

Comparison of pollen and macrofossils in packrat (*Neotoma*) middens: A chronological sequence from the Waterman Mountains of southern Arizona, U.S.A.

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ABSTRACT

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Pollen percentages in moss polsters and soil samples were compared with percent plant cover along 30-m transects in desertscrub vegetation, Waterman Mountains, Arizona, in the northeastern Sonoran Desert. These data were used to interpret pollen assemblages and associated plant macrofossils from 14 packrat (*Neotoma* sp.) middens radiocarbon dated from 1320 to 22,450 yr B.P.

A macrofossil:pollen index (*MPI*) was used to compare the presence and relative abundances of pollen and macrofossils in midden samples. In general, pollen and macrofossils from Sonoran Desert middens reflect similar vegetation signals. Calculation of Sørensen's Similarity Index (*SI*) comparing the presence or absence of midden pollen and macrofossils indicates greater similarities for Sonoran desertscrub than pinyon-juniper woodland. *SI* values from the Waterman series are greater for all age samples, compared to samples from other desert locations, perhaps reflecting greater species richness and summer rainfall in the northeastern Sonoran Desert.

The pollen and macrofossil assemblages reflect a middle and late Wisconsin (22,450–ca. 11,500 yr B.P.) pinyon–juniper woodland with sagebrush and Joshua tree on limestone slopes. A transitional early Holocene juniper woodland/chaparral was replaced by 8900 yr B.P. by a mesic Sonoran desertscrub of saguaro, catclaw acacia, blue paloverde and velvet mesquite. The presence of the latter three on exposed rocky locations, now restricted mostly to riparian washes, indicates moister conditions during the middle Holocene than today. Essentially modern vegetation developed by ca. 4000 yr B.P. Changes over the last ca. 1300 years suggest that modern climate is the most xeric in the entire record.

Introduction

In the American Southwest paleoecological analysis was pioneered using pollen assemblages from pluvial lake and marsh sediments (references in Martin, 1963; Martin and Mehringer, 1965). The use of pollen assemblages to characterize paleovegetation fell largely into disuse within the drier portions of the region with the discovery and expansion of the analyses of plant macrofossils preserved in packrat or wood rat (*Neotoma* spp.) middens (see references in Van Devender et al., 1987; Betancourt et al., 1990). One investigator

even suggested that analysis of companion pollen assemblages from packrat middens would be “redundant,” because more specific identifications could be obtained from analysis of the macrofossil assemblages alone (Wells, 1976). However, other workers have shown that examination of pollen within middens provides complementary information on species presence (King and Van Devender, 1977). While macrobotanical remains in middens come largely from the rocky habitat within the packrats' foraging range of about 30 m (Finley, 1958), midden pollen represents both local and regional vegetation (Davis and Anderson, 1987).

Whether pollen input into packrat middens is predominantly from local, extralocal, or regional sources is in dispute (King and Van Devender, 1977; Thompson, 1985; Davis and Anderson, 1987, 1988; Van Devender, 1988). Separating these sources is problematic and important in the reconstruction of paleocommunities.

In this paper we focus on the interpretation of pollen from fossil middens from the northeastern Sonoran Desert of southern Arizona (Fig. 1). Modern pollen from moss polsters and soil are compared to coverage of plants on line-intercept transects to assess the relationship of pollen to vegetation in Sonoran desertscrub. Pollen from the packrat middens was compared with the associated plant macrofossils using similarity and macrofossil pollen indices to understand the inherent biases in

both analytical methods. The combined pollen and macrofossil record from the middens are used to reconstruct the local vegetation and climate of the Waterman Mountains for the last 22,450 years.

Similar techniques can be used to extract additional paleoecological information from middens found in other regions of the world. Animals that construct middens of plant debris are found in Africa, the Middle East and Australia (Fall et al., 1990; Nelson et al., 1990; Scott, 1990). Pollen analysis could become part of basic research in those regions as well.

Environmental Setting

The Waterman Mountains are a desert range just south of Silver Bell and 40 km west-northwest

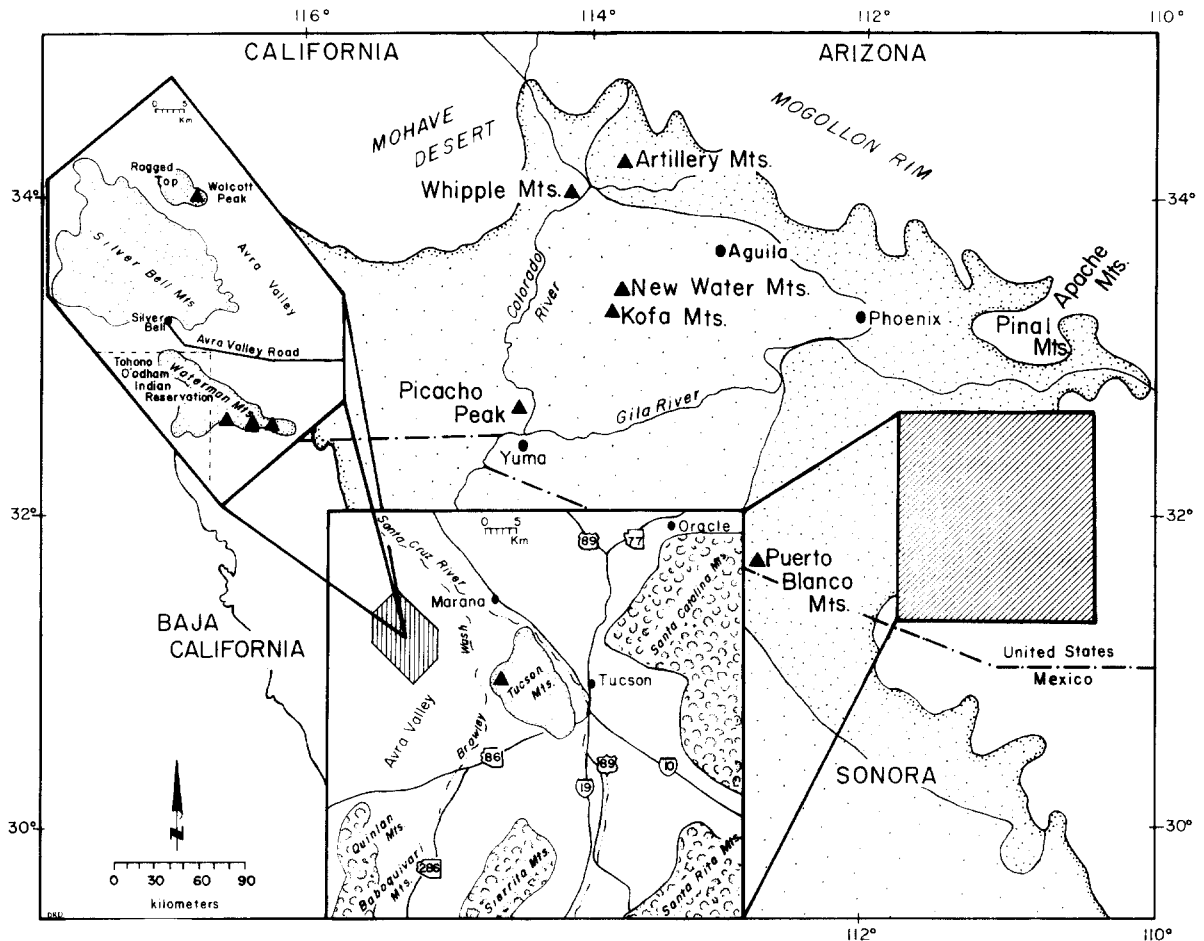


Fig. 1. Map of areas discussed in the text. Limits of the Sonoran Desert after Shreve (1964).



Fig.2. East end of limestone ridge in Waterman Mountains study area, Pima County, Arizona. Vegetation is an Arizona-Upland Sonoran desertscrub. Trees scattered on slope are *Cercidium microphyllum* (foothills paloverde). Shrubs are mostly *Parthenium incanum* (mariola) with occasional *Encelia farinosa* (brittlebush) and *Ambrosia deltoidea* (triangleleaf bursage). *Carnegiea gigantea* (saguaro) is at lower left. Packrat midden from vertical crevice in cliff was radiocarbon dated at 22,450 yr B.P. Macrofossils of *Pinus monophylla* (singleleaf pinyon) and *Juniperus* spp. (junipers) indicate a pinyon-juniper woodland was in the area in the middle Wisconsin glacial period.

of Tucson in Pima County, Arizona (Figs.1 and 2). The range is a northwest-southeast ridge that is approximately seven kilometers long by four wide, and ranges from 730 m to 1180 m elevation. It is bound on the east by the Avra Valley and on the north by the granitic and volcanic Silver Bell Mountains. The western half of the range is on the Tohono O'odham (=Papago) Indian Reservation. Geologically, the Watermans are an isolated block of Paleozoic Concha limestone that has been uplifted, tilted and highly fractured. The dissolution of the calcareous rocks has left occasional rockshelters and vertical crevices along joints that are dry enough for the deposition and preservation of packrat middens.

The climate of the Waterman Mountains is characteristic of the northeastern Sonoran Desert with infrequent winter freezes, hot summers and biseasonal rainfall (Sellers and Hill, 1974; N.O.A.A., 1980). During summer, equatorial heating strengthens the Bermuda High. Air masses move to the northwest across northern Mexico, Texas, and New Mexico and to the north-northeast from the Gulf of California providing summer monsoonal precipitation. In winter, precipitation

arrives from frontal storms moving east from the Pacific. The mean annual precipitation for Silver Bell at 825 m elevation is 312 mm/yr with 51.3% falling from July through September. Mean temperatures are 27.4°C annual, 17.3°C for January and 37.3°C for July. Recorded extremes are -8.3°C and 44.4°C. Winter freezes are infrequent, occurring a few times each winter.

The Sonoran Desert is the arid and semiarid subtropical area centered around the Colorado River and the Gulf of California in southwestern Arizona, southeastern California, northwestern Sonora and much of the Baja California Peninsula (Shreve, 1964; Brown and Lowe, 1980; Fig.1). The Waterman Mountains are in the relatively well-watered Arizona Upland Subdivision of the northeastern Sonoran Desert (Shreve, 1964; Turner and Brown, 1982). The vegetation on rocky slopes and bajadas in the study area at 730-795 m elevation is a diverse, mixed desertscrub dominated by *Cercidium microphyllum* (foothill paloverde), *Olneya tesota* (ironwood), and *Carnegiea gigantea* (saguaro) with *Acacia constricta* (whitethorn), *A. greggii* (catclaw) and *Prosopis velutina* (velvet mesquite) occasional along riparian washes and at

shady cliff bases. Important composites in the community include *Ambrosia deltoidea* (triangle-leaf bursage), *Brickellia baccharidea* and *B. coulteri* (brickell bushes), *Encelia farinosa* (brittlebush) and *Parthenium incanum* (mariola). Other prominent shrubs include *Aloysia wrightii* (oreganillo), *Ephedra nevadensis* (Mormon tea), *Fouquieria splendens* (ocotillo), *Larrea divaricata* (creosotebush), *Lycium berlandieri* and *L. parishii* (wolfberries) and *Hyptis emoryi* (desert lavender). Cacti are conspicuous including *Carnegiea gigantea*, *Ferocactus cylindraceus* (California barrel cactus) and *Opuntias*, both cylindropuntias or chollas (*O. acanthocarpa*, *O. bigelovii*, *O. fulgida*, *O. leptocaulis*) and platyopuntias or prickly pears (*O. chlorotica*, *O. phaeacantha*).

Relatively few additional species occur on the xeric slopes of Waterman Peak above the study area. Most of the range supports paloverde-saguaro desertscrub; a small area of relict desertgrassland is on the north slope of Waterman Peak. The bottom of Avra Valley (580–670 m) a few kilometers to the east originally supported a simple desertscrub dominated by *Larrea divaricata* and *Ambrosia dumosa* (white bursage) on sandy soils. Large areas of Avra Valley have been converted to agricultural fields and disturbance communities.

Methods

Modern vegetation was characterized by three 30 m line-intercept transects on the north slope, and two on the south side of the ridge. The percentage of the line covered by each species provides an estimate of its importance in the vegetation (Mueller-Dombois and Ellenberg, 1974). Total coverage can exceed 100%; subtraction of overlap gives the percent of ground cover.

Modern pollen samples were collected on 13 August 1987 adjacent to each of the vegetation transects in order to compare modern pollen and vegetation. Moss polsters were preferred over soil samples. Available evidence suggests that polsters integrate pollen deposition over as many as 15 years (Davis, 1983), thus averaging season to season variation. Potter and Rowley (1960) indicated that composition of the soil pollen assemblage is highly dependent upon season of collection. Single

polsters were collected along four transects; 15 soil sample pinches were taken and subsequently mixed along the south slope transect (SS in Figs.3 and 4; see Adam and Mehringer, 1975).

The modern and fossil pollen assemblages were processed using a modified Faegri and Iversen (1975) technique, with the addition of *Lycopodium* spores for calculation of pollen concentration (Stockmarr, 1971). The resulting assemblages were mounted in silicone oil. Usually 300 grains (minimum of 250) exclusive of native spores were counted for the pollen sum. Grains were identified by comparison to the reference collection at the Laboratory of Palynology, Northern Arizona University, as well as published sources. The following identification conventions were used: *Boerhaavia*-type includes *Commicarpus scandens*; *Cirsium*-type includes *Psilostrophe*; Euphorbiaceae includes *Argythamnia* (= *Ditaxis*) and *Euphorbia* (subgenera

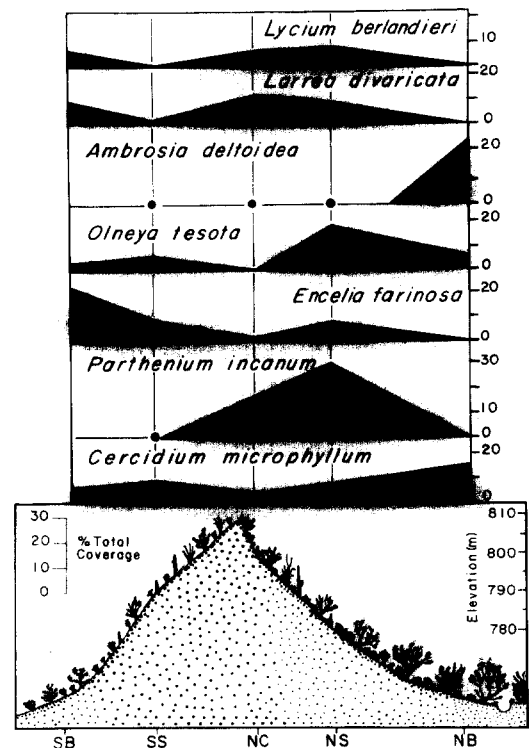


Fig.3. Percent coverage for the seven most important woody plants in a south-north vegetation transect over a limestone ridge in Waterman Mountains. Transect codes after Table II: SB=south base, SS=south slope, NC=north cliff, NS=north slope, NB=north base.

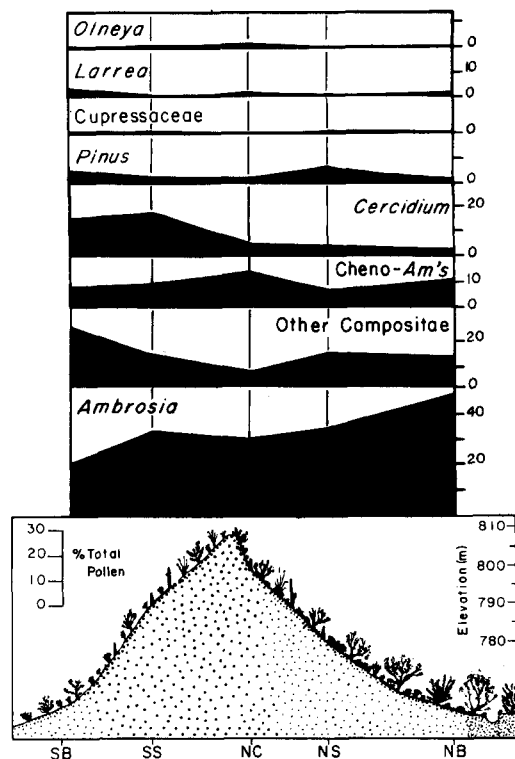


Fig.4. Percent of total pollen for the six most common pollen types from moss polsters and soil samples in south-north transect over a limestone ridge in Waterman Mountains. Transect codes after Table II: SB=south base, SS=south slope, NC=north cliff, NS=north slope, NB=north base.

Chamaesyce and *Poinsettia*) but not *Croton* or *Jatropha*; *Ferocactus*-type includes *Echinocactus*; *Sphaeralcea*-type includes *Abutilon* and *Herissantia*; Other Compositae includes all long-spined taxa but not *Ambrosia*, *Artemisia*, *Cirsium*-type, or *Trixis*. Percentages of plant coverage and pollen both reflect the local vegetation. Note, however, that pollen percentages for the various taxa are mutually dependent (Davis, 1963), whereas percent plant cover for one species is unrelated to that of another within the same transect or set of transects.

A series of 14 packrat middens were dated and analyzed from rockshelters at 795 m elevation in the Waterman Mountains. Most of the middens were found in shelters on the north- and south-facing slopes of a limestone ridge, with a single sample from an east slope (Table I). Twenty radiocarbon dates ranging from 22,450 to 1320 yr B.P. were obtained on packrat pellets and plant debris

(Table I). Small samples were dated with the Accelerator Mass Spectrometer (AMS) to confirm or refute unusual associations and detect possible contaminants. Concordant dates were averaged to give composite dates following Long and Rippe-teau (1974). Two dates revealed contamination by older materials and were not averaged.

The fossil packrat middens were processed by disaggregation in water, dissolving the amberat (urine) matrix and freeing the plant debris. The resulting plant materials were wet-sieved through a 20-mesh (850 μ m) sieve, washed, dried, sorted under a dissecting microscope and identified using reference specimens in the University of Arizona Herbarium. Voucher specimens for 195 species growing in the Waterman Mountains were deposited in the University of Arizona Herbarium.

Results: Modern pollen and vegetation

Modern vegetation and pollen data were collected to determine the pollen representation of the local vegetation relative to source distance. These data facilitate vegetation reconstruction from the midden series. Coverage of vegetation on the five 30-m transects ranged from 55.5% to 105.9% (av. 78.7%). The vegetation on exposed bedrock on the steep south slope was more open (60.7% exposed surface) than the talus of the north slope (29% exposed surfaces; Table II, Fig.3). Fifty plant species in 21 families were identified on the transects on 13 and 19 August 1987. Winter-spring annuals were missed because of time of sampling; however, the absence of summer annuals was probably due to severe summer drought. An intensive survey of the flora of the entire Waterman Mountains over several years and seasons yielded 246 species of vascular plants in 58 families (Van Devender, unpubl.). The most important families are Compositae (15.2%), Gramineae (14.8%), Euphorbiaceae (6.6%), Cactaceae (5.3%) and Leguminosae (5.3%). A total of 105 species in 37 families were found in rocky habitats within 30 m of the six packrat midden rockshelters. The most prevalent families near the midden sites are Gramineae (17.1%), Cactaceae (9.5%), Compositae (8.6%), Euphorbiaceae (6.7%), Malvaceae (6.7%) and Leguminosae (4.8%).

TABLE I

Radiocarbon dates from packrat middens from the Waterman Mountains, Pima County, Arizona. * = dates on obvious contaminants

Sample	Slope	Date (yr B.P.)	Lab. no.	Material dated
Pollen-Macrofossil Zone I				
WAM 13A1	East	22,450 ± 640	A-5116	Midden debris
WAM 9A1	South	22,380 ± 380	A-4776	<i>Neotoma</i> sp. fecal pellets
WAM 2	Northeast	21,510 ± 240	AA-2497	<i>Juniperus</i> sp. twigs
		17,030 ± 380	A-4710	<i>Neotoma</i> sp. fecal pellets
		19,270 ± 205	av. AA-2497 & A-4710	
WAM 1B	North	12,690 ± 150	A-4552	<i>Neotoma</i> sp. fecal pellets
WAM 1D	North	12,530 ± 140	A-4551	<i>Neotoma</i> sp. fecal pellets
Pollen-Macrofossil Zone II				
WAM 11B	South	11,740 ± 110	AA-3577	<i>Prosopis velutina</i> seeds
		11,280 ± 150	A-5069	<i>Neotoma</i> sp. fecal pellets
		11,510 ± 90	av. AA-3577 & A-5069	
WAM 9A2	South	11,470 ± 170	A-4777	<i>Neotoma</i> sp. fecal pellets
WAM 9B	South	9920 ± 130	A-4778	<i>Neotoma</i> sp. fecal pellets
Pollen-Macrofossil Zone III				
WAM 9C	South	*11,560 ± 120	AA-3258	<i>Juniperus</i> sp. twigs, seeds
		8910 ± 110	A-4779	<i>Neotoma</i> sp. fecal pellets
WAM 10	South	*10,070 ± 100	AA-3259	<i>Juniperus</i> sp. twigs, seeds
		8360 ± 135	AA-3353	<i>Stipa speciosa</i> florets
		8260 ± 130	A-4780	<i>Neotoma</i> sp. fecal pellets
		8310 ± 95	av. AA-3353 & A-4780	
		*1100 ± 80	AA-3270	<i>Cercidium microphyllum</i> twig
WAM 12A	South	6195 ± 80	AA-3578	<i>Larrea divaricata</i> twigs
		5920 ± 120	A-5070	<i>Neotoma</i> sp. fecal pellets
		6060 ± 65	av. AA-3578 & A-5070	
WAM 9D	South	5540 ± 70	A-4781	<i>Neotoma</i> sp. fecal pellets
		4845 ± 80	AA-3354	<i>Stipa speciosa</i> florets
		5190 ± 55	av. A-4781 & AA-3354	
Pollen-Macrofossil Zone IV				
WAM 5	Northeast	3880 ± 80	A-4708	<i>Neotoma</i> sp. fecal pellets
WAM 1A	North	2600 ± 40	A-4559	<i>Neotoma</i> sp. fecal pellets
WAM 1E	North	1320 ± 45	A-4558	<i>Neotoma</i> sp. fecal pellets

Forty-three pollen or spore types were identified from the moss polsters and soil sample (Table II; Fig.4). Preservation of the pollen was generally good with 8.5–14.2% (av. = 11.5%) deteriorated pollen. In general the pollen and vegetation were well-correlated with the same rank order for life-form groups: i.e., trees and shrubs, herbs, grasses and succulents. However, pollen assemblages present a biased view of vegetation, a structural configuration defined on the height, size, spacing, density, and longevity of individual plant species. Comparison of percentages of pollen and vegetation along the transects (Table II, Figs.3 and 4)

indicate some general biases in the pollen: (1) trees, especially *Olneya tesota*, and shrubs are modestly under-represented, (2) subshrubs are strongly over-represented, mostly due to *Ambrosia deltoidea*, (3) cacti are poorly represented, (4) perennial grasses are moderately under-represented; addition of annual grasses to coverage would accentuate the bias, and (5) annuals are poorly represented not only in the pollen assemblage, but on the plant coverage transects as well.

We compared the occurrence of each pollen type with the occurrence of the associated plant. Though the small sample size does not permit

rigorous statistical treatment, we facilitated comparisons by classifying each pollen type into four categories based on pollen representation relative to importance in local vegetation.

Group 1: Pollen types were rarely encountered or recognized even when the plant was found on the transects (Table II). Most of the pollen types are large, entomophilous and easily recognizable to genus. These include members of the Boraginaceae (*Tiquilia*), Cactaceae (*Echinocereus*, *Ferocactus*-type, *Mammillaria*), Krameriaceae (*Krameria*), Leguminosae (*Calliandra*) and Malvaceae (*Hibiscus*, *Horsfordia*). The absence of pollen of these groups largely represents vector specificity (poor wind dispersal). The presence of these pollen types in a sample almost certainly represents local occurrence of the plant. Pollen grains of the Boraginaceae are small and may be overlooked in the sample counts.

Group 2: Pollen types were inconsistent in their occurrence (i.e., sometimes present when the plant is not, or absent when the plant is present). Plants whose pollen fits into this group (*Acacia*, *Cirsium*-type, *Ephedra nevadensis*-type, *Fouquieria*, *Opuntia*, *Phoradendron* and *Trixis*) are found sporadically and in low abundance on the transects; most are also poor pollen producers and/or dispersers. *Opuntia* has a large grain that is readily fragmented; this complicates discrimination between cylindropuntias (chollas) or platyopuntias (prickly pears). The *Cirsium*-type pollen probably represents *Psilostrophe cooperi* (paper daisy) transported from the lower bajada to the north-facing cliff; *Cirsium* no longer occurs in the Watermans. *Ephedra nevadensis*-type (woodland jointfir) pollen in the assemblages probably represents scattered individuals of *E. nevadensis*, a variant of *E. viridis*-type of Martin (1963) that is common in the Sonoran Desert. However, the pollen was not found in samples on the north slope near the plants but on the south slope, apparently blown over the ridge.

Group 3: Both plant and pollen were generally represented although in variable quantities. Pollen and plant percentages could be under-, over-, or equally-represented with respect to plant coverage. Pollen prevalence can be further classified as (a) sporadic and of low pollen percentage [*Aloysia*,

Carnegiea, *Crossosoma*, Labiatae (probably *Hyptis emoryi*), *Menodora*, *Sphaeralcea*-type], (b) consistently found in high percentages (Other Compositae), or (c) approximately equal representation of pollen/spores and plant coverage (*Cercidium*, Gramineae, *Notholaena*) percentages. Several were under-represented with respect to plant occurrence (*Cercidium*, Gramineae, *Larrea*, *Lycium*, *Olneya*), while other pollen taxa [*Ambrosia*, Other Compositae (probably *Encelia farinosa*)] over-represent plant occurrence. Pollen of *Ambrosia deltoidea* from the lower bajada on the north slope (Fig.3) was apparently blown throughout the study area (Fig.4). As a result the rank order of the seven most common pollen taxa are completely different than the seven most common species on the transects (Table II).

Group 4: Pollen types were found when the plant was not encountered on or near the transect. In the Chenopodiaceae–*Amaranthus* (Cheno–*Am*) category, a few *Atriplex canescens* grow in the study area. Five species of annual *Amaranthus* and *Chenopodium* were rarely encountered elsewhere in the Watermans; they could occur near the transects in years with unusual winter–spring or summer precipitation. Cheno–*Am* were probably enriched in the samples as the grains are easily recognized and highly resistant to deterioration (O'Rourke, 1986). Some of the pollen could be from the few local *A. canescens* which can produce prodigious amounts. The relative percentages (7.2–15.2%, av. = 10.8%) suggest that most of the pollen was blown in from Avra Valley where *A. canescens*, *A. polycarpa* (all scale), and *Amaranthus palmeri* (pigweed) can be common in disturbed areas. Although *A. canescens*, *A. lentiformis* (quail brush) and *A. semibacata* (Australian saltbush) are cultivated in the Tucson area (Duffield and Jones, 1981), native sources are closer to the study area.

The presence, size, abundance and pollen and seed production in winter–spring or summer annuals (unrecorded in the transects) are highly correlated with the amount and distribution of rainfall. Winter–spring annuals including *Plantago insularis* (Indian wheat) and eight species in different genera of Cruciferae grow in the study area. *Boerhaavia erecta* and *B. wrightii* (spiderlings) are summer

TABLE II (continued)

Pollen/Spore Taxa	Transect species	Common name	North Slope						South Slope						Combined samples			
			Base		Slope		Cliff		Slope		Cliff		Base		P	C	C	
			P	C	P	C	P	C	P	C	P	C	P	C				
<i>Notholaena</i> -type (psilate)	<i>Notholaena jonesii</i>	Jones' cloak fern			2.8		4.6	N	5.8		5.1						3.7	
<i>Plantago</i>		Plantain					0.4										0.1	
		N =	4	6	5	6	9	8	2	5	5	2	5	2	15	16		
		Total % =	2.0	1.6	6.8	5.9	31.4	31.3	6.2	7.6	8.3	0.7	10.9	9.4				
		Total N =	16	17	17	19	28	20	17	20	22	15	40	50				
		% Coverage	67.3		105.9		104.9		56.9		55.5		78.1					
		% Coverage minus overlap	65.8		71.0		71.0		39.3		46.0		58.6					
		Pollen sum	264		250		282		258		253		1307					
		% Deteriorated grains	9.8		14.0		11.0		14.2		8.5		11.5					
		% Unknowns	0.8		0.4		2.5		0.8		0.4		1.0					

annuals that could grow near the transects in wet years.

Other pollen types not encountered on the transects clearly represent long distance transport: i.e. *Ephedra trifurca*-type, *Quercus*, Cupressaceae (*Juniperus*, *Cupressus*), *Artemisia*, *Pinus* and *Morus*. *Ephedra trifurca* (longleaf jointfir) occurs on fine-grained soils in Avra Valley. Another complication is that our reference sample of *E. nevadensis* from the Watermans also contained small amounts of *E. trifurca*-type pollen. Although *Ephedra*'s are commonly thought to produce pollen that is transported long distances in significant amounts, a recent study by Buchman et al. (1989) found that near Tucson most *E. trifurca* pollen fell to the ground within 5 m of the plant. At least in this case, concentrations exceeding trace levels probably indicate local occurrences of the plants.

The nearest *Quercus* are a few relict *Q. turbinella* (shrub live oak) on Wolcott Peak (12 km N.N.W.) and in the Tucson Mountains (38 km E.S.E.) and a few ornamental oaks in Tucson (40 km E.S.E.; Duffield and Jones, 1981). Cupressaceae are very common ornamentals in Tucson (O'Rourke, 1982). The most important cultivars are *Cupressus sempervirens* (Italian cypress), *Juniperus* spp. (five species) and *Thuja orientalis* (arbor vitae). There are a few ornamental trees 8 km E.N.E. and 13 km E.N.E. of the site.

Isolated individuals and populations of woodland plants probably contribute little pollen to the regional pollen rain. The Baboquivari and Quinlan mountains (45 km S.) reach 2355 m and 2095 m elevation, respectively, and support a well-developed pinyon-juniper-oak woodland dominated by *Pinus discolor* (border pinyon) in association with *Juniperus deppeana* (alligator bark juniper), several *Quercus* (*Q. arizonica*, *Q. emoryi*, *Q. hypoleucoides* and *Q. oblongifolia*), *Artemisia ludoviciana* (white sage) and *A. dracunculus* (tarragon). The massive Santa Catalina Mountains (55 km E.) rise to 2790 m and support more extensive woodlands and forests with all of these species plus additional *Pinus* (*P. leiophylla*, *P. ponderosa*, *P. strobiformis*) and *Quercus* (*Q. palmeri*, *Q. reticulata*, *Q. turbinella*) and *Cupressus arizonica* (Arizona cypress). The *Pinus* pollen in the samples are too large for *P. discolor* indicating that mon-

tane species in the Santa Catalinas or *P. halepensis* (Aleppo pine), a commonly cultivated Mediterranean species, are likely sources for the Waterman Mountains pollen. The nearest *Morus microphylla* (Texas mulberry) are a few trees on the north side of Wasson Peak in the Tucson Mountains (C. D. Bertelsen, pers. commun., 1990; 35 km E.S.E.). It is an uncommon tree in the larger mountains. The *Morus* pollen in the samples is probably from cultivated *M. rubra* (red mulberry) in Marana or Tucson (O'Rourke, 1986).

The low levels of *Artemisia* pollen (0.4–0.8%, av. 0.2%) are significant since the herbaceous species (*A. carruthii*, *A. dracunculus*, *A. ludoviciana*) that are common in the mountains of southern Arizona are not generally thought to produce large amounts of pollen. The nearest *Artemisia* are populations of *A. ludoviciana* above 1100 m on the north slope of Silver Bell Peak (J. Wiens, pers. commun., 1990; 7 km N.N.W.). In a pollen transect from the middle of Avra Valley east to Wasson Peak, *Artemisia* pollen was restricted to higher areas in the Tucson Mountains where *A. ludoviciana* occurs (Hevly et al., 1965). A few species of *Artemisia* such as *A. caucasica* (silver spreader), *A. dracunculus* (tarragon) and *A. ludoviciana* are occasionally planted as ornamentals or spice herbs.

Results: Midden fossils

A total of 54 pollen and spore types were identified from 14 packrat middens (Table III). Figure 5 shows a summary of major pollen types and associated macrofossils from these middens. Complete pollen counts and relative abundances of selected macrofossil taxa are shown in Table III; more detailed macrofossil data and discussion will be published elsewhere.

Pollen concentration: Table IV compares pollen concentration (grains/gm) in fossil middens from three vegetation types for midden examples from the Waterman Mountains and other southwestern sites (Davis and Anderson, 1987). Median and mean values are similar for the two studies within and between the vegetation types. However, pollen concentration from individual middens spans up to three orders of magnitude within a given vegeta-

TABLE III

Pollen (*P*) percentages and macrofossil (*M*) relative abundances from packrat middens from the Waterman Mountains, Pima County, Arizona. Ages of samples in thousands of years follow Table II. Pollen taxa in two life form categories are in parens after first entry. Macrofossils were selected to correspond to pollen taxa; all others were excluded. Relative abundance scale: 1 = rare, 2 = uncommon, 3 = common, 4 = very common, 5 = abundant, * = probable contaminant. Relative abundances of combined macrofossil taxa given next to corresponding pollen taxa the first time only. Distribution codes: n = within 100 m of midden rockshelter, a = in the local area but more than 100 m from the rockshelter, W = elsewhere in the Waterman Mountains, r = mostly or completely restricted to riparian habitats below the rockshelter, d = more distant, no longer in the Watermans, s = seasonal, could be near the rockshelter in wet years

Pollen taxa	Macrofossil Taxa	Common name	22.5		22.4		19.3		12.7	
			<i>P</i>	<i>M</i>	<i>P</i>	<i>M</i>	<i>P</i>	<i>M</i>	<i>P</i>	<i>M</i>
	Trees and shrubs									
<i>Acacia</i>	<i>Acacia greggii</i>	Catclaw acacia					0.6	2r		
<i>Artemisia</i>		Sagebrush	6.2		4.2	2	11.5		5.8	3
	<i>Artemisia tridentata</i> -type	Big sagebrush				2d				3d
<i>Bursera</i>	<i>Bursera microphylla</i>	Elephant tree								
<i>Celtis</i>	<i>Celtis pallida</i>	Desert hackberry								
	<i>Celtis reticulata</i>	Netleaf hackberry		1d						
<i>Cercidium</i>		Paloverde	*0.2		*0.3		*1.3		*0.2	
	<i>Cercidium floridum</i>	Blue paloverde								
	<i>Cercidium microphyllum</i>	Foothills paloverde								
Chenopodiaceae-										
<i>Amaranthus</i>		Goosefoot/pigweed	0.8	2	1.9		1.3	2	0.2	
	<i>Atriplex polycarpa</i>	All scale						1d		
	<i>Ceratoides lanata</i>	Winter fat								
cf. <i>Crossosoma</i>	<i>Crossosoma bigelovii</i>	Ragged rock flower		1n						
Cupressaceae		Juniper, cypress	73.4	5	38.1	5	15.3	5	65.0	5
	<i>Juniperus erythrocarpa</i>	Redberry juniper		5d						
	<i>Juniperus osteosperma</i>	Utah juniper		5d						5d
	<i>Juniperus</i> sp.	Juniper				5d		5d		
<i>Ephedra nevadensis</i> -type	<i>Ephedra</i> sp.	Mormon tea								
<i>Ephedra trifurca</i> -type		Jointfir	0.3		0.6		1.9		0.3	
	<i>Ephedra</i> sp.	Jointfir		1d		4d		2d		
<i>Fouquieria</i>	<i>Fouquieria splendens</i>	Ocotillo							*0.2	
Labiatae		Mints	2.8				0.6		0.8	2
	<i>Hyptis emoryi</i>	Desert lavender								
	<i>Salvia pinguifolia</i>	Rock sage								2d
<i>Larrea</i>	<i>Larrea divaricata</i>	Creosotebush								
<i>Lycium</i>		Wolfberry		2				2		1
	<i>Lycium berlandieri</i>	Wolfberry								
	<i>Lycium</i> sp.	Wolfberry		2n				2n		1n
<i>Olneya</i>	<i>Olneya tesota</i>	Ironwood								
Other Compositae		Composites	10.9	3	5.8	3	11.5	3	1.4	3
	<i>Encelia farinosa</i>	Brittlebush		*2n						
<i>Pinus</i>	<i>Pinus monophylla</i>	Singleleaf pinyon	1.7	4d	33.7	4d	5.7	2d	19.6	4d
<i>Prosopis</i>	<i>Prosopis velutina</i>	Velvet mesquite			0.3				0.5	
<i>Quercus</i>	<i>Quercus</i> cf. <i>turbinella</i>	Shrub live oak	73.4		38.1				0.3	2d
Rhamnaceae	cf. <i>Ziziphus obtusifolia</i>	Greythorn					1.3			
<i>Rhus</i>	<i>Rhus</i> cf. <i>trilobata</i>	Skunk bush		2d				2d		
Rosaceae		Roses							0.3	
<i>Sarcobatus</i>		Greasewood			0.6					
cf. <i>Vauquelinia</i>	<i>Vauquelinia californica</i>	Arizona rosewood	0.2			3d		2d		1d

TABLE III (continued)

Pollen taxa	Macrofossil Taxa	Common name	22.5		22.4		19.3		12.7	
			P	M	P	M	P	M	P	M
	Subshrubs									
<i>Ambrosia</i>	<i>Ambrosia? deltoides</i>	Triangleleaf bursage	1.2		1.9		6.4		0.3	
<i>Boerhaavia</i> -type		Spiderling			0.3		2		0.2	
	<i>Commicarpus scandens</i>									
<i>Eriogonum</i>		Buckwheats	0.2							
	<i>Eriogonum wrightii</i>	Wild buckwheat								
Euphorbiaceae		Spurges		2			2			
(Labiatae)	<i>Argythamnia lanceolata</i>	Lanceleaf ditaxis								
(Other Compositae)	<i>Monardella arizonica</i>	(Mints)				2n				
	<i>Brickellia coulteri</i>	Brickellbush								
	<i>Brickellia</i> sp.	Brickellbush	2n							
	<i>Ericameria cuneata</i>	Cuneate terpenine bush						2d		3d
	<i>Ericameria laricifolia</i>	Turpentine bush						2d		
	<i>Gutierrezia sarothrae</i>	Snake weed	3d		2d			3d		
<i>Sphaeralcea</i> -type		Mallows	1				1.3	2	0.8	
	<i>Abutilon</i> sp.	Indian mallow								
	<i>Sphaeralcea</i> sp.	Globe mallow	1a					2a		
<i>Trixis</i>	<i>Trixis californica</i>	(Composite)					0.6			
	Succulents									
Cactaceae		Cacti								2
	<i>Coryphantha vivipara</i>	Biscuit cactus								2d
	<i>Echinocereus</i> sp.	Hedgehog cactus								
<i>Carnegiea</i>	<i>Carnegiea gigantea</i>	Saguaro				2n				
<i>Ferocactus</i> -type		Barrel cacti	2		2					
	<i>Echinocactus</i>	Turk's head cactus				2a				
	<i>horizonthalonius</i>									
	<i>Ferocactus cylindraceus</i>	California barrel		2n						
<i>Mammillaria</i> -type		Fishhook cactus								
	<i>Mammillaria grahamii</i>	Fishhook cactus								
	<i>Mammillaria tetrancistra</i>	Fishhook cactus								
<i>Opuntia</i>		Cholla, prickly pear	2		2		3			2
	<i>Opuntia acanthocarpa</i>	Buckhorn cholla								
	<i>Opuntia bigelovii</i>	Teddy bear cholla								
	<i>Opuntia chlorotica</i>	Pancake pear	2W		2W		3n			
	<i>Opuntia phaeacantha</i>	Variable prickly pear								
	<i>Opuntia versicolor</i>	Staghorn cholla								
	<i>Opuntia</i> cf. <i>whipplei</i>	whipple cholla	2d							2d
cf. <i>Yucca</i>		<i>Yucca</i>	2		2		0.6	2		2
	<i>Yucca</i> cf. <i>baccata</i>	Banana yucca	2d		2d					2d
	<i>Yucca brevifolia</i>	Joshua tree			2d		2d			
	Grasses									
Gramineae	15 genera, 23 species	Grasses	0.9	4	0.6	2	2.5	3		2
	Herbs									
<i>Allionia</i>	<i>Allionia incarnata</i>	Windmills								
(<i>Ambrosia</i>)	<i>Ambrosia confertiflora</i>	Slimleaf bursage								
(<i>Artemisia</i>)	<i>Artemisia ludoviciana</i>	White sage								
(<i>Boerhaavia</i> -type)	<i>Boerhaavia wrightii</i>	Spiderling								
	<i>Boerhaavia</i> sp.	Spiderling						2s		
Caryophyllaceae (Chenopodium- <i>Amaranthus</i>)										
	<i>Amaranthus</i> cf. <i>albus</i>	Tumble pigweed		2W						
	<i>Amaranthus fimbriatus</i>	Fringed amaranth						1s		
<i>Cirsium</i> -type	<i>Cirsium</i> sp.	Thistle	0.3		2d			2d		

TABLE III (continued)

Pollen taxa	Macrofossil Taxa	Common name	22.5		22.4		19.3		12.7	
			P	M	P	M	P	M	P	M
Cruciferae		Mustards								
	<i>Descurainia pinnata</i>	Tansy mustard								
	<i>Draba cuneifolia</i>	Whitlow grass								
	<i>Lepidium lasiocarpum</i>	Peppergrass								
	<i>Lesquerella</i> sp.	Bladderpod								
	<i>Streptanthus carinatus</i>	Silver bell								
(<i>Eriogonum</i>)	<i>Eriogonum abertianum</i>	Wild buckwheat								
(<i>Euphorbiaceae</i>)	<i>Argythamnia</i> cf. <i>neomexicana</i>									
	<i>Euphorbia</i> spp.	Spurges		2s				2s		
<i>Kallstroemia</i>	<i>Kallstroemia</i> sp.	Summer poppy		3s					0.2	
(<i>Labiatae</i>)	<i>Hedeoma nanum</i>	Mock pennyroyal								
Leguminosae	<i>Astragalus nuttalianus</i>	Loco weed	0.3				3.8			
Liliaceae		Lilies								
<i>Mirabilis</i>	<i>Mirabilis</i> cf. <i>multiflora</i>	Colorado four o'clock								
Monolate spore		Mesic ferns								
cf. <i>Nicotiana</i>		Wild tobacco								
<i>Notholaena</i> -type	<i>Notholaena</i> sp.	Cloak fern	0.6				0.6		0.5	0.3
Onagraceae		Primroses								
(Other Compositae)	<i>Perityle emoryi</i>	Rock daisy								
	<i>Viguiera</i> cf. <i>annua</i>	Annual goldeneye								
<i>Phacelia</i>	<i>Phacelia</i> sp.	Caterpillar weed								
<i>Plantago</i>		Plantain								0.3
	<i>Plantago insularis</i>	Indian wheat								
	<i>Plantago</i> sp.	Plantain								
cf. <i>Tidestromia</i>	<i>Tidestromia lanuginosa</i>	Espanta vaqueras							0.2	0.3
<i>Verbena</i> -type	<i>Verbena</i> sp.	Vervain				2d		2d		
Umbelliferae		Parsley family		2				3		
	<i>Bowlesia incana</i>	Hairy bowlesia		1s				1s		
	<i>Daucus pusillus</i>	Wild carrot		2s				3s		
		Deteriorated grains (%)			11.2		29.9		2.5	
		Unknowns (%)					3.8		1.1	
		Pollen sums	644		312		157		652	
		Concentration ($\times 10^3$)	185.5		29.0		74.3		90.1	

tion type. These results suggest that the variability of pollen concentration within a single vegetation type limits its use in midden studies. This variability is probably a result of variation in midden composition, as well as the mode of pollen incorporation. In all cases adequate pollen was present for analysis.

Comparison of pollen and plant macrofossils

In the previous section, we have showed that certain pollen types are frequently associated with local occurrence of the producing plant, while others are distributed regionally. In this section we

(1) investigate the relationship between pollen and plant macrofossils found within the fossil middens using the Macrofossil: Pollen Index (*MPI*; Thompson, 1985) and (2) calculate Sørensen's Index of Similarity (*SI*; Mueller-Dombois and Ellenberg, 1974) comparing pollen and plant assemblages within each midden. Both analyses will examine how the different data sets approximate each other.

Macrofossil: pollen index: There is some debate about what the pollen and macrofossil data mean relative to local and regional vegetation. King and Van Devender (1977) regarded the two sets as relatively distinct fossil assemblages, while Thompson (1985) considered the pollen and plant macro-

12.5		11.5		11.5		9.9		8.9		8.3		6.1		5.2		2.6		1.3	
<i>P</i>	<i>M</i>	<i>P</i>	<i>M</i>	<i>P</i>	<i>M</i>	<i>P</i>	<i>M</i>	<i>P</i>	<i>M</i>	<i>P</i>	<i>M</i>	<i>P</i>	<i>M</i>	<i>P</i>	<i>M</i>	<i>P</i>	<i>M</i>	<i>P</i>	<i>M</i>
	2		3	1.0	3		2		1		2	0.3			1		2		3
			1s				2s								1s				
			3n		1s		1s										2n		3n
	2s		2s		3s		2s		1s		2s				1W		2W		1s
									1W		1W								1W
									3W										
	2n		2n		2n		2n		2n		2n		2n		2n		2n		2n
			3s		2s		2s		2s	0.3	2s		2s		1s	0.3	4s		4s
		0.5	2W	0.3			2W		1W		1W		1W		1W				1W
									2W										
								0.4	1d		1.9								
						0.3													
												0.3							
		1.0	2n	0.6		1.3	2n	4.2	3n	0.6	3n			1.4	1n	5.9		3.6	2n
		0.3		0.3		0.3				0.3								0.4	
							1d								2d				
									1d										
					1s														3.2
			2	0.3	1		2		2	0.3	2						1		
			2s														1s		
			2s		1s		2s		2s		2s								
								0.4						1s					1s
					2d		2d			0.3	2d	0.3					0.4		0.4
	2		1		2		2		1		1				0.4				
											1s								
	2n		1s		2s		2s		1s										
2.1		0.5		12.0		7.5		12.3		16.7		10.7		13.5		11.7		10.7	
		0.5		1.3		2.2		2.7		6.2		1.3		1.1		0.4		6.0	
388		388		308		318		261		323		297		281		256		281	
350.6		533.5		91.4		108.7		88.8		157.0		64.9		152.0		52.3		380.1	

fossils to be representative of nearly the same information. Here we calculate the MPI 's to determine whether an individual taxon from the Waterman Mountains series is better represented by the pollen or plant macrofossil assemblages.

Plant macrofossils from middens are most often tallied on a 5-point internal relative abundance (*RA*) scale. For a sample of about 800 grams (before washing) typical numbers of identified specimens would be: 1 = rare (single specimen), 2 = uncommon (2–30 specimens), 3 = common (30–100), 4 = very common (100–200), and 5 = abundant (above 200). Comparable values for the pollen percentages were established as follows: 1 =

< 1% pollen, 2 = 1–9%, 3 = 10–24%, 4 = 25–49% and 5 = > 50%. The MPI is calculated by summing the differences between the relative abundances of macrofossil (*M*) and pollen (*P*) for each taxon (*i*) from all middens in which that taxon was represented by either data type and dividing by the number of samples (*N*).

$$(MPI) = \Sigma(M_i - P_i) / N$$

The index can vary from –5, where the taxon is represented by pollen percentages > 50% and plant macrofossils are absent, to +5, where the taxon is represented by abundant plant macrofossils and the pollen is lacking, with 0 an equal representation

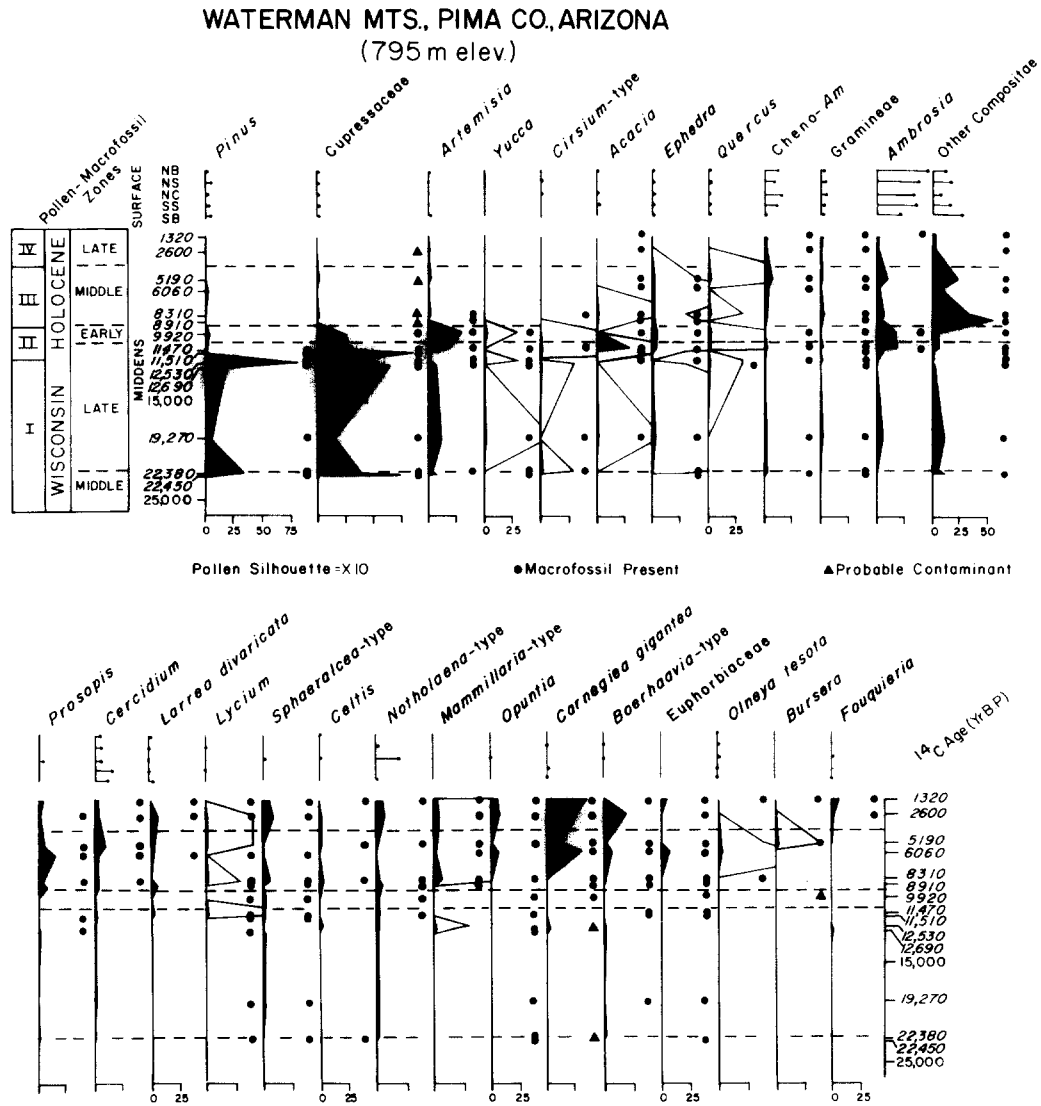


Fig.5. Pollen percentages from packrat middens from the Waterman Mountains, Pima County, Arizona. Radiocarbon ages in italics after Table I. Expanded (open) scale for several pollen types is percentage \times 10. Solid dot indicates presence of macrofossils of the pollen taxa in the middens (Table III). Solid triangles indicate probable contaminant macrofossils.

of macrofossils and pollen. For most taxa, the extreme values were rarely reached, although many taxa were found exclusively as pollen or plant macrofossils in individual samples.

Table V shows the *MPI* values calculated for 27 common taxa from the midden series. Index values range from -1.79 for *Ambrosia* to $+2.64$ for *Acacia*. About half of the taxa are distributed between -1.00 and $+1.00$, indicating pollen and plant macrofossils are likely to be showing similar

vegetation signals. Of these taxa, 40.7% had negative *MPI*'s indicating better representation by pollen than macrofossils. However, *Ambrosia* and *Quercus* ($MPI = -1.75$) were more commonly found in the pollen assemblages than as macrofossils. *Ambrosia* produces large quantities of pollen that is widely dispersed and easily transported to the midden rockshelters from beyond the forage distance of a packrat. Low levels of macrofossils may also reflect a negative dietary bias for aromatic

TABLE IV

Pollen concentration (grains/gm) for middens containing remains of pinyon-juniper and juniper woodland and Sonoran Desert macrofossil assemblages

Vegetation	Study	Range (grains/gm)	Mean	Median	(N)
Pinyon-juniper woodland	this paper	29,000– 350,600	145,900	90,100	5
	Davis and Anderson (1987)	14,819– 629,508	123,148	299,435	13
Juniper woodland	this paper	91,400– 533,500	244,533	108,700	3
	Davis and Anderson (1987)	23,686– 280,135	129,577	114,112	8
Sonoran desertscrub	this paper	23,003– 442,040	136,826	85,594	6
	Davis and Anderson (1987)	4870– 112,695	60,881	73,642	7

Ambrosia leaves. Many taxa such as *Acacia*, *Allionia*, *Kallstroemia*, *Lycium*, *Opuntia*, and *Rhus* have rather large positive indices, indicating that the pollen assemblage tends to underrepresent the taxon. Many species within these taxa have large grains, low production, and insect dispersal. Incorporation of floral parts within the midden or attachment of pollen to vegetative remains may be the most common source of pollen for these taxa.

Artemisia ($MPI = -0.50$), *Juniperus*, *Cheno-Am*, Gramineae and *Pinus* are important genera for interpretation. *Artemisia* pollen often dominates Pleistocene pollen assemblages from sediments but is less abundant in middens. *Artemisia tridentata* and its relatives (*A. bigelovii*, *A. nova*) produce large quantities of wind-dispersed pollen while common herbaceous species such as *A. ludoviciana* are less prodigious. In the Waterman Mountains series *Artemisia* pollen was present throughout the record but only important in three Wisconsin samples (5.8–18.2%). The Wisconsin (22,450, 12,690 and 12,530 yr B.P.) middens yielded uncommon to common macrofossils of *A. tridentata*-type on mesic north- and east-facing sites. *Artemisia ludoviciana* leaves were present in a late Wisconsin (11,510 yr B.P.) and an early Holocene (9920 yr B.P.) sample. It may be underrepresented in midden macrofossil assemblages

because its leaves deteriorate easily. The richest Wisconsin pollen samples (11.5 and 18.2%) lacked *Artemisia* macrofossils; a middle Wisconsin (22,380 yr B.P.) sample had *A. tridentata*-type leaves but no pollen. *Artemisia* pollen was present in three younger (8310, 5190 and 2600 yr B.P.) samples without macrofossils at low levels (0.3–1.1%) similar to levels found in two modern samples (0.4–0.8%). Such low levels probably reflect pollen transported from more distant areas rather than the few Holocene relicts of *A. ludoviciana* on Waterman Peak.

Juniperus produces large quantities of pollen and occurs somewhat more abundantly as a plant macrofossil than as pollen ($MPI = +0.83$). Many packrats preferentially collect juniper leaves, leaving the potential for over-representation in fossil middens. In soils and sediments, *Pinus* pollen is widely dispersed and often overrepresents its local abundance. These data suggest that *Pinus* was not over-represented in this series ($MPI \pm -0.30$), a fact previously noted for Sonoran Desert (King and Van Devender, 1977) and Great Basin (Thompson, 1985) middens.

The *Cheno-Am* pollen is somewhat better represented than macrofossils ($MPI = -0.36$) in the assemblages and in some samples reflects the abundances of annual *Amaranthus*. However, its per-

TABLE V

Macrofossil: pollen index (*MPI*: after Thompson, 1985) for selected taxa from Waterman Mountains packrat middens

Taxon	Number of middens	<i>MPI</i>
<i>Ambrosia</i>	14	-1.79
<i>Quercus</i>	8	-1.75
* <i>Ephedra trifurca</i> -type	11	-0.64
<i>Artemisia</i>	12	-0.50
<i>Celtis</i>	7	-0.43
<i>Notholaena</i> -type	12	-0.42
<i>Cheno-Am</i>	14	-0.36
<i>Fouquieria</i>	3	-0.33
<i>Pinus</i>	10	-0.30
<i>Larrea</i>	7	-0.29
<i>Cercidium</i>	12	-0.08
<i>Sphaeralcea</i> -type	12	+0.33
<i>Prosopis</i>	10	+0.50
<i>Boerhaavia</i> -type	13	+0.62
Other Compositae	14	+0.79
<i>Juniperus</i> sp.	12	+0.83
<i>Carnegia</i>	9	+1.44
<i>Ephedra nevadensis</i> -type	6	+1.50
<i>Vauquelinia</i>	9	+1.67
<i>Yucca</i>	7	+1.71
Gramineae	14	+1.78
<i>Kallstroemia</i>	11	+2.00
<i>Opuntia</i>	12	+2.08
<i>Lycium</i>	12	+2.17
<i>Allionia</i>	7	+2.29
<i>Rhus</i>	7	+2.43
<i>Acacia</i>	11	+2.64

*Comparing *Ephedra trifurca*-type pollen to *Ephedra* sp. which could represent other species as well.

centages (0.2–7.0%, av. = 1.9%) are unusually low compared to surface values in the Watermans (10.8%) and other regional studies. Hevly et al. (1965) found 10–50% *Cheno-Am* pollen in soil samples on a transect from Avra Valley to Wasson Peak in the Tucson Mountains with an average of 24% for Tumamoc Hill, a biological reserve within the Tucson metropolitan area. King (1977) found 15–25% *Cheno-Am* pollen in Tumamoc soils.

The low levels (0.3–3.1%, av. = 1.9%; *MPI* = +1.78) of Gramineae pollen in the middens is surprising considering its abundances in the modern samples (av. = 3.9%), the modern vegetation (8.0% total coverage) and macrofossils in middens (*RA* = 4 in eight samples; Table III). Gramineae values in soils along the Avra Valley to Wasson

Peak transect ranged from 5% to over 30% with an average of 7.4% for Tumamoc Hill (Hevly et al., 1965). King (1977) recorded higher percentages for grasses (10–25%) in soils on Tumamoc Hill, as did O'Rourke (1986; 5–15%). These results indicate that the pollen type is under-represented in middens versus soil samples.

Considerable variation between samples is apparent for some taxa (Table III). For instance, *Prosopis* pollen in general tracks macrofossil abundance but is under-represented. In some middens it was represented by abundant pollen and in others by only macrofossils. In samples where macrofossils of *Cercidium* were common, pollen was consistently under-represented. The traces of *Cercidium* pollen, especially in samples older than 8910 yr B.P., were probably younger contaminants adhering to the midden surface.

Pollen analysis was significant for identification of several taxa, including Carophyllaceae, *Ephedra trifurca*-type (*MPI* = -0.64), cf. *Nicotiana*, a monolet spore (Filicales), Onagraceae and *Sarcobatus*, not found as macrofossils. Onagraceae pollen was found in five middens, but their macrofossils are not easily recognized. The monolet spore in the 9920 yr B.P. sample indicates the presence of a more mesic-adapted fern than the *Astrolepis*, *Cheilanthes* and *Notholaena* found in the Watermans today. The pollen and spores of most of these types are not widely dispersed indicating their presence near the shelters.

The plants identified as macrofossils but not as pollen provide some insight into the limitations of midden pollen analysis. Pollen was not noted in the middens for taxa in 21 families (Table VI). Four of the pollen taxa were found in the modern polster/soil samples: i.e. *Astragalus*-type, *Janusia*, *Menodora* and cf. *Phoradendron*. While many of the taxa are minor components of the community, others include the dominant trees and shrubs: *Berberis* sp., *Canotia holacantha*, *Horsfordia* cf. *newberryi*, *Jatropha cardiophylla*, *Koerberlinia spinosa*, *Krameria parvifolia* and *Menodora scabra*.

Absence of these pollen types could be due to several factors. Members of the Boraginaceae and *Parietaria* are small (5–7 μ m) and may be easily overlooked, especially when extraneous material is present within the preparation. Other types pro-

TABLE VI

Plants identified as macrofossils but not as pollen from Waterman Mountains packrat middens, Pima County, Arizona

Agavaceae:	<i>Agave deserti</i> (desert agave)
Berberidaceae:	<i>Berberis</i> sp. (barberry)
Boraginaceae:	<i>Cryptantha barbiger</i> (bearded nievitas) <i>Cryptantha maritima</i> (desert nievitas) <i>Cryptantha micrantha</i> (purpleroot nievitas) <i>Cryptantha pterocarva</i> (wingnut nievitas) <i>Lappula redowskii</i> (stickseed) <i>Lithospermum</i> sp. (puccoon) <i>Plagiobothrys arizonicus</i> (blood weed) <i>Tiquilia canescens</i> (oreja de perro)
Capparidaceae:	<i>Koerberlinia spinosa</i> (allthorn)
Celastraceae:	<i>Canotia holacantha</i> (crucifixion thorn)
Convolvulaceae:	<i>Ipomoea</i> sp. (morning glory)
Euphorbiaceae:	<i>Jatropha cardiophylla</i> (limber bush)
Geraniaceae:	<i>Erodium texanum</i> (stork's bill)
Krameriaceae:	<i>Krameria parvifolia</i> (range ratany)
Leguminosae:	<i>Astragalus nuttalianus</i> (loco weed)
Malpighiaceae:	<i>Janusia gracilis</i> (desert vine)
Malvaceae:	<i>Horsfordia</i> cf. <i>newberryi</i> (yellow felt plant)
Oleaceae:	<i>Menodora scabra</i> (twinberry)
Portulacaceae:	<i>Portulaca</i> sp. (purslane) <i>Talinum</i> sp. (flame flower)
Ranunculaceae:	<i>Anemone tuberosa</i> (windflower) <i>Myosurus cupulatus</i> (mousetail)
Rubiaceae:	<i>Galium stellatum</i> (desert bedstraw)
Scrophulariaceae:	<i>Castilleja</i> sp. (Indian paintbrush)
Solanaceae:	<i>Physalis</i> sp. (ground cherry) <i>Solanum elaeagnifolium</i> (silverleaf nightshade)
Sterculiaceae:	<i>Avenia microphylla</i>
Urticaceae:	<i>Parietaria</i> cf. <i>hespera</i> (pellitory)
Viscaceae:	<i>Phoradendron juniperinum</i> (juniper mistletoe)

duce small quantities of pollen, often with large grains, that are dispersed by insects. *Berberis* has large, fragile grains that readily deteriorate. Members of the Capparidaceae and Celastraceae have nondescript, medium-sized (ca. 17 μm), tricolporate grains that would be counted as unknowns. In some cases grains such as *Ipomoea* can be damaged in acetolysis to be unidentifiable (M. K. O'Rourke, pers. commun., 1989). Others may have been present and not recognized due to poor preservation. Additional rare types might have been encountered if more grains were identified per sample.

The discrepancy in the visibility of the pollen of annuals leads to some significant observations about different biases in inferring rainfall patterns from fossil assemblages. The Waterman Mountains

flora is rich (ca. 34%) in ephemeral species that are restricted to either the winter–spring or summer seasons. Although 51% of the annual rainfall falls in summer, many more annuals grow only in the cool season (ca. 73%). The macrofossil assemblages appear to sample selected winter–spring annuals (i.e., Boraginaceae) very well; others (i.e., Onagraceae, Polemoniaceae) are better sampled by pollen. The pollen record misses the Boraginaceae, an important part of the spring flora. The macrofossil record samples Cruciferae, Euphorbiaceae, Umbelliferae and Verbenaceae somewhat better than pollen but probably less than their importance in the flora. Both methods only provide minimal information about other spring annuals (*Phacelia*, Polygonaceae). The Caryophyllaceae pollen may represent *Silene antirrhina* (sleepy catchfly), a spring annual not found in the middens. Both methods record *Allionia* (windmills), *Boerhaavia*-type and *Kallstroemia* (summer poppy), important summer rainfall indicators that vary considerably from year to year depending on rainfall. Identification of macrofossils to species in Chenopodiaceae, Cruciferae, Euphorbiaceae and Gramineae allows their separation into spring and summer species. These considerations as well as a general bias toward trees and shrubs which are less well correlated with rainfall seasonality suggest that pollen assemblages provide a general view of the flora with a strong bias toward summer. The macrofossil assemblages provide a balanced view of the seasonal annual flora but are also biased toward summer when compared to the modern flora.

Sørensen's similarity index: A total of 54 pollen types were found in the analyses, several identified only to family. For the plant macrofossils, at least 117 types were identified, most at the specific level. In order to calculate *SI*, the macrofossil taxa were combined into the same taxonomic categories as the pollen data. Elimination of macrofossil taxa not represented by pollen taxa increases *SI* values somewhat. *SI* was calculated as follows:

$$SI = \frac{2C}{A + B},$$

where *A* = number of macrofossil taxa, *B* = number of pollen taxa and *C* = number of common taxa.

Maximum possible value of *SI* is 1.00 where pollen and macrofossil occurrence are identical although values above 0.9 are rarely encountered in biological systems. Index values ranged from 0.30 to 0.67 (av.=0.49) with 5–20 shared taxa (Fig.6). For comparison, we calculated *SI* for two other data sets from the Sonoran Desert. For 14 woodland middens from the Sonoran Desert in southeastern California and western Arizona ranging in age from 8910 to >30,000 yr B.P. (King and Van Devender, 1977), *SI* varied from 0.16 to 0.48 (av.=0.34; Fig.6). Macrofossil numbers were from updated tables in our files and included the taxa in associated pollen categories as well as additional pollen taxa identified in the Waterman samples. Similarity indices from Organ Pipe Cactus National Monument on 11 middens ranged from 0.25 to 0.49 (av.=0.37; Davis and Anderson, unpubl.; Fig.6). A sample dated at 14,120 yr B.P. contained a juniper woodland assemblage (*SI*=

0.32); the remainder are from Sonoran desertscrub samples.

Pollen and plant macrofossils in the Waterman middens are more similar, especially those in the middle and late Holocene, than for either of the other studies. Because of low similarities, King and Van Devender (1977) concluded that the midden pollen spectra reflected the regional vegetation with a strong, variable local component. In light of more recent studies (Thompson, 1985; Davis and Anderson, 1987), this statement may be overly simplistic.

The *SI* values for the five Waterman middens younger than 8310 yr B.P. in Pollen-Macrofossil Zones III and IV average 0.61, while the average for eight middens from Zones I and II is 0.44. This suggests that pollen and plant macrofossil assemblages in this midden series are more similar for Sonoran desertscrub than for woodland. In other words, the pollen assemblages of desertscrub middens have a more "local" characteristic, while that of the older woodland middens have a more "regional" character.

Similarly indices between pollen and macrofossils in middens from the more westerly Sonoran Desert study areas did not show a significant increase in the Holocene or with shifts from pinyon-juniper to juniper woodland to desertscrub. The *SI*'s for Waterman samples were greater at most ages, probably reflecting the study areas' position farther east along the gradient of increasing summer rainfall. The biseasonal rainfall regimes of the northeastern Sonoran Desert support vegetation with greater species richness, especially in summer grasses and annuals.

The lower similarities of the Pleistocene and early Holocene middens may be due to pollen production and liberation strategies. The tree component of vegetation is better sampled by pollen in woodlands than in desertscrub. Dominant species in woodlands are wind pollinated and produce larger quantities of pollen that can be dispersed long distances. In contrast many of the species in the modern Sonoran Desert flora are entomophilous and produce pollen dispersed by specific vectors. Thus midden pollen assemblages are complex mixtures that reflect various transport mechanisms and distances and differential pollen production.

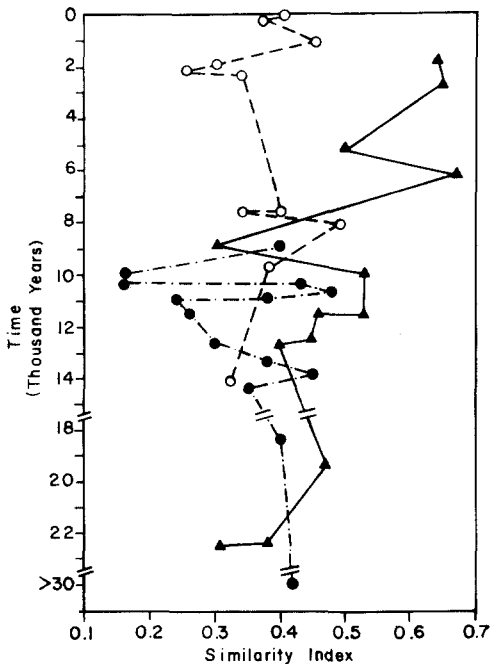


Fig.6. Sørensen's similarity indices comparing pollen and macrofossils in a packrat midden versus age for samples from the Waterman Mountains (solid triangles), Organ Pipe Cactus National Monument (dotted line with open circles; Davis and Anderson, unpubl.) and other Sonoran Desert sites (dashed line with closed circles; King and Van Devender, 1977).

preservation, size, morphology and recognizability (Davis and Anderson, 1987); the relative importance of each variable would change with shifting climate and vegetation.

Discussion

Several patterns have emerged in the analyses of modern and fossil pollen from the Sonoran Desert. The Waterman Mountains midden pollen assemblages resemble other woodland samples from the Sonoran Desert (King and Van Devender, 1977) in several ways. Samples were dominated by *Ambrosia*, *Cheno-Am* and Cupressaceae with moderate amounts of *Pinus*, *Ephedra torreyana* (= *E. trifurca*)-type pollen was consistently more common than *E. viridis* (= *E. nevadensis*)-type although *E. nevadensis* was present as macrofossils. Pollen was often absent for macrofossil taxa in various groups including trees and shrubs (*Acacia*, *Crossosoma*, *Larrea*, *Rhus*), succulents (*Ferocactus*, *Nolina*, *Opuntia*, *Yucca*), parasites (*Phoradendron*) and herbs (*Boerhaavia*, Boraginaceae, *Cirsium*-type, Cruciferae, *Mirabilis*, *Sphaeralcea*-type, Umbelliferae).

Two pollen types considered to be widely dispersed and representing the regional flora in other areas may be locally derived in the Sonoran Desert middens. Pinyon is only slightly better represented by pollen than macrofossils in the midden series ($MPI = -0.30$). Pines no longer grow in the Waterman Mountains today, but low pine pollen percentages were still found in the modern surface samples (1.4–6.0%) and in the late Holocene (1320 and 2600 yr B.P.) desertscrub middens (0–0.4%). Thompson (1985) found that surface samples tend to include larger amounts of non-local pollen than do modern middens. However, the *Pinus* in the surface samples are large grains (>70 μm) transported either from cultivated trees (*P. halepensis*) or from regional forest species (*P. ponderosa*, *P. strobiformis*) rather than the small grains of a pinyon (sensu Fine-Jacobs, 1985) in the older middens. The low MPI , along with the occurrence of macrofossils of *P. monophylla* in the Wisconsin middens suggest that the *Pinus* pollen was primarily from local trees masking input from more distant stands. Juniper pollen was better repre-

sented by macrofossils than pollen ($MPI = +0.83$). Wisconsin assemblages from much of the Southwest are dominated by juniper (Van Devender et al., 1987); a source of concern is the preference for juniper exhibited by some packrat species (Dial, 1988). The pollen in the middens probably represents predominantly local sources with an unknown lesser contribution from more distant sources.

Vegetation reconstruction: The above information provides a better understanding of the relationship of pollen and macrofossils in midden assemblages to each other and their use in reconstructing local and regional paleovegetation. Four zones can be recognized in the pollen-macrofossil assemblages that resemble the regional macrofossil sequence for the Sonoran desert (Van Devender, 1990).

Zone 1: The Wisconsin pollen samples are dominated by *Juniperus*, *Pinus*, with modest amounts of *Artemisia* and Other Compositae and lesser amounts of *Acacia*, *Ambrosia*, *Cheno-Am*, *Cirsium*-type, *Ephedra trifurca*-type, Gramineae, *Notholaena*-type, *Quercus*, *Sarcobatus*, *Sphaeralcea*-type and *Yucca*. Dispersal of modern pollen suggests fossil pollen of these taxa could have been from both local and distant sources; macrofossils indicate local sources for most of them. The *Pinus* are the small grains characteristic of the pinyons (*P. edulis*, *P. monophylla*, etc.). Larger grains from more mesic forest species (*P. flexilis*, *P. ponderosa*, *P. strobiformis*) were absent. The nearest sagebrush (*A. bigelovii*) today are on the southern edge of the Colorado Plateau (at least 265 km N.N.E.). The Other Compositae pollen in the Wisconsin samples tracks relative abundances of macrofossils of several subshrubs including *Ericameria cuneata* (cuneate turpentine bush), *E. laricifolia* (turpentine bush) and *Gutierrezia sarothrae* (snakeweed).

The *Ambrosia* pollen is of interest because the herbaceous perennial *A. confertiflora* (slimleaf bursage) and the modern spring-flowering desert subshrubs (*A. deltoidea*, *A. dumosa*) did not appear in the macrofossil record until later. The Wisconsin pollen could reflect an undetected expansion of *A. eriocentra* (woollyfruit bursage), a common spring-flowering subshrub in the Mohave Desert, or the pollen of *A. aptera* (blood weed) transported

from expanded marshes along the Santa Cruz River. The modern pollen indicates that *Ambrosia* is readily transported.

Phyllaries, seeds and spines of *Cirsium* sp. (thistle) in the samples indicate *Cirsium* rather than *Psilostrophe* as the source for the pollen. Today the nearest *Cirsium* are occasional *C. neomexicanum* in the Tucson Mountains (35 km E.S.E.).

The *Ephedra* pollen in the Wisconsin and most of the early Holocene samples was *E. trifurca*-type while macrofossils in six late Wisconsin and Holocene samples were *E. nevadensis* (Table III). Seeds only identifiable to genus in three Wisconsin samples and the 8910 yr B.P. sample could represent another species. The modern pollen suggest that a three-leaved species and not the local two-leaved *E. nevadensis* was contributing pollen to the middens. If the pollen was from *E. trifurca*, a plant typically found on deep soils or sand dunes, it represents transport by wind. Another possibility is that *E. torreyana* (Torrey jointfir), a three-leaved species of rocky slopes in the Mohave Desert, expanded its range but has not been detected in the macrofossil record. Apparently *E. nevadensis* was producing relatively small amounts of pollen in the past as it does in the area today.

Opuntia pollen was not found in the Wisconsin samples although seeds of *O. chlorotica* and *O. whipplei* (Whipple cholla) were found. Its absence is not surprising considering the fragility of the grains and poor representation in the modern pollen.

Traces (0.3–0.6%) of *Sarcobatus* pollen in samples dated at 22,380 and 11,470 yr B.P. probably reflect long distance transport by wind. *Sarcobatus vermiculatus* (greasewood) is a characteristic plant in modern Great Basin desertscrub on the Colorado Plateau. The main portion of its range begins above the Mogollon Rim (265 km E.N.E.) although there is a disjunct population in alkaline soils along the Gila and Salt rivers from Tempe to near Sacaton (80 km N.N.W.). Macrofossils of this plant have not been identified from Sonoran Desert packrat middens.

Macrofossil assemblages in the Wisconsin samples were dominated by *Juniperus* sp., *J. osteosperma* (Utah juniper) and *Pinus mono-*

phylla in association with *Artemisia tridentata*-type, *Opuntia chlorotica* (silver dollar cactus), *O. whipplei* (Whipple cholla) and *Rhus* cf. *trilobata* (skunk bush). The nearest population of *J. osteosperma* is 140 km N.N.E. of the Waterman Mountains (Little, 1971). Late Wisconsin (11,900 to 17,950 yr B.P.) middens from 1555 m on Pontotoc Ridge in the Santa Catalina Mountains (55 km E.) were dominated by *Cupressus arizonica* (Arizona cypress; Van Devender et al., 1987), a potential contributor to regional Cupressaceae pollen. The nearest stand of *P. monophylla* is 125 km N.N.E. *Yucca brevifolia* is a characteristic desertscrub dominant in the Mohave Desert of southeastern California, southern Nevada, southern Utah and northwestern Arizona. The nearest population is in western Arizona (240 km N.W.; Rowlands, 1978). In the Wisconsin the range of *Y. brevifolia* expanded greatly into the Sonoran Desert in the Colorado River Valley. It was found as low as 240 m with *Larrea divaricata* from Picacho Peak just north of Yuma in California (Cole, 1986). The Waterman records are the easternmost in the modern Sonoran Desert.

The Waterman Mountains midden records are similar to Wisconsin series from other areas in the Arizona Upland subdivision of the Sonoran Desert. The pollen assemblages most resemble a 14,120 yr B.P. sample from the Puerto Blanco Mountains in Organ Pipe Cactus National Monument (Davis and Anderson, 1987) and samples dated at 18,320 and >30,000 yr B.P. from the Artillery Mountains of western Arizona (King and Van Devender, 1977). The expanded woodlands with Mohave and Great Basin Desert elements have been interpreted as reflecting paleoclimates with cool summers, mild winters and increased precipitation predominantly from Pacific winter frontal storms (Van Devender et al., 1987).

Zone II: This transitional period includes the regional Wisconsin–Holocene boundary at about 11,000 yr B.P. (Van Devender et al., 1987). Samples dated at 11,510 and 11,470 yr B.P. are in the latest Wisconsin although the decline in *Pinus monophylla* and development of an early Holocene juniper woodland/chaparral appears to have been somewhat earlier in the Watermans than the

11,000 yr B.P. found in other areas in the Sonoran Desert (Van Devender, 1990).

In the pollen, the vegetation change was reflected by a dramatic decline in *Pinus* and modest increases in *Artemisia* and *Ambrosia*. The low levels of *Pinus* probably reflect the presence of a relict stand of *P. monophylla* on top of Waterman Peak. The increase in *Artemisia* appears to correspond to a shift from *A. tridentata*-type to *A. ludoviciana* macrofossils or an increase in the latter. The increase in *Ambrosia* possibly reflects the local abundance of *A. confertiflora* which is now restricted to the edges of large washes a few kilometers north of the study area. This widespread perennial herb, often found in disturbed soil, commonly flowers in response to summer–fall rains but also in spring in warmer areas. The arrival of or an increase in *Prosopis velutina*, recorded by 11,740 yr B.P. by macrofossils, is another indicator of summer rainfall.

Seeds of several cacti were found in middens earlier than cacti pollen: e.g. *Ferocactus cylindraceus* (12,530 yr B.P.) and *Carnegiea gigantea* (9920 yr B.P.). Macrofossils of *Encelia farinosa*, an Other Compositae pollen type, were first recorded in the 9920 yr B.P. sample.

Relatively low levels of *Ephedra* macrofossils in the Waterman middens of early Holocene age is in marked contrast to midden results from the Lower Colorado River Valley in southwestern Arizona, southeastern California and northwestern Sonora (Van Devender et al., 1987; Van Devender, 1990). Samples in these areas were typically dominated by twigs and seeds of *E. nevadensis* which is now absent or uncommon in the hotter, lower areas. However, the *Ephedra* pollen in middens from both areas was present at relatively low levels with *E. torreyana* (= *E. trifurca*)-type more common. As in the Zone I and the modern pollen, *E. nevadensis* did not produce large amounts of pollen.

The vegetation changes probably reflect increasing summer temperatures rather than a shift to a more xeric climate. Total annual rainfall probably changed little although the contribution from subtropical summer storms increased (Van Devender et al., 1987).

Zone III: The transition to the middle Holocene

is reflected by declines in *Artemisia* and *Juniperus* and increases in *Cercidium*, *Boerhaavia*-type, *Carnegiea*, *Cheno–Am*, *Celtis*, Gramineae, *Larrea*, *Olneya*, *Opuntia*, Other Compositae, *Prosopis* and *Sphaeralcea*-type as Sonoran desert pollen assemblages developed. Increases in Other Compositae pollen closely tracks macrofossil relative abundances of *Encelia farinosa*, a local dominant downslope from the midden rockshelters. *Ambrosia* and *Ephedra trifurca*-type continued to be important. The increase in *Boerhaavia*-type may be from both annual (*B. wrightii*, *Boerhaavia* sp.) and perennial herbs (possibly *B. coccinea*) and may indicate greater summer rainfall than today. The pollen of *Celtis* ($MPI = -0.43$) and *Olneya* are better represented in the middens than the macrofossils. Most of the Holocene *Celtis* is probably from *C. pallida* (desert hackberry) although the traces in a late Wisconsin (12,530 yr B.P.) sample could be from *C. reticulata* (netleaf hackberry), a riparian tree of more mesic areas. *Olneya tesota* pollen and macrofossils were most abundant during this zone.

The 5190 yr B.P. sample contained common and low levels (0.4%) of pollen and ($RA = 3$) seeds and leaves of *Bursera*. Today there is a relict northeastern population of *B. microphylla* on Waterman Peak within a few kilometers of the midden site. This is an aromatic, succulent-stemmed shrub or small tree that is widespread in the more subtropical portions of the Sonoran Desert in Arizona, Sonora and Baja California.

In the macrofossils, most woodland plants (*Juniperus* sp., *Berberis* sp., *Quercus turbinella* and *Yucca* cf. *baccata*) disappeared from the midden sites by 8910 yr B.P., leaving a Sonoran desertscrub dominated by *Acacia greggii* and *Encelia farinosa* in association with *Carnegiea gigantea*. The only woodland remnants in the sample were *Artemisia ludoviciana* and *Rhus* cf. *trilobata*. Subsequent middle Holocene samples dated at 8310 and 6060 yr B.P. record increases in *C. gigantea*, *Ferocactus cylindraceus*, *Opuntia bigelovii*, and *Prosopis velutina* with the arrival of *Cercidium floridum* (blue paloverde) and *Larrea divaricata*. An AMS date on *L. divaricata* twigs from a Waterman midden verifies its presence in the eastern Sonoran Desert by 6195 yr B.P. (Table I).

Acacia greggii, *Cercidium floridum* and *Prosopis*

velutina are presently rare or absent on the exposed limestone slopes and mostly restricted to riparian wash habitats below. Similar occurrences found in the Puerto Blanco Mountains were interpreted to indicate paleoclimates that were wetter, mostly in summer, and with more frequent winter freezes than today (Van Devender, 1987). These species occur today as codominants with *Carnegiea gigantea* and *Encelia farinosa* in relatively mesic desertscrub communities on exposed slopes at the upper elevational and northern limits of the Sonoran Desert.

Zone IV: The first record of *Cercidium microphyllum*, the modern dominant tree, was in a transitional macrofossil assemblage dated at 3880 yr B.P. associated with *Acacia greggii*, *Cercidium floridum*, and *Prosopis velutina*. Unfortunately a pollen sample was not available. The pollen in two younger samples (2600 and 1320 yr B.P.) was similar to those of Zone III with significant increases in *Boerhaavia*-type and *Carnegiea*, modest increases in *Notholaena*-type, *Opuntia* and *Sphaeralcea*-type and decreases in *Ambrosia* and Other Compositae. Macrofossils indicate that the increase in *Boerhaavia*-type pollen not only indicates the summer rainfall *Boerhaavias* but also the arrival of *Commicarpus scandens*, a subtropical desert shrub. *Carnegiea gigantea* is no longer common in the study area and contributed little pollen to the modern samples. *Cercidium* pollen continued at similar levels although macrofossils record the replacement of *C. floridum* by *C. microphyllum*. The increase of *Notholaena*-type spores probably reflects the presence of three cloak ferns (*Astrolepis cochisensis*, *A. sinuata*, *Notholaena jonesii*) near the site which are poorly sampled as macrofossils. *Prosopis* pollen (3.2%) in the rich 1320 yr B.P. sample (ca. 60 macrofossil taxa) indicates its presence in the area even though its macrofossils were not found. In contrast macrofossils of *Olneya tesota* were in the sample but pollen was not.

As for other areas in the Sonoran Desert, these fossil records indicate the development of essentially modern Sonoran desertscrub communities at about 4000 yr B.P., the beginning of the late Holocene (Van Devender et al., 1987). Apparently a decline in winter freeze frequency allowed subtropical desert plants to reach their northernmost

extent for the Holocene. Smaller amounts of pollen of *Acacia*, *Carnegiea*, *Mammillaria*-type, *Opuntia* and *Prosopis* in modern samples compared to the youngest midden sample are reflections of their decline in importance since 1320 yr B.P. Greater percentages of disturbance types such as *Cheno-Am* and Other Compositae in the same samples may reflect increased agricultural disturbance in Avra Valley east of the study area.

Conclusions

(a) Pollen is an abundant, important component of midden analysis, that can add considerably to the paleoecological reconstruction of a midden series.

(b) Surface pollen assemblages reflect Sonoran desertscrub with biases: (1) cacti are relatively poorly-represented, (2) trees, shrubs, grasses and annuals are moderately under-represented and (3) subshrubs are over-represented, mostly due to the presence of *Ambrosia deltoidea*.

(c) Pollen from middens differs from regional soil samples in the greater abundance of *Juniperus* and reduced levels of *Pinus*, *Cheno-Am* and Gramineae reflecting differences in accumulation and transport mechanisms, area sampled and preservation.

(d) Pollen and macrofossil assemblages from most Sonoran Desert middens appear to reflect similar vegetation patterns. Macrofossil pollen indices indicate that certain pollen types, mostly large grains or aggregates, are under-represented in both the modern transect and in the middens. Their presence in a sample undoubtedly reflects derivation from the local vegetation. Other wind-pollinated taxa such as *Ambrosia* are often over-represented and provide a better representation of the extralocal vegetation than macrofossils. *Juniperus* and *Pinus* are often considered part of the regional flora because of the capacity to produce abundant wind-disseminated pollen. Low levels of these taxa as well as *Ephedra trifurca*-type, *Cheno-Am* and *Quercus* in modern moss polsters and soil reflect transport from disturbed agricultural areas in Avra Valley, urban cultivars in Marana or Tucson, or distant montane woodlands or forests. However, the contribution of *Juniperus* and *Pinus* pollen from regional sources in Wisconsin and early

Holocene middens is unknown and masked by production from local trees. In some cases the pollen can provide better representation of plants such as *Ambrosia deltoidea* that are important locally but not within the packrats' foraging range. The pollen of a few taxa such as *Ephedra trifurcata*-type, *Quercus*, and perhaps *Sarcobatus*, probably reflect long-distance transport.

(e) While many taxa are better represented by plant macrofossils, others are better sampled by pollen. A few such as cf. *Nicotiana*, Onagraceae, *Sarcobatus* and a monolete spore fern (Filicales), were only found as microfossils.

(f) Pollen from plant taxa in 21 families identified as macrofossils was not found in the middens. In certain families (i.e., Leguminosae), this may be due to poor resolution of pollen to species. Many of the missing taxa are minor community elements but others represent more important trees, shrubs and leaf succulents. The absence of important winter-spring indicators, especially annual Boraginaceae, Cruciferae and *Plantago*, suggests that paleoclimatic reconstructions based on pollen are biased toward summer rainfall.

(g) Sørensen's similarity indices (*SI*) comparing pollen and plant macrofossils combined into pollen taxa from each midden indicate that the two data sets are more similar for Sonoran desertscrub than for pinyon-juniper or juniper woodland assemblages. This may be due to the larger percentage of zoophilous plants with their relatively poorer pollen production and dissemination in the Sonoran Desert. *SI* values from the Waterman samples in the northeastern Sonoran Desert are greater for all age samples and many reflect greater summer rainfall and species richness.

(h) The pollen and macrofossils in the middens record a pinyon-juniper woodland in the Waterman Mountains in the Wisconsin glacial period. By 11,500 yr B.P., *Pinus monophylla*, *Artemisia tridentata*-type and *Yucca brevifolia* disappeared from the study area leaving a juniper woodland with chaparral elements. By 8900 yr B.P. a mesic Sonoran desertscrub lacking most woodland or chaparral species had developed. In the middle Holocene trees such as *Acacia greggii*, *Cercidium floridum* and *Prosopis velutina* now mostly restricted to nearby washes were found on exposed

rocky slopes, suggesting greater effective precipitation. The modern vegetation developed about 4000 yr B.P. as riparian species retreated from the slopes to the streamsides and *Cercidium microphyllum* and *Fouquieria splendens* arrived in the area, restructuring the desertscrub community. Comparison of midden pollen and macrofossils with modern surface samples and vegetation indicate important readjustments in the desertscrub community in the last 1320 years with declines in *Acacia greggii*, *Carnegiea gigantea*, *Lycium berlandieri*, *Opuntia acanthocarpa*, *O. phaeacantha* and *Prosopis velutina*. Increases in Chenopodiaceae and Other Compositae pollen may reflect increased agricultural disturbance in Avra Valley to the east.

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