

Conclusions

Recent quantitative analysis of 3579 trees recorded in the urban center of Cobá indicates that certain trees are most often located toward the center of the site. Certain architectural features followed the same pattern. The relation suggests agreement between the residential pattern of Cobá and Diego de Landa's 16th-century class-oriented description of Maya towns before the conquest.

This survey conducted at Cobá established the settlement pattern of continuous architectural remains radiating out in all directions surrounding the administrative and religious core. Spatial analysis of the distribution of vaulted and unvaulted architecture supported Folan's (4) hypothesis that the city was generally organized in concentric rings with the elite residing near the center of the city and the lower classes living in the sur-

rounding zones. The existence of garden cities during the post-Hispanic period (1) seems to be a reflection of a pattern already established by the Late Classic. Furthermore, the distribution of economically and ceremonially important trees in the zones controlled by the elite at Cobá establishes the control over these resources by the lords and priests of Cobá during the Late Classic.

References and Notes

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 14. This article is the result of fieldwork undertaken by W.J.F., Nicolás Caamal, L.A.F., E.R.K., and Jacinto May of the Cobá Archaeological Mapping Project, which was funded by the National Geographic Society's Committee for Research and Exploration. The project was directed by W.J.F. and George E. Stuart. An earlier version of this paper was presented by W.J.F. at the 42nd annual meeting of the Society for American Archaeology, New Orleans, La., 28 to 30 April 1977. The original draft of the Cobá map was drawn by G. E. Stuart.

Development of Vegetation and Climate in the Southwestern United States

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In the past 15 years, analysis of packrat (*Neotoma* spp.) middens has provided several hundred radiocarbon-dated fossil plant assemblages from now arid and semiarid regions in the southwestern United States (Fig. 1). Packrats thoroughly sampled the vegetation on rocky slopes within 100 meters of the dry, protected shelters where middens are built and preserved. Many of the hundreds of plants in the fossil middens have been identified to species, allowing their distributions and autecologies to be used in paleoclimatic reconstructions. Fossil middens allow detailed paleoecological reconstructions of past communities in areas with few other sources

of perishable organic materials. On the basis of the packrat midden record, we describe here the vegetational changes and inferred climates during the past 22,000 years in the warm deserts of the southwestern United States.

Vegetation Chronology

Late Wisconsinan (22,000 to 11,000 years B.P.). Packrat middens dating from the late Wisconsinan glacial maximum, 22,000 to 17,000 years B.P. (radio-carbon years before present), to about 11,000 years B.P. document the occurrence of pinyon-juniper woodlands at middle elevations of 1525 to 550 m in areas now occupied by desertscrub communities. Time series of midden assemblages from single sites or several sites in

a small area show few important changes in composition, suggesting that the pinyon-juniper woodlands were relatively stable throughout this 11,000-year period.

The species of pinyon in the midden samples are Colorado pinyon (*Pinus edulis* Engelm.) and Mexican pinyon (*P. cembroides* Zucc. var. *remota* Little) in the Chihuahuan Desert and border pinyon (*P. cembroides* var. *bicolor* Little) and single-needle pinyon (*P. monophylla* Torr. & Frém.) in the Sonoran and Mohave deserts (Fig. 2). Middens recording this pinyon-juniper woodland extend from Ord Mountain, San Bernardino County (1), and Robber's Roost, Kern County (2), California, on the western side of the Mohave Desert (116°W), to the Guadalupe Mountains, Culberson County (3), and Maravillas Canyon, Brewster County (4), Texas (103°W). In the present Chihuahuan Desert, pinyon-juniper midden records extend from the Big Bend to the Guadalupe Mountains in Texas, and to Bishop's Cap, Doña Ana County, New Mexico (29° to 32°N) (5). In Arizona, pinyon-juniper middens have been found from Montezuma's Head, Ajo Mountains, Pima County, to Desert Almond Canyon and Peach Springs Wash, Grand Canyon, Mohave County (32° to 36°N) (6). The midden sample from Kern County at 35°35'N is the northernmost late Wisconsinan pinyon-juniper midden in California (1, 2, 7,

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8). In Nevada and California north of 36°N, single-needle pinyon may have been restricted to elevations above 1585 m and absent from middle elevation juniper woodlands. Table 1 is a summary of data on pinyon-juniper middens from the Southwest.

midden samples from about 600 to 280 m along the Colorado River in Arizona and California contain juniper woodland assemblages without pinyon (9, 10). A similar juniper woodland at 645 to 425 m is documented by a large series of middens from the Rampart Cave area in the lower

ered. Nonetheless, important dominants in the present Mohave and Great Basin deserts have been found in late Wisconsinan woodland middens from sites at lower elevations and farther south than they occur today (6, 7, 9, 11, 12). These include big sagebrush (*Artemisia tridentata* Nutt.), shadscale (*Atriplex confertifolia* Wats.), blackbrush (*Coleogyne ramosissima* Torr.), mountain mahogany (*Cercocarpus intricatus* Wats.), Joshua tree (*Yucca brevifolia* Engelm.), Whipple yucca (*Y. whipplei* Torr.), and creosote bush (*Larrea divaricata* Cov.). Few characteristic Sonoran Desert plants have been found in late Wisconsinan packrat midden samples.

Summary. Plant macrofossils in ancient packrat middens document the presence of woodland communities in most of the present Chihuahuan, Sonoran, and Mohave deserts in the southwestern United States during the late Wisconsinan (22,000 to 11,000 years before present by radiocarbon dating). Warm desert species were common in the woodlands at lower elevations and mixed conifer and subalpine forests were present at high elevations. Inferred mild, wet winters and cool summers produced unusual plant and animal associations compared to those of today. Montane communities acquired modern aspects and more mesophytic species disappeared from lower woodlands about 11,000 years ago. Early Holocene xeric woodlands and an inferred winter precipitation regime persisted until about 8000 years ago. The present circulation patterns, rainfall regimes, and biotic distributions probably formed as a result of the melting of the continental ice sheets. Southwestern communities appear to have responded quickly to climatic changes compared to the gradual responses of central and eastern United States forest communities.

Packrat middens from higher elevations document past montane conifer communities in some areas. Approximately 13,000 years ago a community of spruce (*Picea* sp.), Douglas fir (*Pseudotsuga menziesii* Franco), southwestern white pine (*Pinus strobiformis* Engelm.), and dwarf juniper (*Juniperus communis* L.) with some Colorado pinyon was at an elevation of 2000 m in an area now in the desert-grassland and woodland ecotone in the Guadalupe Mountains of Texas (3). Spruce and dwarf juniper no longer occur in Texas. In southeastern Utah, at

The lowest late Wisconsinan pinyon record in the Southwest is from a midden sample dated at $12,960 \pm 210$ years B.P. from an elevation of 510 m in the Whipple Mountains, San Bernardino County, California (7). Other late Wisconsinan

Grand Canyon of Arizona (6). Desert-scrub communities probably persisted along the Colorado River at elevations below about 400 to 300 m, but middens older than 11,000 years B.P. with desert-scrub assemblages have yet to be discov-

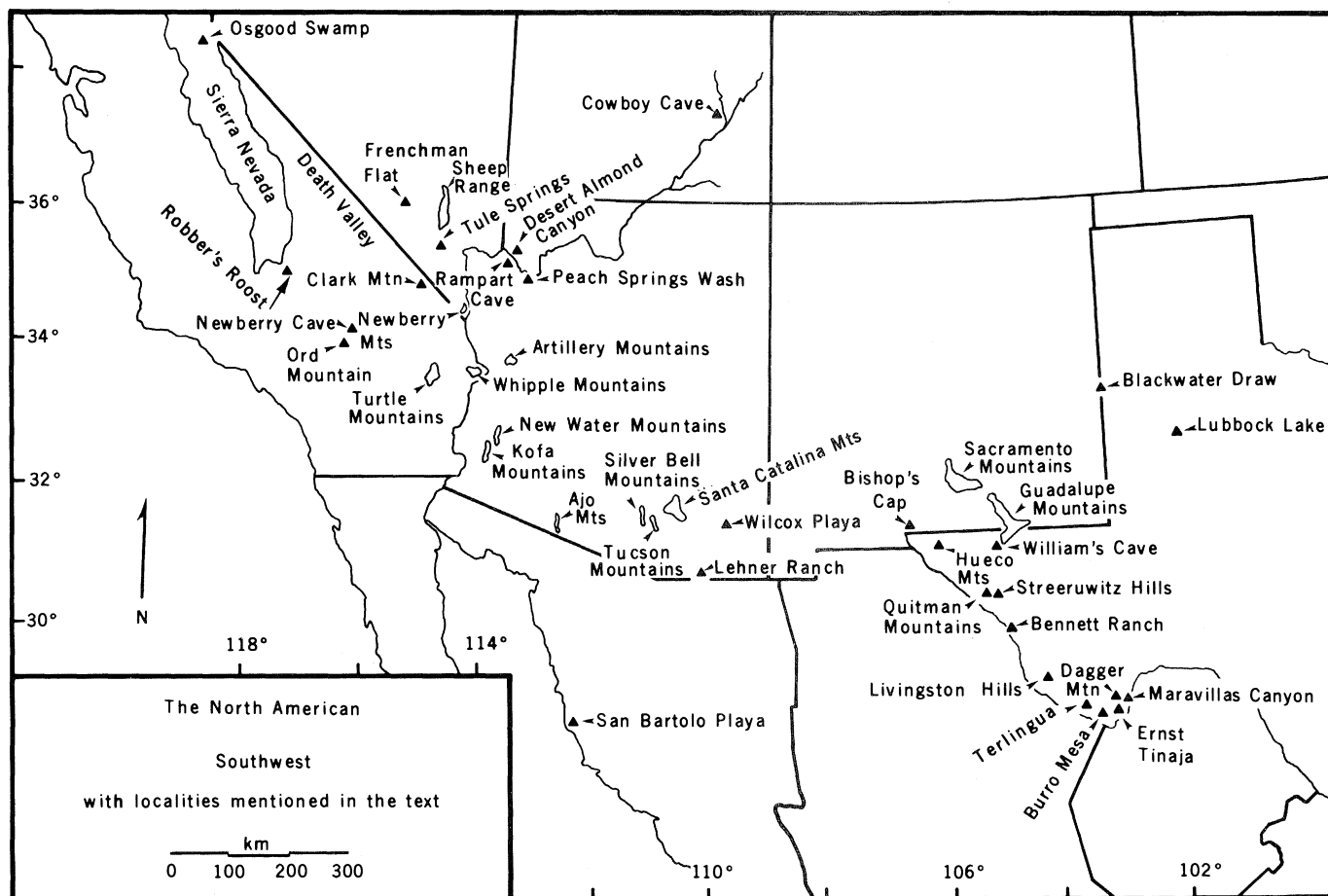
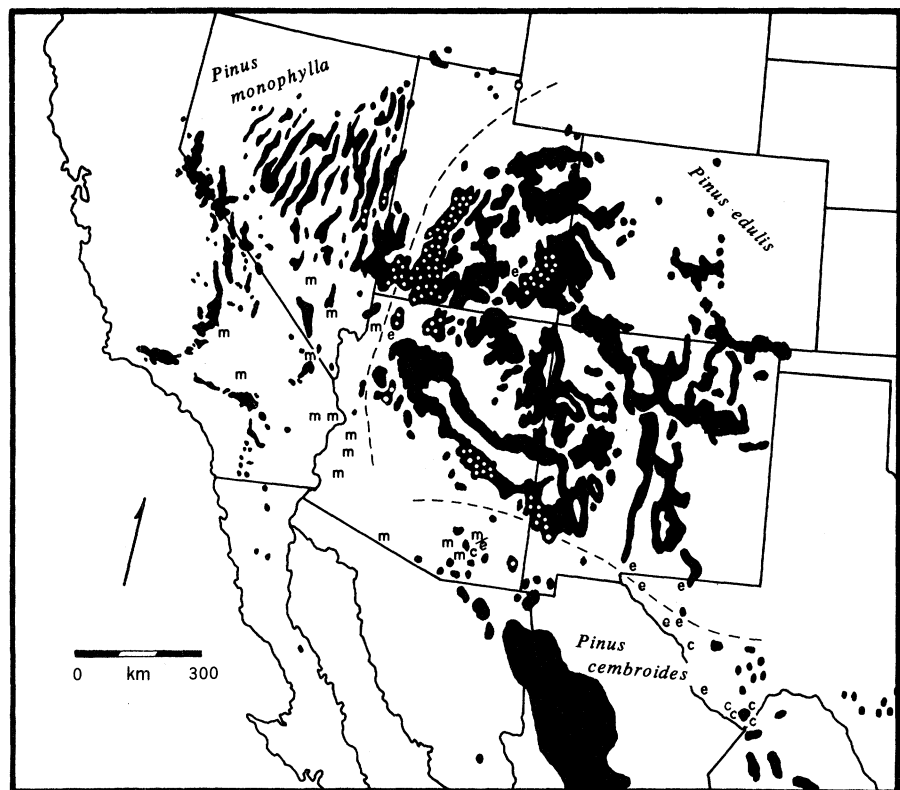


Fig. 1. The southwestern United States with localities mentioned in the text.

Fig. 2. Modern distribution and fossil occurrence of single-needle pinyon (*Pinus monophylla* = m), Colorado (*Pinus edulis* = e), and Mexican pinyon (*Pinus cembroides* = c) (50). Dashed lines show approximate modern species boundaries; stippled areas indicate hybrid populations (51).



Cowboy Cave, Wayne County, spruce and Douglas fir grew at an elevation of 1710 m in a present pinyon-juniper area at 11,000 years B.P. (13). In the Santa Catalina Mountains, Pima County, Arizona, Arizona cypress (*Cupressus arizonica* Greene) and Douglas fir grew at 1555 m near the present upper limit of the Sonoran Desert palo verde (*Cercidium microphyllum* Rose & Jtn.)-saguaro (*Cereus giganteus* Engelm.) community at 13,850 \pm 220 years B.P. and 14,450 \pm 150 years B.P. (laboratory numbers WK-162 and WK-163, on *Cupressus arizonica*). Both border pinyon and hybrids between Colorado and single-needle pinyons are in the latter samples. On Clark Mountain, San Bernardino County, California, limber pine (*Pinus flexilis* James), and white fir (*Abies concolor* Lindl.) occurred with single-needle pinyon as low as 1910 m in a present pinyon-juniper woodland at 12,460 \pm 190 years B.P. (14). Great Basin bristlecone pine (*Pinus longaeva* Bailey, as *P. aristata* Engelm.) was associated with these species in two other sam-

ples from the same site at 23,600 \pm 950 and 28,720 \pm 1800 years B.P. In the Sheep Range, southern Nevada, woodland communities dominated by Utah juniper (*Juniperus osteosperma* Little) and often containing single-needle pinyon,

limber pine and, occasionally, white fir, occupied areas that are now blackbrush desertscrub at 1585 to 1860 m, during the late Wisconsinan. Higher in the Sheep Range, subalpine bristlecone pine-limber pine forest extended from 1900 to 2400 m

Table 1. Late Wisconsinan packrat middens from North America containing pinyon pine. Abbreviations: C, *Cupressus arizonica*; J, *Juniperus* sp.; N, *Neotoma* dung; Picebi, *Pinus cembroides* var. *bicolor*; Picere, *Pinus cembroides* var. *remota*; Pied, *P. edulis*; Pifl, *P. flexilis*; Pilo, *P. longaeva*; Pimo, *P. monophylla*; Pisp, *Picea* sp.; S, *Nothotheriops shastense* dung; TR, this report; U, uriferous material.

Latitude and longitude	Site	Elevation (m)	Age	Material dated	Associates	Pinyon species	Reference
A Chihuahuan Desert							
Big Bend, Brewster County, Texas							
29°16'N, 103°01'W	Ernst Tinaja No. 1	760	15,300 \pm 670 (WK-174)	J	<i>Koeberlinia spinosa</i> , <i>Quercus hinckleyi</i> , <i>Yucca</i> cf. <i>rostrata</i>	Picere	TR
29°16'N, 103°23'W	Burro Mesa No. 1	1200	18,750 \pm 360 (not given)	U	<i>Agave lecheguilla</i> , <i>Berberis trifoliolata</i> , <i>Quercus grisea</i>	Picere	(4)
29°18'N, 103°41'W	Terlingua No. 1	915	15,000 \pm 440 (WK-175)	J	<i>Cercocarpus montanus</i> , <i>Cowania ericaefolia</i> , <i>Yucca</i> cf. <i>rostrata</i>	Picere	TR
29°32'N, 103°06'W	Dagger Mountain No. 1	880	20,000 \pm 390 (not given)	U	<i>Agave lecheguilla</i> , <i>Berberis trifoliolata</i> , <i>Quercus grisea</i>	Picere	(4)
29°32'N, 103°06'W	Dagger Mountain No. 3	850	16,250 \pm 240 (not given)	U	<i>Agave lecheguilla</i> , <i>Celtis reticulata</i> , <i>Quercus pungens</i>	Picere	(4)
29°32'N, 102°49'W	Maravillas Canyon No. 1A	600	11,560 \pm 140 (not given)	U	<i>Agave lecheguilla</i> , <i>Quercus pungens</i> , <i>Yucca rostrata</i>	Picere	(4)
29°32'N, 102°49'W	Maravillas Canyon No. 1C	600	12,550 \pm 130 (not given)	U	<i>Agave lecheguilla</i> , <i>Juglans microcarpa</i> , <i>Quercus pungens</i>	Picere	(4)
29°32'N, 102°49'W	Maravillas Canyon No. 2	600	13,350 \pm 170 (not given)	U	<i>Berberis trifoliolata</i> , <i>Quercus pungens</i> , <i>Yucca rostrata</i>	Picere	(4)
29°32'N, 102°49'W	Maravillas Canyon No. 3	600	14,800 \pm 180 (not given)	U	<i>Berberis trifoliolata</i> , <i>Celtis reticulata</i> , <i>Quercus pungens</i>	Picere	(4)
29°32'N, 102°49'W	Maravillas Canyon No. 1B	600	12,000 \pm 150 (not given)	U	<i>Agave lecheguilla</i> , <i>Quercus pungens</i> , <i>Yucca rostrata</i>	Picere	(4)
29°33'N, 102°49'W	Maravillas Canyon TRV No. 3	600	16,160 \pm 330 (A-1842)	J	<i>Berberis</i> cf. <i>trifoliolata</i> , <i>Quercus</i> sp., <i>Yucca</i> cf. <i>torreyi</i>	Picere	TR
Livingston Hills, Presidio County, Texas							
29°47'N, 104°22'W	Shafter No. 1B	1310	15,695 \pm 230 (A-1581)	J	<i>Quercus hinckleyi</i> , <i>Q. pungens</i> , <i>Yucca</i> cf. <i>rostrata</i>	Pied	(24)

Table 1 (continued).

Latitude and longitude	Site	Elevation (m)	Age	Material dated	Associates	Pinyon species	Reference
<i>Rio Grande, Presidio County, Texas</i>							
30°37'N, 104°59'W	Bennett Ranch No. 1	1035	18,190 ± 380 (A-1831)	N	<i>Berberis haematocarpa</i> , <i>Juniperus</i> sp., <i>Prosopis glandulosa</i>	Picere	TR
30°37'N, 104°59'W	Bennett Ranch No. 3	1035	11,000 ± 320 (A-1801)	J	<i>Agave</i> sp., <i>Nolina</i> sp., <i>Opuntia imbricata</i>	Picere	TR
30°37'N, 104°59'W	Bennett Ranch No. 4	1035	12,030 ± 170 (A-1836)	J	<i>Agave</i> cf. <i>neomexicana</i> , <i>Forsellesia spinescens</i> , <i>Nolina</i> sp.	Picere	TR
<i>Sierra Diablo, Hudspeth County, Texas</i>							
31°07'N, 105°09'W	Streeruwitz Hills No. 1 (P3U)	1430	14,290 ± 290 (A-1843)	J	<i>Agave</i> cf. <i>neomexicana</i> , <i>Berberis trifoliolata</i> , <i>Yucca elata</i>	Pied	TR
31°07'N, 105°09'W	Streeruwitz Hills No. 1 (P4)	1430	18,060 ± 1320 (A-1623)	J	<i>Atriplex canescens</i> , <i>Berberis haematocarpa</i> , <i>Celtis reticulata</i>	Pied	TR
<i>Quitman Mountains, Hudspeth County, Texas</i>							
31°08'N, 105°24'W	Quitman Mountains No. 1	1430	10,910 ± 170 (A-1612)	J	<i>Cercocarpus montanus</i> , <i>Quercus pungens</i> , <i>Symphoricarpos</i> sp.	Pied	(7, 44)
31°08'N, 105°24'W	Quitman Mountains No. 2	1430	12,040 ± 470 (A-1843)	J	<i>Berberis haematocarpa</i> , <i>Cercocarpus montanus</i> , <i>Quercus pungens</i>	Pied	TR
<i>Hueco Mountains, El Paso County, Texas</i>							
31°53'N, 106°09'W	Picture Cave No. 1D	1430	12,030 ± 210 (A-1699)	J	<i>Berberis haematocarpa</i> , <i>Cercocarpus montanus</i> , <i>Quercus pungens</i>	Pied	(17)
31°54'N, 106°09'W	Tank Trap Wash No. 1 (5)	1340	19,610 ± 1150 (A-1710)	Pied	<i>Cercocarpus montanus</i> , <i>Mortonia scabrella</i> var. <i>scabrella</i> , <i>Quercus pungens</i>	Pied	TR
31°54'N, 106°09'W	Tank Trap Wash No. 2	1340	21,200 ± 990 (A-1772)	J	<i>Cercocarpus montanus</i> , <i>Forsellesia spinescens</i> , <i>Quercus pungens</i>	Pied	TR
31°54'N, 106°09'W	Navar Ranch No. 3B	1370	16,240 ± 430 (A-1645)	J	<i>Berberis trifoliolata</i> , <i>Forsellesia spinescens</i> , <i>Opuntia imbricata</i>	Pied	TR
31°55'N, 106°03'W	Hueco Tanks St. Park No. 1	1420	13,500 ± 250 (A-1624)	J	<i>Quercus toumeyi</i> , <i>Ribes</i> sp., <i>Symphoricarpos</i> sp.	Pied	(17)
<i>Guadalupe Mountains, Culberson County, Texas</i>							
31°55'N, 104°50'W	Cave C-08 midden	2000	13,060 ± 280 (A-1549)	Pisp	<i>Juniperus communis</i> , <i>Pinus strobiiformis</i> , <i>Pseudotsuga menziesii</i>	Pied	(3)
31°54'N, 104°50'W	William's Cave No. 2	1500	12,040 ± 210 (A-1540)	J	<i>Prunus serotina</i> , <i>Quercus</i> sp., <i>Robinia neomexicana</i>	Pied	TR
<i>Bishop's Cap, Doña Ana County, New Mexico</i>							
32°11'N, 106°36'W	Shelter Cave Sloth No. 1	1400	11,330 ± 370 (A-1878)	S	<i>Juniperus</i> sp., <i>Opuntia imbricata</i> , <i>Sphaeralcea</i> sp.	Pied	TR
B Sonoran Desert							
<i>Ajo Mountains, Pima County, Arizona</i>							
32°07'N, 112°42'W	Montezuma Head No. 1A	975	20,490 ± 510 (A-1695)	J	<i>Artemisia tridentata</i> , <i>Quercus turbinella</i> ssp. <i>ajoensis</i> , <i>Yucca brevifolia</i>	Pimo	(7)
32°07'N, 112°42'W	Montezuma Head No. 1B	975	21,840 ± 650 (A-1696)	Pimo	<i>Artemisia tridentata</i> , <i>Opuntia chlorotica</i> , <i>Yucca brevifolia</i>	Pimo	(7)
32°07'N, 112°42'W	Montezuma Head No. 1C	975	17,830 ± 870 (A-1697)	J and Pimo	<i>Artemisia tridentata</i> , <i>Berberis harri-soniana</i> , <i>Yucca brevifolia</i>	Pimo	(7)
32°07'N, 112°42'W	Montezuma Head No. 1D	975	13,500 ± 390 (A-1698)	J	<i>Agave deserti</i> , <i>Artemisia tridentata</i> , <i>Yucca brevifolia</i>	Pimo	(7)
<i>Tucson Mountains, Pima County, Arizona</i>							
32°19'N, 111°12'W	Tucson Mountains No. 3	740	21,000 ± 700 (A-994)	J	<i>Agave</i> sp., <i>Dasyllirion wheeleri</i> , <i>Opuntia chlorotica</i>	Pimo	(27, 44)
<i>Santa Catalina Mountains, Pima County, Arizona</i>							
32°21'N, 110°53'W	Pontatoc Ridge No. 2	1555	13,850 ± 220 (WK-162)	C	<i>Arctostaphylos</i> sp., <i>Pseudotsuga menziesii</i>	Picebi, Pimo × Pied	TR
32°21'N, 110°53'W	Pontatoc Ridge No. 4A	1555	14,450 ± 150 (WK-163)	C	<i>Arctostaphylos</i> sp., <i>Cupressus arizonica</i> , <i>Juniperus</i> sp., <i>Pseudotsuga menziesii</i>	Picebi, Pimo × Pied	TR
<i>Silver Bell Mountains, Pima County, Arizona</i>							
32°27'N, 111°28'W	Wolcott Peak No. 2	860	14,550 ± 800 (A-1286)	J	<i>Celtis pallida</i> , <i>Opuntia phaeacantha</i> , <i>Prosopis juliflora</i>	Pimo	(27, 48)
32°27'N, 111°28'W	Wolcott Peak No. 5	860	12,130 ± 500 (A-1287)	J	<i>Agave</i> sp., <i>Opuntia chlorotica</i> , <i>Quercus turbinella</i>	Pimo	(27, 48)
<i>Picacho Mountains, Pinal County, Arizona</i>							
32°38'N, 111°24'W	Picacho Peak No. 1B	655	11,100 ± 300 (A-1835)	J	<i>Berberis trifoliolata</i> , <i>Ferocactus acanthodes</i> , <i>Quercus</i> cf. <i>turbinella</i>	Pimo	TR
32°38'N, 111°24'W	Picacho Peak No. 1A	655	13,170 ± 200 (A-1827)	J	<i>Artemisia</i> cf. <i>tridentata</i> , <i>Ferocactus acanthodes</i> , <i>Opuntia chlorotica</i>	Pimo	TR
<i>Kofa Mountains, Yuma County, Arizona</i>							
33°24'N, 114°01'W	Burro Canyon No. 1(6)	860	13,400 ± 350 (A-1357)	J	<i>Atriplex confertifolia</i> , <i>Encelia farinosa</i> , <i>Rhus aromatica</i>	Pimo	(27, 48)
33°24'N, 114°01'W	Burro Canyon No. 1(1)	860	14,400 ± 330 (A-1315)	J	<i>Atriplex canescens</i> , <i>Opuntia chlorotica</i> , <i>Quercus turbinella</i>	Pimo	(27, 48)

Table 1 (continued).

Latitude and longitude	Site	Elevation (m)	Age	Material dated	Associates	Pinyon species	Reference
<i>New Water Mountains, Yuma County, Arizona</i>							
33°36'N, 113°55'W	New Water Mountains No. 4	615	10,880 ± 390 (A-1285)	J	<i>Acacia greggii</i> , <i>Ferocactus acanthodes</i> , <i>Larrea divaricata</i> , <i>Quercus turbinella</i>	Pimo	(27, 48)
<i>Whipple Mountains, San Bernardino County, California</i>							
34°16'N, 114°25'W	Redtail Peak No. 5	510	12,960 ± 210 (A-1666)	Pimo	<i>Cercocarpus intricatus</i> , <i>Nolina bigelovii</i> , <i>Yucca whipplei</i>	Pimo	(48)
<i>Artillery Mountains, Mohave County, Arizona</i>							
34°20'N, 113°35'W	Artillery Mountains No. 2	725	18,320 ± 400 (A-1101)	J	<i>Arctostaphylos pungens</i> , <i>Ferocactus acanthodes</i> , <i>Quercus turbinella</i>	Pimo	(27, 48)
34°23'N, 113°28'W	Artillery Mountains No. 3	725	21,000 ± 400 (USGS-196)	J	<i>Acacia greggii</i> , <i>Artemisia tridentata</i> , <i>Larrea divaricata</i> , <i>Quercus dunni</i>	Pimo	(27, 48)
<i>C Mohave Desert</i>							
<i>Turtle Mountains, San Bernardino County, California</i>							
34°20'N, 114°50'W	Turtle Mountains No. 1	850	19,500 ± 380 (not given)	(ng)	<i>Opuntia erinacea</i> , <i>Ribes cf. velutinum</i>	Pimo	(8)
34°20'N, 114°50'W	Turtle Mountains No. 2	730	13,900 ± 200 (not given)	(ng)	<i>Cercocarpus intricatus</i> , <i>Opuntia erinacea</i> , <i>Ribes cf. velutinum</i>	Pimo	(8)
<i>Ord Mountain, San Bernardino County, California</i>							
34°40'N, 116°50'W	Ord Mountain	1220	11,850 ± 550 (UCR-149)	J	<i>Ephedra</i> sp., <i>Opuntia</i> sp., <i>Purshia glandulosa</i>	Pimo	(1)
<i>Newberry Mountains, Clark County, Nevada</i>							
35°15'N, 114°37'W	Sacatone Wash	730	19,620 ± 600 (I-3659)	(ng)	<i>Quercus dunni</i>	Pimo	(49)
35°16'N, 114°37'W	Newberry Mountains No. 1	850	13,380 ± 300 (Gak-1988)	Pimo	<i>Quercus chrysolepis</i> , <i>Q. dunni</i> , <i>Purshia glandulosa</i>	Pimo	(49)
<i>Peach Springs Wash, Mohave County, Arizona</i>							
35°43'N, 113°23'W	Cave of the Early Morning Light No. 1	1300	16,580 ± 460 (A-1718)	J	<i>Artemisia tridentata</i> , <i>Cercocarpus intricatus</i>	Pied	(6), TR
<i>Scodie Mountains, Kern County, California</i>							
35°36'N, 117°57'W	Robber's Roost No. 1C	1130	13,800 ± 400 (A-1763)	J	<i>Artemisia tridentata</i> , <i>Ceanothus</i> sp., <i>Opuntia basilaris</i>	Pimo	(2)
35°36'N, 117°57'W	Robber's Roost No. 1D	1130	12,820 ± 400 (A-1762)	J	<i>Artemisia tridentata</i> , <i>Purshia glandulosa</i> , <i>Quercus turbinella</i>	Pimo	(2)
35°36'N, 117°57'W	Robber's Roost No. 2A	1130	12,960 ± 270 (A-1761)	J	<i>Artemisia tridentata</i> , <i>Purshia glandulosa</i> , <i>Yucca brevifolia</i>	Pimo	(2)
<i>Spring Range, Clark County, Nevada</i>							
36°02'N, 115°23'W	Blue Diamond Road No. 3	1050	15,040 ± 650 (UCR-725)	J	<i>Atriplex canescens</i> , <i>Mortonia scabrella</i> var. <i>utahensis</i>	Pimo	TR
36°02'N, 115°23'W	Blue Diamond Road No. 5	1110	15,800 ± 680 (UCR-726)	J	<i>Agave utahensis</i> , <i>Artemisia tridentata</i> , <i>Forsellesia nevadensis</i>	Pimo	TR
<i>Grand Canyon, Mohave County, Arizona</i>							
36°06'N, 113°56'W	Rampart Cave, Unit B	535	14,810 ± 220 (A-1570)	J	<i>Artiplex confertifolia</i> , <i>Fraxinus anomala</i> , <i>Ribes montigenum</i>	Pimo	(6)
36°07'N, 113°54'W	Desert Almond No. 10	635	12,650 ± 380 (A-1720)	J	<i>Cercocarpus intricatus</i> , <i>Nolina microcarpa</i> , <i>Symphoricarpos</i> sp.	Pimo and Pied	(6)
<i>Sheep Range, Clark County, Nevada</i>							
36°28'N, 115°15'W	Penthouse No. 2 (2)	1580	11,550 ± 150 (A-1774)	J	<i>Ceanothus greggii</i> , <i>Forsellesia nevadensis</i> , <i>Symphoricarpos</i> sp.	Pimo	TR
36°28'N, 115°15'W	Penthouse No. 1 (3)	1600	19,400 ± 300 (A-1772)	J	<i>Ceanothus greggii</i> , <i>Forsellesia nevadensis</i> , <i>Symphoricarpos</i> sp.	Pimo	TR
36°28'N, 115°15'W	Willow Wash No. 4A	1585	21,350 ± 440 (WSU-1858)	J	<i>Artiplex confertifolia</i> , <i>Pinus flexilis</i> , <i>Ribes montigenum</i>	Pimo	TR
36°29'N, 115°15'W	South Crest No. 1 (4) ₂	1990	21,700 ± 500 (LJ-2840)	Pilo/ Pifl	<i>Abies concolor</i> , <i>Cercocarpus intricatus</i> , <i>Philadelphus microphyllus</i>	Pimo	TR
36°29'N, 115°15'W	Flaherty Mesa No. 1	1770	20,380 ± 340 (WSU-1862)	J	<i>Ephedra viridis</i> , <i>Pinus flexilis</i> , <i>Ribes montigenum</i>	Pimo	TR
36°34'N, 115°18'W	Spires No. 2	2040	18,800 ± 130 (USGS-198)	Debris	<i>Artemisia tridentata</i> , <i>Cercocarpus intricatus</i> , <i>Jamesia americana</i>	Pimo	TR
36°37'N, 115°17'W	Deadman No. 1 (1)	1970	17,420 ± 250 (LJ-3707)	Pilo/ Pifl	<i>Chamaebatiaria millefolium</i> , <i>Fallugia paradoxa</i> , <i>Juniperus osteosperma</i>	Pimo	TR
36°37'N, 115°17'W	Deadman No. 1 (4)	1970	18,680 ± 280 (WSU-1857)	J	<i>Atriplex confertifolia</i> , <i>Pinus flexilis</i> , <i>Pinus longaeva</i>	Pimo	TR
36°37'N, 115°17'W	Deadman No. 1 (2)	1970	16,800 ± 245 (WSU-1860)	J	<i>Jamesia americana</i> , <i>Opuntia polyacantha</i> , <i>Salvia dorrii</i>	Pimo	TR
36°38'N, 115°17'W	Eyrie No. 3 (1)	1855	16,490 ± 220 (WSU-1853)	J	<i>Ephedra viridis</i> , <i>Opuntia polyacantha</i> , <i>Pinus flexilis</i>	Pimo	TR

between 22,000 and 12,000 years B.P. (9).

Early Holocene (11,000 to 8000 years B.P.). The end of the late Wisconsinan pinyon-juniper woodlands is recorded by the youngest dated woodland middens with pinyon at about 11,000 years B.P. in the Chihuahuan, Sonoran, and Mohave deserts (Table 1). The single-needle pinyon record reported from the Whipple Mountains, San Bernardino County, California, is not directly associated with the radiocarbon age of 8910 ± 380 years B.P. (9). A new age of $12,960 \pm 210$ years B.P. on single-needle pinyon wood is from Redtail Peaks No. 5, a separate midden from the same site.

Xeric, middle-elevation juniper, or juniper-oak woodlands developed synchronously with the disappearance of pinyons in the Southwest. Early Holocene woodlands in the southwestern deserts between 10,000 and 8000 years B.P. have been discussed (7). Similar xeric woodland midden assemblages with radiocarbon ages between 11,000 and 10,000 years B.P. have also been found in all of the warm desert areas in the Southwest (5, 8, 13). The early Holocene xeric woodland period in the Southwest was from 11,000 to 8000 years B.P.

The late Wisconsinan juniper woodlands of Arizona and California below 600 m persisted into the early Holocene with little change. Most xeric woodland species were present in these areas until about 8000 years B.P. (7). Big sagebrush and shadscale appear to have retreated from more southern woodlands by 11,000 years B.P. Blackbrush may have survived until about 10,000 years B.P., and mountain mohagany, Joshua tree, and Whipple yucca until 8000 years B.P. Creosote bush was present in the juniper woodlands. California juniper (*Juniperus californica* Carr.) is a xeric-adapted species that usually occurs below Utah juniper. California juniper may have displaced Utah juniper in the early Holocene woodlands. Unfortunately, the species of the fossil juniper materials are not easily identified, and changes in juniper species have not been well documented.

In the northern Mohave Desert, the late Wisconsinan juniper woodlands below about 1600 m persisted into the Holocene. Several important changes in other taxa occurred during the early Holocene, however. Joshua tree appears to have expanded its range into Death Valley, Inyo County, California, and to the Frenchman Flat area, Clark County, Nevada (8, 15). Creosote bush probably entered the northern part of its present range in Nevada at this time. The oldest radiocarbon age reliably associated with

creosote bush in the Sheep Range is 8100 ± 120 years B.P. (Penthouse 1, 1:A-1771, on *Neotoma* fecal pellets). This sample is a midden containing juniper found at an elevation of 1560 m on a southeast-facing slope, 100 m above the local limit of creosote bush, and 400 m below the present lower limit of Utah juniper. As modern pinyon-juniper woodlands displaced the earlier bristlecone-limber pine forests in southern Nevada in the early Holocene, single-needle pinyon also may have expanded into lower areas such as the Spotted Range (8), or even into the Great Basin to the north (16).

Early Holocene creosote bush-white bursage (*Ambrosia dumosa* Payne) communities were well developed below about 300 m. Middens with this assemblage from the Wellton Hills, Yuma County, Arizona, at 175 to 160 m were radiocarbon dated at $10,750 \pm 400$ to 8150 ± 260 years B.P. (7). A similar assemblage from Picacho Peak, Imperial County, California, at 245 m was dated at 8650 ± 280 years B.P. (A-1876, on *Opuntia basilaris*) (12). Creosote bush-white bursage communities are characteristic of low-elevation areas in the Lower Colorado Valley section of the Sonoran Desert and the Mohave Desert.

Packrat middens at elevations higher than about 1800 m document a transition from late Wisconsinan forests to essentially modern communities in the early Holocene. In the Guadalupe Mountains of Texas, a Douglas fir-southwestern white pine forest at 2000 m was replaced by a juniper grassland community after 11,500 years B.P. (3). The disappearance of spruce and dwarf juniper from this site between 13,000 and 11,500 years B.P. probably records an earlier climatic event. Macrofossils of two species of sedge (*Carex* sp.) and horsetail (*Equisetum* sp.), and pollen of spruce, Douglas fir, and birch (probably *Betula fontinalis* Sarg., water birch) suggest that relatively mesic conditions may have persisted in the dry canyon at Cowboy Cave, Utah, until 8700 years B.P. (13).

In the Sheep Range of Nevada, mesic juniper communities from 1585 to 1860 m were replaced by xeric juniper woodland before 9500 years B.P. The juniper woodlands were in turn replaced by mixed scrub and blackbrush desertscrub by 7500 years B.P. Late Wisconsinan bristlecone-limber pine forests from 1900 to 2100 m disappeared before 9500 years B.P. and were replaced by the pinyon-juniper woodland that still exists at these sites. In a mesic canyon at 2400 m, a midden with an age of $10,060 \pm 130$ years B.P. (LJ-3729, on bristlecone and

limber pine needles) contains bristlecone, limber, ponderosa (*Pinus ponderosa* Laws.), and pinyon pine, Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), and white fir. Ponderosa pine, Rocky Mountain juniper, and white fir are dominant species in the present community. Older late Wisconsinan middens from the same site contain bristlecone and limber pines and dwarf juniper, but lack ponderosa pine, Rocky Mountain juniper, and white fir (11).

Middle and late Holocene (8000 years B.P. to present). The youngest records of displaced woodland plants in present deserts are about 8000 years old in the Chihuahuan Desert in Texas, the Sonoran Desert in Arizona and California, and the Mohave Desert in Arizona, California, and Nevada (7, 8). The end of the early Holocene woodlands in these now warm deserts appears to have been a rapid, widespread, synchronous event about 8000 years B.P. Packrat middens indicative of modern desert vegetation younger than 8000 years B.P. are common, but few have been dated by carbon-14 analysis. The oldest creosote bush middens are dated at 5800 ± 250 years B.P. (UCR-135, on *Larrea divaricata*) and 5880 ± 250 years B.P. (UCR-134, on miscellaneous twigs) from the Lucerne Valley (1), and 7400 ± 150 years B.P. (UCLA-560, on uriniferous material) from Newberry Cave (8), both from San Bernardino County, California. Similar early Holocene creosote bush middens were mentioned earlier. King's (1) Lucerne Valley study documented a continuation of the creosote bush community into the late Holocene.

At the beginning of the middle Holocene, woodland species migrated northward, retreated to higher elevations in the mountains, and disappeared in the lowlands. Desert-adapted species increased in abundance and dispersed into new areas. Creosote bush-white bursage communities expanded greatly into the lowlands of the Sonoran and Mohave deserts. Joshua tree was restricted to higher elevations to the north on the edges of the Mohave Desert. It was associated more often with creosote bush and blackbrush than with pinyon and juniper (15). As rocky slopes became more xeric, catclaw (*Acacia greggii* Gray) became a riparian species in the washes of the Sonoran and Mohave deserts. Important dominant species, such as foothills palo verde, saguaro, and ironwood (*Olneya tesota* Gray), apparently moved into the United States from the Mexican lowlands around the head of the Gulf of California. Ocotillo (*Fouquieria splendens* Engelm.) is a widespread, dis-

tinctive, southwestern species that has not been found in any late Wisconsinan or early Holocene middens despite its frequent occurrence at fairly high (up to 1350 m) elevations today. It may have invaded most of the Southwest during the middle Holocene. Later fluctuations in the structure and composition of the plant communities in the Sonoran and Mohave deserts were of small magnitude and were relatively minor events within the present vegetational regime.

In the Chihuahuan Desert in New Mexico and Texas, a middle Holocene grassland community probably preceded the formation of the present, diverse, succulent desertscrub communities at elevations of 1200 to 2000 m. Important perennials in the latter communities, such as creosote bush, lechuguilla (*Agave lecheguilla* Torr.), mariola (*Parthenium incanum* H.B.K.), Big Bend silver leaf (*Leucophyllum minus* Gray), white thorn (*Acacia neovernicosa* Isely), and many others may have been present in small edaphic microhabitats in middle Holocene grasslands. The establishment of desertscrub communities in the northern Chihuahuan Desert is probably the last major vegetational change in the Southwest (excluding historic changes). Midden samples from an elevation of 1430 m from Picture Cave, Hueco Mountains, El Paso County, Texas, record modern desertscrub communities at 1530 ± 120 and 1700 ± 100 years B.P. (A-1706 and A-1726, on *Opuntia phaeacantha*-type) (17). A series of seven middens from 1130 to 1310 m from Rocky Arroyo and Last Chance Canyon, Eddy County, New Mexico, document modern desertscrub communities between 4000 years B.P. and the present (18).

Late Wisconsinan Climate

Evidence from deep sea cores, the Greenland ice sheet, and pollen-stratigraphic sites document the cyclic nature of Quaternary climates. The durations of glacial periods have been on the order of 100,000 years and interglacial periods only on the order of 10,000 to 20,000 years (19, 20). Therefore, the woodlands and forests recorded by packrat midden materials at low elevations in the Southwest probably represent typical environments throughout much of the Quaternary. The present Holocene deserts do not represent general conditions during this period.

The nature of the late Wisconsinan climate in the Southwest is controversial and deserves discussion. The term "pluvial climate" is used in the Southwest,

where continental glaciation did not occur. The most noticeable effect of "glacial climates" beside vegetation changes was the filling of now dry playa lakes when the continental ice sheets were well developed (21). The term "pluvial" climates carries a connotation of wetter climate due to an actual increase in precipitation. However, in most geological and biological systems it is difficult to separate the effects of precipitation and temperature. Inferences of the late Wisconsinan climate in the Southwest have ranged from a model of lower winter temperature or annual temperatures (22, 23) to a model of mild winters and cool summers (24), and from a model of decreased precipitation with maintenance of the present seasonal distribution of precipitation (25) to a model of greatly increased winter precipitation (7, 25). Many of these models have been generated to satisfy pluvial lake water budgets or have been based on the distributions of solifluction deposits that are assumed to imply lowered snowlines in the past.

The species and composition of fossil assemblages from packrat middens provide insight into paleoclimates. The number of species living in comparable habitats decreases with increasing latitude or elevation. This is commonly attributed to the limiting effects of lower winter temperatures and shorter growing seasons with increasing altitude and latitude. Colder and longer winters during the late Wisconsinan may be expected to have resulted in less diverse woodland and forest assemblages and a lack of desert species in the packrat middens. Instead, most fossil assemblages are equally or more diverse than their modern counterparts. In most instances they are mixtures of woodland and warm desert species. Middens in the Sonoran and Mohave deserts do contain important Great Basin species such as big sagebrush and shadscale, but simple cold steppe or steppe desert assemblages have not been found south of 36°N.

Galloway (22) provided a strong case for acceptance of the cold-dry model of late Wisconsinan climate in the Southwest. He postulated a 1300- to 1400-m lowering of timberline due to a temperature decrease of 10° to 11°C for all seasons and a 10 to 20 percent reduction in precipitation. His thesis was based on cursory observations of undated solifluction deposits in New Mexico (22). More recently, after a literature review of similar deposits, Brakenridge (23) inferred a 1000-m snowline depression, 7° to 8°C cooling in all seasons, and a precipitation somewhat less than today. If an environmental lapse rate of 6°C per 1000 m is ap-

plied to the data used by Galloway and Brakenridge, the implied magnitudes of lowering of vegetational zones are 1750 m and 1250 m, respectively. Cooling of lesser magnitude would not be enough to fill the playa lakes without increased precipitation.

Plant macrofossils in middens and cave fills in the Guadalupe Mountains of Texas, 175 km south of Galloway's Sacramento Mountains study area, provide a test of these inferences. Macrofossil assemblages at an elevation of 2000 m contained species of subalpine (spruce and dwarf juniper), montane (Douglas fir and southwestern white pine), and woodland (Colorado pinyon and juniper) affinities about 13,000 years B.P. (3). The association of subalpine plants with more xerophytic species suggests that this site was near the lower limit of the spruce forest. The lower limit of modern conifer forest with spruce is about 2430 m of elevation, 110 km to the northwest in the massive Sacramento Mountains. Spruce and dwarf juniper no longer occur in the Guadalupe Mountains and a modern analog with a physiographic setting comparable to the paleocommunity is not available. Earlier full-glacial communities at this site were probably a little more mesic.

A midden from William's Cave at 1500 m in the Guadalupe Mountains records a pinyon-juniper woodland at $12,040 \pm 210$ years B.P. Middens from other Trans-Pecos Texas sites, including Maravillas Canyon, Brewster County (4) (Table 1), Bennett Ranch, Presidio County, and the Hueco Mountains, El Paso County, record few changes in local pinyon-juniper woodland communities from elevations of 600 to 1350 m between 16,000 to 18,000 years B.P. and 11,000 years B.P. Late Wisconsinan pinyon-juniper middens from other Trans-Pecos sites document similar woodlands throughout this period. The full-glacial vegetation at William's Cave was probably little if any more mesic than the 12,000 years B.P. pinyon-juniper woodland. Even the most modest inference of 1000-m vegetational lowering in the Galloway-Brakenridge models would predict a mixed conifer forest with Douglas fir, southwestern white pine, ponderosa pine, or even spruce at William's Cave. If the timberline was depressed 1000 m then the subalpine forest was greatly compressed, and inferred paleotemperatures of Galloway and Brakenridge only relate to elevations above 2000 m and not to the Southwest in general.

Many of the fossils in packrat middens contain species that are indicators of winter temperatures. Beaked yucca

(*Yucca rostrata* Engelm.) and crucifixion thorn (*Castela stewartii* C.H. Mull.) are now restricted to Chihuahuan desert-scrub communities in the Big Bend region in Texas and south into Mexico. They were in a pinyon-juniper woodland at 1310 m in the Livingston Hills, Presidio County, Texas, well north of their present range at $15,695 \pm 230$ years B.P. (26). A related crucifixion thorn (*C. emoryi* Gray) was in a juniper-Joshua tree community at 550 m at $11,450 \pm 400$ years B.P. (A-1328 on *Yucca brevifolia* Engelm.) on Brass Cap Point, Kofa Mountains, Yuma County, Arizona; now it is restricted to low-elevation desert-scrub communities (27). In the Sheep Range of Nevada, shadscale is now restricted to desert communities below 1600 m. It was present at elevations up to 2150 m in mixed conifer and bristlecone-limber pine communities from more than 48,000 to at least 15,000 years B.P. (11). Big sagebrush grew as far south as Montezuma's Head, in the Ajo Mountains of southwestern Arizona (7), and Shelter Cave, in south-central New Mexico, in the late Wisconsinan. In southern Nevada big sagebrush is now dominant in areas with cooler summers and more winter precipitation than in areas with blackbrush or creosote bush (28). All of these associations suggest that late Wisconsinan winters were mild.

The faunal record does not support an interpretation that late Wisconsinan winter temperatures were cooler than present winter temperatures. Late Wisconsinan faunal assemblages from many sites in the central and eastern United States contain mixtures of northern and southern forms that suggest equable climates with mild winters and cool summers (24). Late Pleistocene cave faunas from the Southwest are mixtures of forest, woodland, and grassland animals. Southwestern packrat middens of late Pleistocene and early Holocene age contain remains of animals now restricted to desert-scrub habitats in woodland assemblages (29). The desert tortoise (*Gopherus agassizi* Cooper) is now restricted to desert-scrub habitats west of the Continental Divide in the Sonoran and Mohave deserts. During the late Wisconsinan it inhabited pinyon-juniper woodlands in the northern Chihuahuan Desert in New Mexico and Texas.

The coldest winter temperatures in the midcontinent and the Great Basin occur when Arctic or polar continental air masses move to the south. "Northers" or "nortes" bring cold air and freezing temperatures south of the Tropic of Cancer in Mexico including all areas in the Chihuahuan Desert. Bryson and Wend-

land (30) suggested that 3500-m-high continental ice sheets prevented cold Arctic air from entering the mid-continent. Moreover, the air above the ice sheets was warmed adiabatically as it descended and they postulated that between 13,000 and 10,000 years B.P. winter temperatures were relatively mild. Elimination of northers would result in warmer winter temperatures in a huge area as far south as Mexico City.

Moisture deficits appear to control the present lower elevational and southern geographical limits of many southwestern plants. Upper elevational and northern limits may be governed by temperature or competition with other species (31). Cooler global climates and the inference of mild winters during the late Wisconsinan suggest that summer temperatures in the Southwest were much cooler than today, resulting in reduced evaporation, water retention in playa lakes, and reduced water stress for plants at the lower limits of their ranges. However, lowered summer temperatures alone are not sufficient to explain most of the fossil plant records. Without greatly lowered annual temperatures, the high water levels in the playa lakes suggest a real increase in precipitation (21, 32). The San Bartolo Playa in the Sonoran Desert, 30 km north of Bahia Kino, Sonora, Mexico, is at 29°N and just slightly above sea level (33). San Bartolo Playa was a large freshwater lake in the late Wisconsinan when the sea level was lowered. The present annual precipitation is about 130 mm. Temperatures and potential evaporation are high. Moisture was surely imported to San Bartolo in the late Wisconsinan to fill the playa unless a cooling of unreasonable magnitude is postulated.

Middens in Arizona, California, and Nevada record a dramatic expansion of woodland, chaparral, and cold desert plants during the late Wisconsinan. Many of the species in the middens now occur in areas to the north or west with greater percentages and absolute amounts of winter rainfall than the midden sites (8). Late Wisconsinan records of woodland species now associated with high summer rainfall are meager. Most annual plants in packrat middens from the western Sonoran and Mohave deserts are species that respond to winter rainfall. The few annuals in the middens that now respond to summer precipitation also germinate, grow, and reproduce in response to fall precipitation and warm temperatures. Increased winter precipitation and reduced summer temperatures can account for most of the observed late Wisconsinan plant distribu-

tions in the Southwest. The apparent stability of late Wisconsinan pinyon-juniper woodlands for 11,000 years suggests that the vegetation was not very sensitive to global temperature fluctuations, but was recording a general climate dominated by moisture.

The presence of the Cordilleran ice sheet, lowered eustatic sea level, colder sea-surface temperatures, and possible cold air drainage from the frozen Arctic Ocean across the Bering Strait, all probably contributed to intensification of the Aleutian Low at lower latitudes than today. This may have resulted in increased frontal storms south of the crest of the Sierra Nevada (36°N) and as far east as Trans-Pecos Texas. Pacific frontal storms usually lose much of their moisture by the time they reach the Chihuahuan Desert, but often cause precipitation as they meet moist air masses from the Gulf of Mexico. Late Wisconsinan winter frontal storms may have begun earlier in the fall than today and lasted later in the spring. Colder sea surface temperatures probably moved the late summer-early fall hurricanes farther south and eliminated this source of precipitation from the Southwest.

Today the Southwest is divided into regions with predominantly winter precipitation in the west and predominantly summer precipitation in the east. We infer a more uniform winter precipitation dominance in both areas in the late Wisconsinan. The xeric juniper woodlands at middle elevations and the bristlecone-limber pine forests at higher elevations in the northern Mohave Desert suggest that southern Nevada was relatively drier than areas south of 36°N (3, 7, 8, 11, 13, 14). This apparent anomaly may be attributed to the Sierra Nevada rain-shadow.

Early Holocene Climate

The documented persistence of woodland until about 8000 years B.P. in the middle-elevation deserts of the Southwest appears to contradict earlier chronologies based on fossil pollen. Essentially modern climate and vegetation after 12,000 to 11,000 years ago have been inferred on the basis of pollen studies (7, 34). The pollen record from Osgood Swamp, in the Sierra Nevada of California, indicates that a shift to modern pine forest began about 11,000 years B.P. and was completed by 10,000 years B.P. (35). Fossil pollen from Tule Springs, Clark County, Nevada, records a major vegetational change about 12,000 years B.P. However, spectra character-

istic of the present Mohave Desert communities did not appear until about 7500 years B.P. (34). The pollen record from Lehner Ranch Arroyo, Cochise County, Arizona, indicates that a major vegetational change marking the beginning of the Holocene occurred 11,200 years B.P. (36). Changes in montane conifer distributions appear to be well reflected in lowland sedimentary pollen records. Midden records can provide a calibration of the pollen records and help separate local pollen from that transported from the nearest mountains.

The midden record confirms the loss of pinyon and other mesic species as well as big sagebrush and shadscale from middle-elevation woodlands by 11,000 years B.P. At higher elevations the transition from late Wisconsinan subalpine communities to woodland and montane communities approaching modern composition also occurred at this time. Thus, the midden record and the pollen stratigraphic records are complementary and not in opposition. For the packrat midden record and stratigraphic pollen record in the Southwest, we suggest that a climatically defined Pleistocene-Holocene boundary be placed at 11,000 years ago, a time of consistent, widespread, contemporaneous vegetational change throughout the Southwest. Environmental changes at about 11,000 years B.P. are also reflected by the upper boundaries of sedimentary deposits at Tule Springs, Nevada (34), the Lehner Ranch Arroyo, Arizona (36), Blackwater Draw, New Mexico (37), and the Lubbock Lake Site, Texas (38). The youngest records of extinct large mammals are in the same units at these sites.

The climate of the early Holocene appears to have been characterized by a continuation of the late Wisconsinan winter precipitation regime. Its persistence for 3000 years into the Holocene implies that "glacial" and "pluvial" climates were not synchronous and the "pluvial" climates are the result of "glacial" climates. As the Cordilleran ice sheet dissipated, the Aleutian Low and the winter storm track assumed their present position. The persistence of the Laurentide ice sheet probably delayed development of the Bermuda High and summer monsoonal rain west of the Continental Divide. Early Holocene middens from the Sonoran Desert lack many characteristic Sonoran Desert species and suggest that summer rains had not begun.

If the late Wisconsinan winters were mild and were caused by the blocking effect of the Cordilleran and Laurentide ice sheets, colder winters may have be-

gun after about 11,500 years B.P. (30) as the ice-free corridor opened between the two ice sheets in western Alberta (39). The same corridor that allowed Paleoindians to enter the mid-continent would have allowed northerners south of the Laurentide ice sheets in the winter. Lower winter temperatures probably caused range changes in many plants and animals by 11,000 years B.P. (24). Early Holocene northerners have been suggested as a causal factor in the extinction of some late Pleistocene megafauna. However, we consider this unlikely because: (i) megafaunal extinctions occurred in many different climatic regimes throughout the Western Hemisphere; (ii) the magnitude of the difference between the climate of the late Wisconsinan and that of today in the Southwest was small compared to the ecological amplitudes of most large herbivores (40); and (iii) similar climatic events at the end of earlier glacial stages were not marked by similar extinctions.

Middle and Late Holocene Climates

The present climatic and vegetational regimes were established after about 8000 years B.P. Winter precipitation was reduced in or withdrawn from much of the Southwest. The summer monsoon expanded, resulting in the present geographic difference in seasonality of rainfall and the related segregation of the biota. The middle Holocene warm period has been termed the Altithermal, the Xerothermic, and the Hypsithermal (41, 42). The term Altithermal connotes a dry climate as well as a warm period. It has been uncritically extended from the Great Basin, characterized by winter rainfall, to areas in the Southwest that have predominantly summer precipitation. Atmospheric circulation patterns that would result in dry conditions in the Great Basin are unlikely to cause summer droughts in the Chihuahuan Desert. The term Altithermal should be discarded or should be restricted to the northern Mohave Desert and Great Basin, where a warm and dry middle Holocene climate is documented (11, 16, 43). Summer rainfall in areas now characterized by summer monsoons probably was greater than at present because warmer global temperatures favor the development of the Bermuda High (28, 44). The present northern Chihuahuan Desert is relatively high in elevation and the present climate is marginal for desert-grassland or succulent desertscrub communities. Middle Holocene wet climates probably favored development of grass-

land. Widespread loss of well-developed, mature soils on bedrock during the middle and late Holocene probably augmented the development of xeric microhabitats and desert vegetation (45). The establishment of northern Chihuahuan desertscrub communities in the late Holocene is the most recent major vegetational change in the Southwest induced by climate.

Vegetational Dynamics

The ecological impact of Quaternary climatic changes in the Southwest traditionally has been expressed in terms of the elevational displacement of vegetation zones, with modern analogs being used to interpret fossil pollen spectra and macrofossil assemblages (4, 8, 46). Estimates of lowering of vegetation zones range from about 350 to 1000 m, with larger estimates at higher elevations and latitudes (7). However, simple vertical displacements are unrealistic because plant species responded differentially to climatic changes and not as community units. Modern analog communities with compositions similar to the fossil assemblages in middens are often difficult to find. Warm desert species such as catclaw, barrel cacti (*Echinocactus polycephalus* Engelm. & Bigel., *Ferocactus acanthodes* Brit. & Rose), and brittlebush (*Encelia farinosa* Gray, *E. frutescens* Gray) were common associates of late Wisconsinan woodland dominants in the Mohave and Sonoran deserts. Other xerophytes such as creosote bush and white bursage that now are common associates of the above desert species were uncommon or absent from these woodland assemblages. In southern Nevada and the Grand Canyon in Arizona, pinyon-juniper woodland now occurs below forest in the vegetational gradient. In the late Wisconsinan, juniper expanded much more than pinyon, and a pinyon-juniper zone may not have been present at all. In the Chihuahuan Desert, juniper woodlands and juniper grasslands are important communities on the upper peripheries of the desert. In the late Wisconsinan, pinyon-juniper woodlands were present at all elevations between 1500 m and the Rio Grande at 600 m, and xeric juniper communities have not been found.

In Davis' (19) recent summaries of the late Quaternary history of the eastern deciduous forest, she concluded that the plant communities have not yet reached equilibrium in response to postglacial climates. Lag times of differing durations have been observed for the estab-

lishment of several important tree species. Migration rates were differentially affected by successional processes such as dispersal capability, soil development, and biotic competition. In contrast, we conclude that new communities with relatively stable composition were established soon after climatic changes occurred in the Southwest. The most important difference between the Southwest and the Appalachian, New England, and mid-continent areas discussed by Davis is the low precipitation in the Southwest.

The vegetation zones in the Southwest are arranged vertically in an altitudinal moisture gradient, with drier desert communities below woodlands and with forests on the mountain tops. Mountains modify the local climate through orographically induced precipitation and adiabatically cooled temperatures. Mountains serve as both source areas and refugia for mesophytic plants in fluctuating environments. Most woodland species found in late Wisconsinan or early Holocene packrat middens in present desert areas are now living on mountains within 100 to 200 km of the site (Fig. 2). The forests of the Southwest are often restricted to montane islands of small areal extent and are potentially vulnerable to local extinctions. Dispersal of forest species can be expected to have occurred in the past when vegetation zones were lowered sufficiently for intermountain connections or when larger target areas increased the chances of long-distance dispersal. Brown's (47) work on the montane mammals of isolated mountains in the Great Basin suggests that dispersals of boreal species occurred in the late Wisconsinan and extinctions in the Holocene.

Changes in composition of montane plant communities during the Holocene were relatively minor because these communities adjusted quickly to climatic changes. Desert species persisted at low elevations in the southern Mohave Desert and around the Gulf of California, and at higher elevations in woodlands in the late Wisconsinan and early Holocene. Changes in abundance and dispersals of desert species, in some cases over fairly long distances, appear to have been rapid. We suggest that the rapid responses to climatic changes exhibited by desert and woodland species are related to an observation that their present distribution is highly dependent on precipitation. The present distributions of forest species apparently reflect differences in regional temperature regimes, as well as precipitation. Competition exists in all of

these communities, but competitive advantages are strongly related to local climatic regimes. The biota of the Southwest is far more stressed by the current climatic regimes than it was by the "rigors" of the late Wisconsinan climate.

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