A 22,000-year record of vegetation change in the north-central Sonoran Desert

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Abstract

Plant macrofossils from eleven packrat (*Neotoma* sp.) middens provide a history of vegetation change over the last 22,140 years at Eagle Eye Mountain, near the northern border of the Sonoran Desert in Arizona. This site is located in the Arizona Upland subdivision. Departures and arrivals of various perennial plant species during the Holocene were similar to other records from more southerly sites and support earlier generalizations of Van Devender [Van Devender, T.R., 1990. Late Quaternary vegetation and climate of the Sonoran Desert, United States and Mexico. In: Betancourt, J.L., Van Devender, T.R., Martin, P.S. (Eds.), Packrat Middens: The Last 40,000 Years of Biotic Change. University of Arizona Press, Tucson, pp. 134–165.] regarding the tempo and mode of late Quaternary changes in the Arizona Upland. Evergreen woodland containing *Pinus monophylla* (singleleaf pinyon), *Juniperus osteosperma* (Utah juniper), and *Quercus turbinella* (shrub live oak) occupied the site during full glacial times. The latter two species, but not *P. monophylla*, persisted into the early Holocene and were joined by a limited number of desertscrub species, including *Acacia greggii* (catclaw), *Carnegiea gigantea* (saguaro), and several other succulents. With the arrival of many other species during the middle Holocene, a desertscrub community that differed considerably from the modern vegetation developed. *Acacia greggii* and *Cercidium floridum* (blue paloverde) were the principal large woody species on exposed hillslopes. Assemblages similar in composition to the modern desertscrub did not appear until approximately 4000 years ago, when the more xerophytic *Cercidium microphyllum* (foothills paloverde) arrived and *C. floridum* disappeared from hillslopes. The delayed arrival of *C. microphyllum* in comparison to other Sonoran Desertscrub species with similar climatic tolerances is attributed to the limited dispersal distance of its seeds by seed-eating heteromyid rodents. At 4540 and 6425 yr B.P., the cold-intolerant shrub *Encelia farinosa* was present on northeasterly aspect exposures where it is absent today, suggesting slightly warmer winter conditions during the middle Holocene. The presence of the tree *Cercidium floridum* and the perennial, C-4 grass *Setaria leucopila* on exposed slopes during the middle Holocene indicates substantially moister conditions during that time than in the late Holocene or today. At sites on the xeric limits of the modern distributions of both species, average annual precipitation is from 50% to 100% greater than that presently received at Eagle Eye Mountain. In particular, the responses of *S. leucopila* and cacti during the middle Holocene indicate substantial increases in warm-season precipitation. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Holocene; *Neotoma*; packrat middens; paleoclimate; Quaternary; Sonoran Desert

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1. Introduction

Organic materials collected by packrats (*Neotoma* spp.) and preserved in urine-impregnated midden deposits in dry rock shelters have provided a unique record of late Quaternary environmental change in the arid and semiarid parts of western North America (Betancourt et al., 1990). Plant macrofossils contained in ancient middens from the present-day Chihuahuan, Sonoran, and Mojave deserts have demonstrated that during the last glacial period, these regions were generally occupied by woodlands containing pinyon pine, juniper, and shrub oaks. Macrofossils from Holocene middens record sequential changes in vegetation from these ice-age woodlands to modern desertscrub during the last 11,000 years.

In the Sonoran Desert of southern Arizona, southern California, and adjacent Mexico, approximately 200 radiocarbon-dated middens have been studied

(Van Devender, 1990). Despite this considerable research effort, the geographic coverage of these studies has been patchy. The northern portion of the Sonoran Desert within the United States contains two geographic subdivisions: the extremely arid Lower Colorado River Valley subdivision and the semiarid Arizona Upland subdivision (Shreve, 1964; Turner and Brown, 1982; Fig. 1). Data from long time series of middens (ten or more middens from a single locality spanning Late Pleistocene through Holocene ages) have been reported from twice as many sites in the Lower Colorado compared to the Arizona Upland. Similarly, a greater total number of middens from all localities have been radiocarbon-dated and studied from the Lower Colorado (Table 1).

Significant gaps remain in our knowledge of vegetation history of the Arizona Upland. Although the latitudinal range of the Arizona Upland extends from approximately 30° in north-central Sonora, Mex-
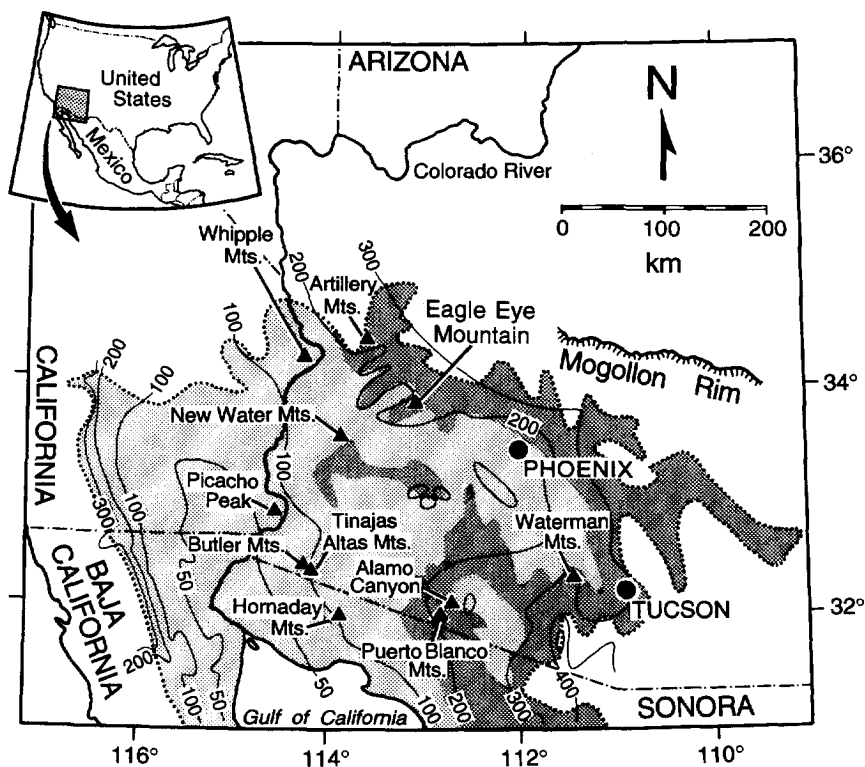

Fig. 1. Map of the northern Sonoran Desert region showing location of the Eagle Eye Mountain study site and other woodrat midden studies discussed in the text. The limits of the Sonoran Desert are shown with the bold dotted line. Dark-shaded areas indicate the Arizona Upland vegetation subdivision; light-shaded areas indicate the Lower Colorado River subdivision. Isohyets of average annual precipitation (mm) were redrawn from the map in Turner and Brown (1982).

Table 1

Comparison of midden studies conducted to date in Lower Colorado and Arizona Upland subdivisions of the Sonoran Desert

Sonoran Desert		Elevation (m)	Nr. of dated middens	Reference
Subdivision name	Site name			
Lower Colorado	Hornaday Mts.	240	10	Van Devender et al. (1990)
	Butler Mts.	240–255	9	Van Devender (1990)
	Picacho Peak, California	240–300	24	Cole (1986, 1990)
	Tinajas Altas	330–580	21	Van Devender (1990)
	Whipple Mts., California	320–525	30	Van Devender (1990)
	Kofa Mts.	550	1	Betancourt et al. (1986)
Total			95	
Arizona Upland	Puerto Blanco Mts.	535–605	21	Van Devender (1987)
	New Water Mts.	605–615	3	Van Devender (1990)
	Picacho Peak, Arizona	655	4	Van Devender et al. (1991)
	Tucson Mts.	710–890	3	Van Devender (1973)
	Waterman Mts.	795	14	Anderson and Van Devender (1991)
	Castle Mts.	820	1	Betancourt et al. (1986)
	Wolcott Peak	860	3	Van Devender and Wiens (1993)
	Artillery Mts.	725	3	Van Devender (1990)
	Ajo Mts.	975	4	Van Devender (1990)
	Alamo Canyon	915	6	Van Devender (1990)
Total			62	

ico, to nearly 35° in west-central Arizona, the two long midden series from the Arizona Upland (Puerto Blanco and Waterman Mountains; Van Devender, 1987, 1990; Anderson and Van Devender, 1991) are both located at approximately 32°N latitude (Fig. 1). Three other middens have been studied from a single site at the northern margin of the Sonoran Desert (Artillery Mountains, Fig. 1; Van Devender, 1973, 1990), but are early Holocene to Late Pleistocene in age (10.2, 18.3, and <30 ka dates), and therefore provide no information about vegetation changes during the last 10,000 years.

In this paper we present data from a series of eleven radiocarbon-dated packrat middens of Late Pleistocene through late Holocene age from a single locality in the northern part of the Arizona Upland subdivision. Macrofossil assemblages from these middens serve to test previous conclusions regarding the nature and timing of vegetation changes in the Arizona Upland during this time period (Van Devender, 1987, 1990). In addition, quantitative data on present-day perennial vegetation occupying various aspect exposures at the site are used to strengthen paleoclimatic interpretations based on macrofossil evidence.

2. Study area

Fossil packrat middens were collected from Eagle Eye Mountain, 6 km south of Aguila, Maricopa County, Arizona (33.89°N, 113.17°W). Eagle Eye Mountain and nearby Eagle Eye Peak (Fig. 2) are composed of andesitic volcanic breccia capping strongly metamorphosed, coarse sandstones and conglomerates. Together, these small mountains are slightly more than 1 km wide at the base and rise approximately 120 m above the surrounding basin floor. A distance of approximately 1 km separates Eagle Eye Mountain from the northeastern end of the Harquahala Mountains, a larger mountain range about 35 km long (southwest to northeast axis), 12 km wide, and exceeding 1500 m in elevation. The town of Aguila (661 m elevation) receives an annual average of 190 mm precipitation (Turner and Brown, 1982). Because Eagle Eye Mountain (basal elevation = 730 m with peaks exceeding 850 m) is over 100 m higher in elevation than Aguila and is located so near the Harquahala Mountains where marked orographic uplift contributes to locally increased precipitation, the average annual precipitation at Eagle Eye Mountain probably slightly exceeds 200 mm.

3. Methods

3.1. Field collection of middens

Middens were collected from rock shelters of varying sizes on Eagle Eye Mountain at elevations of approximately 800–825 m (Fig. 2) from 27 to 30 May 1989. The collection site of each midden was marked with an aluminum tag bearing field note reference numbers of J.R. McAuliffe. Tags were attached to individual sites with steel spikes driven into the remaining mass of the sampled midden or into nearby fissures in the bedrock within a rock shelter. Information taken from each collection site included a sketch showing the position of the midden within the shelter, any apparent stratigraphic relationships of the midden deposit, and the part of the deposit removed for a sample. Midden samples were removed

with chisels, the upper and lower sides were marked, and sealed in individual plastic bags. Aspect orientation and inclination of the slope were measured at the opening of the each shelter.

3.2. Laboratory methods and analyses

In the laboratory, exterior dust rinds containing potential contaminants were removed from midden samples with a chisel. Freshly exposed cross-sections were examined for any apparent depositional discontinuities, such as internal dust rinds representing depositional hiatuses. Wherever such a discontinuity was present, the sample was cleaved along the plane of the discontinuity and each newly exposed surface was cleaned. This subdivision and cleaning yielded 31 separate samples. The samples were separately soaked in water to dissolve the cementing
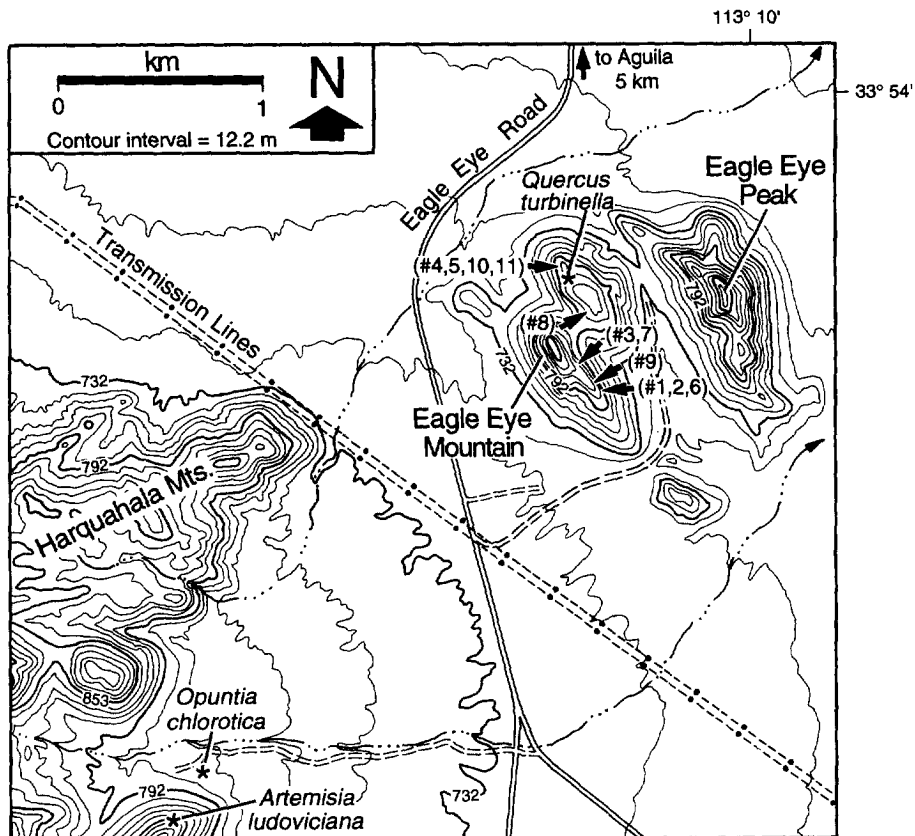

Fig. 2. Detailed map of Eagle Eye Mountain study area. Collection sites of midden samples 1–11 are indicated with bold arrows. Locations of plant species discussed in text are shown with labelled asterisks.

urine. Various materials were subsequently collected in a 250 μm sieve and oven-dried. Macrofossil contents in each sample were preliminarily examined to assess the presence or absence of dominant indicator species (listed in Table 3) discussed in earlier studies of Arizona Upland sites (Van Devender, 1987). Using these tallies, hypothetical relative ages were assigned to the samples. This initial ranking of hypothesized relative ages was made before radiocarbon dating and provided a test of the hypothesis of similar late Quaternary vegetation responses in the Arizona Upland.

From the 31 samples, 11 samples representing the spectrum of different species compositions observed in preliminary observations (and corresponding distribution of hypothesized relative ages) were selected for radiocarbon dating and detailed macrofossil analyses. These samples generally had prewashed weights of approximately 500 g (Table 3). Approximately 10–15 g of dried fecal pellets were removed from each sample and sent to the University of Arizona Laboratory of Isotope Geochemistry for radiocarbon dating. All dates reported in this paper represent radiocarbon years before 1950 (^{14}C yr B.P.).

Plant macrofossils from the samples were identified, usually to species, by comparison with reference materials in the University of Arizona Herbarium. Relative abundances of 1–5 (1 = rare, 5 = abundant) were assigned to each species in a sample. In these rankings, a species represented by a single specimen within a sample was scored 1, the most common taxon a 5, and the remaining species ranked in between. The 1–5 internal rankings of relative abundances are readily comparable between samples. More elaborate quantitative methods requiring exact counts of all identified specimens greatly increase the analytical effort without significantly improving or changing final results (see Spaulding et al., 1990, p. 70). Ephemeral plants and short-lived perennial herbs identified from middens were classified as either winter- or summer-active, based on species accounts in Kearney and Peebles (1960).

3.3. Measurement of modern vegetation

Vegetation composition was measured next to eighteen different midden shelters. Since these shel-

ters were located at the bases of cliff faces, all perennial plant species were recorded from a hemicircle of 30 m radius centered at the shelter opening, an area where packrats concentrate most of their foraging and collecting (Finley, 1990). Within a smaller 12.6 m radius semicircle directly in front of the opening (= 250 m^2 sampling area), data were collected on density of each species and canopy size (areal coverage) of the median-sized individual of each species. These data were recorded in classes on a log$_2$ scale according to the *log-series sampling method* of McAuliffe (1991). The sum of the logarithmic scores for density and average individual canopy coverage yields an estimate of total canopy cover per species on a log$_2$ scale. The antilogarithm base 2 of the difference between this sum and the logarithm base 2 of total plot area provides an arithmetic estimate of the proportion of total plant canopy cover per species. The log-series method was used because it is rapid and provides more complete data on species, including less common ones, since large areas can be rapidly assessed (McAuliffe, 1991; Ward et al., 1993), and was successfully used in quantifying existing perennial vegetation in another packrat midden study (Hunter and McAuliffe, 1994). For species absent from the smaller log-series sample plot but present in the larger 30 m radius plot, a value of 0.1% relative cover was arbitrarily assigned for the purpose of quantitative analyses. Two-way Indicator Species Analysis (TWINSPAN; Gauch, 1982) was used to classify sampling sites according to vegetational similarities, using data from plots on relative canopy cover of perennial plant species. Ordered tables produced in the TWINSPAN analysis were re-arranged to list sites according to aspect exposure in an order of increasing absolute departure from geographic north.

In addition to the data on perennial plants taken from plots at each midden collection locality, the occurrences of various perennial plant species around the entire base and accessible slopes of Eagle Eye Mountain and nearby areas in the Harquahala Mountains were recorded in May 1989 and March 1996. Additional modern distributional information for selected species was obtained from label data on specimens in the University of Arizona and the Desert Botanical Garden herbaria.

4. Results

4.1. Modern vegetation

The perennial vegetation of Eagle Eye Mountain is typical of that found throughout much of the Arizona Upland subdivision (Shreve, 1964; Turner and Brown, 1982). The small tree *Cercidium microphyllum* (foothills paloverde) is the dominant species, usually accounting for one-quarter to more than one-half of all perennial plant cover. This tree species exhibited no systematic variation in relative cover on different aspect exposures (Table 2 Fig. 3A). In contrast, *Encelia farinosa* (brittlebush), co-dominant with *C. microphyllum* on southerly exposures, was completely absent from north and northwestern exposures (Table 2; Fig. 3B). The TWINSPAN classification of vegetation sites showed that the relative abundance of *E. farinosa* was the principal source of variation in vegetation composition among sample

Table 2
Ordered table of vegetation data [a]

Species	Vegetation sample sites																	
	6	7	8	3	17	4	1	18	5	14	9	2	13	16	15	12	10	11
Acacia constricta	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Acacia greggii	4	1	–	1	2	–	–	–	–	–	–	–	–	–	2	–	–	–
Menodora scabra	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Aloysia wrightii	1	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–
Viguiera deltoidea	1	2	–	1	3	1	1	1	–	1	–	–	–	–	–	–	–	–
Brickellia desertorum	1	1	1	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–
Galium stellatum	1	1	1	–	1	1	–	1	1	1	–	1	–	–	–	–	1	1
Sphaeralcea ambigua	1	1	2	1	2	1	2	1	2	1	1	1	1	1	1	1	1	1
Salazaria mexicana	2	3	–	1	1	1	–	1	1	3	–	1	–	–	–	1	1	1
Ephedra nevadensis	1	–	–	1	1	–	1	–	–	–	1	1	–	–	–	–	1	–
Brickellia atractyloides	1	–	–	1	1	1	–	–	–	–	–	1	–	–	–	1	–	–
Brickellia coulteri	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–
Stephanomeria pauciflora	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Janusia gracilis	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Cercidium microphyllum	4	5	5	5	3	5	5	5	5	5	5	5	2	4	4	4	5	5
Lycium spp.	1	1	1	–	2	1	1	1	1	1	1	1	3	–	2	1	1	1
Trixis californica	1	1	1	1	1	1	–	–	1	1	1	1	1	–	–	1	1	1
Larrea tridentata	1	1	1	–	2	3	4	3	4	1	1	1	2	1	5	3	2	1
Aristida sp.	–	–	1	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–
Machaeranthera pinnatifida	1	–	–	–	1	–	–	–	–	1	1	1	1	1	–	1	1	1
Eriogonum fasciculatum	–	–	–	1	1	1	1	–	1	1	1	1	1	–	–	1	1	1
Muhlenbergia porteri	–	–	1	–	–	–	–	–	–	1	–	1	–	1	–	1	–	–
Erioneuron pulchellum	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Fouquieria splendens	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–
Ambrosia deltoidea	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	1	1	–
Hyptis albida (= *emoryi*)	–	1	1	1	–	2	1	–	1	–	1	1	3	1	–	2	1	1
Carnegiea gigantea	–	–	1	–	–	1	–	–	–	1	1	1	1	1	1	–	1	–
Mammillaria grahamii	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Peniocereus greggii	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Opuntia bigelovii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
Ferocactus cylindraceus	–	–	–	–	–	–	1	–	–	–	1	1	–	–	–	1	1	1
Encelia farinosa	–	–	–	–	–	2	1	1	1	3	4	3	5	5	1	2	4	3
Total number of species	14	12	11	10	16	14	15	9	11	13	14	18	11	8	8	14	17	12
Aspect exposure	N			NE + NW			E + W		SW + SE						S			

[a] Sites arranged from left to right by absolute departure from geographic north. Values 1–5 represent relative cover groups, where 1 = <5% relative cover, 2 = 5–12.5%, 3 = 12.5–25%, 4 = 25–50%, 5 = >50% relative cover.
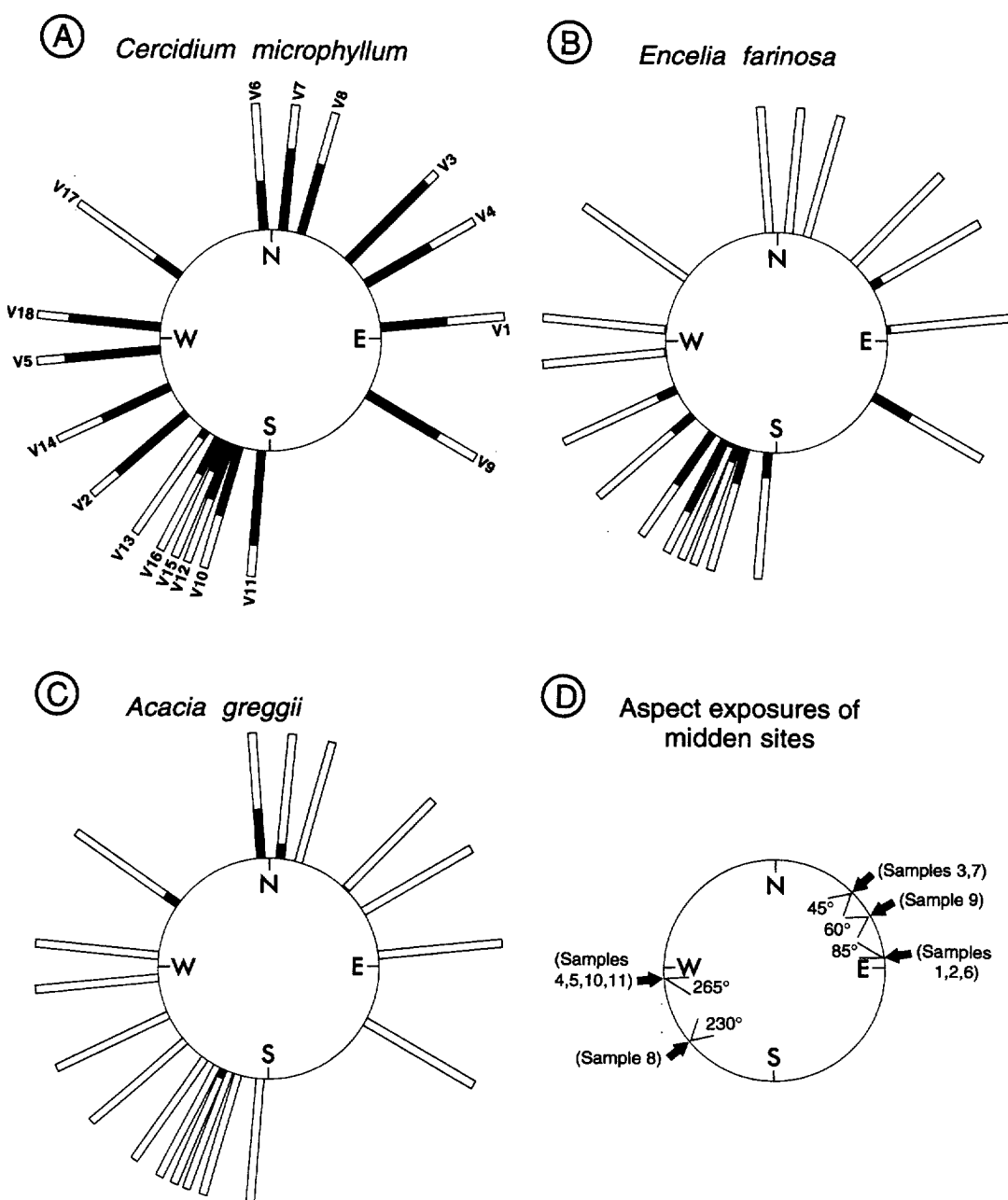
Fig. 3. (A, B, C) Rose diagrams showing variation in relative cover of some perennial plant species on different aspect exposures. Solid portion of each bar represents the percentage of relative canopy cover with total bar length equal to 100%. Notation *V1* to *V18* refers to the 18 vegetation samples. (D) Aspect exposures of the 11 woodrat midden samples.

sites. All sites on northern and northwest aspects were classified in a group in which relative cover of this plant was less than 5%, and with only one exception, sites on eastern, southern, and southwestern aspects were contained in the other group where relative cover of *E. farinosa* exceeded 5%.

The cold-sensitive columnar cactus, *Carnegiea gigantea* (saguaro) was infrequent on northern exposures, but more common on southerly exposures. Woody species that were moderately to strongly restricted to more northerly aspects included *Acacia greggii* (catclaw), *Aloysia wrightii* (honey bush), and *Viguiera deltoidea* (desert goldeneye); (Table 2; Fig. 3C). Some of the sampling sites at the bases of cliffs receive considerable runoff from upper catchment areas. This augmentation of incident precipitation by runoff from other areas apparently contributes to the local presence of *A. greggii*, especially in one southerly exposure.

In the extensive searches around the entire perimeter of Eagle Eye Mountain, single old, mature individual *Prosopis velutina* (velvet mesquite) and *Quercus turbinella* (shrub live oak) were found on northerly exposures at bases of cliffs. These two woody species are today usually limited to the more mesic microhabitats along washes (*P. velutina*) or considerably higher elevations where precipitation is greater (*Q. turbinella*). These local microhabitats are more mesic than the surrounding area due to northern exposure and augmentation of incident precipitation by considerable runoff from upper slopes.

4.2. Preliminary analysis of plant macrofossils and test of hypothesized chronology

Based on initial examinations of the presence or absence of dominant indicator species, the ancient middens formed five distinct groups that were designated before the samples were radiocarbon dated (Table 3). Group I consisted of a single sample containing *Pinus monophylla* (singleleaf pinyon pine), *Juniperus osteosperma* (Utah juniper), and *Q. turbinella*. Group II consisted of a single midden sample with *J. osteosperma* and *Q. turbinella*, but lacked *P. monophylla*. Samples in Group III contained *A. greggii* and *C. gigantea*, but lacked *C. microphyllum* and *Larrea tridentata* (creosotebush). Group IV contained *C. microphyllum*, *A. greggii*, and in some cases, *C. gigantea*. Group V contained either *C. microphyllum*, *L. tridentata*, or both, but *A. greggii* was not detected (although in detailed macrofossil analyses it was later recorded as rare or uncommon). These groups formed a ranking of hypothetical relative ages from oldest (Group I) to youngest (Group

V), based on late Quaternary changes in midden macrofossil assemblages from two other Arizona Upland sites (Van Devender, 1987, 1990); e.g. midden Groups I, II, III–IV, and V corresponded with Late Pleistocene, early Holocene, middle Holocene, and late Holocene, respectively (Table 3).

4.3. Detailed analysis of plant macrofossils

The eleven radiocarbon-dated samples provide a 22,000-yr record of vegetation change from the Late Pleistocene through the late Holocene. For purposes of discussion and direct comparison with other Sonoran Desert chronologies of Van Devender (1987, 1990), the record is divided into Late Pleistocene (>11 ka), early Holocene (11–8.9 ka), middle Holocene (8.9–4.0 ka) and late Holocene (4.0 ka–present).

The single midden of Late Pleistocene age (22,140 yr B.P.) contained abundant *Juniperus osteosperma* with lesser amounts of *Pinus monophylla* and *Quercus turbinella* (Fig. 4; Table 4 . Understory shrubs associated with these trees and large shrubs were *Ericameria laricifolia* and *E. cuneata* (turpentine bushes), *Artemisia tridentata*-type (sagebrush), and *Ephedra nevadensis* (Nevada joint-fir). The only succulent species present in this midden was *Yucca baccata* (banana yucca; Fig. 5).

A single early Holocene midden (10,440 yr B.P.) records the apparent loss of *Pinus monophylla* on an easterly exposure. Plant species that persisted from the Late Pleistocene into the early Holocene were *Juniperus osteosperma*, *Quercus turbinella*, *Ericameria laricifolia*, *Ephedra nevadensis*, and *Yucca baccata*. *Artemisia ludoviciana* (white sage) made its only appearance in the midden record in this early Holocene midden. Although *A. ludoviciana* apparently disappeared from Eagle Eye Mountain for the remainder of the Holocene, in 1996 it was documented 3 km to the southwest on a steep, relatively mesic, north-facing hillslope at the base of the Harquahala Mountains (Fig. 2). The few desertscrub species that made their first appearance in the early Holocene midden include *Acacia greggii* and four succulent species including *Carnegiea gigantea*, *Ferocactus cylindraceus* (California barrel cactus), *Opuntia chlorotica* (silver dollar prickly pear), and *Agave deserti* (desert agave; Figs. 4 and 5; Ta-

Table 3

Groupings of middens according to presence/absence of plant macrofossils arranged from hypothesized oldest (sample 1) through youngest (sample 11) middens [a]

Midden sample	Species [b]								Group	Lab No.	Pre-washed sample weight (g)	Age ^{14}C yr B.P.	Actual chronological order
	Pi	Ju	Qu	Pr	Ac	Ca	Ce	La					
1	*	*	*						I	A-5963	292	22, 140 ± 350	1
2		*	*						II	A-5964	402	10, 440 ± 70	2
3					*	*			III	A-5965	511	6, 425 ± 75	3
4					*	*			III	A-5966	528	5, 130 ± 65	5
5					*	*			III	A-5967	504	5, 335 ± 90	4
6					*	*	*		IV	A-5968	514	4, 040 ± 70	7
7				*	*		*		IV	A-5969	888	4, 540 ± 85	6
8							*		V	A-5970	517	1, 885 ± 60	10
9							*	*	V	A-5971	405	1, 595 ± 50	11
10						*	*	*	V	A-5972	440	3, 340 ± 60	8
11							*	*	V	A-5973	636	2, 980 ± 65	9

[a] Asterisks indicate detection of plant macrofossils of the species indicated, based on preliminary examinations.

[b] Abbreviations of species names: Pi, *Pinus monophylla*; Ju, *Juniperus osteosperma*; Qu, *Quercus turbinella*; Pr, *Prosopis velutina*; Ac, *Acacia greggii*; Ca, *Carnegiea gigantea*; Ce, *Cercidium microphyllum*; La, *Larrea tridentata*.

ble 4). Although *O. chlorotica* and *A. deserti* are today absent from Eagle Eye Mountain, populations of both species are found nearby at similar elevations in the Harquahala Mountains (pers. observations on *O. chlorotica*, Fig. 2; records of *A. deserti* from the Desert Botanical Garden herbarium).

The middle Holocene is represented by five samples ranging in radiocarbon age from 6435 to 4040 yr B.P. (samples 3–7). During the 4000-yr gap in the record preceding the 6.4 ka sample, many species that were common in the Late Pleistocene and early Holocene middens, including *Ericameria laricifolia*, *Juniperus osteosperma*, and *Quercus turbinella* disappeared as many desertscrub species arrived. The 6435 yr B.P. sample yielded the earliest records from the site of *Cercidium floridum* (blue paloverde), a variety of shrubs including *Encelia farinosa*, *Galium stellatum* (desert bedstraw), *Hyptis albida* (= *H. emoryi*, desert lavender), *Larrea tridentata*, *Trixis californica* (trixis), *Viguiera deltoidea*, and the woody vine *Janusia gracilis* (desert vine; Fig. 4; Table 4).

Cercidium microphyllum does not appear in the midden record until the end of the middle Holocene at 4540 yr B.P. (Fig. 4; Table 4). The consistent absence of *C. microphyllum* from three slightly older, middle Holocene middens (5.1, 5.3, and 6.4 ka) provides strong evidence that this small tree did not

arrive until near the end of the mid-Holocene. Two late middle Holocene middens (4.5, 4.0 ka) contained macrofossils of both *C. floridum* and *C. microphyllum*, indicating a short period during which the two species may have coexisted with *Acacia greggii* on the same slopes. *Prosopis velutina*, another small tree, appeared only in the 4540 yr B.P. sample (Fig. 4; Table 4).

The middle Holocene middens generally contain more cactus species at greater relative abundances than in late Holocene samples (Figs. 5 and 6), although *C. gigantea* was absent from the 6425 yr B.P. sample. In addition to the greater abundance of cacti during the middle Holocene, the warm-season, perennial C-4 grass, *Setaria leucopila* (bristlegrass), made its only appearance in moderate abundances in the 6425 and 4540 yr B.P. samples (Fig. 5).

In the four late Holocene middens, *Cercidium microphyllum*, *Encelia farinosa*, and *Larrea tridentata* were the dominant woody species, while *C. floridum* was absent. *Acacia greggii*, although not detected in the preliminary examinations (Table 3), was later detected in low abundances (Fig. 4). Cacti also declined in abundance and number of species (Figs. 5 and 6). Most of the xerophytic shrub species that made their first appearances in the middle Holocene have persisted until today. The only perennial plant species that was apparently at the site for the entire
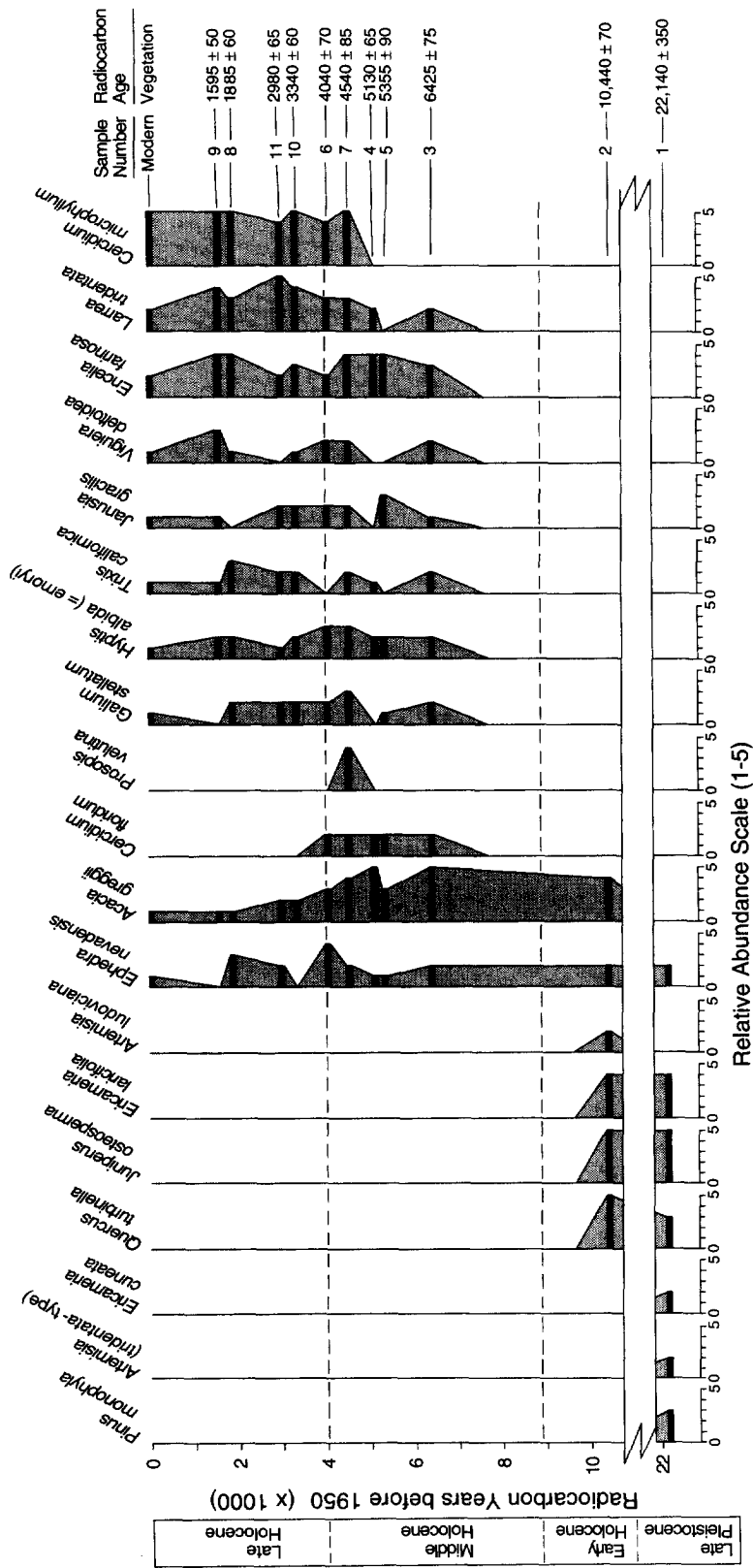
Fig. 4. Macrofossil abundance diagrams for woody plants from the Eagle Eye Mountain woodrat middens. Values for modern vegetation represent the average of relative cover scores 1–5 for the 18 vegetation samples listed in Table 2.
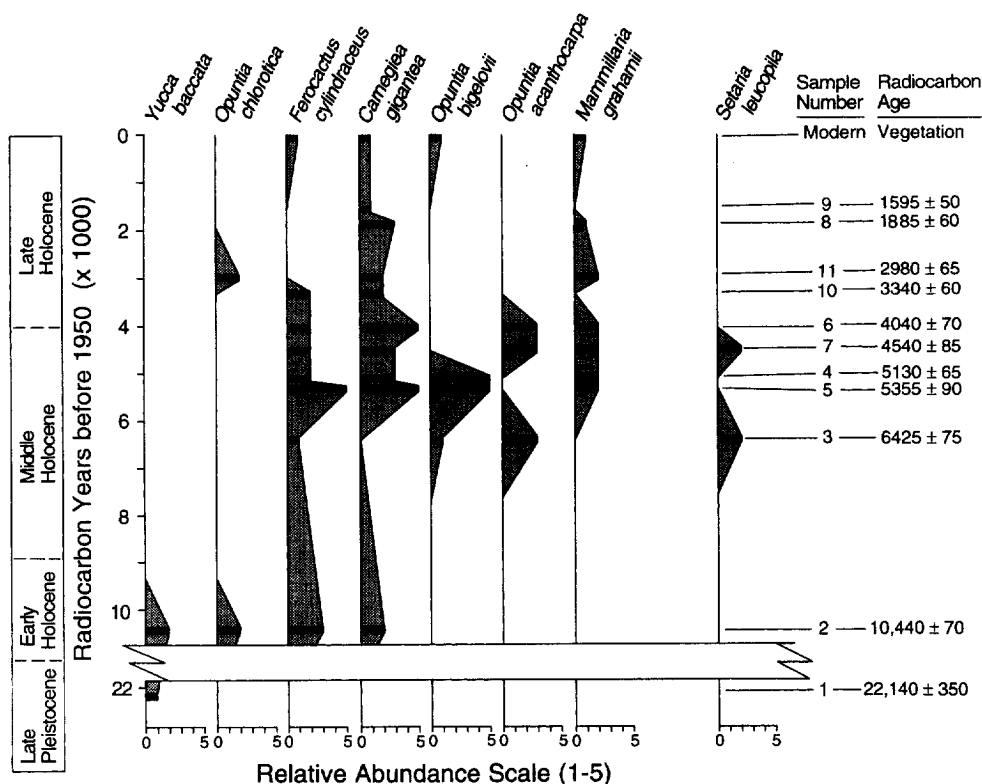
Fig. 5. Macrofossil abundance diagrams for succulents and one perennial grass species from the Eagle Eye Mountain woodrat middens. Values for modern vegetation as in Fig. 4.
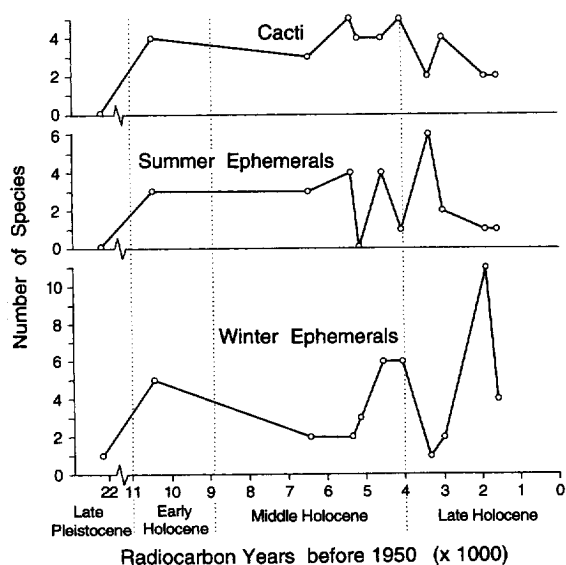

Fig. 6. Number of species of cacti, winter ephemerals, and summer ephemerals as a function of midden age.

22,000 year record was *Ephedra nevadensis*. Median values for relative canopy cover of perennial plants comprising the present-day vegetation are in general similar to relative abundances of their macrofossils in late Holocene middens (Table 2; Fig. 4).

The total number of perennials, including woody, suffrutescent, and succulent species in the single Late Pleistocene sample (9 species) is less than the number found in Holocene middens (mean = 15.4 species/midden, range = 13–21 species). However, this difference may be simply due to a sampling effect since the 292 g Late Pleistocene midden sample weighed half or less than the ten Holocene middens (mean = 534.5 g, range = 402–888 g; Table 3). The numbers of ephemeral and short-lived herbaceous perennial species were even more reduced in the Late Pleistocene middens with only one herbaceous species, whereas the Holocene middens each contained from 5 to 13 species (mean = 8.8). The magnitude of this difference suggests a real increase

Table 4

Plant macrofossil abundance scores for paleomidden samples from Eagle Eye Mountain, Arizona

Taxa	Material identified	Age of sample (radiocarbon years ×1000 before 1950)										
		22.1	10.4	6.4	5.4	5.1	4.5	4.0	3.3	3.0	1.9	1.6
Trees and shrubs:												
Acacia constricta	thorns								2			
Acacia greggii	pods, leaflets, thorns		4	5	3	5	4	3	2	2	1	1
Artemisia tridentata-type	leaves	2										
Cercidium floridum	thorns, twigs, leaflets				2	2	2	2				
Cercidium microphyllum	pods, leaflets, twigs						5	4	5	4	5	5
Crossosoma bigelovii	seeds, pods, leaves			2								
Encelia farinosa	achenes, leaves, bracts, twigs				3	4	4	2	3	2	4	4
Ephedra nevadensis	seeds, twigs, bracts	2?	2?	2?	1?	1?	2	4		2?	3?	
Eriogonum fasciculatum	leaves				1				2			
Fouquieria splendens	twigs									1		
Hyptis albida	fruit, leaves, twigs, seeds				2	2	2	3	3	2	1	2
Juniperus osteosperma	seeds, twigs	5?	5?									
Larrea tridentata	fruit, leaves, twigs, buds				2	2	3	3	4	5	3	4
Lycium sp.	seeds, leaves, twigs					2	3					
Keckiella antirrhinoides spp. *microphylla*	pods, leaves, involucres	2	2									
Pinus monophylla	needles	3										
Prosopis velutina	leaflets, thorns						4					
Quercus turbinella	leaves, twigs, acorns	3	5									
Rhus aromatica	seeds		3?									
Subshrubs, suffrutescent perennials, vines, and woody parasites:												
Artemisia ludoviciana	leaves, twigs			2								
Bebbia juncea	achenes											1
Brickellia atractyloides	achenes, leaves, involucres				2		2					3
Brickellia coulteri	twigs, involucres						2					
Brickellia sp.	achenes									2		
Ditaxis lanceolata	seeds, leaves, capsules									2		
Dyssodia porophylloides	achenes							1				
Ericameria cuneata	leaves	2										
Ericameria laricifolia	leaves	4	4									
Galium stellatum	leaves				2	1	3	2	2	2	2	
Janusia gracilis	fruit, leaves				1	3	2	2	2	2		1
Machaeranthera pinnatifida	achenes						1				4?	2
Phoradendron californicum	fruit, twigs				2	2	2	3		2	2	3
Porophyllum gracile	achenes											
Senna covesii	seeds						2	1				
Sphaeralcea sp.	carpels, twigs, seeds, leaves	2	2	3	1	1	2	2	2	2	4	3
Tiquilia canescens	seeds, leaves									2		
Trixis californica	leaves, involucres				2	1	2		2	2	3	1
Viguieria deltoidea	achenes				2		2	2	1		1	3
Succulents:												
Agave deserti/mckelveyana	leaves			2								
Carnegiea gigantea	seeds, fruit			2	5	3	3	5	2	2	3	1
Echinocereus sp.	seeds					1				2		
Ferocactus cylindraceus	seeds, spines			3	1	5	2	2	2	2		
Mammillaria grahamii	seeds, spines					2	2	2	2	2	1	
Opuntia acanthocarpa	seeds, leaves, wood				3			3	3			
Opuntia bigelovii	seeds				1	5	5					
Opuntia chlorotica	seeds, epidermis			2							1	
Opuntia sp.	spines								2			2
Yucca baccata	leaves	1?	2?									
Long-lived herbaceous perennials:												
Anemone tuberosa	seeds			2								

Table 4 (continued)

Taxa	Material identified	Age of sample (radiocarbon years ×1000 before 1950)										
		22.1	10.4	6.4	5.4	5.1	4.5	4.0	3.3	3.0	1.9	1.6
Perennial grasses:												
Bouteloua repens	floret		2		2							
Bouteloua trifida	floret						1					
Digitaria californica	floret									1		
Erioneuron pulchellum	floret			2	1						2	3
Setaria leucopila	floret			2			2					
Tridens muticus	floret										1	
Ephemerals or short-lived herbaceous perennials, summer season:												
Amaranthus sp.	seeds				2							
Boerhavia erecta intermedia	fruit		2				2		2	2		
Boerhavia wrightii	fruit		2	2	2		3		2	2	2	
Boerhavia sp.	fruit							1				1
Bouteloua barbata	floret								1			
Eriochloa acuminata	floret			1	1		1		2			
Euphorbia micromera/polycarpa	fruit, leaves				2							
Euphorbia revoluta	seed, fruit		2									
Kallstroemia sp.	seed, leaves			2			2					
Panicum sp.	floret								1			
Setaria griesbachii	floret								1			
Ephemerals or short-lived perennials, winter–spring season:												
Amsinckia tessellata	nutlet							1				
Caulanthus lasiophyllus	fruit						1					
Chaenactis carpoclinia	achenes					1						2
Chaenactis stevioides	achenes										2	
Cryptantha barbigera	nutlets		2									
Cryptantha maritima	fruit, seeds										2	
Cryptantha sp.	fruit					1						
Dalea mollis	fruit						2	2			2	
Daucus pusillis	fruit, mericarps		1								2	1
Draba cuneifolia	capsules				1		2				2	
Gilia sp.	fruit							1				
Lepidium lasiocarpum	fruit, inflorescences											2
Lepidium sp.	fruit							2			4	
Lotus sp.	seed, capsules, leaves		1	2			2			1	2	1
Lupinus sp.	seeds, capsules		2	1	1		2	1				
Muhlenbergia microsperma	floret										1	
Pectrocarya recurvata	nutlet										1	
Phacelia crenulata	seeds, capsules					1					2	
Plagiobothrys acanthocarpus	seeds								2			
Plantago fastigiata	seeds, bracts							2			2	
Silene antirrhina	fruit						1					
Thysanocarpus curvipes	fruit	1	1									
Vulpia sp.	floret										1	
Ephemerals or short-lived perennials, summer or winter–spring active:												
Allionia incarnata	seeds	1		1	1		2					
Cirsium sp.	phyllaries		2									
Ditaxis sp.	capsule		1					1				2
Euphorbia sp.	fruit, leaves							3				
Muhlenbergia sp.	floret										1	
Parietaria hespera	fruit		1				2					
Perityle emoryi	achenes					1			2			2
Physalis sp.	seeds, fruit			2	4	1	2	3	3	2	2	2

in the diversity of ephemerals and herbaceous perennials in the Holocene.

The numbers of winter- versus summer-active ephemerals throughout the Holocene are extremely variable and exhibit no clear, systematic pattern (Fig. 6). Although the predominance of summer- versus winter-active ephemerals are inversely related at dates of 4.0, 3.3, and 2.0 ka, taken as a whole, the numbers of winter- versus summer-active ephemerals for all Holocene samples are not significantly negatively correlated (Spearman rank correlation = -0.45, $p = 0.19$).

5. Discussion

5.1. Patterns of vegetation change

Vegetation change at Eagle Eye Mountain during the late Quaternary has generally been similar to the changes documented at two other major Arizona Upland sites (Puerto Blanco Mountains and Waterman Mountains; Van Devender, 1987, 1990; Anderson and Van Devender, 1991). The concordance between the original groupings and hypothesized relative ages of midden samples based on their dominant macrofossil contents and the actual chronological position of these groups (i.e. Late Pleistocene; early, middle, and late Holocene; Table 3) indicates that the timing and types of late Quaternary vegetation changes described by Van Devender (1990) are generally applicable to other Arizona Upland sites nearer the northern margin of the Sonoran Desert.

5.2. Comparisons of the Eagle Eye Mountain record with other midden studies and modern plant distributions

Middens with radiocarbon dates exceeding 11,000 yr from Eagle Eye Mountain and the Artillery and Waterman mountains (Van Devender, 1990; Anderson and Van Devender, 1991) indicated that woodland/chaparral of Pinus monophylla and Juniperus osteosperma, often with Quercus turbinella in the understory, occupied these sites during the last glacial stage. Modern vegetation assemblages containing these species are commonly found in Arizona in a broad band below the Mogollon Rim to

the north and northeast of the study site (Fig. 1) at elevations of approximately 1210–1800 m, approximately 400–1000 m higher than the Eagle Eye and Waterman midden localities. A tridentate-leaved sagebrush (either Artemisia bigelovii or A. tridentata) was also a member of this pinyon–juniper–shrub live oak assemblage at Eagle Eye Mountain at 22.4 ka and at the Waterman Mts. at 12.5 and 12.7 ka. Both Artemisia species are presently restricted to the northern half of Arizona, approximately 200–250 km north of these midden localities, at elevations exceeding 1500 m.

Pinus monophylla disappeared around the Pleistocene–Holocene transition, but since the early Holocene record from Eagle Eye Mountain is represented by only one midden sample, additional middens from the latest Pleistocene and earliest Holocene are needed to more precisely constrain the timing of this change. Juniperus osteosperma and Q. turbinella persisted into the early Holocene on eastern exposures. These woodland/chaparral species were joined by Acacia greggii and several cacti: Carnegiea gigantea, Ferocactus cylindraceus, and Opuntia chlorotica.

Timing of the disappearances of J. osteosperma and Q. turbinella in the midden record is poorly constrained because of the large temporal gap between the 10,440 yr B.P. sample where both were present and the 6425 yr B.P. and later middens where both were absent. In several other studies in the Sonoran Desert, the early–middle Holocene transition, marked by the disappearance of Juniperus spp. was about 9000 yr B.P. (Van Devender, 1990). The single Q. turbinella located at the site today in a mesic microenvironment may represent a relict from this period rather than a recent event of dispersal and establishment. This oak is capable of regeneration through persistent basal sprouting; consequently genetic individuals can potentially persist as clones for thousands of years (Neilson and Wullstein, 1983).

Many desertscrub species that arrived during the earlier part of the middle Holocene were components of a desertscrub community that differed considerably from the modern vegetation. All three Arizona Upland midden sequences (Eagle Eye, Waterman, Puerto Blanco mountains) indicate that Acacia greggii and Cercidium floridum were the principal large woody species on exposed hillslopes during the mid-
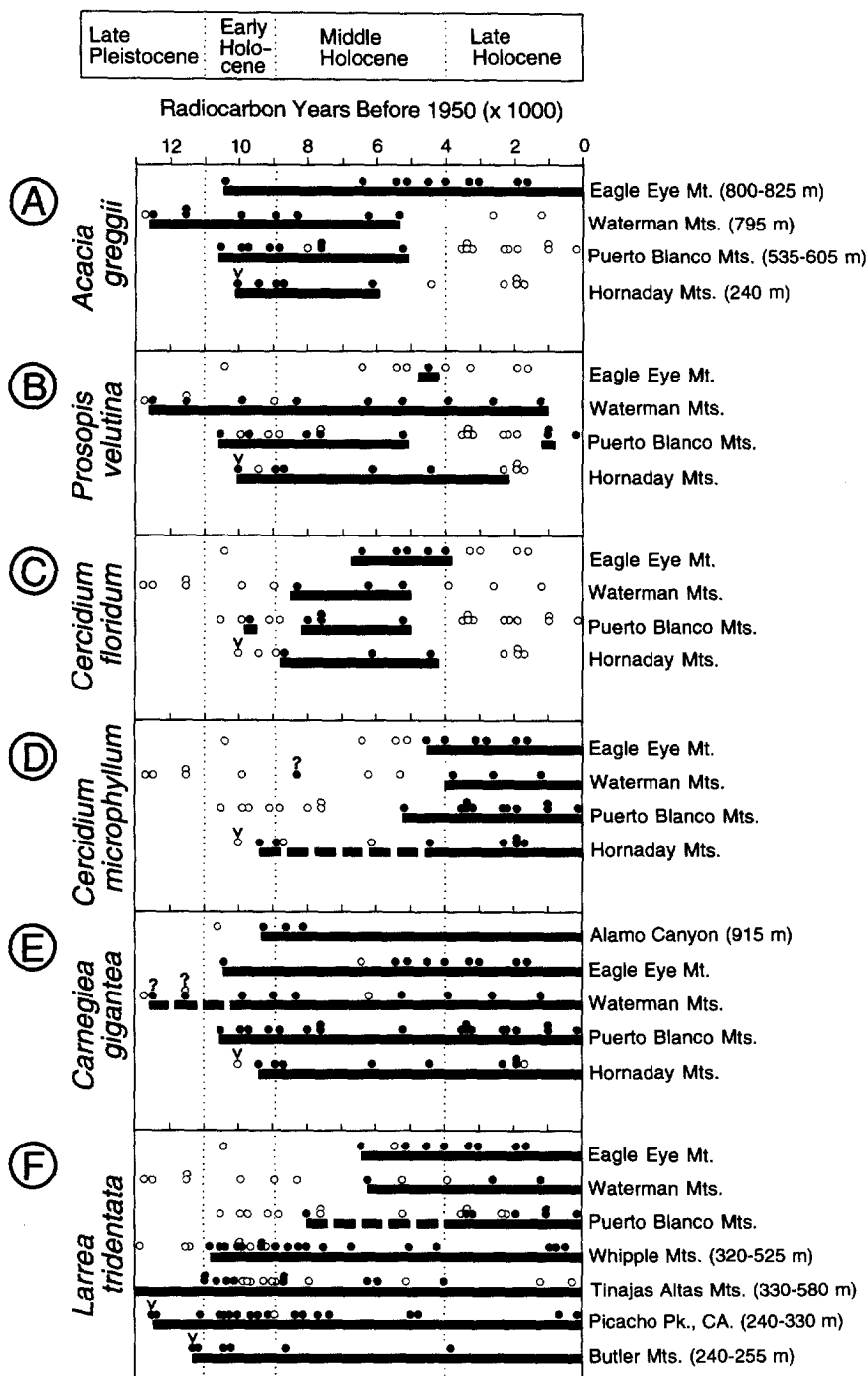
Fig. 7. Comparisons of presence/absence data for selected species during the last 13,000 years at various sites throughout the northern Sonoran Desert. Each dot represents a midden record; dots indicate presence and circles represent absence. The solid bars indicate the period over which the species was present at each site; dashed lines indicate questionable presence based on intervening samples from which the species was absent. Question marks above individual record indicate probable contaminants. The V positioned above a record indicates the oldest midden in the sequence (Hornaday Mts., Picacho Peak, and Butler Mts.). Midden sequences from all other sites extend to dates older than 13 ka.

dle Holocene (Fig. 7A,C). At each of these sites, *C. floridum* is today absent from the more xeric hillslopes and is restricted to more mesic environments along larger ephemeral streams. In the Puerto Blanco and Waterman mountains, *Prosopis velutina* was also present from the early to middle Holocene (Fig. 7B); it was found at Eagle Eye Mountain in a single midden dated at 4540 yr B.P.

The history of *Acacia greggii* at Eagle Eye Mountain differs from the records of this species at the Puerto Blanco and Waterman mountains (Fig. 7A). At both of these more southerly sites in the Arizona Upland, *A. greggii* disappeared from the midden record at the end of the middle Holocene. However, at Eagle Eye Mountain, this small tree persisted into the late Holocene, although apparently at lower abundances (Fig. 4). Today it is most common in the somewhat more mesic, north-facing cliffbase microhabitats (Fig. 3C). The persistence of *A. greggii* at Eagle Eye Mountain also reflects general compositional differences between modern Arizona Upland vegetation in the northern versus more southerly or easterly sites. Eagle Eye Mountain is near the transition between Mojave and Sonoran deserts, a zone in which *A. greggii* generally becomes a more important vegetation component. *Acacia greggii* is also commonly found in some relatively xeric interior chaparral communities that discontinuously border the northern margin of the Sonoran Desert (Pase and Brown, 1982).

The Eagle Eye, Waterman, and Puerto Blanco mountains midden sequences all show that *Cercidium microphyllum* arrived relatively late compared to other desertscrub species. The arrival of *C. microphyllum* and the formation of relatively modern desertscrub assemblages were used as indicators of the beginning of the late Holocene (Van Devender, 1987, 1990; Fig. 7D). At the Eagle Eye and Puerto Blanco mountains, *Cercidium floridum* and *C. microphyllum* coexisted during a short period between 4000 and 4500 yr B.P. during the transition from middle to late Holocene (Fig. 7C,D).

The late arrival of *Cercidium microphyllum* in the northern part of the Sonoran Desert is not readily explained by limitations to its spread imposed by climate. *Cercidium microphyllum* and *Carnegiea gigantea* are subtropical species that are similarly sensitive to extended freezing temperatures (Steenbergh

and Lowe, 1977), as indicated by nearly identical northern and upper elevational limits of their present geographic ranges in Arizona (Turner et al., 1995). Additionally, their nearly identical westward distributional limits along the Arizona–California border indicate similar responses to diminished precipitation, especially their dependence on summer precipitation which decreases from east to west (Turner et al., 1995). Given the similarities of their modern distributions in response to temperature and precipitation, it is hard to attribute the arrival of *Cercidium microphyllum* 6000 years after *Carnegiea gigantea* at sites throughout Arizona to different responses to Holocene climate regimes. An alternative hypothesis for the great difference in their arrival times is the contrasting manner in which seeds of each species are dispersed. The appearance of *C. gigantea* very near the beginning of the early Holocene in midden records throughout the Arizona Upland (Fig. 7) may have been due to the rapid, long-distance dispersal of its small seeds by frugivorous birds. For example, *Zenaida asiatica* (white-winged dove) consume the ripened fruits of *C. gigantea* (Steenbergh and Lowe, 1977; Olin et al., 1989) and potentially can disperse viable seeds many kilometers in a single day.

In contrast, *Cercidium microphyllum* seeds are typically dispersed over much shorter distances by small, seed-eating rodents (McAuliffe, 1990). Immediately upon ripening, entire fruits drop to the ground during a brief period lasting only a few weeks in early summer. During the time when fruits fall to the ground, seeds are removed from the pods by pocket mice (*Chaetodipus* spp., *Perognathus* spp.) and kangaroo rats (*Dipodomys* spp.). These rodents collect seeds from beneath trees rapidly and nearly completely; seeds rarely remain on the soil surface long after fruitfall ceases (McAuliffe, 1990). Seeds not immediately eaten are moved only a short distance away from the parent tree and are buried in underground caches for later retrieval. Some buried seeds are never relocated and eventually germinate. Because the rodents are so efficient at collecting and burying the seeds, the seeds are probably not available to be regularly picked up in large numbers by long-distance travellers such as birds. The considerably more limited dispersal distance of seeds of *C. microphyllum* may explain the tree's lag in arrival in the northern part of the Sonoran Desert. Similarly,

dispersal of seed by birds versus rodents may have also contributed significantly to differences in northward dispersal rates of various hardwood tree species in eastern North America during the Holocene (Vander Wall, 1990).

If the delayed arrival of *C. microphyllum* was due to these limitations of seed dispersal, its first occurrence in Holocene midden records should be earlier in the southern parts of the Sonoran Desert (at sites nearer its hypothesized Late Pleistocene distribution) and should become increasingly recent at more northerly or northeasterly sites. The presence of *C. microphyllum* in midden samples dated at 10,000 and 9570 yr B.P. from the more southerly Hornaday Mountains in the Pinacate Region of northwestern Sonora, Mexico (Van Devender et al., 1990, Figs. 1 and 7D) is consistent with this hypothesis and indicates that this area may have been extremely close to the geographic range of this subtropical desertscrub species during the Late Pleistocene. The oldest record of *C. microphyllum* macrofossils in middens from the Puerto Blanco Mountains, 100 km east of the Hornaday Mountains is 5240 yr B.P., at a time when the tree was absent from Eagle Eye Mountain, 220 km to the north (Fig. 7D). The arrival of *C. microphyllum* in the Puerto Blanco Mountains may have been earlier, but the timing of its arrival is poorly constrained because a 2320-year gap in the midden record precedes the 5240 yr B.P. record (Fig. 7D). The earliest record of *C. microphyllum* in the Waterman Mountains at 3880 yr B.P. is also poorly constrained because a 1300-year gap precedes this record (Fig. 7D).

Slightly different modes of seed dispersal may similarly have contributed to the arrival of *Cercidium floridum* approximately 3000–4000 yr before *C. microphyllum* in the northern Sonoran Desert. Unlike the very brief period over which nearly all fruits of *C. microphyllum* fall to the ground upon ripening, the fruits of *C. floridum* are retained on branches for several months after complete ripening; some fruits remain for up to a year (personal observations). The significantly longer retention of fruits on branches of *C. floridum* would make seeds more available for collection and potential long-distance dispersal by seed-eating birds including *Zenaida asiatica* and *Z. macroura* (mourning dove).

The appearance of *A. greggii* throughout the region in early Holocene middens (Fig. 7) may also be partly related to longer retention of ripe fruits in branches, making seeds more available to long-distance dispersal by birds. However, significant differences in climatic tolerances and paleodistributions are major factors responsible for the arrival of *A. greggii* long before *Cercidium floridum*. *Acacia greggii* had a more northerly distribution than either *Cercidium* species during the Late Pleistocene. Whereas macrofossils of *Cercidium* spp. have not been found in any Late Pleistocene middens from southern Arizona, several middens from southern Arizona with ages of 19.3 to 11.1 ka have contained *A. greggii* in association with *P. monophylla*, *Juniperus* spp., and *Q. turbinella* (Anderson and Van Devender, 1991; Van Devender et al., 1994). This difference in paleodistributions of *Cercidium* spp. and *A. greggii* is reflected in their modern northern distributional limits (*Cercidium* spp., 34.8°N; *A. greggii*, 36.5°N). Additionally, at latitudes in Arizona where *Cercidium* spp. and *A. greggii* are both found, the upper elevational limit of *A. greggii* is approximately 600 m higher than that of either *Cercidium* species (Turner et al., 1995).

Although the timing of the arrival of *Cercidium microphyllum* at Eagle Eye Mountain is well constrained, the earliest arrivals of many other desertscrub species are poorly constrained because of the 4000-year gap in the middle Holocene record between 6.4 and 10.4 ka (Fig. 4). The midden record for the Puerto Blanco and Waterman mountains also contain similar gaps (5.2–7.6 ka and 6.2–8.3 ka, respectively). These large temporal gaps in the early–middle Holocene midden records of sites in the Arizona Upland make it impossible to narrowly constrain the arrival times of many desertscrub species, including *Larrea tridentata* (Figs. 4 and 7F). In contrast, several sites in the Lower Colorado subdivision, including Picacho Peak and the Whipple Mountains in California, and the Tinajas Altas and Butler mountains in Arizona have yielded excellent series with numerous middens from the first half of the Holocene that allow better resolution of arrivals and departures times of many species. The large number of middens with ages between 11 ka and 7 ka from these sites in the Lower Colorado subdivision contrasts strongly with the relatively few middens of this age range from the Eagle Eye and

Waterman sites (Fig. 7F). Clearly, many questions regarding the pace of northerly movement of a variety of desertscrub species into the Arizona Upland will be resolved only with the discovery and study of additional midden material of early to middle Holocene age.

5.3. Holocene paleoclimate interpretations

5.3.1. Temperature regimes

Van Devender (1990) suggested a greater frequency of catastrophic winter freezes in the Puerto Blanco Mountains during the middle Holocene due to the absence of several cold-sensitive desertscrub plants during this period. However, comparison of middle Holocene occurrences of cold-sensitive *Encelia farinosa* with its current distribution at Eagle Eye Mountain according to aspect exposure does not indicate more frequent catastrophic freezes. *Encelia farinosa* is currently limited to more southerly exposures on Eagle Eye Mountain; the most northerly aspect where it presently occurs is 60°NE (Fig. 3B; Table 2). The absence of *E. farinosa* from northerly aspects is due to the intolerance of this shrub to frosts which are longer and more severe on northerly aspects at this elevation (Turner et al., 1995). However, vegetation sampling site V3 (45°N) where *E. farinosa* is today absent (Fig. 3B) is located at the opening of the shelter where midden samples with radiocarbon ages of 4.5 ka and 6.4 ka yielded very common *Encelia farinosa* achenes (Fig. 4; Table 4). The presence of this frost-intolerant shrub at this slightly more northerly aspect exposure during the middle Holocene suggests a temperature regime either as warm or slightly warmer than today's, especially in terms of an increase in winter temperatures or a decrease in unusual, catastrophic freezes.

This conclusion of slightly elevated middle Holocene temperatures based on comparisons of modern versus ancient aspect distributions of *E. farinosa* is consistent with other independent reconstructions of Holocene temperature changes. Analyses of stable hydrogen isotopes contained within cellulose of plant macrofossils from ancient packrat middens provide evidence of temperatures between 10,000 and 4000 years ago that were approximately 2°C higher than modern mean annual temperatures (Long et al., 1990). Reconstructions of average body sizes of packrats at various times in the past from the relationship between body size and fecal pellet sizes also reflect a slight temperature elevation during the middle Holocene (Smith et al., 1995).

5.3.2. Precipitation regimes

The presence of *Cercidium floridum* on exposed slopes during the middle Holocene at Eagle Eye Mountain and other Arizona Upland sites (Fig. 7) indicates moister conditions during that time than in the late Holocene or today, as the local distribution of this tree at these sites is now restricted to more mesic habitats along larger ephemeral watercourses. However, in localities along the more mesic, northern and eastern limits of the Arizona Upland at elevations between 1000 and 1200 m, *C. floridum* is occasionally present on exposed, southerly hillslopes in vegetational associations that include *A. greggii*, *P. velutina*, and occasionally, *C. gigantea*. The compositions of these assemblages resemble those represented in middle Holocene middens from Eagle Eye Mountain. Examples of these modern-day hillslope assemblages containing *C. floridum* are found in Yavapai County, Arizona along U.S. Highway 89 between Congress and Yarnell and along Castle Hot Springs Road, 50 and 65–70 km east of Eagle Eye Mountain, respectively. Similar assemblages are also found 225 km east-southeast of Eagle Eye Mountain in Gila County, in foothills of the Pinal Mountains, 5 km south of Miami, Arizona (Fig. 8). Based on precipitation records from nearby weather stations (data from Pase and Brown, 1982; Turner and Brown, 1982), average annual precipitation at the two Yavapai County sites is slightly more than 300 mm and the third site near the town of Miami receives an annual average of 400 mm. These precipitation amounts are 50% to 100% greater than the amount received today at Eagle Eye Mountain.

Other species provide further evidence for greater precipitation during the middle Holocene. The perennial C-4 grass *Setaria leucopila* (bristlegrass) and cacti are more abundant in middle Holocene middens than in late Holocene times. Van Devender (1987) showed similar responses of *Setaria macrostachya* (plains bristlegrass, including *S. leucopila*) during the middle Holocene in the Puerto Blanco Mountains. At that site, this grass species was consistently present throughout the early and middle Holocene,
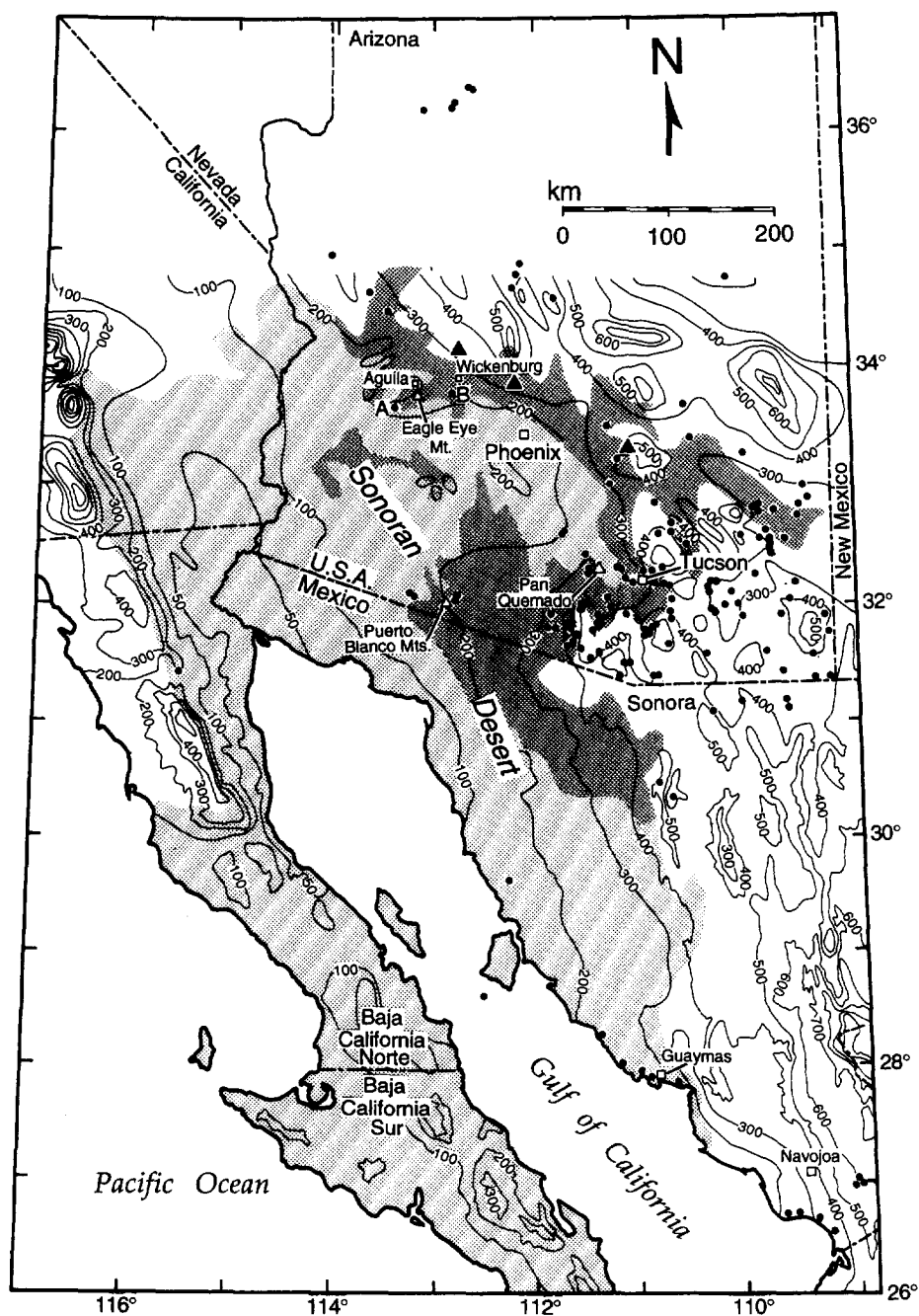
Fig. 8. Modern plant distributions. Small solid dots represent localities of documented specimens of *Setaria leucopila*. Large, solid triangles indicate the three localities discussed in the text where *Cercidium floridum* is found on exposed hillslopes. Cities and towns are shown as small open squares and other localities discussed in text indicated as small, open triangles. Precipitation isohyets redrawn from Turner and Brown (1982).

but was absent from the five most recent middens with ages less than 2.3 ka. There was a similar expansion of another perennial, C-4 grass, *Aristida ternipes* var. *gentilis* (= *A. hamulosa*) at 5020 yr B.P. in the Whipple Mountains (Van Devender, 1990). At Eagle Eye Mountain, *Opuntia acanthocarpa* (buckhorn cholla) is present during the middle Holocene at the same time when *S. leucopila* was present (Fig. 5), but today this cactus is completely absent from sampling areas around all midden shelters (Table 2), but becomes conspicuously abundant on alluvial fan surfaces 0.5–1.0 km southwest nearer the Harquahala Mountains where orographic effects contribute to greater precipitation. The responses of *S. leucopila* and cacti during the middle Holocene suggest that warm-season precipitation was greater at that time than at present.

With few exceptions, herbarium records indicate that *S. leucopila* is typically absent from parts of the Sonoran Desert receiving less than 200 mm average annual precipitation. In Arizona, *Setaria leucopila* most commonly occurs in semiarid grasslands of the southeastern part of the state where average annual precipitation exceeds 300 mm (Fig. 8). *Setaria leucopila* is present today in Arizona Upland communities toward the eastern margin of the Sonoran Desert where summer monsoonal precipitation (June–August) is considerably greater than that now experienced at Eagle Eye Mountain. For example, *S. leucopila* is occasionally abundant on the more mesic, northerly exposures of rhyolitic hills (Pan Quemado) located 35 km west of Tucson near the Waterman Mountains (Fig. 8; Wiens, 1996; pers. observation, January 1993). This area receives an estimated annual average of 280 mm precipitation, 43% of which (= 120 mm) is received from June through August (based on weather records from Silverbell, located at the same elevation, 10 km away). In contrast, Eagle Eye Mountain receives approximately 200 mm average annual precipitation, but only 30% of this total (= 60 mm) is received from June through August (precipitation data from Turner and Brown, 1982).

Herbarium records also show that *S. leucopila* is absent through the extremely arid lowlands of the Sonoran Desert near the northern end of the Gulf of California in Mexico, but reappears at more humid coastal and inland sites in southern Sonora, Mexico near Guaymas (Fig. 8), as summer monsoonal

precipitation increases markedly from north to south (Douglas et al., 1993). Guaymas, Sonora annually receives an average of 233 mm precipitation, of which 117 mm is received between June and August.

Setaria leucopila has only been collected from two locations near Eagle Eye Mountain. One was immediately west of Eagle Eye Mountain (site 'A', Fig. 8) from a much higher, more mesic elevation (1524 m in a riparian area amidst woodland and chaparral) in the Harquahala Mountains. The other locality 36 km east of Eagle Eye Mountain at 820 m elevation in the Vulture Mountains (site 'B', Fig. 8) is associated with a sharp increase in precipitation to the east. Whereas Aguila (6 km north of Eagle Eye Mountain) annually receives only 190 mm average precipitation, the town of Wickenburg (639 m elevation), 41 km east of Aguila and 10 km north of the Vulture Mountains receives an annual average of 274 mm precipitation (July–August total = 92 mm). Taken together, these herbarium records and associated precipitation data indicate that a threshold of average summer precipitation required for persistence of *S. leucopila* is approximately 100–120 mm. This amount is 67% to 100% greater than presently received at the site, an increase consistent with information on precipitation amounts that foster the presence of *C. floridum* on exposed slopes at higher elevations.

In addition to mid-summer monsoonal precipitation, another moisture source, tropical cyclones in the eastern Pacific, could have contributed to some of the plant responses in the Arizona Upland during the middle Holocene. These tropical cyclones or 'chubascos' occasionally track into the region in late summer to early fall (September–October). Paleoclimatic reconstructions for the American Southwest have largely overlooked this important moisture source and have instead dichotomized precipitation as either monsoonal or winter frontal and have attributed past paleoecological records to changes in one or the other of these two sources.

When waters of the eastern Pacific are anomalously warm during El Niño conditions, these tropical Pacific cyclones apparently tend to recurve from their normal west-northwest courses to the northeast toward the northwestern coast of Baja California and Sonora, Mexico, into the Sonoran Desert region (Webb and Betancourt, 1990). As these trop-

ical storms dissipate over land, they yield widely distributed, heavy rainfall, often over a several-day period, and have produced the largest flood and filling events of dry lake beds in southern Arizona during this century (Waters, 1989; Webb and Betancourt, 1990). Precipitation delivered in the Sonoran Desert by these storms, especially those occurring in September, can provide a significant moisture source to plants that are principally active during the warm season. By extension, the warm-season precipitation signal indicated by the midden record from Eagle Eye Mountain may be to some degree the result of moisture from tropical cyclonic activity. Given the marked hydrological impacts of these cyclonic storms in historic times, Waters (1989) suggested that two high lake stands in Willcox Playa (pluvial Lake Cochise) in southeastern Arizona during the latter half of the middle Holocene may have been caused by a greater incidence of tropical cyclones tracking into the region. These high lake level stands are synchronous with the period over which the midden record from Eagle Eye Mountain indicates greater warm-season precipitation than at present. Further investigations involving paleohydrological, paleoecological, and climate modeling efforts are clearly necessary to better resolve the sources of warm-season precipitation in the Sonoran Desert region during the Holocene.

5.4. Remaining problems

The Eagle Eye midden record provided a general validation of previous reconstructions of vegetation in a new area of the Arizona Upland near the northern border of the Sonoran Desert. A paleoclimatic inference of greater freeze frequencies in the middle Holocene (Van Devender, 1987) was contradicted based on a documented expansion of frost-intolerant *Encelia farinosa* onto more northerly aspect exposures during the middle Holocene. Detailed comparisons of modern-day distributions of two species, *C. floridum* and *S. leucopila* indicate that substantially greater amounts of precipitation, especially warm-season precipitation, was received in the latter half of the middle Holocene.

Although the three long series of middens (Eagle Eye, Puerto Blanco, and Waterman mountains) and various shorter sequences (Table 1) provide a

remarkably coherent picture of the history of vegetation and paleoclimate in the Arizona Upland, several important questions remain unanswered due to significant gaps in the midden record. The single early Holocene sample which indicates the persistence of juniper–oak woodlands is consistent with other midden records from the region (Van Devender, 1990), model reconstructions of early Holocene precipitation regimes (COHMAP Members, 1988), and inferences of greater precipitation at this time based early Holocene filling of Lake Cochise (Willcox Playa) in southeastern Arizona (Waters, 1989). Although the Eagle Eye Mountain record indicates warmer, moister conditions in the latter half of the middle Holocene, it is unclear whether these conditions were continuous with elevated temperature and precipitation regimes of the early Holocene. Regionally, other lines of proxy climate data indicate substantial variation within the middle Holocene. For example, detailed studies of shoreline deposits surrounding Willcox Playa indicate an absence of lake-filling events in the first half of the middle Holocene, but show two distinct lake stands in the latter half of the middle Holocene (Waters, 1989). Clearly, more middens from the early Holocene and first half of the middle Holocene are needed to resolve many remaining questions regarding changes in plant communities over time and the paleoclimatic regimes that contributed to these changes.

The Arizona Upland forms the northern and northeastern margin of the Sonoran Desert with more mesic interior chaparral in central Arizona to the north and semi-desert grasslands to the east. During the Pleistocene glacials, the Arizona Upland region was occupied by woodland/chaparral with *Pinus monophylla*, *Juniperus osteosperma*, and *Quercus turbinella*. A series of Late Pleistocene midden samples from Pontatoc Ridge at 1555 m in the Santa Catalina Mountains near Tucson indicated that these Late Pleistocene woodlands merged into mixed coniferous forests (Van Devender, 1990). The Arizona Upland and adjacent communities presently form a broad arc from central New Mexico to northwestern Arizona below the Mogollon Rim. Mid- to late Wisconsin pollen samples from sites north of the Mogollon Rim were dominated by *Picea* (spruce), *Pseudotsuga* (Douglas fir), and *Pinus*, indicators of dense regional mixed-conifer forests (Whiteside,

1965; Hall, 1985; Anderson, 1993). Discovery and study of additional long series of middens from elevations of the Arizona Upland anywhere east of Eagle Eye Mountain and north of Tucson would yield invaluable insight into the late Quaternary history of this important regional ecotone.

Acknowledgements

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