

Reconstruction of past desert vegetation along the Colorado River using packrat middens

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Abstract

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The paleoecological reconstruction of Pleistocene deserts along the Colorado River of western North America is attempted using data from fossil packrat middens. The Colorado River drainage is set into a physiographic context along a gradient from the hyperarid Colorado Desert to the moist high elevations on the Colorado Plateau. The Pleistocene and modern distributions of individual plant species along this corridor are compared emphasizing records from the Picacho Peak area of the Colorado Desert and the eastern Grand Canyon.

In general, plant species are now distributed 700–900 m higher in elevation and 400–700 km further up-river than they were during the late Wisconsin, however, some plant species have not conformed to the general pattern emphasizing the individualistic nature of species distributions in time.

Introduction

The Colorado River forms the main drainage of the southwestern deserts of the United States. The river traverses magnificent canyons and stark deserts on its way from the peaks of the Rocky Mountains to the Gulf of California. In this paper, I will characterize the modern and late Wisconsin vegetation along this gradient from high peaks to hyperarid deserts.

The reconstruction of the Wisconsin vegetation will be accomplished using data from fossil packrat middens along the Colorado River corridor from the State of Colorado to Mexico. I will focus upon studies of the two areas along the gradient that I am most familiar with, the Colorado Desert and the Grand Canyon. These results will then be set into a larger context of fossil records along the river corridor. This paper will emphasize

the differences between late Wisconsin and modern vegetation rather than temporal aspects of vegetation change and paleoclimatic reconstructions which have been the subject of extensive speculation elsewhere (Van Devender and Spaulding, 1979; Spaulding et al., 1983; Betancourt, 1984; Spaulding, 1985; Cole, 1985; Van Devender et al., 1987).

Plant species in this paper are classified using the taxonomic ranks of Benson and Darrow (1981) except at higher elevations where Lehr (1978) is used. Benson and Darrow's (1981, p. 37) "conservative" use of specific ranks is more compatible with the actual information discernable from plant macrofossils, and aids in the understanding of regional processes.

The packrat midden method

Packrat middens are accumulations of debris resulting from the foraging and collecting

practices of cricetid rodents of the genus *Neotoma*. About twenty species of these North American rodents share in a curious habit of collecting debris (plant parts, bones, rocks) and carrying it back to their den area. Various known as packrats, woodrats, or go-atters, they are also called trade rats after their habit for "trading" the item they are carrying for the next item encountered. Packrat middens are the resulting "garbage pile" of debris surrounding and protecting the nest area (Finley, 1958).

The middens surrounding dens are often used as urination perches. The urine is especially viscous, perhaps because packrats often utilize water from succulent desert plants (Lee, 1963), containing high concentrations of resins and calcium oxalate. As a result, the middens can solidify into rocklike deposits, cemented together with a matrix of crystallized rat urine (Wells, 1976). The crystallized urine, often referred to as amberat, will form masses resembling hardened asphalt or molasses.

I believe that these solid (indurated) middens also serve a protective function of sealing the nest entrance against larger predators and that their construction may represent a behavioral adaptation to predation.

The packrat's habit of collecting plant parts and encasing them into a solid deposit is a bonus for paleoecologists. The crystallized urine not only envelops and mummifies the plant macrofossils but, as a result of its cohesiveness, can attach the midden deposit to a rock wall where it is suspended away from ground moisture. As long as the deposit remains dry, the plant parts concealed within will not decay. Furthermore, the surface of the amberat is hygroscopic, and cracks in middens will seal through a re-hydration of the surface during infrequent humid periods (Spaulding, 1985).

The attachment of an indurated midden to a rock wall also allows it be used as a geomorphological datum. The age of a midden gives a minimum age for the formation of that rock surface. Comparison of midden distribution and ages may yield estimates of erosion rates

for rock shelters (Cole and Mayer, 1982; Betancourt, 1984, p. 12).

Plant macrofossils

Midden deposits can survive longer than 50,000 years in suitable situations, and contain abundant plant macrofossils, many identifiable to the species level (Wells, 1976; Van Devender et al., 1987). This is important in a region dominated by plants from the sunflower, grass, and pea families and having an abundance of conifer species, most of which are difficult to distinguish using fossil pollen alone.

Midden assemblage can be thought of as a relevé representing approximately one hectare centered at the midden (Spaulding et al., 1990). Although packrats may travel as far as 100 m to collect some items, the midden most accurately reflects the plant species within about a 10–30 m radius of the site (Horton and Wright, 1944; Finley, 1958; Cole, 1981). Presence/absence data comparing the modern middens with the nearby vegetation show high similarity, and abundant plants are usually represented by abundant specimens (Cole and Webb, 1985).

This information on local vegetation can be further enhanced through the study of fossil pollen from middens (King and Van Devender, 1977; Davis and Anderson, 1988). Although local pollen may predominate, a regional pollen signal will also be present (Thompson, 1985). Because the macrofossil and pollen record emphasize different taxa and a different source area, the two records can be used to gain a more complete picture of paleovegetation. In addition, the study of the isotope geochemistry of plant macrofossils has potential for adding other paleoenvironmental information (e.g. Leavitt and Long, 1983).

Packrat middens also contain fossil bones, especially where they have been deposited in or near the roosts of raptorial birds (e.g. Mead and Phillips, 1981). Packrat middens have yielded such items as keratinaceous horn sheaths of extinct mountain goats (Mead, 1983), hooves of extinct equids, and dung of extinct ground sloths (Phillips, 1977).

Individualistic distributions along physiographic gradients

Because past plant associations are usually interpreted in the context of modern communities, paleoecological reconstructions are heavily influenced by the scientists' conception of modern plant communities. However, this perspective can be misleading as conceptual units defined in the present may have been less meaningful in the past. Many plants have been individually distributed in time (Davis, 1976; Birks, 1981). Some common plant associations probably developed only recently in the post-glacial and did not exist during the Wisconsin. Similarly, some past plant associations have no modern counterpart (Delcourt and Delcourt, 1985; Overpeck et al., 1985). Using a spatial analog for temporal change, the use of modern community concepts in the classification of paleocommunities is similar to classifying the vegetation of Utah using a key to Arizona plant communities. Some communities may fit well into the scheme, while others may defy clear classification.

An alternate strategy for paleoecological reconstruction is to consider the past individualistic distribution of species along physiographic gradients. Although, much else has changed, the basic physiography controlling the regional climatic gradients has changed little within the past 100,000 years. As a result, a physiographic context may be more useful for paleoenvironmental reconstruction than a biological context.

Two physiographic units which aid in the understanding of the past vegetation of the Colorado River drainage are the Colorado Desert and the Colorado Plateau.

The Colorado Desert

The Lower Colorado trough has been called the Colorado Desert (Jaeger, 1957), the lower Colorado Valley subdivision of the Sonoran Desert (Turner and Brown, 1982), and the Lower Colorado Valley (Shreve, 1951). This arid center of the North American deserts was known as "La Palma de la Mano de Dios" ("the

hollow of God's hand") to the Mexicans, but was named the Colorado Desert in 1853 by William Blake because it lay along the Colorado River (Jaeger, 1957).

The Colorado Desert forms the arid core of the North American Deserts. Within it, high temperatures combine with high summer insolation to produce mean annual values of pan evaporation exceeding 3658 cm, the highest on the continent (U.S. Geological Survey, 1970). Precipitation averages less than 50 mm/yr at many low elevation stations (Turner and Brown, 1982) and the area has the highest precipitation variability (>40%) on the continent (Van Royan, 1954). These arid conditions combine to create a precipitation/potential evapotranspiration ratio less than 0.03% (Fig.1), making it, and Death Valley, the only "hyperarid" deserts in North America (Meigs, 1953).

The Colorado Plateau

The Colorado Plateau is a high, broad plateau encompassing much of the northern portions of the states of Arizona and New Mexico and the southern portions of Utah and Colorado. The area has a distinctive geology (Hunt, 1956), and many unusual botanical features (Reveal, 1979). Physiographically, the Colorado Plateau represents the southeastern portion of the highlands between the Sierra Nevada and Rocky Mountains termed the Intermountain Region by Cronquist et al. (1972) and the Intermountain Plateau by Cole (1981) (Fig.2). This physiographic unit differs from the more southerly deserts in its higher elevation, its latitude, and its location in the rain shadow of the Sierra Nevada.

The concept of the Intermountain Plateau helps in explaining the abrupt northern border of the Mojave and Sonoran Deserts and the low species diversity of the western Great Basin. The elevational difference between the southern deserts and the Intermountain Plateau accentuates the latitudinal cline decreasing both summer and winter temperatures. The atmosphere, dried by its trip over the crest of the Sierra, can reach both higher

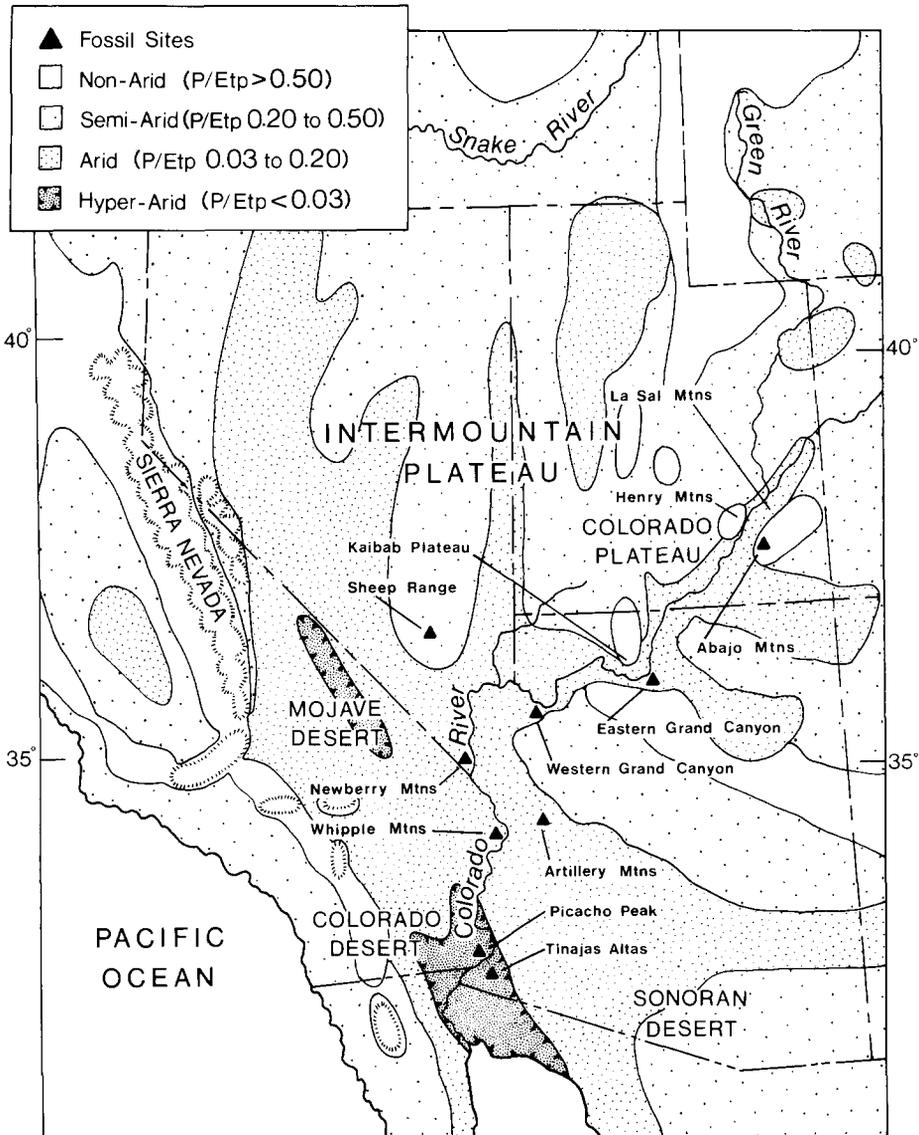


Fig.1. Map of the deserts of the southwestern United States as defined by the ratio of precipitation to potential evapotranspiration (modified from Meigs, 1953).

and lower temperatures increasing the continentality of climates on the Intermountain Plateau.

Results

Picacho Peak

Twenty five packrat middens from near Picacho Peak (Fig.2), demonstrate the Late

Wisconsin and early Holocene vegetation of this low elevation Colorado Desert site (Cole, 1986). Fossil middens from this site are listed with their radiocarbon dates and principal macrofossils in Table I and the major species present are shown in Fig.3.

This series is from the most xeric North American desert site with a Pleistocene midden record and it records the presence of desert scrub vegetation for the last 13,000 years.

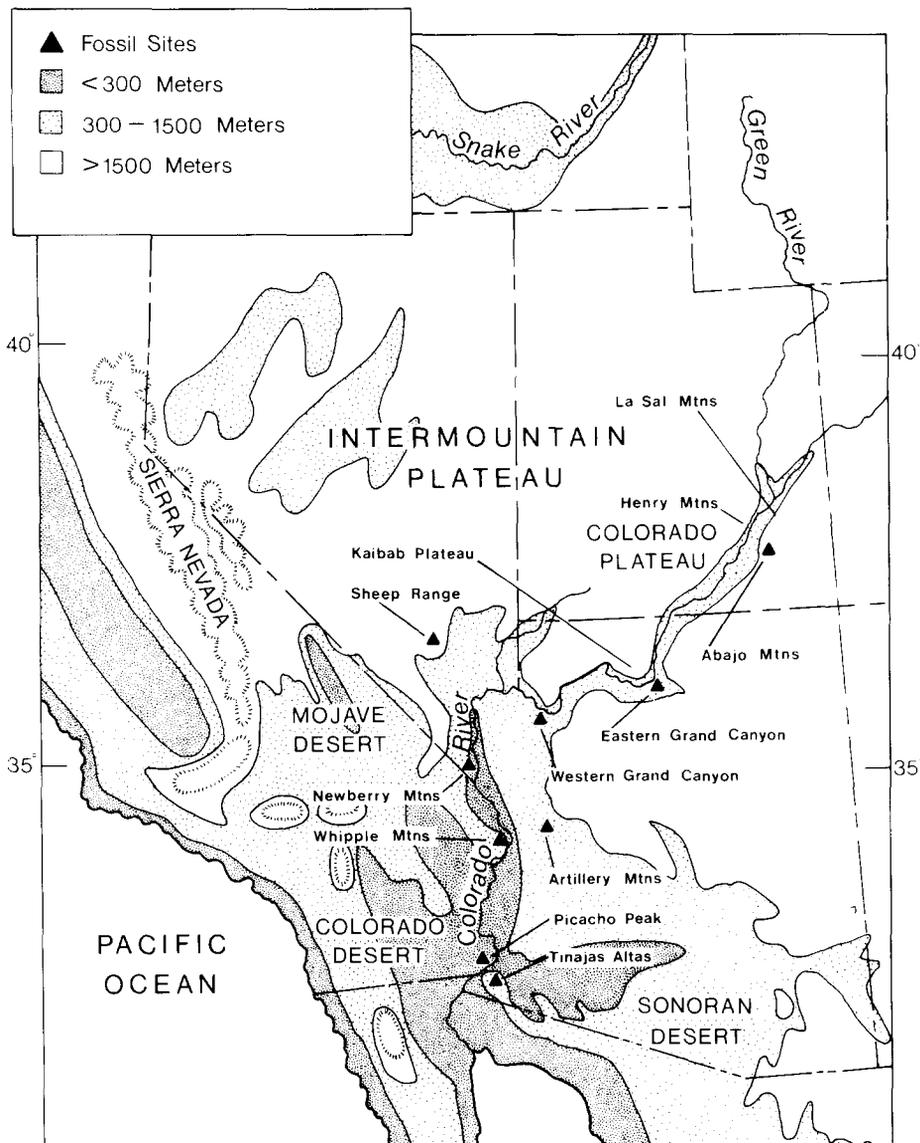


Fig.2. Map of the Colorado River corridor showing elevation and principal packrat midden sites adjacent to the Colorado River.

Precipitation is low at this site because of its low elevation (285 m), its position well away from mountain masses and the resultant orographic rainfall, and its location west of the main Arizona monsoon rains. However, the site is still very high in elevation compared to the Salton Trough and the broad expanse of low plains which existed around the head of the Gulf of California during the Pleistocene because of lowered sea levels.

Creosote bush (*Larrea tridentata*), a major dominant of all warm North American Deserts, is very abundant throughout the record. The oldest Pleistocene assemblage from this site contains fossils of plants which now grow further up the Colorado River such as Joshua tree (*Yucca brevifolia*) and black-brush (*Coleogyne ramosissima*). These two plants, present only in the oldest middens, disappear during the early portion of the Pleistocene-Holocene

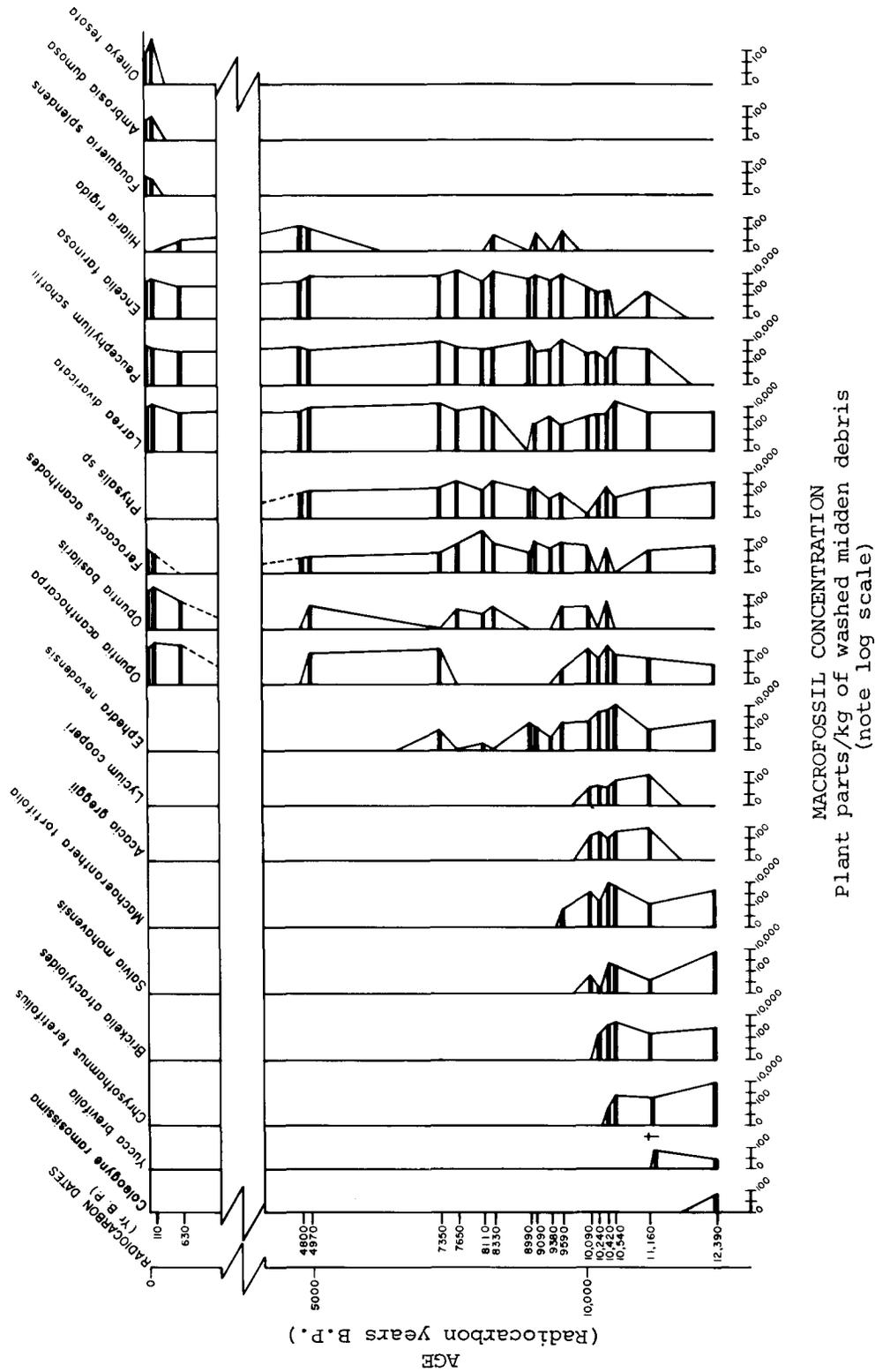


Fig. 3. Concentration of principal microfossils in the midden series from Picacho Peak, California. Note the logarithmic scale for concentration. Radiocarbon dates from Table I are shown at left. + = Possible contaminant. (From Cole, 1986).

TABLE I

Radiocarbon ages and principal fossil contents of 20 packrat middens from Picacho Peak, California

| Radiocarbon date (yr B.P.) | Midden number | Elev. (m) | Slope aspect | Principal macrofossils |
|----------------------------|---------------|-----------|--------------|------------------------------------|
| 12,390 ± 340* | 17D2 | 285 | NE | Chte, Samo, Latr, Mato, Cora, Yubr |
| 11,160 ± 190 | 15 | 275 | NE | Latr, Pesc, Acgr, Lyco, Chte, Samo |
| 12,500 ± 360* | 15 | 275 | NE | Yubr |
| 10,640 ± 320* | 15 | 275 | NE | Latr |
| 10,540 ± 250 | 23B | 280 | NE | Latr, Epne, Mato, Brat, Pesc, Acgr |
| 10,420 ± 110 | 17B | 285 | NE | Mato, Epne, Latr, Opac, Samo, Brat |
| 10,240 ± 220 | 16 | 245 | NE | Epne, Latr, Pesc, Acgr, Enfa, Mato |
| 10,090 ± 170 | 5D | 270 | SW | Latr, Mato, Opac, Pesc, Enfa, Epne |
| 9590 ± 190 | 6B | 280 | NE | Pesc, Enfa, Epne, Feac, Latr, Mato |
| 9380 ± 300 | 5B | 270 | SW | Pesc, Enfa, Latr, Feac, Epne, Opba |
| 9090 ± 150 | 26 | 280 | E | Enfa, Pesc, Feac, Latr, Epne |
| 8990 ± 110 | 22 | 300 | NW | Pesc, Enfa, Epne, Feac |
| 8330 ± 120 | 10 | 275 | SW | Enfa, Pesc, Latr, Feac, Opba |
| 8110 ± 160 | 8C | 275 | NE | Latr, Pesc, Feac, Enfa, Epne, Opba |
| 7650 ± 120 | 9B | 275 | SW | Enfa, Pesc, Latr, Feac, Opba |
| 7350 ± 90 | 17A | 285 | NE | Pesc, Latr, Enfa, Epne, Feac, Opac |
| 4970 ± 80 | 21 | 290 | NE | Latr, Pesc, Enfa, Opac, Opba, Hiri |
| 4800 ± 80 | 18 | 250 | NE | Pesc, Latr, Enfa, Hiri, Feac |
| 630 ± 140 | 11 | 275 | SE | Latr, Opac, Pesc, Enfa, Opba |
| 110 ± 40 | 24 | 280 | NW | Latr, Olte, Pesc, Opac, Opba, Enfa |
| modern debris | 25 | 280 | NW | Pesc, Latr, Opac, Olte, Enfa, Opba |
| modern debris | 7 | 270 | SW | Pesc, Latr, Opba, Opac, Enfa, Feac |

*Tandem accelerator mass spectrometer date. Laboratory numbers and dated materials are available in Cole (1986).

Key to macrofossils: Acgr = *Acacia gregii*; Brat = *Brickelia atractyloides*; Chte = *Chrysothamnus teretifolius*; Cora = *Coleogyne ramosissima*; Enfa = *Encelia farinosa*; Epne = *Ephedra nevadensis*; Latr = *Larrea tridentata*; Feac = *Ferocactus acanthodes*; Hiri = *Hilaria rigida*; Lyco = *Lycium* cf. *cooperi*; Mato = *Machaeranthera tortifolia*; Olte = *Olneya tesota*; Opac = *Opuntia acanthocarpa*; Opba = *Opuntia basilaris*; Pesc = *Peucephyllum schottii*; Samo = *Salvia mohavensis*; Yubr = *Yucca brevifolia*.

transition (ca. 12,000 yr B.P.), while other species such as Mojave sage (*Salvia mohavensis*) and rabbit brush (*Chrysothamnus teretifolius*) do not disappear until 10,000 yr B.P. Woody buckwheat (*Eriogonum fasciculatum*) and Mormon tea (*Ephedra nevadensis*) disappear during the early to middle Holocene.

Interesting aspects of this midden chronology include the presence of catclaw acacia (*Acacia gregii*) and peach thorn wolfberry (*Lycium cooperi*) on rocky slopes during the Pleistocene-Holocene transition. These plants are now restricted to washes in the area suggesting that during the early Holocene there was higher summer precipitation (Kutzbach, 1981; Spaulding and Grumlich, 1986) and/or deeper soils (Bull and Schick,

1979; Wells et al., 1987) upon these now bare slopes. These early Holocene assemblages of now riparian desert shrubs upon high slopes are similar to those found further to the east in the Sonoran Desert by Van Devender (1987).

The eastern Grand Canyon

Fifty-two packrat middens from the eastern Grand Canyon are listed with their radiocarbon dates and principal macrofossils in Table II. A generalized reconstruction of the vegetation zones of the Grand Canyon region during the last 24,000 years is shown in Fig. 4.

Most species occurred 600–1000 m lower in elevation than today during the late Wisconsin. However, the plant associations have

TABLE II

Radiocarbon ages and principal fossil contents of 52 fossil packrat middens from the eastern Grand Canyon

| Radiocarbon date (yr B.P.) | Midden name | Elev. (m) | Slope aspect | Principal macrofossils |
|----------------------------|-------------|-----------|--------------|------------------------------------|
| 950–1220 m | | | | |
| 34,300 ± 3570 | CC2 | 1100 | NE | Jumo, Opun, Juos, Artr, Agut, Prfa |
| 29,400 ± 1800 | CC3 | 1100 | NE | Jumo, Opun, Juos, Prfa, Rost, Atco |
| 17,400 ± 450 | HC4 | 1100 | SE | Juos, Atco, Oper, Symp, Artr |
| 16,400 ± 190 | GC1 | 1100 | NE | Juos, Opun, Atco, Rost, Chmi, Pttr |
| 13,800 ± 330 | HC3 | 1100 | E | Juos, Opun, Atco, Agut |
| 12,900 ± 200 | CC1* | 1100 | N | Juos, Opun, Fran, Enfr, Rhus, Ephd |
| 12,380 ± 370 | Ch3 | 970 | W | Juos, Oper, Atco, Artr, Symp, Cora |
| 12,030 ± 220 | HC8a | 1100 | W | Juos, Opun, Agut |
| 12,015 ± 365 | Ch4 | 970 | W | Juos, Oper, Agut, Artr, Cora |
| 10,760 ± 260 | BC1 | 950 | NE | Juos, Pttr, Feru, Fran, Eped, Opun |
| 10,150 ± 120 | HCl | 1100 | W | Juos, Ephd, Fran, Oper, Arlu, Prfa |
| 10,110 ± 100 | HC2a | 1200 | W | Juos, Ephd, Arlu, Pttr, Rhus, Fran |
| 9400 ± 270 | CL1 | 1220 | SW | Juos, Opun, Agut, Fran, Rhus |
| 8957 ± 96 | HM1 | 1100 | W | Juos, Fran, Pttr, Rhus, Oper, Arlu |
| 1345 ± 135 | Ch5 | 970 | W | Oper, Prju, Opba, Enfa, Ephd |
| < 1000 | HC2b | 1200 | W | Oper, Ephd, Rhus, Agut, Arlu, Yuan |
| < 1000 | HM1b | 1100 | W | Ephd, Enfr, Alwr, Oper, Opun, Prfa |
| 1400–1470 m | | | | |
| 20,630 ± 470 | HM11 | 1450 | W | Juos, Agut, Ribe, Atco, Rost, Opun |
| 18,630 ± 310 | HM6 | 1450 | W | Juos, Rost, Ribe, Psme, Atco, Hodu |
| 16,165 ± 615 | CH2 | 1450 | N | Psme, Abco, Artr, Juos, Symp, Ribe |
| 13,830 ± 790 | HM4 | 1470 | W | Juos, Rost, Opun, Ribe, Ephd, Atco |
| 13,780 ± 240 | Bi2 | 1450 | W | Opun, Psme, Abco, Rost, Ribe, Pifl |
| 14,170 ± 470 | Bi2 | | | |
| 13,540 ± 170 | HM7 | 1450 | W | Juos, Opun, Rost, Psme, Abco, Fran |
| 13,470 ± 420 | Bi8b | 1450 | W | Opun, Psme, Rost, Ribe, Abco, Pifl |
| 13,340 ± 150 | Bilc | 1450 | W | Juos, Rost, Opun, Psme, Oskn, Ribe |
| 12,600 ± 540 | Bilc | | | |
| 11,530 ± 290 | Bi8a | 1450 | W | Opun, Psme, Fran, Juos, Rost, Pifl |
| 10,290 ± 150 | Bi3 | 1450 | W | Juos, Oper, Pied, Fran, Agut, Ceoc |
| 8470 ± 100 | Bi4 | 1460 | W | Oper, Ephd, Juos, Agut, Fran, Cein |
| 6830 ± 175 | Ch1 | 1430 | N | Juos, Fran, Opun, Ephd, Agut, Pttr |
| 6800 ± 220 | Bi6b | 1450 | W | Oper, Agut, Juos, Ephd, Fran, Come |
| < 1000 | Ch10 | 1400 | W | Juos, Qutu, Prju, Ephd, Agut, Arlu |
| 1600–1900 m | | | | |
| 23,350 ± 1110 | Ch9 | 1770 | SW | Psme, Abco, Pifl, Juos, Rubu, Hodu |
| 18,800 ± 800 | Ch8b | 1770 | SW | Pifl, Psme, Abco, Artr, Hodu, Juos |
| 18,490 ± 660 | Ch8C | 1770 | SW | Pifl, Psme, Abco, Rubu, Hodu, Juos |
| 15,840 ± 310 | Cl2 | 1600 | NE | Psme, Abco, Juos, Pifl, Ribe, Rost |
| 14,050 ± 500 | Cl3 | 1600 | NE | Psme, Abco, Juos, Opun, Chmi, Oskn |
| 9070 ± 350 | CH7 | 1770 | NW | Psme, Pied, Juos, Fran, Qutu, Pipa |
| 8900 ± 340 | BC3 | 1900 | S | Juos, Psme, Pied, Pipa, Qutu, Pttr |
| 8590 ± 110 | BC2 | 1900 | S | Juos, Psme, Pied, Qutu, Pttr, Pipa |
| 8430 ± 400 | BC2 | | | |
| 7110 ± 180 | Ch8a* | 1770 | SW | Agut, Juos, Qutu, Cein, Psme, Pifl |
| 2300 ± 90 | Sul | 1620 | N | Juos, Pied, Fran, Pttr, Come, Cein |

TABLE II (continued)

| Radiocarbon date (yr B.P.) | Midden name | Elev. (m) | Slope aspect | Principal macrofossils |
|----------------------------|-------------|-----------|--------------|------------------------------------|
| 2000–2200 m | | | | |
| 23,385 ± 772 | Na9d | 2020 | S | Psme, Pifl, Abco, Pice, Juos, Juco |
| 18,130 ± 350 | Na9c | 2020 | S | Pifl, Psme, Pice, Abco, Juco, Hodu |
| 17,950 ± 600 | Na9b | 2020 | S | Pifl, Pice, Psme, Abco, Juco, Pamy |
| 12,660 ± 230 | Na6 | 2050 | NW | Psme, Pifl, Pice, Abco, Juco, Pamy |
| 13,110 ± 240 | Na6 | | | |
| 12,170 ± 210 | Na7a | 2050 | NW | Psme, Abco, Pifl, Pice, Juco, Pamy |
| 7870 ± 140 | Na9a | 2020 | S | Juos, Agut, Qutu, Pied, Ophh, Cein |
| 5510 ± 80 | GP4 | 2200 | N | Juos, Psme, Fran, Oper, Pied, Pipo |
| 1220 ± 70 | Na4 | 2070 | SW | Pied, Juos, Qutu, Agut, Cein, Rhus |
| 1170 ± 80 | Na10 | 2050 | NW | Pied, Psme, Pttr, Juos, Oskn, Qutu |
| < 1000 | GP6a | 2170 | W | Pied, Juos, Come, Artr, Cein, Psme |
| < 1000 | GP9 | 2170 | SE | Juos, Pied, Ephd, Oper, Agut, Cein |

*Midden contains contaminants.

Laboratory numbers and dated materials are available in Cole (1981).

Key to macrofossils: Abco = *Abies concolor*; Agut = *Agave utahensis*; Alwr = *Aloysia wrightii*; Arlu = *Artemisia ludoviciana*; Artr = *Artemisia tridentata*; Atco = *Atriplex confertifolia*; Cein = *Cercocarpus intricatus*; Ceoc = *Cercis occidentalis*; Chmi = *Chamaebatiaria millifolium*; Come = *Cowania mexicana*; Cora = *Coleogyne ramosissima*; Enfa = *Encelia farinosa*; Enfr = *Encelia frutescens*; Ephd = *Ephedra* sp.; Feru = *Fendlera rupicola*; Fran = *Fraxinus anomala*; Hodu = *Holodiscus dumosus*; Jumo = *Juniperus* cf. *monosperma*; Juos = *Juniperus californica* var. *osteosperma*; Opba = *Opuntia basilaris*; Oper = *Opuntia erinacea*; Ophh = *Opuntia phaeocantha*; Opun = *Opuntia* sp.; Oskn = *Ostrya knowltoni*; Pamy = *Pachystima myrsinites*; Pied = *Pinus edulis*; Pice = *Picea engelmannii/punens*; Pipo = *Pinus ponderosa*; Prfa = *Prunus fasciculata*; Prju = *Prosopis juliflora*; Psme = *Pseudotsuga menziesii*; Pttr = *Ptelea trifoliata* var. *pallida*; Qutu = *Quercus turbinella*; Rhus = *Rhus* sp.; Ribe = *Ribes* sp.; Rost = *Rosa* cf. *stellata*; Rubu = *Rubus* sp.; Yuan = *Yucca angustissima*.

Key to localities: BC = Bass Canyon; Bi = Bida Cave; CC = Cottonwood Canyon; Ch = Chuar Valley; Cl = Clear Creek; GC = Grapevine Canyon; GP = Grandview Point; HC = Hance Canyon; HM = Horseshoe Mesa; Na = Nankoweap (Novinger Butte); Su = Supai Formation above Horseshoe Mesa.

changed in character during the last 20,000 years. Some modern species of the Canyon such as pinyon (*Pinus monophylla/edulis*) and ponderosa pine (*P. ponderosa*) were not common enough to be sampled in Pleistocene middens and probably migrated into the canyon from the Mogollon Rim, or up the canyon during the Pleistocene–Holocene transition. Other species common in Pleistocene middens such as limber pine (*Pinus flexilis*), buffalo-berry (*Shepherdia canadensis*), mountain lover (*Pachystima mersinites*), and common juniper (*Juniperus communis*), shifted northward and are now absent or too infrequent to be represented in a midden record.

The assemblages present during the early Holocene were especially unique, unlike either the Wisconsin or modern ones. Low elevations supported a woodland of juniper (*Juniperus*

californica), single-leaf ash (*Fraxinus anomala*), and hop tree (*Ptelea trifoliata* var. *pallida*). High elevations contained a diverse forest including ponderosa pine (*Pinus ponderosa*) which rarely grows on such steep sites today. These unique assemblages, like the early Holocene assemblages at Picacho Peak, suggest higher summer precipitation and/or relictual Pleistocene soils.

The presence of ponderosa pine on steep sites and retention of juniper at low elevations (Van Devender, 1977) while pinyon migrated into its modern elevational range support a model of vegetational inertia (Cole, 1985). This model proposes that species may be remain at low elevations following a climatic warming by the retention of Pleistocene soils or simply by the presence of mature plants producing abundant propagules. However, new species invading an area may be retarded by competition with

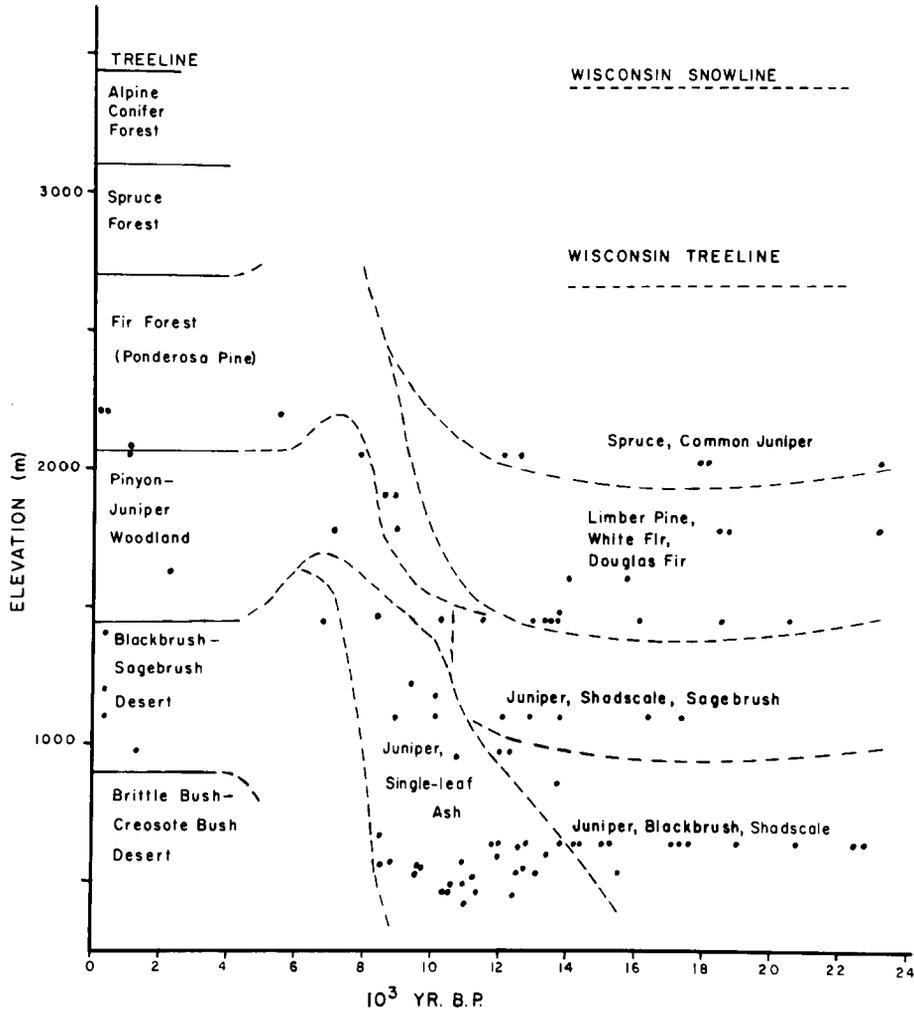


Fig. 4. Elevational zonation of major plant associations over the last 24,000 years from the Grand Canyon vicinity, Arizona (modified from Cole, 1985).

established plants despite their better adaptations to the climatic regime. As a result, migrational lags involve far more than seed dispersal. Dispersed seeds must be abundant and frequent enough that they can become established during infrequent favorable years and still compete with established, but perhaps relictual, vegetation.

Wisconsin distribution of selected species along the Colorado river gradient

The Picacho Peak and Grand Canyon records can be placed into a regional perspec-

tive through the consideration of other fossil localities along the river corridor. The Pleistocene records here are almost exclusively late Wisconsin in age (20,000–12,000 yr B.P.) and are used as the best approximation for distributions during the majority of the Wisconsin.

The modern and Pleistocene distributions of major trees and shrubs with respect to river distance and elevation are shown in Fig. 5. In general, species present in the Pleistocene middens are now located 700–900 m higher in elevation, and 400–700 km further upriver. However, individual plant species have responded in different ways to the climatic



Fig.5. Vegetational transect along the Colorado River during the late Wisconsin (24,000-12,000 Ka, "Pleistocene") and modern times.

and ecologic alterations of the last 15,000 years.

Spruce

Pleistocene spruce needles have been found at remarkably low elevations on sandstone in southeastern Utah in what is now arid desert. Betancourt (1990) reports needles of Colorado blue spruce (*Picea pungens*) at two sites near Glen Canyon at 1310 and 1390 m elevation. Blue spruce fossils are also common at Fishmouth Cave (1585 m) south of the Abajo Mountains (Betancourt, 1984). However, the proximity of streams or seep zones to these sites and the presence of xerophytic species in the assemblages suggest that the low elevation Pleistocene distribution of blue spruce was probably restricted to moist microhabitats on sandstone. In general, species reach lower elevations on sandstone than on limestone in both the modern associations and Pleistocene middens.

Englemann spruce (*Picea engelmannii*) is a frequent component of Pleistocene middens at the highest sampled elevations. It is abundant in middens from Allen Canyon Cave in the Abajo Mountains at 2195 m (Betancourt, 1984), and Nankoweap in the eastern Grand Canyon at 2020–2050 m (Cole, 1982, 1990). The Nankoweap sites are on limestone, well away from local seeps or travertine demonstrating that spruce must have been widespread at this elevation at least 500 m below its modern lower limit. It most likely was also distributed further downstream on high elevation portions of the Coconino and Shivwits Plateaus.

Limber pine

The dominant fossil in the higher elevation Late Wisconsin records from the Grand Canyon and Glen Canyon is limber pine. Needles of this tree are abundant in most Pleistocene middens above 1400 m, but surprisingly, it is now absent from the Grand Canyon, where it may be limited by high temperatures, low precipitation, or competition from other species. Limber pine often grows on rocky outcrops (Lepper, 1974) at low to mid-eleva-

tions in the Rocky Mountains (Peet, 1978). The Pleistocene lower limit of limber pine was 850–1000 m lower than its modern lower limit in the San Francisco Peaks, 100 km south of the Grand Canyon (Cole, 1981).

Douglas fir

Douglas fir (*Pseudotsuga menziesii*) is abundant in middle elevation Pleistocene middens from the Grand Canyon (Cole, 1981) and Abajo Mountains (Betancourt, 1984) where it was distributed about 720–800 m lower than today. Fossil Douglas fir needles have been identified from as far west as the Etna Locality in Meadow Valley Wash, Nevada (Spaulding, 1981; Wells, 1983) 100 km to the west of its modern distribution. However, it did not extend much farther into the arid Great Basin as it is not found in the Pleistocene record from the Sheep Range, slightly farther west (Spaulding, 1981).

True firs (*Abies* spp.) are often found within the same elevational zone as Douglas fir. White fir (*Abies concolor*) is associated with Douglas fir in the middens from the Grand Canyon, while sub-alpine fir (*Abies lasiocarpa*) is associated on the sandstone substrates in southeastern Utah (Betancourt, 1984).

Juniper

Juniper (*Juniperus californica* vars. *californica* and *osteosperma*) is usually the most abundant macrofossil in low elevation middens. Juniper seems to be a preferred food item of some, if not most, desert packrat species (Vaughn and Dial, 1990). My experience with modern midden deposits has led me to believe that at least a few juniper branchlets will be found in a midden if one tree is within 50 m of the nest site. Paleoclimatic reconstructions based upon juniper are complicated by the fact that California juniper (*Juniperus californica*) and Utah juniper (*J. californica* var. *osteosperma*) are not readily distinguishable using branchlets alone, especially in the lower Colorado River drainage where their modern ranges are adjacent. The difference may be critical as California juniper can grow as low

as 1000 m in the Colorado Desert and is often a desert shrub, while Utah juniper is typically found above 1200 m as part of the pinyon–juniper woodland. Because of these taxonomic problems and the packrats predilection for juniper, the presence of a few juniper branchlets in a midden dominated by fossils of desert shrubs may not necessarily represent a “woodland”, especially if the other macrofossils are all desert shrubs.

During the Wisconsin, juniper grew at or near base level along much of the Colorado River below Glen Canyon. Juniper branchlets are the dominant Pleistocene macrofossil from Stanton’s Cave, at 927 m elevation in the eastern Grand Canyon (Hevly, 1984) and were dominant in the lowest packrat middens throughout the Grand Canyon (Cole, 1982; Van Devender and Mead, 1976; Phillips, 1977).

The Wisconsin lower elevational limit of juniper seems to have been about 300 m. It is present in fossil middens as low as 320 m near the Whipple Mountains (Wells and Hunziker, 1976) but is absent from the Picacho Peak series (245–285 m). The lowest record for juniper is 240 m from the Butler Mountains (Van Devender et al., 1987), just west of the Tinajas Altas.

Calculating the elevational displacements of juniper is complicated by the different elevational limits of varieties on different substrates and edaphic situations. In the western Grand Canyon, modern juniper woodland is more than 1000 m higher in elevation than the Wisconsin middens containing juniper (Phillips, 1977). However, there are also isolated junipers at seeps within the elevational range of the middens (Phillips, 1977, p. 61). The cooler and/or wetter climate of the Wisconsin surely would have concentrated more moisture at these seeps and within the shaded canyons. On the other hand, the Picacho Peak site is located well away from cliffs and large drainages, and may only lack juniper because it lacks moist microhabitats.

One other juniper species, Rocky Mountain juniper (*Juniperus scopulorum*), is present at

high elevation sites, especially on sandstone above the eastern Grand Canyon (Betancourt, 1990).

Pinyon pine

The past and present distribution of the pinyon pines (*Pinus edulis*, *P. monophylla*) demonstrate changes more complex than can be explained using simple elevational displacement (Betancourt, 1987). Today pinyon dominates the middle elevations in the Grand Canyon, but it is only present in two Pleistocene middens, both in the western Grand Canyon (Van Devender and Spaulding, 1979; Phillips, 1977). During the Wisconsin, the Grand Canyon was probably near the upstream and northerly limits of pinyon, and although small unrecorded populations may have been present, it was not abundant enough to have been sampled in fossil middens above the middle Grand Canyon (Cole, 1990). Pinyon was more widespread at middle to high elevations in the Colorado Desert as demonstrated by the fossils collected from the Newberry mountains (Leskinen, 1975), the Tinajas Atlas Mountains, and the Whipple Mountains (Van Devender et al., 1987).

The midden data suggest that pinyon has expanded as much as 800 km upriver and 600 km to the north while retreating northward from its more southerly fossil localities (Van Devender et al., 1987). Other fossil records indicate that it was present south of the Grand Canyon along the Mogollon Rim during the Wisconsin (Jacobs, 1985) and that it occurred as close as Wupatki National Monument, 50 km south of the canyon, during the Wisconsin–Holocene transition (Cinnamon and Hevly, 1988).

Ponderosa pine

Despite its large modern range across the Colorado Plateau, ponderosa pine was also absent, or too infrequent to be recorded, along the Colorado River during the Late Wisconsin. The absence of this species suggests summer-dry conditions during the Late Wisconsin as it can tolerate cold, but not dry conditions,

as indicated by its absence today from the summer-dry interior of the Great Basin.

Sagebrush

Sagebrush (*Artemisia* cf. *tridentata*) is a frequent macrofossil in Pleistocene middens along much of the Colorado River. This plant has unpalatable, resinous leaves and is not known to be a preferred food item of packrats. In addition, the plant usually grows on fine-grained substrates (clay, shale, or fine-grained alluvium) well away from the rocky outcrops where middens are located. Despite these factors which would make sagebrush unlikely to be a frequent macrofossil, it is still well represented in some fossil middens. Sagebrush leaves are especially abundant in Pleistocene middens from the Tapeats Sandstone (ca. 1100 m) in the eastern Grand Canyon, suggesting dominance on the Tonto Platform. Sagebrush pollen is the dominant taxa in the Pleistocene sediments of Stanton's Cave (Hevly, 1984) in the eastern Grand Canyon, and Rampart Cave in the western Grand Canyon (Martin et al., 1961). Sagebrush pollen is also abundant in the Pleistocene middens from the Colorado Desert and Pleistocene macrofossils of sagebrush have been found as low as 365 m in the Whipple Mountains (King and Van Devender, 1977).

Species of sagebrush with tridentate leaves have a wide modern distribution, but they are most dominant in plant communities above the Grand Canyon. The fossil records from packrat middens and pollen suggest that sagebrush was much more abundant at middle to low elevations during the Pleistocene.

Shadscale

A frequent associate of sagebrush on fine-grained substrates, shadscale (*Atriplex confertifolia*) has been found in many of the same Pleistocene middens. It is abundant in middens from the middle (Cole, 1982), and low (Mead and Phillips, 1981) elevations of the Grand Canyon and from middens above 600 m in the Kofa and New Water Mountains, 100 km south of the Artillery Mountains (King and Van Devender, 1977).

Blackbrush

Blackbrush (*Coleogyne ramosissima*) is abundant today at middle elevations in the upper Colorado River corridor. Its northern extent is limited by the relatively high elevations over the rest of the Intermountain Plateau. Late Wisconsin fossils have been recovered from the lowest portion of the eastern Grand Canyon (970 m, Cole, 1981), downriver all the way to Picacho Peak, near the Gulf of California (275 m, Cole, 1985). Both the upriver and southerly limits have migrated 500–700 km up the river, and 700 m upslope, since the Wisconsin.

Shrub live oak

Shrub live oak (*Quercus turbinella*) is not found in the Pleistocene records of the Grand Canyon, but is present in middens from the Whipple and Artillery Mountains (King and Van Devender, 1977). The presence of this chaparral species at high elevations in the Colorado Desert suggests a cooler, equable, climate for this area (Van Devender and Spaulding, 1979). The absence of this species and other chaparral elements from the Pleistocene Grand Canyon, coupled with the abundance of shadscale and sagebrush, suggests a cold/dry, continental climate (Cole, 1982).

Creosote bush

Creosote bush (*Larrea tridentata*) is now an omnipresent shrub in the low elevation deserts. Although it may be a recent disjunct from South America (Wells and Hunziker, 1976), it was present during the Wisconsin along the lowest elevations of the Colorado River. Van Devender et al. (1987) reported a radiocarbon date of $18,700 \pm 1050$ yr B.P. (AA-536) on creosote bush from the Tinajas Altas, and Cole (1985) reported a date of $12,390 \pm 340$ yr B.P. (AA-578) from Picacho Peak. Both dates were obtained from *Larrea* leaves with a Tandem accelerator mass spectrometer (Van Devender et al., 1985).

Pollen identified as *Larrea* was identified in Pleistocene sloth dung from a lower level of Rampart Cave (Martin et al., 1961). This

record, although only a tentative identification (P.S. Martin, pers. comm., 1988), may come from early to mid-Wisconsin levels. Plant cuticles from sloth dung from Gypsum Cave, 75 km to the west of Rampart Cave, were also identified as creosote (Laudermilk and Munz, 1934).

The upper elevational limit of creosote in the Wisconsin was probably around 500 m although it has not been found in any middens above 330 m. It grows well on flat alluvium well away from midden deposits and may have been more widely distributed than midden records indicate. Today creosote bush grows up to 1220 m in elevation, suggesting a vertical displacement of from 720 to 910 m. During the Holocene, it has migrated about 400 km up the Colorado River and may still be in the process of moving upstream. Creosote reaches up to 600 m above river level near its up-stream limit (Martin, 1971). This suggests that it may be migrating in a "front", not strictly limited by climate, but rather by its slow migrational advance into an area with marginal rates of seedling establishment.

Discussion

Individualistic distributions in time and space

Reconstructions of paleovegetation from packrat middens often emphasize the individualistic nature of vegetational response to climatic change. For example, the Wisconsin abundance of limber pine on the Colorado Plateau and the modern dominance of ponderosa pine contrast with other species which have simply migrated up the river corridor in response to the warming climate. Some plants, such as single leaf ash, appear to have a wider modern than Wisconsin distributions. Other plants, such as desert spanish bayonet (*Yucca whipplei* var. *caespitosa*), had wider distributions during the Wisconsin.

The individualistic nature of plant distributions through time comes as little surprise to ecologists who see modern distributions in space as individualistic (Gleason, 1926; Whittaker, 1975). Because the landscape of western

North America is mountainous, major changes in temperature and precipitation are reflected differentially in different places producing past communities with no modern analog. For example, the Wisconsin association of spruce and xerophytic species such as *Yucca angustissima*, *Opuntia polyacantha*, and *Ephedra* near the Abajo Mountains (Betancourt, 1984) probably resulted from the presence of moist seeps in alluvium adjacent to dry sandstone outcrops. Although the canyons of southeast Utah do not extent high enough to support this association today, a parallel is present where pinyon and juniper persist at the base of rock walls supporting *Cercocarpus intricatus*, blackbrush, and other desert shrubs.

Past associations with no modern analog have been often reported (Overpeck et al., 1985). Conversely, some modern communities, such as the ponderosa pine forest, may have had no past analog. These no past analog communities are difficult to verify as our paleovegetational record is not yet complete enough for the negative evidence to be convincing.

Physiographic ecotones

Despite the individualistic movements of species, sharp changes in community structure usually occur at the same places in the Wisconsin assemblages as in the modern vegetation (Cole, 1990). Ecotones, whether between local assemblages or between major biomes, occur at major breaks in physiographic continua. These major breaks were probably present during the Wisconsin as they are today. For example, the low Mojave Desert communities of the late Wisconsin appear to have been limited to those areas which are now hyperarid (Fig.1). The higher elevation Mojave Desert communities filled much of what is now the Colorado and Sonoran Desert (Van Deventer, 1990).

Conclusions

Plant macrofossils from fossil packrat middens are ideal for reconstructing past distribu-

tions of plant species because of the precision in plant identification and location of the past assemblages along the elevational gradient. Along the Colorado River corridor, most plant species are now distributed 700–900 m higher in elevation and 400–700 km further up-river than they were during the late Wisconsin. However, plant species seem to be individualistically distributed in time as some species did not conform to this general pattern.

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