Holocene Vegetation and Climate in the Puerto Blanco Mountains, Southwestern Arizona

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Plant macrofossils from 21 pack rat (Neotoma sp.) middens at 535-605 m from the Puerto Blanco Mountains, southwestern Arizona, provide an excellent history of vegetation and climate for the last 14,120 yr B.P. in the Sonoran Desert. A late Wisconsin juniper-Joshua tree woodland gave way to a transitional early Holocene desertscrub with sparse Juniperus californica (California juniper) by 10,540 yr B.P. Important Sonoran Desert plants including Carnegiea gigantea (saguaro) and Encelia farinosa (brittle bush) were dominants. Riparian trees such as Acacia greggii (catclaw acacia), Prosopis velutina (velvet mesquite), and Cerdicium floridum (blue palo verde) grew on dry, south-facing slopes in a middle Holocene Sonoran desertscrub in a warm, wet summer climate with frequent winter freezes. Modern subtropical Sonoran desertscrub formed about 4000 yr B.P. as summer rainfall and winter freezes declined. Cercidium microphyllum (foothills palo verde), Sapium biloculare (Mexican jumping bean), Olneva tesota (ironwood) and Stenocereus thurberi (organ pipe cactus) became dominant as riparian trees retreated to wash habitats. The inferences of a latest Wisconsin/early Holocene summer monsoonal maximum by J. E. Kutzbach (1983), Modeling of Holocene climates. In "Late-Quaternary Environments of the United States," Vol. 2, "The Holocene" (H. E. Wright, Ed.), pp. 271-277. Univ. of Minnesota Press, Minneapolis) are not supported for the Southwest. Apparently the persistence of late Wisconsin circulation patterns offset any increases in insolation. © 1987 University of Washington.

Plant remains preserved in ancient pack rat (Neotoma) middens allow excellent reconstructions of the local history of vegetation and climate in the North American deserts for 30,000 yr of the last glacial/interglacial cycle (Spaulding, et al., 1983; Van Devender and Spaulding, 1979). In the late Wisconsin prior to about 11,000 yr ago, most of the present warm deserts supported woodlands dominated by pinyons, junipers, and shrub oaks. In Arizona, pinyon-juniper-oak woodlands dominated by Pinus monophylla (singleleaf pinyon) grew at 1555-610 m. In the modern Sonoran Desert, juniper woodland and creosote bush desertscrub with Juniperus californica (California juniper) grew as low as 305 and 240 m, respectively (Van Devender et al., 1985).

Pack rat middens are hard, dark, shiny organic deposits that are built by rodents in the genus *Neotoma*. In open areas, they build their houses near shrubs or large rocks out of a variety of local plant materials, including thorny branches and cactus joints. Middens are areas near entrances to internal passages where fecal pellets, plant fragments, and general debris are deposited during house cleaning (Finley, 1958). In dry rock shelters where the house is small or absent, the midden can become cemented with urine and preserved for tens of thousands of years. Pack rats are very efficient samplers of the plants within about 30-50 m of the shelter. Radiocarbon dating allows the midden assemblages to be placed in time. Series of radiocarbon-dated midden assemblages from a single cave or several caves in a small local area provide detailed records of the local vegetation history.

In this study, plant macrofossils were analyzed in a chronological series of pack rat midden assemblages from the heart of the Sonoran Desert in southwestern Arizona. This sequence not only provides a detailed Holocene vegetation history for a unique subtropical desert, but allows paleoclimatic reconstruction in an area dominated by summer monsoonal rainfall and limited by severe winter freezes. The data will help evaluate recent paleoclimatic models based on changes in the earth's oribtal parameters that suggest that summer monsoon was best developed in the Southwest in the latest Wisconsin and the early Holocene (Kutzbach, 1983; Spaulding and Graumlich, 1985). The study area is well suited to evaluating whether the middle Holocene was a period of Altithermal drought (Antevs, 1955) or of increased summer rainfall (Martin, 1963).

ENVIRONMENTAL SETTING

The Puerto Blanco Mountains are a small desert range reaching 960 m elevation in Organ Pipe Cactus National Monument, Pima County, Arizona (31°58-59'N, 112°47-48'W; Fig. 1). A suite of subtropical Sonoran Desert plants including Stenocereus thurberi (organ pipe cactus), Lophocereus schottii (senita cactus), Sapium biloculare (Mexican jumping bean), Jatropha cinerea, and J. cuneata (limber bushes) reach the United States in this unique desert area (Bowers, 1980). The massive Ajo Mountains, 9 km northeast of the midden sites, rise to 1465 m elevation and support desert-grassland and sparse chaparral. The present vegetation near the sites is a xeric Sonoran desertscrub dominated by Encelia farinosa (brittle bush), Cercidium microphyllum (foothills palo verde), Sapium biloculare, and Stenocereus thurberi (Fig. 2). The area is at the xeric lower edge of the Arizona Upland Subdivision of the Sonoran Desert (Shreve, 1964; Turner and Brown, 1982).

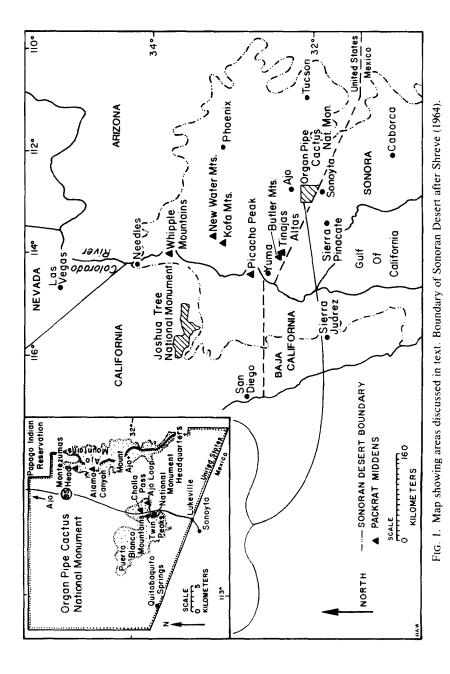
The climate of Organ Pipe Cactus National Monument is characteristic of the northeastern Sonoran Desert with biseasonal rainfall from Pacific winter frontal storms and the summer monsoon, hot summers, and infrequent winter freezes. Total annual rainfall at the Visitor Center at 510 m elevation is 233 mm/yr (Sellers and Hill, 1974). Using an elevational lapse rate calculated from nearby weather stations, the top of Mount Ajo at 1465 m receives an estimated 457-510 mm/yr.

METHODS AND RESULTS

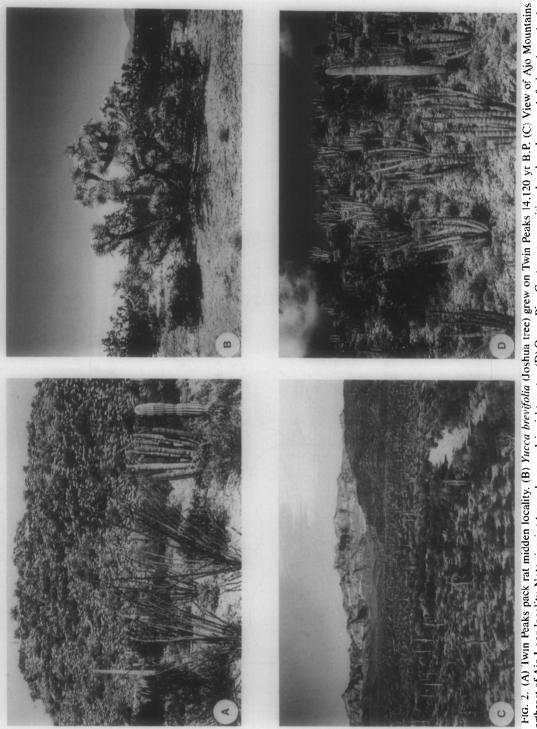
In the present study, 21 pack rat midden samples were collected from rhyolitic rockshelters at 535–605 m from three areas (Ajo Loop, Cholla Pass, Twin Peaks) in the Puerto Blanco Mountains within 3 km of the Organ Pipe Cactus National Monument Visitor Center (Fig. 2). Most of the samples were collected from xeric, south-facing slopes. The subtropical vegetation on these slopes is exceptionally sensitive to fluctuations in rainfall and to grazing.

Detailed plant lists and collections were made within 30-50 m of each rockshelter and a composite flora was prepared for the entire study area. Voucher specimens of unusual plants were deposited in the herbaria at the University of Arizona and Organ Pipe Cactus National Monument. Pack rat midden samples were washed in water, oven-dried, and sorted. Weights after washing ranged from 63 to 377 g. Plant macrofossils were identified using reference collections in the University of Arizona Herbarium and Laboratory of Paleoenvironmental Studies. Internal relative abundances were assigned to each plant taxa in an assemblage on a scale of 1-5. In this scale a single specimen is a 1, the most common taxa a 5, with other abundances ranked between. Although the number of plants in ranks 2-5 varies depending on the total number of identified specimens, the relative abundances between samples are readily compared.

Twenty-one radiocarbon dates on materials from the pack rat middens yielded ages from 14,120 to 30 yr B.P. with fairly continuous coverage from the late Wisconsin to present (Table 1). The only individual species dated were twigs of *Juniperus californica* and *Encelia farinosa*. The latter date was obtained using the University of Arizona tandem accelerator mass







Sample	Elevation (m)	Radiocarbon date (yr B.P.)	Lab No.	Material dated
Twin Peaks #1	565	$14,120 \pm 260$	A-3986	Juniperus californica twigs
Cholla Pass #1A	605	$10,540 \pm 250$	A-4276	Neotoma fecal pellets
Twin Peaks #7	565	$9,860 \pm 180$	A-4212	Neotoma fecal pellets
Twin Peaks #5	560	$9,720 \pm 460$	AA-625 ^a	Encelia farinosa twigs
Cholla Pass #1B	605	$9,070 \pm 170$	A-4278	Neotoma fecal pellets
Cholla Pass #1C	605	$8,790 \pm 210$	A-4277	Neotoma fecal pellets
Ajo Loop #1D	550	$7,970 \pm 130$	A-3981	Neotoma fecal pellets
Twin Peaks #6	580	$7,580 \pm 100$	A-3980	Neotoma fecal pellets
Ajo Loop #1G	550	$7,560 \pm 170$	A-3985	Neotoma fecal pellets
Ajo Loop #1A	550	$5,240 \pm 90$	A-4213	Neotoma fecal pellets
Ajo Loop #5B	535	$3,480 \pm 80$	A-4233	Neotoma fecal pellets
Cholla Pass #2	590	$3,440 \pm 90$	A-4279	Neotoma fecal pellets
Ajo Loop #6C	550	$3,400 \pm 100$	A-4235	Neotoma fecal pellets
Ajo Loop #6B	550	$3,220 \pm 100$	A-4234	Neotoma fecal pellets
Twin Peaks #2	580	$2,340 \pm 70$	A-3973	Neotoma fecal pellets
Twin Peaks #3	550	$2,160 \pm 60$	A-3982	Midden debris
Twin Peaks #4	555	$1,910 \pm 50$	A-3998	Neotoma fecal pellets
Ajo Loop #3A	550	990 ± 50	A-3972	Neotoma fecal pellets
Ajo Loop #4	550	980 ± 70	A-4214	Neotoma fecal pellets
Ajo Loop #2C	550	130 ± 50	A-3971	Neotoma fecal pellets
Ajo Loop #2B	550	30 ± 50	A-3970	Neotoma fecal pellets

TABLE 1. RADIOCARBON DATES OF PACK RAT MIDDENS FROM THE PUERTO BLANCO MOUNTAINS, ORGAN Pipe Cactus National Monument, Pima County, Arizona

^a Date from tandem accelerator mass spectrometer.

spectrometer. The remainder of the dates were for pack rat fecal pellets or midden debris. Careful stratigraphic collection and removal of the weathering rind minimizes any contamination problems for these types of radiocarbon samples.

The chronology proposed for the Southwest by Van Devender and Spaulding (1979) with modifications by Van Devender *et al.* (1985) and Van Devender *et al.* (in press) is followed in this paper. The divisions are late Wisconsin, 22,000–11,000 yr B.P.; early Holocene, 11,000–ca. 8900 yr B.P.; middle Holocene, ca. 8900–ca. 4000 yr B.P.; late Holocene, ca. 4000 yr B.P. to present.

The pack rat midden assemblages contained remains of a total of 103 plant taxa with 11-34 ($\bar{x} = 21.8$) taxa per assemblage (Table 2). The plants identified in the samples included woody trees and shrubs (25.2%), subshrubs (14.6%), stem and rosette succulents (16.5%), grasses (14.6%), and herbs (29.1%). Chronological summaries of important trees and shrubs, succulents, and grasses are presented in Figures 3–5. Distributions of plants were determined through personal observations, notes and collections, surveys of the University of Arizona Herbarium, an atlas of Sonoran Desert plant distributions (Hastings *et al.*, 1972), a local flora (Bowers, 1980), and regional floras (Kearney and Peebles, 1964; Munz, 1974; Wiggins, 1980).

VEGETATION HISTORY

Late Wisconsin

The 14,120 yr B.P. sample yielded a xeric juniper-Joshua tree woodland assemblage dominated by Juniperus californica and Yucca brevifolia (Joshua tree). Associates included Salvia mohavensis (Mohave sage), Yucca whipplei (Whipple yucca). Opuntia whipplei (Whipple cholla), Opuntia chlorotica (silver dollar cactus).

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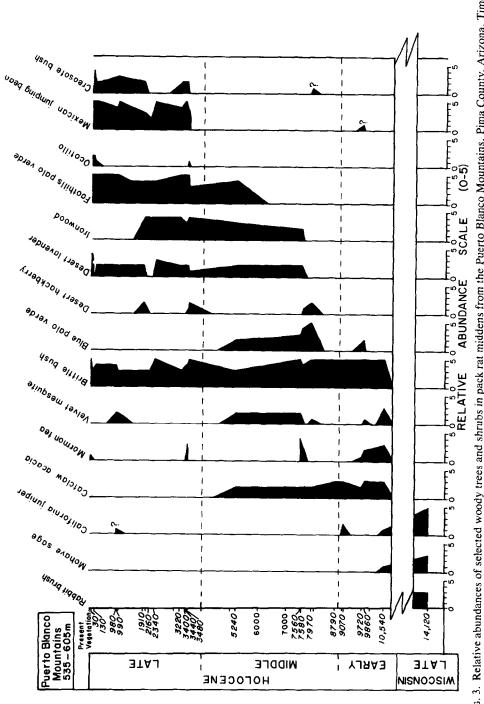
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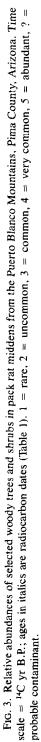
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Species	Common name	14.1	10.5	9.9	9.7	9.1	8.8	8.0	7.6	7.6	5.2	3.5	3.4	3.4	3.2	2.3	2.2	1.9	1.0	1.0	0.1	0.0
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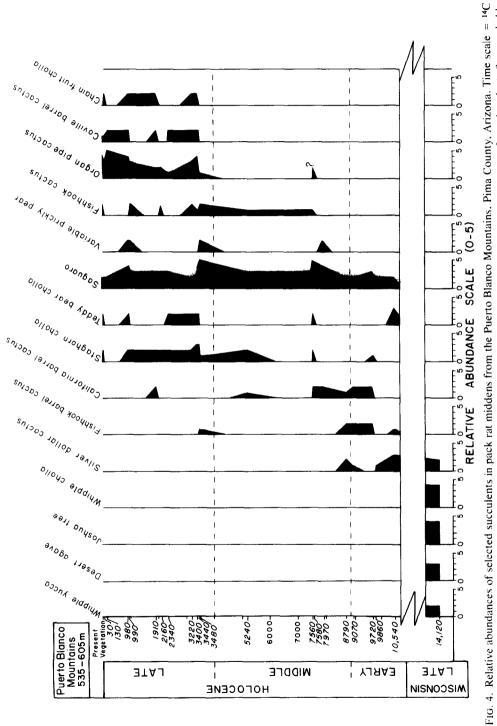
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^a Ages in thousands of	^a Ages in thousands of years for each midden follow Table 1.	w Tab	le I.	.]													.	

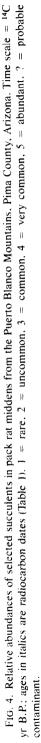
nearby. within 30 m of rockshelter; P = restricted to higher elevations in the Puerto Bianco. Bates, and Ajo mountains; p = elsewhere in the Puerto Bianco Mountains; r =restricted to riparian habitats along wishes below sites; s = clsewhere on south-facing slope, u = uncommon or rare, scattered in Monument; y = probably at site in wettermesic micronabitat on nearby north- or east-facing stope; n on Hats Delow; m exiralocal, no longer occurs in Monument; r clevations in the Ajo Mountains; c year.

HOLOCENE VEGETATION IN ARIZONA









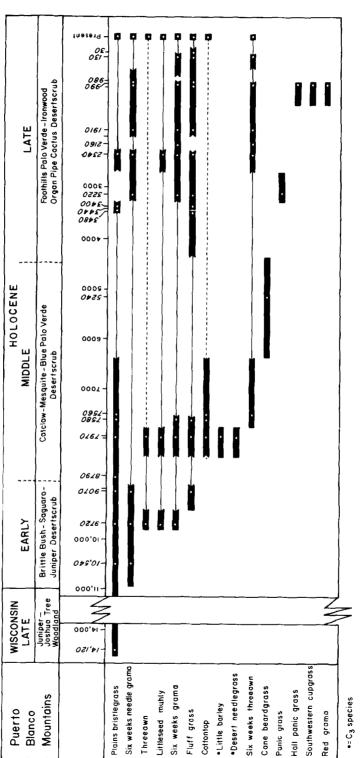


FIG. 5. Temporal distribution of grasses in pack rat middens from the Puerto Blanco Mountains, Pima County, Arizona. Time scale = 14C yr B.P.; ages in italics are radiocarbon dates (Table 1). L. J. Toolin analyst. and *Monardella arizonica*. None of the woody trees and shrubs or succulents in the present Sonoran desertscrub community at the site were in the midden assemblage. *Opuntia chlorotica* is an aborescent prickly pear found at 490–915 m elevation in the Puerto Blanco and Ajo mountains (Bowers, 1980). *Monardella arizonica* is a small, shrubby mint restricted in the Monument to elevations above 915 m in the Ajo Mountains (Bowers, 1980).

The remainder of the important woody plants in the late Wisconsin midden assemblage no longer occur in the area. The nearest Arizona population of *Juniperus californica* is in the Arrastra Mountain area on the Mohave-Yavapai County line (280 km NNW of the study area). The nearest population to the west is in the Sierra Juarez of northern Baja California, Mexico (260 km W; Wiggins, 1980).

Yucca brevifolia is the arborescent yucca that dominates many areas in the Mohave Desert in Utah, Nevada, California, and Arizona (Fig. 2). The nearest Arizona population is north of Aguila in Yavapai County (225 km NNW). In California, the southernmost population is in the Cottonwood Mountains, Riverside County (340 km NW; Rowlands, 1978).

Salvia mohavensis is a shrubby mint found in the Mohave Desert from southern Nevada and southeastern California to west-central Arizona (Munz, 1974). The nearest Salvia mohavensis to the study area is a relict population on Sierra Pinacate in northwestern Sonora (50 km SW; G. Starr, personal communication, 1984). To the west, it occurs in the Sierra Juarez, Baja California (Wiggins, 1980). The nearest Arizona population is in the Sierra Estrella near Phoenix, Maricopa County (225 km NNE).

Yucca whipplei is a common, widespread rosette succulent in the chaparral communities of California and Baja California (Wiggins, 1980). An isolated population of Y. whipplei in the northwestern Mohave Desert in the western Grand Canyon, Arizona (545 km N), was formerly called Y. *newberryi*. The nearest Y. *whipplei* to the midden site is a tiny relict population at 380 m in the Sierra los Alacranes, Sonora (130 km W; T. L. Burgess personal communication, 1985). Otherwise, the nearest Y. *whipplei* is in the Sierra Juarez, Baja California.

Opuntia whipplei is the northwestern representative of a species group that includes O. spinosior (cane cholla) and O. imbricata (tree cholla). It is found from northwestern New Mexico across the Colorado Plateau to Utah and Nevada and south into the western Arizona portion of the Mohave Desert. The nearest Arizona populations are near Oracle on the north side of the Santa Catalina Mountains, Pinal County (195 km ENE), and near Roosevelt Dam, Gila County (240 km NE; Benson, 1982). Today, O. spinosior lives at 460-610 m elevation in desert-grassland in the northern Aio Mountains (19 km NE: Bowers, 1980).

In contrast, the herbs and grasses in the midden samples do not live far away today. In wet years, *Phacelia* sp. (caterpillar weed) and *Lotus* sp. (deer vetch) would probably grow at the site.

Early Holocene

Four samples in the Puerto Blanco Mountains midden series record the early Holocene vegetation. The assemblages are dominated by *Encelia farinosa* and *Acacia* greggii (catclaw acacia) in association with *Ephedra nevadensis* (Mormon tea), *Erio*gonum wrightii (wild buckwheat), and *Pro*sopis velutina (velvet mesquite). Juniperus californica was present at low levels in samples dated at 10,540 and 9070 yr B.P. from 605 m at the Cholla Pass site. Samples dated at 9860 and 9720 yr B.P. from 560-565 m on Twin Peaks lacked juniper. A single leaf of Salvia mohavensis was in the 10,540 yr B.P. sample.

Important succulents in the early Holocene assemblages include *Opuntia chlorotica*, persisting from the late Wisconsin.

and Carnegiea gigantea (saguaro), Opuntia bigelovii (teddy bear cholla), Ferocactus acanthodes (California barrel cactus), and F. cf. wislizenii (fishhook barrel cactus). Carnegiea gigantea is the stately, arborescent cactus whose northeastern range limit sets the boundary of the Sonoran Desert itself (Shreve, 1964; Turner and Brown, 1982). Its appearance in the 10,540 yr B.P. sample suggests that it dispersed into the Organ Pipe area from its ice-age refugium soon after the end of the last glaciation (ca. 11,000 yr B.P.). F. acanthodes is a widespread barrel cactus in the lowlands of the Mohave and Sonoran deserts that is uncommon in the Puerto Blanco Mountains above the sites (Bowers, 1980). F. wislizenii is the barrel cactus characteristic of the Arizona Upland desertscrub, desert-grassland and Chihuahuan desertscrub east to near El Paso, Texas.

Encelia farinosa, Carnegiea gigantea, and Opuntia bigelovii are the only longlived plants in the midden assemblages that now grow near the sites. Acacia greggii and Prosopis velutina no longer grow on rocky slopes and are restricted to riparian wash habitats. Cercidium floridum (blue palo verde) found in the 9720 yr B.P. sample is also restricted to washes. Salvia pinguifolia (rock sage) found in the 7970 yr B.P. sample is presently rare above 915 m in the Ajo Mountains (Bowers, 1980). The single seed of Sapium biloculare in the 9720 yr B.P. sample is probably a contaminant.

Middle Holocene

The final disappearance of woodland plants such as junipers and oaks from the desert lowlands marks the end of the early Holocene. At the Cholla Pass site California juniper disappeared between 9070 and 8790 yr B.P. Five middle Holocene samples between 8790 and 5240 yr B.P. record Sonoran plants that presently live within a few kilometers of the rock shelters but in a desertscrub community with very different composition and structure than today. *Encelia farinosa* and *Carnegiea gi*- gantea continued to dominate the slopes in association with Acacia greggii, Prosopis velutina, and both species of Ferocactus. The riparian Cercidium floridum reappears on south-facing slopes between 7970 and 5240 yr B.P. Hyptis emoryi (desert lavender), a common, widespread subtropical desert shrub, appeared in the 7580 yr B.P. sample. Olneya tesota (ironwood) appearing in the 7560 yr B.P. sample is a large leguminous tree that is characteristic of relatively flat desert areas in much of the Lower Colorado River Valley. Opuntia acanthocarpa (staghorn cholla) is in several middle Holocene samples.

The 5240 yr B.P. sample records the arrival of *Cercidium microphyllum* (foothills palo verde), the dominant tree in the modern Arizona Upland communities. The only long-lived perennials in the middle Holocene samples that presently live at the sites are *Encelia farinosa*, *Cercidium microphyllum*, *Hyptis emoryi*, and *Carnegiea gigantea*.

Late Holocene

The 5240 yr B.P. sample with abundant Cercidium microphyllum and riparian wash trees on rocky slopes was transitional between middle and late Holocene Sonoran Desert communities. In general the late Holocene assemblages recorded a shift to a warmer, drier desertscrub community as many plants (e.g., Acacia greggii, Celtis pallida, Cercidium floridum, Hymenoclea salsola, and Prosopis velutina) retreated from exposed rocky slopes into riparian wash habitats. Encelia farinosa, Cercidium microphyllum, and Olneya tesota were dominant in association with Carnegiea gigantea, Hyptis emoryi, Opuntia acanthocarpa, and Opuntia bigelovii. Other important Sonoran Desert plants appeared in the record by 3400 yr ago including the modern dominants Sapium biloculare and Larrea divaricata. Jatropha cardiophylla (limber bush) is a succulent-stemmed shrub of the Arizona Upland and more subtropical vegetation to the south that was found in the 3440 yr B.P. sample. Since its appearance

in the midden record, Stenocereus thurberi was consistently present and at times dominant. The two columnar cacti (S. thurberi, Carnegiea gigantea) have been desertscrub associates in the late Holocene although their abundances appear to have been independent. Ferocactus covillei (Coville barrel cactus) is a subtropical species that apparently replaced F. acanthodes and F. wislizenii in the late Holocene.

Within the late Holocene, there appear to have been some interesting vegetation changes. Olneya tesota dominated xeric south-facing slopes until after 1910 vr B.P. when it retreated to the flats below. Opuntia cf. fulgida (chain fruit cholla) grew on slopes until this century but is now restricted to flats. Ambrosia deltoidea (triangleleaf bursage), a common dominant in Arizona Upland desertscrub communities, appeared only in the 3480 yr B.P. sample and is now scattered at the base of the hills. Ambrosia dumosa (white bursage), the dominant of lowland desertscrub communities in the Lower Colorado River Valley, is recorded at 2340 and 990 yr B.P. In the Monument today it is mostly restricted to sandy flats along the international border and is rare on rocky slopes.

The samples dated at 980 and 990 yr B.P. record a wet interval in the late Holocene. Species richness was much greater than today (28-34 versus 10 taxa) with more woody trees and shrubs (10 to 6) and succulents (7 to 1), Prosopis velutina, Opuntia leptocaulis (Christmas cactus), and O. phaeacantha (variable prickly pear) are now restricted to shady microhabitats in the wash below the site. The abundance of perennial and ephemeral herbs (nine) and grasses (seven) suggest reliable rainfall in both seasons. Three grasses in one sample (Bouteloua trifida, Eriochloa lemmoni, and Panicum cf. hallii) no longer occur in the Monument.

Historical Period

The differences between the modern vegetation and very young midden samples are surprising. After being present for most of

the Holocene, Carnegiea gigantea is now restricted to the flats or ridge crests and is very rare on open slopes. Many Stenocereus thurberi on the slopes are dead. Ferocactus covillei is rare in the area today; a few living and dead plants are seen. Opuntia acanthocarpa is now much more common on the flats than on the rocky slopes. Young plants were not seen for any of these succulents. Lycium berlandieri (wolfberry) and Croton sonorae (encinilla) are much less common today than previously. A few plants in the late Holocene samples including the grasses mentioned above and Chorizanthe corrugata (corrugated spiny herb; 2340 yr B.P.) apparently no longer occur in the Monument. On the other hand, Cercidium microphyllum, Stenocereus thurberi, Sapium biloculare, Horsfordia newberryi, and Larrea divaricata are presently at their peaks in abundance. Several shrubs including Acalypha pringlei (Sonoran three-seeded mercury), Aloysia wrightii (oreganillo), Fagonia californica, and Jatropha cuneata grow near the midden sites but were not found in the middens.

Livestock grazing in Organ Pipe Cactus National Monument was fairly intense from the late 1930s until 1979 when the last cattle and burros were removed. Some recent vegetation changes seen in the midden record may be due to grazing impact. Palatable herbs such as Abutilon incanum (Indian mallow). Lotus salsuginosus (deer vetch), Lupinus sparsiflorus (blue bonnet), Phacelia distans (caterpillar weed), Physalis crassifolius (ground cherry), and Sphaeralcea ambigua (globe mallow) are well represented in the middens but rare or absent from the area today. The seed banks of many ephemeral and short-lived perennial herbs and grasses may still be recovering from grazing depletions. Exposed rocky slopes may be slower than flats or washes to recover because of stony, shallow soils. On the other hand, Allionia incarnata (windmills), Amsinckia tessellata (fiddleneck), Kallstroemia grandiflora (summer poppy), and Plantago insularis (Indian wheat) are widespread ephemerals readily sampled by pack rats that have never been common on rocky slopes in the study area. The decline on rocky slopes of spiny perennials such as *Opuntia acanthocarpa*, *O. bigelovii*, and *Fouquieria splendens* (ocotillo) are probably not related to grazing. Declines in adult *Carnegiea gigantea*, *Ferocactus covillei*, and *Stenocereus thurberi* are probably not the result of grazing, while the establishment of young plants may be directly related. The local vegetation is clearly recovering from grazing impacts and recent catastrophic climatic events.

COMPARISON WITH OTHER AREAS

Ajo Mountains

Four pack rat middens from 975 m on Montezuma's Head in the Aio Mountains east of the midden study areas record a relatively stable pinyon-juniper-oak woodland dominated by Pinus monophylla (singleleaf pinyon), Juniperus spp. (junipers), and Quercus ajoensis (Ajo oak) from 21,840 to 13,500 yr B.P. (Van Devender and Spaulding, 1979). On reexamination the juniper material was determined to represent J. scopulorum (Rocky Mountain juniper) and a second species with toothed leaf margins. *Quercus ajoensis* is an Ajo Mountains endemic considered a relict of O. ajoensoides, a late Miocene species from Oregon (Tucker and Muller, 1956). More recently it has been considered as a subspecies of Q. turbinella (shrub live oak), the widespread chaparral dominant (Felger and Lowe, 1970). Other important plants in the Montezuma's Head samples include Artemisia tridentata-type (big sagebrush; Artemisia nova or Artemisia tridentata), Atriplex confertifolia (shadscale), and Yucca brevifolia.

A midden dated at 14,500 yr B.P. from 915 m elevation in Alamo Canyon in the central Ajo Mountains was also dominated by *Pinus monophylla*, *Juniperus scopulorum*, and *Quercus ajoensis* with *Artemisia tridentata*-type. However, *Juniperus* californica was abundant and Yucca brevifolia absent. A similar midden assemblage with reduced *P. monophylla* dated 32,000 yr B.P., extending the pinyon-juniper-oak woodland to the middle Wisconsin.

Three Alamo Canyon middens record early Holocene oak-juniper woodland from 10,580 to 8130 yr B.P. dominated by *Quercus ajoensis* with *Juniperus californica* and *J.* cf. *erythrocarpa* (redberry juniper). Both *Q. ajoensis* and *J. erythrocarpa* still occur locally in more mesic areas in the Ajo Mountains. Whereas junipers grew at the site until after 8130 yr B.P., their decline in abundance sometime after 9910 yr B.P. could correspond to the disappearance of *J. californica* about 8900 yr ago in the Puerto Blanco Mountains. Indeed, *J. californica* may have become extinct in both areas at the same time.

Although the midden site is near the present upper elevational limit of *Carne-giea gigantea*, its seeds were common in the Alamo Canyon samples. Three tandem accelerator radiocarbon dates on the seeds yielded results of 8080–9240 yr B.P. (Van Devender *et al.*, 1985). Considering the 10,540 yr B.P. appearance in the Puerto Blanco Mountains, *C. gigantea* apparently arrived in the area simultaneously over a 310-m elevational range. However, *C. gigantea* no longer grows at the midden site, while *Stenocereus thurberi* is nearby.

The late Wisconsin woodland at 565 m elevation in the Puerto Blanco Mountains clearly represents the lower, drier end of the vegetation gradient from the more massive Ajo Mountains.

Lower Colorado River Valley

In the late Wisconsin, California juniper woodland with *Pinus monophylla* has been found as low as 460 m in the Tinajas Altas Mountains, 615 m in the New Water Mountains of southwestern Arizona, and 510 m in the Whipple Mountains of southeastern California (Van Devender and Spaulding, 1979; Van Devender *et al.*, 1985). Middens containing California juniper–Joshua tree assemblages similar to the late Wisconsin Puerto Blanco Mountains sample at 565 m have been found from 550 m in the Kofa Mountains, Arizona, and 320 m in the Whipple Mountains. *Nolina bigelovii* (Bigelow beargrass), an important desert succulent in these middens, was absent from the Puerto Blanco Mountains sample.

The late Wisconsin vegetation of the mountainous lowlands (below 610 m) in Organ Pipe Cactus National Monument was apparently a southeastward extension of the woodland that extended from the modern Mohave Desert throughout the Lower Colorado River Valley, except for the lowest elevations in the Picacho Peak area, California (Cole, 1986). Most of the species coexist today in Arizona around the base of the Hualapai Mountains, Mohave County (280 km NNW), or in southeastern California in the Providence-New York Mountains area (450 km NW; Thorne et al., 1981) and Joshua Tree National Monument (340 km NW; Rowlands, 1978). Many of the plants, with the exceptions of Yucca brevifolia and Opuntia whipplei, extend into Baja California on the drier, eastern slopes of the Sierra Juarez (Wiggins, 1980). Salvia mohavensis and Yucca whipplei have small relict populations in the Sierra Pinacate area of northwestern Sonora.

After about 11,000 yr ago in the early Holocene, a xeric California juniper woodland persisted in the lowlands (275-610 m) of the Lower Colorado River Valley for several thousand years (Van Devender, 1977). The final disappearance of juniper and the transition to desert climate and vegetation of the middle Holocene was found to be about 8900 vr B.P. in the Tinajas Altas Mountains (Van Devender et al., in press), after 8910 yr B.P. in the Whipple Mountains, and 7870 yr B.P. in the New Water Mountains, Arizona. The Puerto Blanco Mountains transition at about 8900 yr B.P. correlates well with the Tinajas Altas and Whipple mountains records.

The final late Holocene transition to the relatively modern vegetation and climate about 4000 yr ago in the Puerto Blanco Mountains is similar to the final establishment of modern desertscrub communities in the Tinajas Altas Mountains, and the Picacho Peak area of southeastern California (Cole, 1986).

PALEOCLIMATES

Many of the 103 taxa identified from the middens are identified to the species level. allowing their present distributions and ecological adaptations to be used in reconstructing paleoclimates. The assemblages include a variety of life forms including freeze-limited subtropical desert trees, shrubs and succulents, and short-lived ephemerals that only grow in the winterspring or summer rainy seasons. Few plants in the flora live more than 100 yr. Response times to climatic changes are relatively short because of catastrophic mortality in droughts or freezes and relatively short distances to seed source areas in Sonora. Thus the plants in midden assemblages provide independent, sensitive proxies for reconstructing different facets of Holocene paleoclimates (Bryson, 1985).

Late Wisconsin

The late Wisconsin California juniper-Joshua tree woodland on Twin Peaks suggests a paleoclimate similar to areas in the Mohave Desert today. The driest areas that support Yucca brevifolia receive a precipitation of at least 110 mm/yr in California and 170 mm/yr in Arizona (Rowlands, 1978). Mixed communities of Y. brevifolia and Juniperus californica probably receive about 280 mm/yr rainfall, mostly from winter Pacific frontal storms. This would represent a minimum increase in annual precipitation for the study area of only 16%, but a major shift in seasonality. The few ephemerals (2) in the sample are winter-spring obligates. The late Wisconsin precipitation inferred from the pinyon-juniper-oak woodland with the

mesic J. scopulorum at 915 m on an open, west-facing slope on Montezuma's Head would be at least 510-560 mm/vr based on comparison with weather records from known J. scopulorum populations below the Mogollon Rim (Sellers and Hill, 1974). This suggests an increase of 55-70% over today. Extrapolation to higher elevations using modern lapse rates suggests that Mount Ajo probably had a precipitation of at least 775-865 mm/yr and easily supported larger conifers such as Pseudotsuga menziesii (Douglas fir) or Pinus ponderosa (Ponderosa pine). The difference in precipitation between the Puerto Blanco and Ajo mountains midden sites was greater in the late Wisconsin than today, suggesting a steeper elevational gradient. Orographic uplift of warm, moist air probably resulted in summer rainfall in the Ajo Mountains. Significant summer rainfall was not present in any areas further west in the late Wisconsin.

As for late Wisconsin temperatures, the summers were probably much cooler, with the July mean as much as $8-11^{\circ}$ C lower; conditions similar to today's winter-spring existed throughout the year. The midden fossils do not give a strong signal about the winter temperatures because most of the species were probably in the lower portions of their elevational ranges and not limited by winter freezes. The absence of Sonoran Desert plants was probably due as much to very cool summers and little summer rainfall as to winter freezes.

Early Holocene

The early Holocene climate of the Puerto Blanco Mountains was transitional between glacial and modern climates. A few California juniper lingered until about 8900 yr B.P. in the Cholla Pass area. The presence of Acacia greggii and Prosopis velutina on south-facing slopes suggests that rainfall increased to perhaps 330 mm/yr, or 30% more than today, as summers warmed, with a greater percentage falling in the summer. A total of 71.4% of the ephemeral herbs (11) and grasses (3) identified in early Holocene samples are winter-spring rainfall obligates. The grasses are opportunistic C-4 species that can also have limited fall or spring activity.

Encelia farinosa, the community dominant, is frost sensitive but regrows rapidly after a freeze. *Carnegiea gigantea* is apparently limited today on its northern range by freezing temperatures during a single midday (e.g., more than 32 hr; Shreve, 1911; Turnage and Hinckley, 1938). The continued presence and abundances of *E*. *farinosa* and *C. gigantea* suggest that hard freezes have not been very frequent at any time in the Holocene.

Middle Holocene

The middle Holocene climatic regime was essentially modern, although the frequencies of events were quite different than today. Early Holocene rainfall levels continued, with a greater shift to summer rainfall and fewer serious summer droughts. Only 37.5% of the ephemeral herbs (4) and grasses (4) in the middle Holocene samples are winter-spring rainfall obligates. Today, desertscrub communities with Encelia farinosa, Carnegiea gigantea, Acacia greggii, Cercidium floridum, and Prosopis velutina grow on open slopes at the upper margin of the Arizona Upland above more typical palo verde-saguaro communities. Good examples can be seen at 915-1065 m below Molino Basin in the Santa Catalina Mountains, Pima County, and north of Magdalena, Sonora. Indeed, a band of similar vegetation marks the northern periphery of the Sonoran Desert in Arizona. Apparently the winter freezes were frequent and severe enough to prevent the expansion of more subtropical plants but not to eliminate E. farinosa and Carnegiea gigantea.

A tooth of *Notiosorex crawfordi* (desert shrew) in the 7580 yr B.P. sample is a faunal record with paleoclimatic implications. This tiny insectivore is widespread in the Southwest, but so secretive it is seldom collected. Mostly it inhabits grasslands at elevations well above the midden study area. The only extant population in Organ Pipe is a small relict in the marsh at Quitobaquito Springs (Y. Petryszyn, personal communication, 1984). The presence of N. crawfordi suggests that summers were less harsh than today, with fewer droughts.

Late Holocene

The late Holocene climate of the Puerto Blanco Mountains, with its essentially modern regime, began after 5240 yr B.P. and probably about 4000 yr B.P. Decreased rainfall with greater frequencies of summer drought forced the retreat of Acacia greggii, Cercidium floridum, and Prosopis velutina from open slopes. Today they survive in riparian communities along large washes (Fig. 2). A total of 54.5% of the ephemeral herbs (17) and grasses (5) are winter-spring rainfall obligates. Apparently reduced frequency of hard freezes allowed the expansion of subtropical desertscrub plants, including Stenocereus thurberi and Sapium biloculare. The expansion of Olneva tesota onto xeric south-facing slopes from the nearby flats between 5240 and 1910 yr B.P. suggests that summer rainfall was somewhat greater than today. The samples at 990 and 980 yr B.P. reflect a wet period that may have been of short duration. Only the 130 and 30 yr B.P. samples reflect the modern climate very well. The present vegetation is even more sparse than the youngest samples, reflecting droughts of the 1970s, the hard freeze of November 1978, and grazing impacts.

DISCUSSION

Organ Pipe Cactus National Monument was established in 1937 to protect a unique subtropical desertscrub vegetation in the United States that is more typical of the Sonoran Desert in Sonora, Mexico. The pack rat midden series from the Puerto Blanco Mountains records a series of plant communities from a late Wisconsin California juniper-Joshua tree woodland through a series of Holocene Sonoran desertscrub communities, culminating in the modern subtropical brittle bush-foothills palo verde-Mexican jumping bean-organ pipe cactus association about 4000 yr ago. Dispersal distances for Sonoran Desert plants from glacial refugia in Sonora were probably 100 km or less, with relatively rapid response times following climatic changes. The dispersal and isolation of subtropical plants into Arizona, such as Bursera microphylla (elephant tree) in the Waterman Mountains, Stenocereus thurberi in the Picacho Mountains, and Justicia candicans (chuparosa) in the Santa Catalina Mountains, are probably late Holocene events. Indeed a tandem accelerator mass spectrometer radiocarbon date for a B. microphylla seed records the arrival of this species in the Tinajas Altas Mountains by 5820 yr B.P. (Van Devender et al., 1985). The present vegetation in the Sonoran Desert is apparently the most xeric association with lowest species richness seen in the present interglaciation. The overall desertscrub community composition has changed continuously as temperature and rainfall fluctuated.

Larrea divaricata is an important, widespread dominant in a myriad of desertscrub communities throughout the warm deserts of North America. After a basic diploid stock migrated from Argentina to the Chihuahuan Desert during some earlier interglaciation, creosote bush dispersed westward giving rise to the tetraploid Sonoran Desert and hexaploid Mohave Desert chromosomal races (Wells and Hunziker, 1976). Pack rat midden sequences from southcentral New Mexico record its arrival in the northern Chihuahuan Desert by 4340 yr B.P. in the San Andres Mountains (Van Devender and Toolin, 1983) and by 3300 yr B.P. in the Sacramento Mountains (Van Devender et al., 1984). In contrast, new tandem accelerator mass spectrometer (TAMS) radiocarbon dates of L. divaricata twigs from pack rat middens document its presence in late Wisconsin woodland and desertscrub communities in the Lower Colorado River Valley. Creosote bush twigs from near Picacho Peak, California, and the Butler Mountains, Arizona, yielded ages of 12,730 and 11,250 yr B.P., respectively (Cole, 1986; Van Devender et al., 1985). A TAMS date of 18,700 yr B.P. from a California juniper-Joshua tree sample at 330 m in the Tinaias Altas Mountains documents its presence in the full-glacial flora (Van Devender et al., in press). In this context, the late Holocene appearance of L. divaricata in the Puerto Blanco Mountains is very interesting. I suggest that these plants were Sonoran Desert tetraploids arriving with other subtropical plants from their ice-age refugia in Sonora. The older Lower Colorado River Valley records were probably Mohave Desert hexaploids. If so, the connection between the creosote bush desertscrub communities of the eastern Sonoran Desert and the northwestern Chihuahuan Desert in southeastern Arizona was probably after 5240 yr B.P. Unfortunately, the chromosomal races are not readily discernible from the midden materials.

The conclusion that the most subtropical climate of the last 11,000 yr was in the late Holocene is interesting for several reasons. The middle Holocene has traditionally been considered to be the "thermal maximum" and has been variously called the Xerothermic (Sears, 1942), the Hypsithermal (Deevey and Flint, 1957), and the Altithermal (Antevs, 1955). The Puerto Blanco middens demonstrate decisively that the middle Holocene climate was warmer and much wetter than today, as inferred by Martin (1963), and not the intense drought proposed for the Altithermal. However, the warm, moist climate did not favor the most subtropical plants. Apparently the frequency of winter freezes was great enough to prevent the expansion of the most cold-sensitive plants until after 5000 yr B.P. and has been lower subsequently. Similar middle Holocene climates at higher elevations in south-central New

Mexico and Trans-Pecos Texas favored desert-grassland over Chihuahuan desert-scrub (Van Devender *et al.*, 1984).

Kutzbach (1983) presented a model of Holocene climates for the entire globe using the possible effects of orbital variations and their consequent changes in solar radiation on climate. He concluded that 10,000 to 9000 vr B.P. was a time of maximum solar insolation in summer, with winter temperatures lower than today. Periods of global warmth are reflected by intensification of the subtropical high pressure cells and summer monsoon circulation patterns. The Puerto Blanco Mountains vegetation record in the eastern portion of the Sonoran Desert, with its dependence on summer rainfall and limitation by winter freezes, presents an opportunity to evaluate the conclusions of the Kutzbach model for the Southwest. Early Holocene summers were apparently cool enough to support California juniper in low desert habitats until at least 9070 yr B.P. Only 28.6% of the ephemeral plants in early Holocene samples are typical summer monsoon species and none are obligates. Although summer precipitation increased from virtually none in the late Wisconsin to perhaps 30% in the early Holocene, peak summer monsoonal activity at 60% was after 8900 yr B.P. in the middle Holocene. Monsoonal activity continued to be high, although more irregular, throughout the late Holocene. The early Holocene was clearly a transitional period from the glacial climate of the late Wisconsin and by no means warmer than today.

Spaulding and Graumlich (1985) attempted to account for early Holocene juniper woodlands in the Lower Colorado River Valley as due to very hot summer temperatures and a summer monsoonal rainfall maximum. This hypothesis is unlikely because *Juniperus californica* is the juniper most strongly correlated with winter rainfall of any in the woodlands bounding the warm deserts of North America. It is abundant in dry chaparral and juniper-Joshua tree woodlands in the western Mohave Desert where there is little or no summer rainfall. Moreover, the woodland vegetation of the early Holocene became increasingly more mesic and better developed west of the Puerto Blanco Mountains at lower elevations toward the source area of winter rainfall. Remnant woodlands in the early Holocene would have fared better to the southeast where summer rainfall increased, if the Spaulding-Graumlich hypothesis were correct.

The Kutzbach paleoclimatic model was global in scale, with a spatial resolution of about 11° lat by 11° long. Presumably the predictions of the model can be tested for a subdivision using paleoclimatic proxy records and not a new independent global data set. Most of the summer monsoonal precipitation reflected in the Puerto Blanco Mountains midden record at 112°47'W is imported into the Sonoran Desert from the Gulf of Mexico (Bryson and Lowry, 1955), a minimum of 15° to the east. The core of the Bermuda High is at about 70-80°W, 38° to the east. The conclusions of the Kutzbach model for the Southwest need to be reevaluated in light of these detailed paleoecological records. Either the conclusions about an enhanced early Holocene insolation maximum are in error or the effects of the lingering Laurentide Ice Sheet on early Holocene circulation patterns offset any major climatic effects in the monsoonal Southwest.

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