Chihuahuan Desert, milder winter temperatures and increased humidity produce more subtropical climates. The frequency of incursions of continental polar or continental Arctic air decreases to the south but occasional frosts will penetrate to the southern edge of the Mexican Plateau.

These precipitation and temperature regimes are reflected in the vegetation: xeric desertscrub communities in the lowlands are gradually replaced by desert-grassland to the north, west, south, and southeast. A relatively mesic mesquite scrub community is found on the coastal plain of the Gulf of Mexico and contiguous low areas in Texas, Coahuila, Tamaulipas, and Nuevo Leon (Muller 1939, 1947). The vegetation of the southeastern portion of the Chihuahuan Desert is much more subtropical than other areas. In desertscrub communities there is a gradual increase to the south in the numbers of species and in the importance of succulents and other frost-sensitive species. Pine-oak woodland and pine forest are present at higher elevations on montane islands in the Chihuahuan Desert and on the surrounding mountain ranges.

Johnston (1977) reported about 1000 species of plants endemic to the Chihuahuan Desert Region. This number includes many widespread plants such as lechuguilla (Agave lechuguilla) and tarbush (Flourensia cernua) as well as more narrow endemics. At least 65 Chihuahuan endemics are restricted to gypsum substrates (Powell and Turner 1977). The Chihuahuan Desert fauna is not as rich in endemics. Again, some Chihuahuan animals such as Merriam’s spiny lizard (Sceloporus merriami), Trans-Pecos ratsnake (Elaphe subocularis), gray-banded kingsnake (Lampropeltis mexicana), Chihuahuan lyre snake (Trimorphodon bescutatus vilkinsoni) are widespread while bolson tortoise (Gopherus flavomarginatus), Cuatro Ciénegas alligator lizard (Gerrhonotus luguoi), bolson fringe-toed lizard (Uma exsul), Durangam night lizard (Xantusia vigilis extorris) and bolson night lizard (X. bolsonae) have very restricted distributions (Webb 1970, Morafka 1977). In general, the numbers of all species, as well as endemics of both plants and animals, increase to the south.

**Pleistocene Vegetation of the Chihuahuan Desert**

In Well’s (1966) packrat midden study, he found a pinyon-juniper-oak woodland dominated by Texas pinyon (Pinus remota) at three sites in the Big Bend of Texas that now support Chihuahuan desertscrub vegetation. Bryant and Larson’s (1968) analysis of pollen in sediments from caves near Del Rio suggested that this woodland was still present in the early Holocene (ca 9000 years ago) just east of the Chihuahuan Desert. Meyer’s (1973) study of the pollen in spring deposits in the Cuatro Ciénegas Basin in central Coahuila showed little change in the vegetation in the last 20,000 years.

In the last 6 years I, with the help of co-workers (B. L. Everitt, R. D. Worthington, W. G. Spaulding, A. M. Phillips, J. L. Betancourt, J. J. Toolin, R. S. Thompson, D. H. Riskind), have discovered fossil packrat middens from a number of Chihuahuan Desert sites ranging from the San Andres (33°11'N) and Sacramento mountains (32°50'N), south-central New Mexico, along a latitudinal gradient into the Big Bend (29°12'N), Texas, and the Bolson de Mapimi in Coahuila and Durango, Mexico (26°N; Fig. 1). These results are in the following publications, arranged from north to south: Van Devender et al. (1984) (Sacramento Mountains), Van Devender and Everitt (1977) and Thompson et al. (1980) (Shelter Cave, Bishop’s Cap, New Mexico), Van Devender (1980) (Last Chance Canyon and Rocky Arroyo, Guadalupe Mountains, New Mexico), Van Devender et al. (1977, 1979) (Guadalupe Mountains, Texas), Van Devender and Riskind (1979) (Hueco Mountains, Texas), Van Devender et al. (1978) (Livingston Hills, Chinati Mountains, Texas), and Van Devender (1978) (Bolson de Mapimi, Mexico). Many of the early Holocene and late Wisconsin records and radiocarbon dates are summarized in Van Devender 1977, Van Devender and Spaulding 1979, Lanner and Van Devender 1981, and Spaulding et al. 1983.

**Biochronologies**

The current emphasis is to build detailed local vegetation chronologies along a latitudinal gradient through the Chihuahuan Desert. Differences in composition and the timing of change can help infer atmospheric circulation patterns through time and the role of dispersal in the development of the vegetation. The chronology from the Sacramento Mountains is published (Van Devender et al. 1984). Other chronologies have been completed for the San Andres Mountains, New Mexico, Hueco Mountains (32°N; Fig. 2), Maravillas Canyon (29°33'N; Fig. 3), and Rio Grande Village area (29°12'N; Fig. 4), Texas.

All of the vegetation sequences are similar in showing step-wise changes in vegetation with the most mesic in the late Wisconsin and the most xeric in the last 5000 years in the late Holocene. In all areas the end of the late Wisconsin is marked by a reduction of the more mesic plants including Colorado pinyon (Pinus edulis), P. remota, and Rocky Mountain juniper (Juniperus scopulorum) about 11,000 years ago. With the exception of the Rio Grande Village sequence, the early Holocene vegetation
was a transitional xeric oak-juniper woodland. The middle Holocene was a desert-grassland period lacking both woodland and many important Chihuahuan desert scrub plants. The development of the modern communities was in all cases a late Holocene event. Certainly creosote bush (Larrea divaricata), ocotillo (Fouquieria splendens), and lechuguilla (Agave lechuguilla) are late arrivals in the northern Chihuahuan Desert. The vegetation changes that mark the boundaries between the early, middle, and late Holocene have some temporal variability but were completed by 8000 and 4000 years ago, respectively.

The Rio Grande Village chronology differs from the other records, even the one from Maravillas Canyon, 40 km to the north, in several important ways. Important Chihuahuan plants, including Agave lechuguilla and crucifixion thorn (Koeberlinia spinosa), were common in the late Wisconsin pinyon-juniper-oak woodland. The Big Bend was probably the Ice Age refugium for some of the plants that are important in Chihuahuan desert scrub communities to the north. Samples dated at 10,390 ± 230 BP (average of A-2937 on Koeberlinia spinosa and A-3129 on Prosopis glandulosa; Tunnel View #5B) and 8980 ± 130 BP (average of A-2936 on Lycium puberulum and A-3128 on Opuntia phaeacantha; Tunnel View #5A) document the early development of honey mesquite (Prosopis glandulosa) dominated desert-grassland in the early Holocene instead of a xeric woodland. Although this is the earliest record of a shift to desert-grassland in the entire Southwest, the community was very different from the modern one. Prominent plants such as blind prickly pear (Opuntia rufida), false agave (Hechtia scariosa), candelilla (Euphorbia antisyphilitica), and resurrection plant (Selaginella lepidophylla) probably migrated into the Big Bend in the late Holocene.

The two late Wisconsin midden assemblages from the Bolson de Mapimi contained remains of woodland plants in assemblages rich in succulents (Van Devender 1978). The sample from Sierra de la Misericordia, near Bermejillo, Durango, was dated at 12,280 ± 345 BP (average of A-1895 and A-1896 on midden debris) and contained Pinus remota and Juniperus sp. The sample from Puerto de Ventanillas (43 km NE San Pedro de las Colonias), Coahuila, at 12,700 ± 165 BP (Wk-165 on Juniperus sp.) only contained Juniperus sp. (Fig. 5). These sites on the dry end of the gradient from Cuatro Cienegas to the center of the Bolson de Mapimi suggest that the Cuatro Cienegas pollen record (Meyer 1973) is much too conservative and may have been dominated by the local hygroic vegetation near the permanent springs. Although woodland plants expanded into desert lowlands as they did to the north, the Ice Age climates were not harsh enough or so different from today's that the wealth of endemic succulents, including Opuntia rufida, were displaced southward. The Bolson de Mapimi was probably the refugium for any Chihuahuan Desert plants displaced out of the Big Bend during the late Wisconsin.

PALEOCLIMATES

The Pleistocene has traditionally been divided into four glacial periods. However, the results of studies of oxygen isotope ratios from deep sea
Fig. 2. A. Limestone ridge with rock shelters in western Hueco Mountains, El Paso Co., Texas; Navar Ranch midden series, 1340 m elevation. B. Close-up of Tank Trap Wash midden site. C. Chronological sequence of relative abundances of selected plants from packrat middens from the shelters. Tandem linear accelerator radiocarbon date of 4080 ± 1500 BP (AA-382) verifies the full-glacial record of Prosopis glandulosa.
Fig. 3. A. Limestone ridge in Maravillas Canyon, Black Gap Wildlife Refuge, Brewster Co., Texas. B. Cave at 635 m elevation. C. Chronological sequence of relative abundances of selected plants from packrat middens from the cave (modified results of Wells [1966] included).
FIG. 4.  A. View of the Sierra del Carmen, Coahuila, from just above the tunnel near Rio Grande Village, Big Bend National Park, Brewster Co., Texas. The lowest elevations in the Chihuahuan Desert (550–600 m) are along the Rio Grande in the center of photo. B. Packrat midden site at 680 m on limestone near tunnel. C. Chronological sequence of relative abundances of selected plants from packrat middens from several sites in the area. Tandem linear accelerator radiocarbon date of 22,600 ± 1500 BP (AA-382) verifies the full-glacial record of Prosopis glandulosa.
cores have demonstrated that there have been many more glacial/interglacial cycles, perhaps as many as 15–20 in the 1.8 million years included in the Pleistocene. These studies have also demonstrated that each glacial period has been on the order of 80,000–100,000 years while interglacial periods have been only 10,000–20,000 years (Imbrie and Imbrie 1979). The packrat midden chronologies have documented that relatively modern conditions were only established in the last 4000 years in the present interglacial. Thus, the modern climate and biotic relationships that we know and consider as “pristine” a few centuries ago, may be representative of as little as 4% of the time since the Pliocene. The glacial periods with woodlands widespread at the expense of the deserts is clearly the more typical situation. With these kinds of major and minor environmental fluctuations throughout the Quaternary, stable equilibria in the biota may never be achieved, or not for long. In the late Wisconsin, fairly uniform woodland vegetation appears to have been relatively stable for 10,000–20,000 years in some records and are the best cases for community equilibria.

The paleoclimate inferred for the northern Chihuahuan Desert (32–33°N) during the maximum expansion of the Wisconsin continental glacier (18,000 BP) included mild winters, greatly cooled summers, and somewhat greater annual precipitation strongly shifted to the winter from Pacific frontal sources at the expense of the summer monsoons from the Gulf of Mexico (Lanner and Van Devender 1979). The warmth of the summers and the proportion of summer rainfall increased to the south as it does today. In general, full-glacial and modern climates were different at all latitudes with the greatest in the north and the least in the south.

ENDEMISM IN THE CHIHUAHUAN DESERT

The uplift of the Rocky Mountains and Sierras Madre in the middle Tertiary, roughly 20–25 million years ago, had a profound effect on the circulation of the atmosphere and led to regional climatic differentiation and the segregation of plants into relatively simple new formations. By the latest Miocene, about 5–8 million years ago, such new formations as tundra, coniferous forests, grasslands, and deserts were well-developed (Axelrod 1979). Most of the groups of plants and animals that are successful today have their evolutionary roots in this Mio-Pliocene revolution. The evolution of most of the Chihuahuan Desert endemic species occurred at this time or later.

The advent of glacial climates in the Pleistocene has had profound effects on the Chihuahuan Desert biota in many ways, including changes in distribution of species, composition of communities, extinction, speciation, and in species richness. During each glacial, woodland plants expanded greatly into the lowlands while many desertscrub species were displaced southward. During each interglacial, the woodland plants retreated to the north or onto moutain islands as first desert-grassland, then desertscrub, plants expanded to higher elevations and latitudes. Considering the number and frequency of glacial/interglacial cycles, the magnitude of the changes in distribution, and difference in dispersal rates, community composition has been very dynamic for most of the Pleistocene.

The role of Pleistocene climatic fluctuations in evolving new species can be seen in the distribution and floristic affinities of narrow endemics in the Chihuahuan Desert. On the northern periphery of the Chihuahuan...
Desert in south-central New Mexico and adjacent Trans-Pecos Texas there are few narrow endemics. A few examples include high rolls rabbitbush (Chrysothamnus spathulatus) (Anderson 1964) and Sibara grisea (Rollins 1982) from the Sacramento and Guadalupe mountains, Rhodes Canyon penneyroyal (Hedeoma todesii) (Irving 1979) in the San Andres Mountains, and Navar Ranch rock daisy (Perityle huecoensis) (Powell 1983).

To the south the number of both narrow and widespread endemics increases dramatically. The affinities of most of these plants are with the Sierra Madre Oriental of northeastern Mexico. The narrow endemics represent both old relics and younger species in groups that are rapidly evolving. Several of the older species have closely related vicariant species in the Sonoran Desert in Arizona and California. These include crucifixion thorns (Castela stewartii/C. emoryi), crucifixion thorns (Canotia wendii/C. holacantha), cliff roses (Cowania ericaefolia/C. subintegra) and diamond chollas (Opuntia anteojeensis/O. ramosissima) (Pinkava 1976).

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LATITUDINAL SPECIES GRADIENTS

The total number of species and often the number of species in a single genus increases to the south. This latitudinal gradient in species richness was explained in terms of climate by Fischer (1960) but has subsequently been viewed as the result of the biotic interactions involved in competition, species packing, co-evolution, and resource partitioning (MacArthur 1972, Brown and Gibson 1983). The detailed paleoecological record from the last glacial/interglacial cycle of the Chihuahua Desert suggests that the distribution patterns can be best interpreted as historical, environmental phenomena.

Speciation is most likely to occur when a population becomes isolated. In the north, the differences between modern and glacial climates were so great that the probability of extinction of isolated populations at the end of either a glacial or interglacial was very high. Speciation has only occurred in special habitats such as cliff faces, cold air sinks, and gypsum deposits. To the south, as the difference between modern and glacial climates becomes less, the probability of extinction decreases as that of speciation increases. The climate was stable only in the sense that the environmental extremes of cold, heat, and drought have never been great enough to cause major extinctions. The repeated climatic fluctuations in the Pleistocene and the resulting changes in the distributions of organisms have provided a great many opportunities for speciation in isolation. Gypsum beds and playa surfaces have been repeatedly exposed and limestone sierras have repeatedly become islands as pluvial lakes filled. The combination of repeated opportunities for speciation in isolation in a fluctuating climate and of low extinction rates in an equable climate readily explains the accumulation of species at lower latitudes. Biotic interactive processes may be important in structuring communities at any one time, but the latitudinal diversity gradient appears to be a legacy of climates of the past and present.

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