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Middle- and late-Wisconsin paleobotanic and paleoclimatic records from the southern Colorado Plateau, USA

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Abstract

The Colorado Plateau is a distinct physiographic province in western North America, which presently straddles the transition between summer-wet and summer-dry climatic regimes to the south and northwest, respectively. In addition to climate, the diversity of environments and plant communities on the Colorado Plateau has resulted from extreme topographic diversity. Desert lowlands as low as 360 m elevation are surrounded by forested plateaus, and even higher peaks greater than 3800 m elevation. This environmental diversity provides a unique opportunity to study the history of biotic communities in an arid region of North America. Although the Colorado Plateau harbours numerous potential sites, the paleoecological record of the Plateau is poorly known. Potential deposits for analysis include packrat middens, alluvial and cave sites at lower elevations, and lake, bog and wetland sites at higher elevations. Forty-six sites have been analysed across the nearly 337,000 km^2 region, of which 27 contain records that span Marine Oxygen Isotope Stage (IS) 2 data, with IS 3 information coming from only 12 sites. Most IS 2 and 3 sites are clustered along the lowland regions of the Colorado River corridor and the uplands of the Mogollon Rim area. We compiled selected data from long paleoecological records to examine patterns of vegetation and climate change across the southern Colorado Plateau for the middle and late Wisconsin. During the middle Wisconsin, mixed conifers covered middle-elevations presently dominated by ponderosa pine (*Pinus ponderosa*), and juniper (*Juniperus*) woodland grew at elevations today covered by blackbrush (*Coleogyne*) and sagebrush (*Artemisia*) desert. During the late Wisconsin, boreal conifers, primarily Engelmann spruce (*Picea engelmannii*), replaced the mixed conifer association. Estimates of mean annual temperatures (MAT) during IS 3 were at least 3–4ºC cooler than today, whereas IS 2 MAT estimates are at least 5ºC colder. Our investigation of millennial-scale climatic variability within the region provided equivocal results. The packrat midden sequence could not distinguish vegetation changes that might be associated with Heinrich events in the North Atlantic. From the lake records, however, many Heinrich events were associated with generally drier intervals, often with elevated sagebrush pollen concentrations. Future paleoecological investigations should concentrate on the northern Colorado Plateau, as well as the eastern and western

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margins. Additional sites, along with closer-spaced sampling in regions already studied, will be important in determining the history of important climatic phenomena such as the timing of the Arizona monsoon.

Keywords: Quaternary; paleoecology; Colorado Plateau; pollen; plant macrofossils; packrat middens

1. Introduction

The Colorado Plateau is a unique physiographic province in western North America, located between the Rocky Mountains to the east and north, and the Basin and Range province to the west and south. Covering an area of roughly 337,000 km^2, with an average elevation of 1525 m, the Colorado Plateau covers parts of the states of Utah, Arizona, Colorado and New Mexico (Fig. 1). The elevational range varies from ca. 360 m at the lower reaches of the Grand Canyon of the Colorado to ca. 3850 m at the crest of the San Francisco Peaks. Geologically, the region consists of extensive areas of nearly horizontal sedimentary rock formations, punctuated locally by volcanic terrains, drainage systems defined by deeply incised, steep-walled canyons, and extensive areas of bare rock (Hunt, 1967).

The spine of the Colorado Plateau is the Colorado River, which rises high in the Rocky Mountains, dissects the Colorado Plateau, and exits the Grand Canyon at the Grand Wash Cliffs on its way to the Sea of Cortez. Major tributaries include the Green (draining the north), San Juan (draining the east) and Little Colorado (draining the southeast) rivers. These riparian corridors have played an important, but passive, role in biotic movements of the past and present (Benson and Darrow, 1981).

Perhaps because of its sparse human settlement and rugged terrain, surprisingly little is known about the Late Pleistocene paleoecology of the Colorado Plateau. Much of our knowledge is confined to the core and southern portions of the Plateau. Betancourt (1990) synthesised current late-Quaternary paleobotanical research on the low to middle elevations (ca. 900–2200 m) of the region, primarily from packrat (*Neotoma*) middens collected from the central Plateau. Thompson et al. (1993) summarised paleoenvironmental data for the entire western U.S., including the Colorado Plateau, for the period since ca. 18,000 yr BP. Cole (1982, 1985, 1990) concentrated on the late-Quaternary vegetation changes from the eastern Grand Canyon, while other workers (Wright et al., 1973; Jacobs, 1985; Hevly, 1985; Anderson, 1993) have studied individual sites at the southern margin, or at higher elevations, on the Plateau.

Considering the vast diversity of environments on the Colorado Plateau, the uneven spacing of sites, and the variety of paleoenvironmental proxies, an exhaustive treatment of the late-Quaternary paleoecology of the entire province must await future efforts. Our objective here is to summarise major aspects of the paleobotany and paleoenvironments of the late- and middle-Wisconsin period — Oxygen Isotope Stages (IS) 2 and 3 — of the southern Colorado Plateau in part to suggest a research agenda for the future, as well as to examine regional expression of global climate.

Why is it important to understand the paleoenvironments of the Colorado Plateau? Due to its geographic position and elevation, the Colorado Plateau plays a key role in the North American monsoons, similar to the influence that the Tibetan Plateau exerts on the Southeast Asian monsoon (Tang and Reiter, 1984; Adams and Comrie, 1997). In both cases, a high-elevation land mass serves as an efficient summertime heat source for the otherwise-cool air aloft, thermally inducing a trough and thus driving monsoonal flow. Like the Tibetan system, a large springtime snowpack in the southern Rockies favors cold continental temperatures that tend to inhibit monsoon development (Gutzler and Preston, 1997). During glacial periods, snowpacks on the Colorado Plateau may have been sufficient to exert a similar influence on monsoonal flow. On a variety of scales, from interannual to glacial–interglacial, when the southwest is wet, the northwest is dry and vice versa. In general terms, the average position of the polar jet stream and winter storm tracks migrate from north to south of a pivot point at 40°N (Dettinger et al., 1998). It is uncertain if this pivot point is the same for Milankovitch and sub-Milankovitch time scales as for interannual/interdecadal variations, although an average value of 35°N latitude is suggested from paleoenvironmental data (Thompson et al., 1993).

The occurrence of significant river corridors oriented north–south probably assisted in channeling migration and gene flow to and from the interior of North America. Our understanding of Colorado Plateau paleoecology will allow us to determine routes and rates of migration, which may help anticipate future shifts in biotic distributions with changing climates. Lastly, the topographic diversity of the Plateau provides ample opportunity to study biogeographic phenomena, such as long-distance dispersal, vicariance and island biogeography. Large portions of the Plateau are protected or semi-protected federal lands, including the newly established 0.7 million ha Grand Staircase-Escalante National Monument. Paleoecological research can help establish historical baselines for land management decisions on all parts of the Colorado Plateau.

1.1. Modern climate

Although large uplands such as the Colorado Plateau exert considerable influence on regional climates (Ruddiman and Kutzbach, 1991), modern climatic syntheses of the entire Plateau climate are few. Until recently, potential syntheses have suffered from a low density of recording stations, as well as a considerable variation in elevation between stations. For the compilation of historic precipitation series Richmond (1987) used data from 1859 to 1983 AD, collected from only 40 sites on, and 10 sites immediately off, the Plateau. Station density was low; stations were 80–150 km apart. In addition, only a narrow range of elevations was represented. Forty-seven percent of all stations were located between 1525 and 1830 m (5000 and 6000 ft) elevation, and 78% of recording stations were found between 1220 and 2130 m (4000 and 7000 ft) elevation. Average annual precipitation at these sites varied from 14 cm (Lee's Ferry, AZ; 975 m) to 59 cm (Telluride and Steamboat Springs, CO; 2063 and 2667 m, respectively). Summer (July through September) had the greatest precipitation at most stations, although at eleven sites, winter (December through February) precipitation exceeded that of summer.

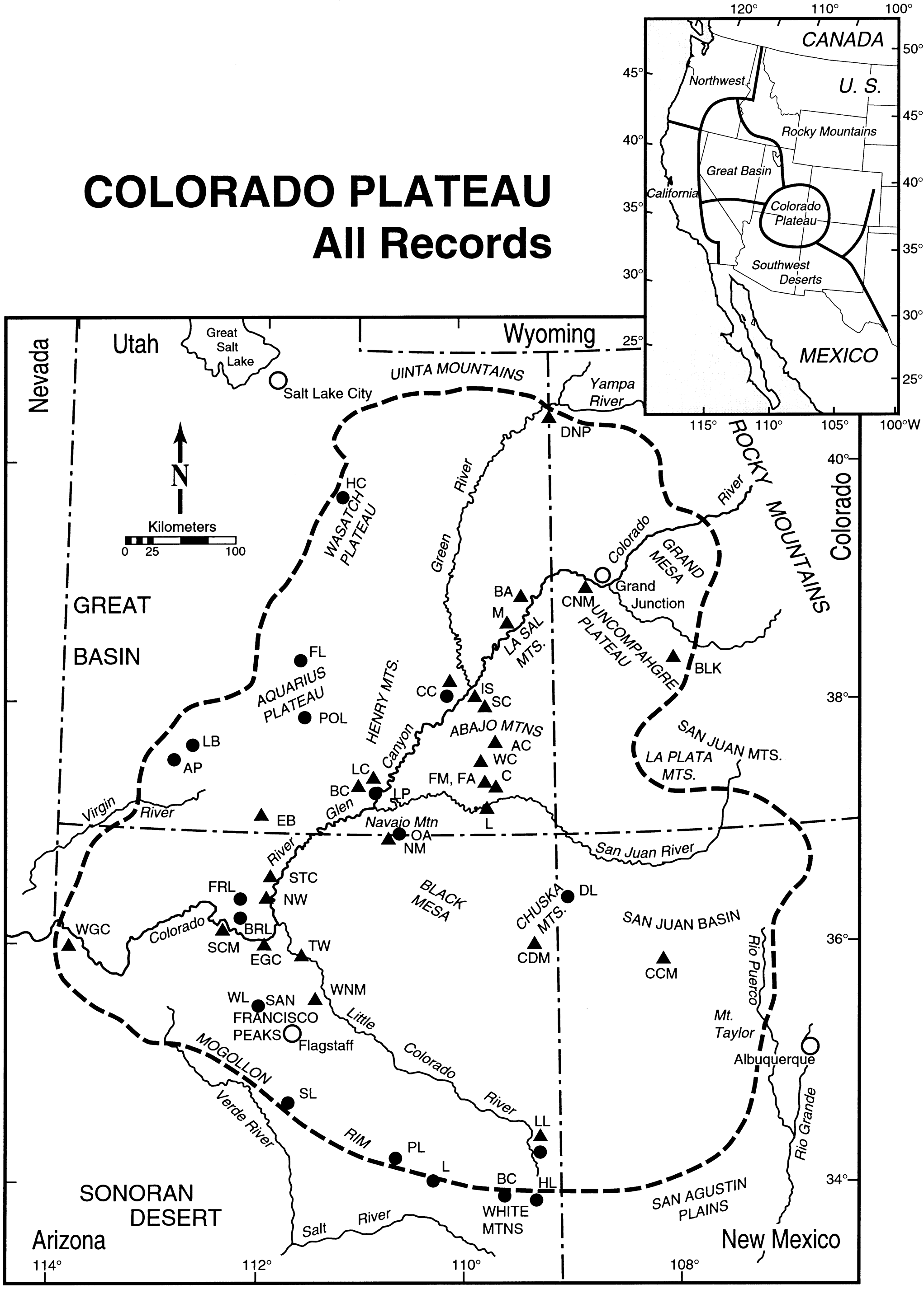
Hereford and Webb (1992) examined 24 stations to link historic variations in summer rainfall with stream erosion and deposition in the southern Colorado Plateau. They concluded that June 15–October 15 rainfall tended to be normal to above normal during El Niño events. Winter precipitation in the southern Colorado Plateau also tended to be above normal during ENSO episodes (D'Arrigo and Jacoby, 1991).

Mock's diagrams (Mock, 1996) depict changes in month-to-month precipitation for western North America, including the Colorado Plateau. Early winter (December and January) precipitation is spatially heterogeneous, and is strongly influenced by elevation. However, late winter (February and March) trends show increasing precipitation throughout the Plateau, resulting from increased cyclogenesis in the Great Basin to the west. By May the trend is reversed, with drier conditions lasting into June. Precipitation changes for July and August are strongly positive throughout the southwest. This summer monsoon impacts the southern 3/4 of the Plateau, but brings very little moisture to the Wasatch Plateau and Uinta Basin in the north. However, in September, drier conditions prevail again, as precipitation decreases throughout the southern 3/4 of the Plateau with the weakening of the summer monsoon. This trend lasts through October and November for most of the Plateau, though increases are demonstrated for the Wasatch Front to the west and the western Rocky Mountains to the east.

These patterns clearly demonstrate the spatial heterogeneity of climate on the Colorado Plateau (Mock, 1996). In general, precipitation decreases from high elevation sites to low elevation sites. In addition, summer precipitation decreases from the southern Colorado Plateau northward (Higgins et al., 1997), and it may be assumed that the amount of summer precipitation falling in the north is related to the strength of the summer monsoon. These relationships have important consequences for modern, and probably former, biotic distributions on the Plateau.

1.2. Modern vegetation

Modern vegetation of the southern Colorado Plateau and adjoining regions has been described by numerous authors, beginning with Merriam (1890), whose studies led to a description of vegetation



● = stratigraphic record (lake, etc.)

▲ = packrat midden locality

belts, termed 'life zones', based upon elevational changes within the province. Subsequent refinements of the vegetation classification for different portions of the Plateau include Shreve (1942), Lowe (1964), and Phillips et al. (1989) for the southern Colorado Plateau, Dixon (1935) for southwest Utah, Graham (1937) and Goodrich and Neese (1986) for northeast Utah, and Weber and Wittmann (1996) for western Colorado. General texts include Kearney and Peebles (1960) and Welsh et al. (1987). Although it is convenient to think of vegetation zones organised by elevation, a more realistic concept is that individual plant species are distributed independently of one another, each species having developed its own response and distribution along an elevational gradient (Gleason, 1939; Whittaker, 1970; Phillips et al., 1989).

Betancourt (1990) summarized the modern distribution of vegetation with respect to elevation across the southern Colorado Plateau. The alpine zone occurs above 3480 m elevation on the San Francisco Peaks, the La Sal Mountains, and the Markagunt and Tushar plateaus. On the San Francisco Peaks, common alpine species include golden avens (*Geum turbinatum*), sedges (*Carex* sp.), Parry lousewort (*Pedicularis parryi*), and other forbs (Little, 1941; Schaack, 1970). Common tree species in the subalpine (spruce-fir) zone at ca. 2900–3480 m include Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Several high-elevation pines, including limber (*Pinus flexilis*), bristlecone (*P. aristata*) and western bristlecone (*P. longaeva*), occur locally, but never in abundance (Betancourt, 1990). A mixed-conifer forest at ca. 2600–2900 m elevation includes Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*) and Colorado blue spruce (*Picea pungens*), with local abundance of quaking aspen (*Populus tremuloides*), and at lower elevations, ponderosa pine (*Pinus ponderosa*).

The forest assemblage below the mixed-conifer zone is dominated by ponderosa pine, to ca. 2100 m elevation. The ponderosa pine forest type is found extensively along the southern boundary of the Plateau — the Mogollon Rim. Other trees found locally include Gambel oak (*Quercus gambelii*), Rocky Mountain juniper (*Juniperus scopulorum*) and quaking aspen. Pinyon–juniper woodlands occupy extensive plateaus from ca. 1600 to 2100 m. Dominant trees include Colorado pinyon (*Pinus edulis*), Utah juniper (*Juniperus osteosperma*) and one-seed juniper (*J. monosperma*).

The desertscrub zone interfingers with, and is more heterogeneous than, the pinyon–juniper assemblage. For instance, the big sagebrush (*Artemisia tridentata*) communities on Fishtail Mesa (1860 m; Jameson et al., 1962) and Boysag Point (1675 m; Schmutz et al., 1967), Grand Canyon National Park, include Mormon tea (*Ephedra viridis*), four-wing saltbush (*Atriplex canescens*), prickly-pear cactus (*Opuntia* spp.) and many grasses (*Oryzopsis hymenoides*, *Bouteloua eriopoda*, and *Sporobolus cryptandrus*). At slightly lower elevations, typified by 1400 m elevation in San Juan County, Utah, a mixed shrub community dominated by blackbrush (*Coleogyne ramosissima*), shadscale (*Atriplex confertifolia*) and Mormon tea (*Ephedra torreyana*) is found (Turner, 1982). At even lower elevations in the Grand Canyon, species typical of the Mohave desert dominate. Brittlebush (*Encelia farinosa*) and beavertail cactus (*Opuntia basilaris*) are common below ca. 1000 m elevation (Cole, 1981). Southwestern Utah and the Grand Canyon region define the eastern boundary of other important desert species such as creosotebush (*Larrea divaricata*) and ocotillo (*Fouquieria splendens*). Terminology follows Kearney and Peebles (1960).

2. The dataset

Sites compiled here include both published and unpublished data. We considered only those records that contained primary paleoecological data. We excluded from consideration many studies conducted in concert with archaeological investigations, as well

Fig. 1. Location map of the general physical features on the Colorado Plateau, and locations of major paleobotanical sites, in relation to other physiographic regions of western North America (base map after Betancourt, 1990; inset after Thompson et al., 1993). Dots = stratigraphic sites (mostly lakes, bogs, meadows and alluvial profiles); triangles = non-stratigraphic sites (primarily packrat middens). Site abbreviations see Table 1.

Table 1
Location of major paleobotanical sites on the Colorado Plateau.

State	Record type[a]	Site	Elevation (m)	Approximate age range (cal. yr BP × 10^3)	References
Arizona	M	Rampart Cave (RC)	530	9.5–22.6	Phillips and Van Devender, 1974; Phillips, 1977;
	M	Vulture Cave (VC)	645	1.2–36.0	Phillips, 1977; Mead and Phillips, 1981
	M	Shinumu Creek (SH)	700	16.6	Van Devender and Mead, 1976
	M	Peach Springs Wash (PS)	855	14.0	Van Devender and Mead, 1976
	M	Stanton's Cave (SC)	900	12.9–37.0	Dryer, 1994
	M	Eastern Grand Canyon (EGC)	950–2200	0.0–36.6	Cole, 1982; Cole, 1990
	M	Nankoweap Region (NR)	1082–1273	15.2–46.9	Coats, 1996
	M	Tappan Wash (TW)	1310–1370	1.0–13.7	Van Devender and Spaulding, 1979
	M	Wupatki National Monument (WNM)	1490–1525	0.0–16.5	Cinnamon, 1988; Cinnamon and Hevly, 1988
	M	Canyon de Chelly/Canyon del Muerto (CDM)	1770	1.8–13.0	Betancourt and Davis, 1984
	S and M	Lyman Lake (LL)	1880	0.0–32.7	Koehler (unpublished)
	S	Stoneman Lake (SL)	2047	0.0–10.0	Hasbargen, 1994
	S	Potato Lake (PL)	2222	0.0–32.7	Whiteside, 1965; Anderson, 1993
	S	Jacob Lake (JL)	2285	0.0–26.5	Jacobs, 1983
	S	Walker Lake (WL)	2500	0.0–49.6	Berry et al., 1982; Adam et al., 1985; Hevly, 1985
	S	Fracas Lake (FL)	2512	0.0–13.0	Weng and Jackson, 1999
	S	Bear Lake (BL)	2768	0.0–13.0	Weng and Jackson, 1999
	S	Hay Lake (HL)	2780	0.0–43.2	Jacobs, 1983, 1985
	S	Benny Creek (BC)	2865	0.0–>29.1	Merrill and Péwé, 1977
Utah	M	The Maze (Canyonlands) (M)		0.0–0.8	McMullin (unpublished)
	S	Lake Pagahrit (LP)	1250	0.5–5.8	Phillips, 1995
	S	Escalante Basin (EB)	1140–1200	8.4–26.6	Withers and Mead, 1993
	S	Bechan Cave (BC)	1310	13.7–15.5	Davis et al., 1984; Mead et al., 1986

Table 1 (continued)

State	Record type [a]	Site	Elevation (m)	Approximate age range (cal. yr BP × 10^3)	References
	M	Bison Alcove (Arches) (BA)	1317	1.8–23.8	Sharpe, 1991
	M	Island-in-the-Sky (Canyonlands) (IS)	1340–1400	0.4–35.4	Mead and Agenbroad (unpublished)
	M	Cottonwood Cave (C)	1390	6.9–18.7	Betancourt, 1990
	M	Long Canyon (Glen Canyon) (LC)	1390	2.4–20.7	Betancourt, 1990
	S	Oak Alcove (OA)	1442	0.0–13.5	Smith et al., 1996
	M	Falling Arch (FA)	1460	2.4–23.4	Betancourt, 1990
	M	Salt Creek (Canyonlands) (SC)	1490–1830	0.0–39.9	Mead and Agenbroad (unpublished)
	M	Navajo Mountain (NM)	1510–2390	1.8–16.7	Koehler (unpublished)
	M	The Loop (L)	1525	1.2–10.5	Betancourt, 1990
	M	Fishmouth Cave (FM)	1585	2.3–16.8	Betancourt, 1984
	S and M	Cowboy Cave (CC)	1782	0.0–15.5	Spaulding and Petersen, 1980; McVickar, 1991
	M	White Canyon (WC)	1820	11.0–>41.3	Mead et al., 1987
	M	Sand Canyon Alcove (Dinosaur) (DNP)	1920	3.2–11.2	Sharpe, 1991
	M	Allen Canyon Cave (AC)	2200	1.8–13.3	Betancourt, 1984
	S	Posey Lake (POL)	2653	0.0–8.1	Shafer, 1989
	S	Fryingpan Lake (FL)	2720	0.0–9.2	Shafer, 1989
	S	Huntington Canyon (HC)	2740	9.5–14.6	Gillette and Madsen (1993)
	S	Lowder Creek Bog (LB)	3278	0.0–15.5	Anderson et al. (1999)
	S	Alpine Pond (AP)	3278	0.0–2.8	Anderson et al. (1999)
Colorado	M	Colorado National Monument (CNM)	1890–2139	0.0–8.5	Koehler (unpublished)
	M	Black Canyon of the Gunnison (BLG)		5.5–6.0	Koehler (unpublished)
New Mexico	M	Chaco Canyon (CC)	1860–2020	0.0–12.5	Betancourt and Van Devender, 1981
	S	Dead Man Lake (DL)	2780	0.0–>31.2	Wright et al., 1973

[a] M = midden; S = sediment.

as those from herbivore dung. Notable exceptions to this exclusion include Chaco Canyon, Stanton's Cave, Bechan Cave, and Rampart Cave (Table 1). Thus our dataset includes 46 sites or records.

Primary chronological control for each record is by radiocarbon dating. However, we have converted each radiocarbon date to a calendar year. From the present to 19,262 ^{14}C years, we used the CALIB 3.0 program of Stuiver and Reimer (1993). From the period of 19,262 to 27,120 ^{14}C years, we used a linear interpolation between the two sets of equivalent ^{14}C and U–Th ages given by Bard et al. (1990). The conversion assumes that U–Th ages and calendar ages are equivalent. From 27,120 to 50,000 ^{14}C years we used a relationship suggested by Mazaud et al. (1991) and Thouveny et al. (1993) which relates the variations in the geomagnetic dipole field strength and the production of ^{14}C. The results suggest that the difference between ^{14}C and calendar ages is ca. 3000 years at about 30,000 cal yr BP, while decreasing to near zero by ca. 50,000 cal. yr BP (P.J. Bartlein, pers. commun., 1996).

2.1. *Types of deposits*

Few geographic regions can match the variety of paleobotanical deposits found on the Colorado Plateau. Sediments include stratigraphic deposits from lakes, bogs, alluvium, and caves, as well as non-stratigraphic deposits, primarily packrat middens and herbivore dung. Natural lakes and bogs on the Colorado Plateau are generally limited to higher elevations, where high evaporation is balanced by greater precipitation. Caves and alcoves containing stratigraphic deposits are abundant at middle to low elevations throughout the Plateau; in contrast to organic remains from lakes and bogs, organic remains in cave sediments are preserved by desiccation (Davis, 1990). Alluvial deposits have also been studied for pollen and plant macrofossil content. Most studies presented to date come from low to middle elevation sites.

Packrat (*Neotoma*) middens are found throughout the arid west, and have become an important source of paleoenvironmental information from middle to low elevation sites (Betancourt et al., 1990a). Though primarily examined for species identifications of plant macrofossils, recent studies have included analyses of pollen (Anderson and Van Devender, 1995), insects (Elias et al., 1992), vertebrates (Mead and Phillips, 1981), stomatal density/carbon isotopes in leaves (Van de Water et al., 1994), and packrat body size estimates from faecal pellets (Smith et al., 1995; Smith and Betancourt, 1998). The dung of extinct mammals in both packrat middens and cave sediments has also been analysed for its paleobotanical content (Davis et al., 1984; Mead et al., 1986; Mead and Agenbroad, 1992).

Our compilation of late-Quaternary paleobotanical records includes 20 stratigraphic deposits and 28 packrat midden records (Table 1).

2.2. *Spatial site distribution*

The locations of all stratigraphic (dot) and non-stratigraphic (triangle) paleobotanical records on the entire Colorado Plateau are shown in Fig. 1. Most sites are located in Utah and Arizona. The majority of middle- to low-elevation packrat midden records occur near the axis of the Colorado River and its major tributaries; the San Juan, Little Colorado and Green rivers. The majority of stratified sites, primarily lake and bog records, occur on the southern edge of the Plateau, along the heavily forested Mogollon Rim, or on the higher elevations of the western plateaus of southwestern Utah. Significant geographic gaps in the total record occur on the northern quarter of the Colorado Plateau (the Wasatch Plateau of Utah, and the Uinta Basin of Utah and Colorado), much of northeastern Arizona and northwestern New Mexico, northeast of the Little Colorado River valley, and northwestern Arizona.

Sites are located along a near-continuous range of elevations, from ca. 1550 to over 3200 m elevation (Fig. 2). Most sites below ca. 2100 m elevation come from packrat midden localities. Many are from a single cave or shelter, but at least seven series occur at a range of elevations within a given locality. Stratigraphic deposits are found primarily above ca. 2100 m elevation. The distribution of lake and bog sites is not as continuous as for packrat midden sites; no sites are presently available for elevations of ca. 2200–2500 m and for 2700–3278 m. Although the highest elevation on the Colorado Plateau is ca. 3850 m, no site has been analysed above 3278 m.

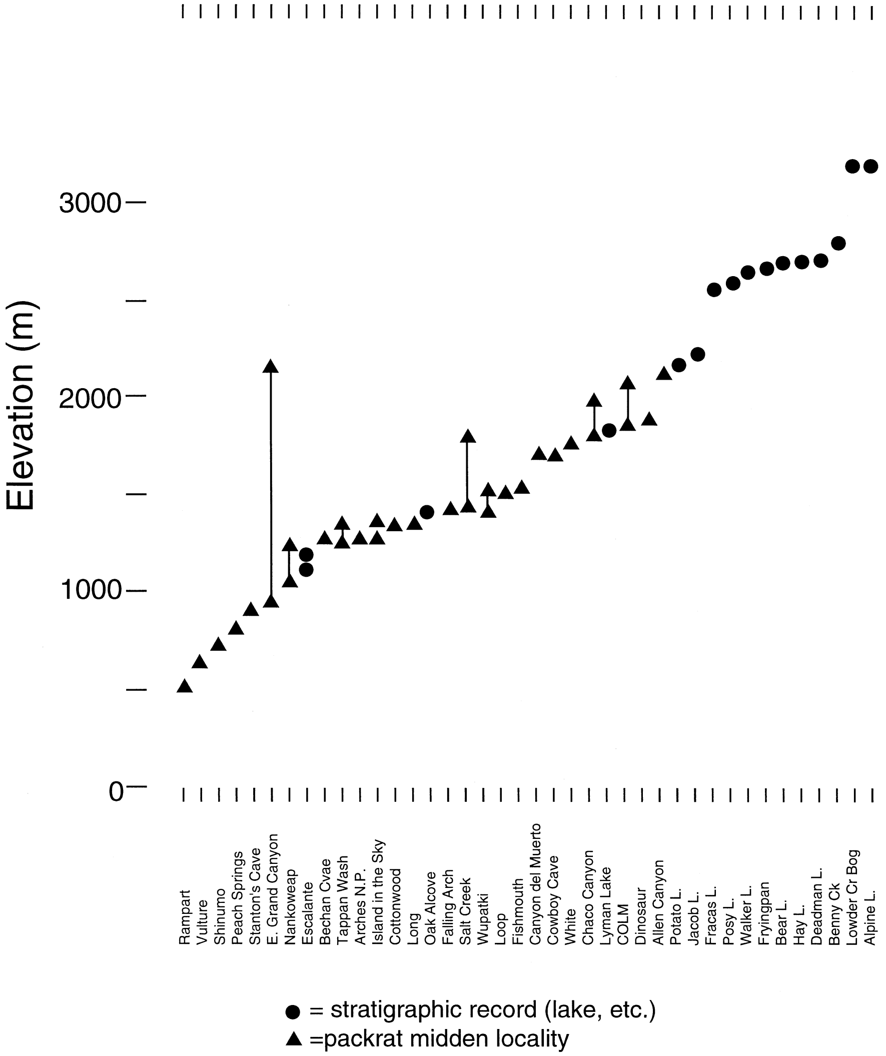


Fig. 2. Distribution of major paleobotanical (pollen and plant macrofossil) sites on the Colorado Plateau by elevation. Dots = stratigraphic records; triangles = packrat midden sites.

2.3. Temporal site distribution

For the purposes of this paper we assigned the ages of the paleobotanical records to Marine Oxygen Isotope Stages (IS) based on age assignments in Martinson et al. (1987). Isotope Stage (IS) 1 sites date from the present to 14,059 cal. yr BP; IS 2 sites date from 14,060 to 27,500 cal. yr BP; and IS 3 sites date from 27,501 to 59,000 cal. yr BP. At present, no late-Quaternary paleoecological data from anywhere on the Colorado Plateau date to IS 4 or earlier.

Forty-two sites include data from IS 1 (Fig. 3). The number of sites including IS 2 and 3 data is considerably smaller: 28 sites for IS 2, and only 11 sites for IS 3 (Fig. 3). In addition, most of the IS 3 localities occur on the southern Colorado Plateau. Virtually all of these are in Arizona, including packrat midden sites in the Grand Canyon, and lake sites found along the largely unglaciated Mogollon Rim.

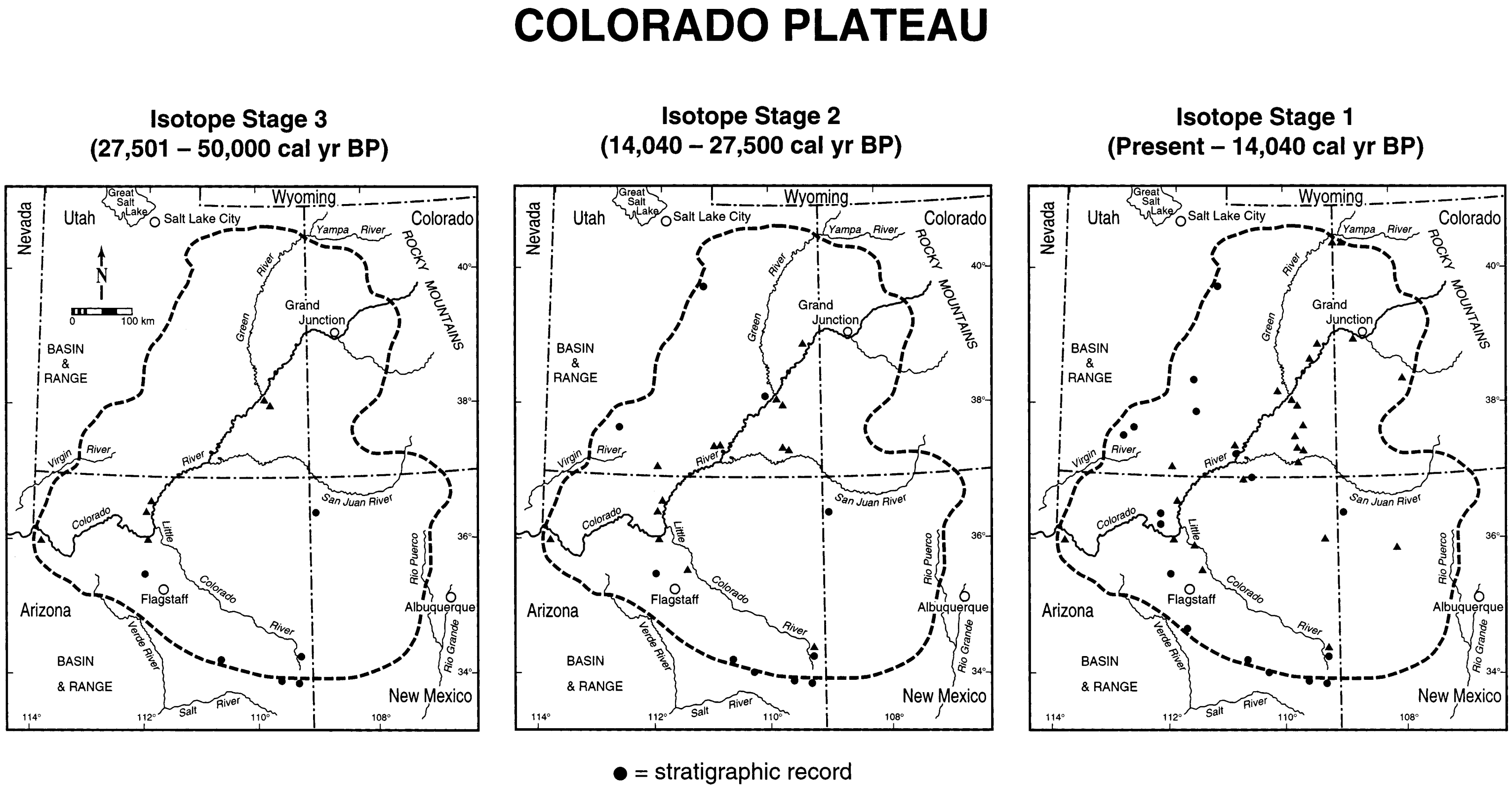


Fig. 3. Location of paleobotanical sites on the Colorado Plateau with pollen and/or plant macrofossil data from specific time periods: (left) sites with data from Marine Oxygen Isotope Stage (IS) 3 (27,500–50,000 cal. yr BP); (middle) sites with data from Marine Oxygen Isotope Stage 2 (14,040–27,500 cal. yr BP); (right) sites with data from Marine Oxygen Isotope Stage 1 (present–14,040 cal. yr BP). Dots = stratigraphic sites; triangles = packrat midden sites.

3. Records of Marine Oxygen Isotope Stages 2 and 3

In this section we examine the vegetation and climate history deduced from selected published and unpublished records spanning IS 2 and 3, mostly from the southern Colorado Plateau. For purposes of presentation, we divide our discussion into two groups: high-elevation stratigraphic sites, and low- to middle-elevation packrat midden locations.

3.1. High-elevation stratigraphic records (above 2200 m)

3.1.1. Potato Lake, Arizona

One of the longest, well-dated records from the Mogollon Rim of Arizona is Potato Lake (Whiteside, 1965; Anderson, 1993), a small solution depression at 2222 m elevation (Fig. 1). Presently the site is surrounded by the largest continuous ponderosa pine stand in North America (Hanks et al., 1983). Analysis of a 9.4-m-long core by Anderson (1993) recorded ca. 35,000 radiocarbon years of vegetation and climate change. An open forest of Engelmann spruce, white fir and Douglas fir, with an understorey of sagebrush (*Artemisia*), grasses (Poaceae) and composites (Asteraceae), grew around Potato Lake during IS 3 time (Fig. 4). Apparently, conditions were not warm enough to allow the establishment of ponderosa pine near the lake during this middle-Wisconsin interstade. Algal and aquatic macrophyte data suggest that lake levels were higher than today, but that the period of ca. 25,000 to 30,000 yr BP (ca. 28,400 to 33,000 cal. yr BP) was the driest of IS 3. During IS 2, white fir and Douglas fir were reduced near the lake, leaving a closed forest primarily of Engelmann spruce. The vegetation during IS 2 reflects colder conditions than before, while the aquatic fossil remains indicate that lake levels were probably at their highest during this period. Near-modern vegetation was established by ca. 10,400 ^{14}C yr BP (12,400 cal. yr BP) with the immigration of ponderosa pine into the area. The record at Potato Lake and midden records from Allen Canyon Cave (2200 m) in southeastern Utah (Betancourt, 1984), the latter ca. 300 km north of Potato Lake, suggest that subalpine forest covered much of the Colorado Plateau above 2200 m during the mesic periods of IS 2 and 3, and at the beginning of IS 1.

3.1.2. Walker Lake, Arizona

The record from Walker Lake extends even further back into IS 3 than that for Potato Lake. Walker Lake is located in the bottom of a small cinder cone, at 2500 m elevation northwest of the San Francisco Peaks (Fig. 1). This ca. 50,000-year-long record contains several hiatuses, but remains the longest, nearly continuous record on the Colorado Plateau (Berry et al., 1982; Adam et al., 1985; Hevly, 1985). Unlike Potato Lake, no macrofossils were reported from Walker Lake sediments. Walker Lake lies today on the transition from ponderosa pine to mixed-conifer forest; ponderosa pine dominates the south-facing slopes, but limber pine, white fir, Douglas fir and quaking aspen grow on slopes of north-facing aspect.

Pollen of ponderosa or high elevation white pines, pinyon pine, oak (*Quercus*) and sagebrush dominate the spectra of the early IS 3 record; spruce (*Picea*) and fir (*Abies*) pollen do not become important at the site until ca. 35,000 cal. yr BP (Fig. 5). Along with the increasing importance of spruce and fir in the later part of IS 3 is a decline in pinyon pine and oak. Walker Lake apparently dried out completely for periods of nearly 1000 to 5000 years during IS 3, in what must have been intervals of variable, yet generally drier climate than the succeeding IS 2 climates. One depositional hiatus occurs from ca. 30,000–34,000 cal. yr BP, coeval with the low-water period at Potato Lake. For much of IS 2 time, non-arboreal pollen types (e.g., sagebrush, grasses, cheno-ams [Chenopodiaceae–*Amaranthus*]) become more important, while maximum spruce and fir pollen percentages are found between ca. 22,000 and 24,000 cal. yr BP. One interpretation of the pollen assemblage is that it represents an open limber pine forest with abundant sagebrush in the understorey. Apparently the Walker Lake basin either dried out for shorter periods of time, or remained wet throughout IS 2.

In general, the record from Walker Lake shows that spruce and fir were probably less important, and pine and sagebrush were more important, than at Potato Lake.

3.1.3. Hay Lake, Arizona

Hay Lake is a small lake of 16 ha, located in the White Mountains at ca. 2780 m elevation (Fig. 1). The sedimentary record spans the last ca. 38,000

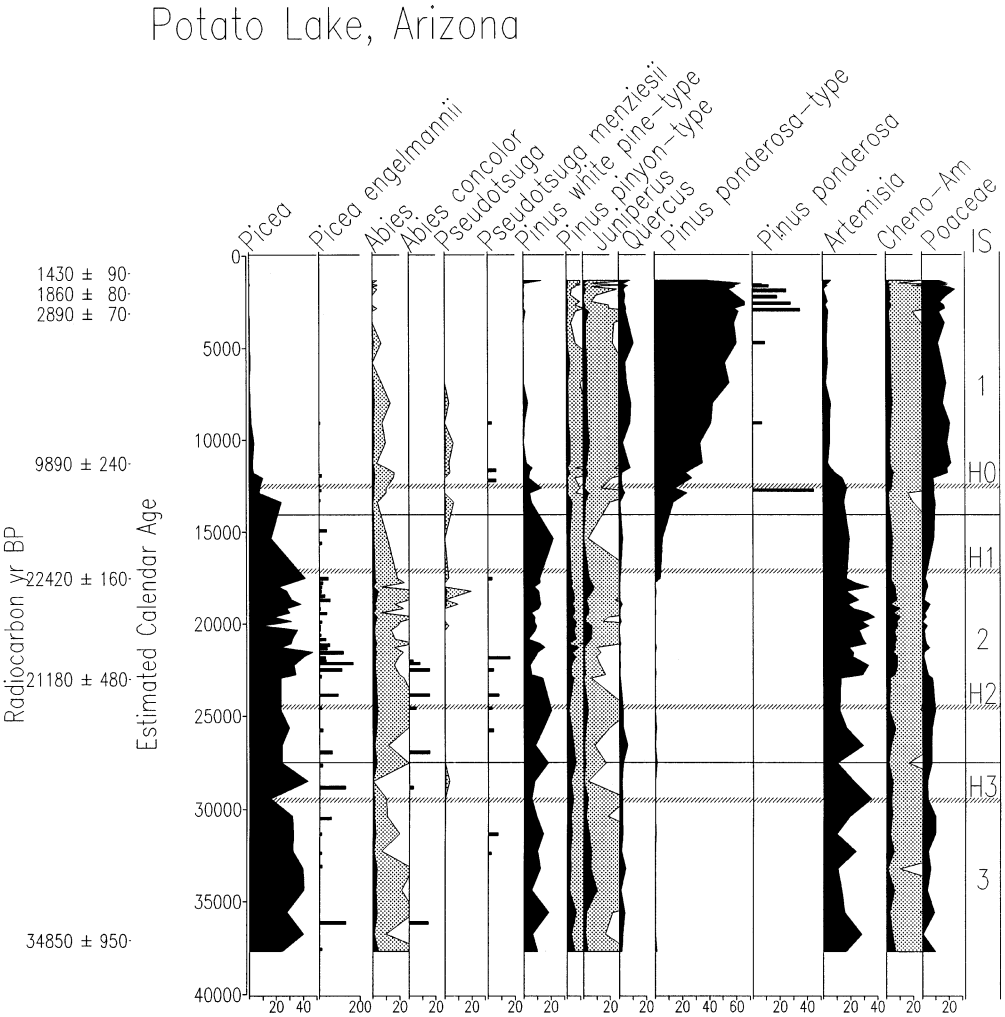


Fig. 4. Summary pollen percentage (solid curves) and plant macrofossil concentration (solid dark lines) diagram from Potato Lake, Arizona (2222 m elevation; Anderson, 1993). Stippled curves represent 10× exaggeration of pollen percentages. Estimated chronology is in calendar years BP, by methodology outlined in text. *IS* = Isotope Stage. Location of radiocarbon dates in the profile is on the left of the diagram (see original reference for decisions on date acceptance). Horizontal crosshatched lines are approximate ages of Heinrich events (after P. Bartlein and C. Whitlock, pers. commun., 1996).

cal. yr (Fig. 6; Jacobs, 1983, 1985). On south-facing slopes around the lake, mixed-conifer forest of ponderosa pine, Douglas fir, southwestern white pine (*Pinus strobiformis*), white fir and quaking aspen dominates. Spruce fir forest is found in cooler, wetter areas of the drainage basin.

IS 3 pollen data are characterized by high percentages of pine pollen (mostly subalpine types, such as bristlecone, limber or southwestern white; and pinyon), with some spruce and sagebrush (Fig. 6). Jacobs (1983) suggested that Hay Lake was surrounded by a mixed conifer forest, with a diverse herbaceous understorey. Pinyon pine was probably more widespread at lower elevations than today, suggesting cooler summers and greater-than-present winter precipitation. Near the end of IS 3, spruce increased near the lake. Pollen size measurements suggested that either ponderosa or lodgepole pine (*P. contorta*) may have been present near the lake.

IS 2 is characterised by high spruce and grass

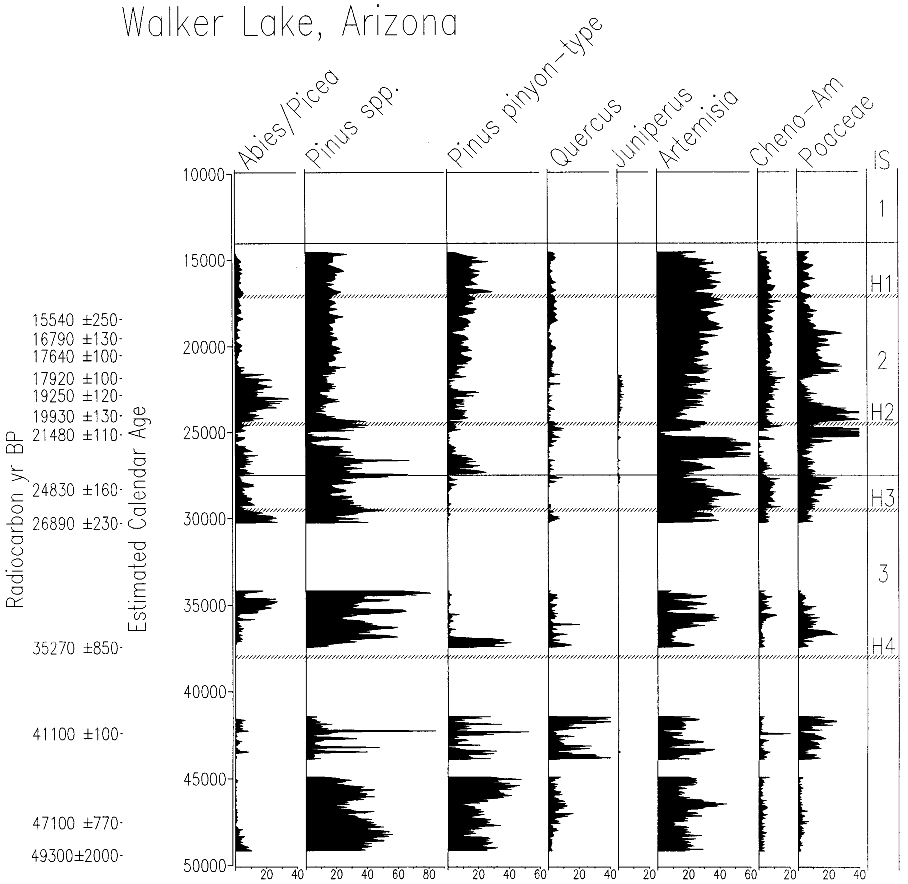


Fig. 5. Summary pollen percentage (solid curves) diagram from Walker Lake, Arizona (2500 m elevation; Berry et al., 1982; Adam et al., 1985; Hevly, 1985). Estimated chronology is in calendar years BP, by methodology outlined in text. *IS* = Isotope Stage. Location of radiocarbon dates in the profile is on the left of the diagram. Horizontal crosshatched lines are approximate ages of Heinrich events (after P. Bartlein and C. Whitlock, pers. commun., 1996).

pollen, with declines in pine pollen. These changes were interpreted as representing a high elevation parkland at the forest–tundra ecotone, with a conservative estimate for treeline depression of ca. 570 m.

Winter precipitation was greater than today during IS 3, but not as much as during IS 2. The greater available moisture permitted pinyon pine to greatly expand its range, compared to today, at lower elevations. IS 3 summers were cooler than today, but probably not as cool as during IS 2 (Jacobs, 1983).

3.1.4. Dead Man Lake, New Mexico

Dead Man Lake is one of many small depressions in the gently rolling landscape of the Chuska Mountains, northwestern New Mexico (Fig. 1; Wright and Bent, 1968). Elevation of the lake is ca. 2780 m. Ponderosa pine dominates the mixed-conifer forest surrounding the lake; additional species include Douglas fir, quaking aspen and, locally, Gambel oak.

Eleven meters of sediment preserve approximately 35,000 cal. yr of record (Fig. 7; Wright et al., 1973). IS 3 pollen spectra are characterised by high sagebrush (early IS 3; their pollen zone 5) and spruce (later IS 3; their zone 4), with variable pine and grass. The abundant sagebrush pollen suggested alpine conditions to Wright et al. (1973); the subsequent increase in spruce indicated development of a spruce parkland, and consequently movement of treeline to a higher elevation, relative to the lake's position, signaling a climatic warming.

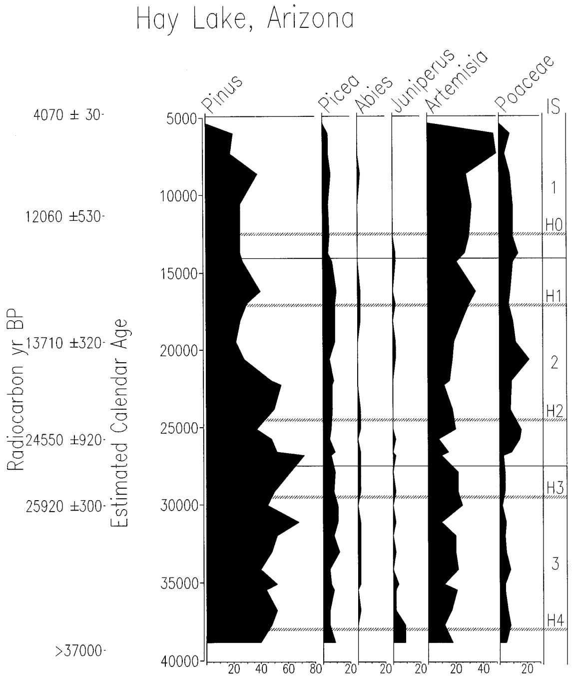


Fig. 6. Summary pollen percentage (solid curves) diagram from Hay Lake, Arizona (2780 m elevation; Jacobs, 1983, 1985). Estimated chronology is in calendar years BP, by methodology outlined in text, and based upon chronology in Jacobs (1985). *IS* = Isotope Stage. Location of radiocarbon dates in the profile is on the left of the diagram. Horizontal crosshatched lines are approximate ages of Heinrich events (after P. Bartlein and C. Whitlock, pers. commun., 1996).

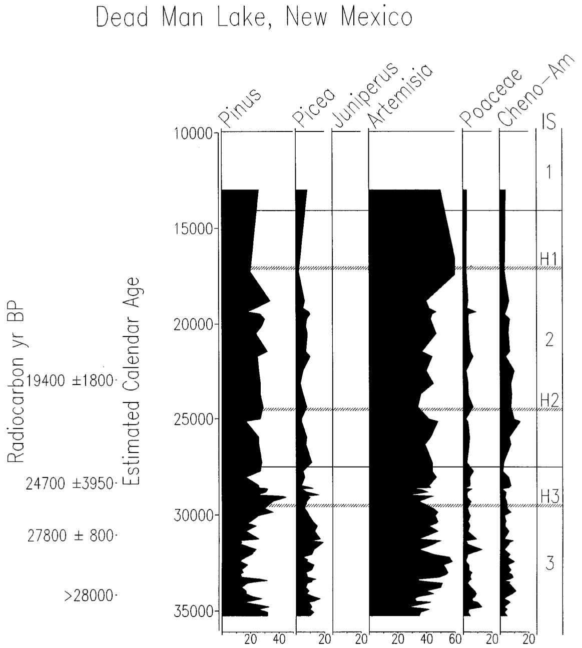


Fig. 7. Summary pollen percentage (solid curves) diagram from Dead Man Lake, Arizona (2780 m elevation; Wright et al., 1973). Estimated chronology is in calendar years BP, by methodology outlined in text. *IS* = Isotope Stage. Location of radiocarbon dates in the profile is on the left of the diagram. Horizontal crosshatched lines are approximate ages of Heinrich events (after P. Bartlein and C. Whitlock, pers. commun., 1996).

During early IS 2 (pollen zone 3) time, increased percentages of limber pine-type pollen indicated a subsequent lowering of treeline relative to the lake, and a return of alpine conditions. This was followed during late IS 2 (pollen zone 2) by a return to spruce parkland conditions dominated by sagebrush, suggesting somewhat warmer conditions.

Based primarily on present lapse rates for the Chuskas, upper elevation treeline during the Wisconsin was lowered by 900 m, while the lower elevation treeline was depressed only 500 m. Such ‘telescoping’ of vegetation zones was based on the assumption that ponderosa pine did not extend down to the base of the Chuska Mountains, and that pinyon–juniper woodlands covered much of the San Juan Basin. Pine pollen size statistics indicated to the authors that ponderosa pine grew in a narrow belt below ca. 2200–2300 m elevation, while the upper elevation of pinyon pine was depressed to ca. 1900–2000 m. However, midden records from both sides of the Chuska Mountains and elsewhere in the southwest indicate that the northern limits of ponderosa and pinyon pine occurred hundreds of kilometers south during the last glacial. Instead, species such as limber pine, blue spruce, Douglas fir, and Rocky Mountain juniper occupied the lowlands surrounding the Chuska Mountains (Betancourt and Davis, 1984; Betancourt, 1990). As with Hay Lake, much of the ponderosa and pinyon pollen encountered in IS 2 and 3 profiles in the Chuska Mountains may represent long-distance pollen transport from woodlands and forests along the base of the Mogollon Rim and what are now the hot deserts of the southwest.

3.2. Low-elevation packrat midden records (below 2200 m)

3.2.1. Western Grand Canyon, Rampart Cave region, Arizona

One of the earliest vegetation reconstructions using packrat midden data comes from sites at ca. 440 to 675 m in the western Grand Canyon (Fig. 1; WGC = Rampart Cave [RC], Vulture Cave [VC], Shinumu Creek [SH], Peach Springs Wash [PS]; Phillips and Van Devender, 1974; Van Devender and Mead, 1976; Phillips, 1977, 1984; Mead and Phillips, 1981). Rampart Cave (530 m) has been of particular interest due to the occurrence of Shasta Ground Sloth (*Nothrotheriops shastensis*) remains; the general area contains a record stretching to ca. 36,000 cal. yr BP.

Both IS 3 and 2 middens are dominated by juniper and single-leaf ash (*Fraxinus anomala*), with lesser amounts of cacti (*Echinocactus, Echinocereus, Opuntia basilaris, O. whipplei*), squaw-bush (*Rhus trilobata*), and banana yucca (*Yucca baccata*) (Phillips, 1977). Phillips (1977) considered middens deposited between ca. 36,000 and 27,500 cal. yr BP to be interstadial, but no species are limited to IS 3 time only.

The full-glacial, dating from ca. 27,500 to 17,000 cal. yr BP (IS 2), preserved the most mesophytic assemblage of plants, including additional species of blackbrush, snakeweed (*Gutierrezia lucida*), beargrass (*Nolina microcarpa*), and gooseberry currant (*Ribes montigenum*). During the late-glacial (IS 2), until ca. 14,000 cal. yr BP, more desert species were present, mixed with the woodland species. These desert species included Utah agave (*Agave utahensis*), spiderling (*Boerhaavia coulteri*), desert thorn (*Lycium andersonii*), desert almond (*Prunus fasciculata*), and catclaw acacia (*Acacia greggii*). Between ca. 14,000 and 10,000 cal. yr BP, woodland species decreased and most of the modern desert species were represented in the middens.

Though the occurrence of woodland species as low as 440 m elevation during the Pleistocene represents a minimum displacement of ca. 1000 m elevation for those species, at least 50% of the species identified in the middens are low desert plants which presently occur within the area (Phillips, 1977). These assemblages are unusual in the Grand Canyon today, and provide an excellent example of the individualistic distribution of species along environmental gradients. The displaced woodland suggested to Phillips that during IS 3 and 2, climates were wetter (even more mesic in early IS 2), and summers were cooler than today. The mixed assemblage of woodland and desert species suggested mild winters. Precipitation came largely during the winter, as demonstrated by the large number of winter annual species, and the absence of summer annuals.

3.2.2. Eastern Grand Canyon, Arizona

Cole (1981, 1982, 1990) studied vegetation changes from packrat middens for the eastern Grand Canyon (Fig. 1). The dataset includes a total of 52 dated middens, stretching over an elevational range of ca. 950–2200 m. Most data represent IS 2, although at least two middens are older than 32,000 cal. yr BP.

During IS 3 time, elevations which presently support blackbrush–sagebrush desert (ca. 1000 m) supported an open woodland of juniper (both single-seed and Utah), with big sagebrush and several rosaceous shrubs; shadscale was particularly abundant below 1200 m elevation. Presence of these taxa represents an elevational depression of ca. 800–1000 m (Cole, 1990). No data exist for the IS 3 distribution of montane conifers in the eastern Grand Canyon.

IS 2 middens are found at a wider ranger of elevations. Once again, juniper woodland dominated up to ca. 1450 m elevation. Above this, to ca. 2200 m elevation, a mixed conifer forest of Douglas fir, limber pine and Engelmann spruce with white fir dominated the landscape. Engelmann spruce is abundant only in the highest elevation middens, which also contain the modern spruce-forest understorey species common juniper (*Juniperus communis*) and mountain lover (*Pachystima myrsinites*). Cole (1990) considered these occurrences to be evidence of lowering of ca. 720–800 m. The only glacial records of pinyon pine in this area of the Colorado Plateau are from Wupatki National Monument, along the Little Colorado River. Four middens collected from 1490 to 1525 m elevation on limestone record pinyon pine and Rocky Mountain juniper between 16,300 and 12,800 cal. yr BP (13,700 and 10,800 ^{14}C yr BP; Cinnamon and Hevly, 1988).

Transitional development of the modern vegetation in the Grand Canyon occurred between ca. 12,900 and 9500 cal. yr BP (11,000 and 8500 ^{14}C yr BP), with the replacement of spruce by fir forest above 2200 m elevation, mixed conifer by ponderosa pine, Douglas fir and Utah juniper at ca. 1900–2100 m, mixed conifer–juniper by pinyon–juniper woodland at ca. 1200–1500 m, and juniper–Great Basin desertscrub by juniper and ash (*Fraxinus* sp.) at lower elevations (Cole, 1990).

3.2.3. Central Colorado Plateau, Utah

At least thirteen midden sites are found within the core of the Colorado Plateau (Fig. 1), but only three key sites are reviewed here. A single, unpublished site provides IS 3 data from the central Plateau region. Salt Creek Canyon in Canyonlands National Park (Mead and Agenbroad, unpublished) is oriented north–south; elevations within the canyon vary from ca. 1900 m at the head to ca. 1490 m at the mouth. The region today is within the pinyon–juniper and big sagebrush parkland.

Rocky Mountain juniper, limber pine and Douglas fir were common at middle elevations in Salt Creek Canyon during IS 3, while a mixture of Rocky Mountain and Utah junipers with mountain mahogany (*Cercocarpus intricatus*) occurred at the mouth of the canyon. During IS 2 time, mixed conifer assemblages of spruce, limber pine, Douglas fir and Rocky Mountain juniper persisted at all elevations of the canyon, with an understorey of rabbitbrush (*Chrysothamnus nauseosus*), big sagebrush, and rosaceous shrubs (Mead and Agenbroad, unpublished). Essentially modern vegetation occupied the site by ca. 9500 cal. yr BP.

Allen Canyon Cave, adjacent to the Abajo Mountains, Utah, occurs at 2200 m elevation; because of the complex topography of the area, modern vegetation is a mixture of pinyon–juniper woodland and oak chapparal elements with a few Douglas fir and ponderosa pine (Betancourt, 1984, 1990). However, IS 2 vegetation at Allen Canyon Cave contained species typical of spruce–fir forest, including Engelmann spruce, subalpine fir, limber pine, common juniper and Douglas fir (ca. 13,300 cal. yr BP; Betancourt, 1984, 1990). Between 12,500 and 11,250 cal. yr BP, Engelmann spruce and subalpine fir were replaced by blue spruce, ponderosa pine, and Gambel oak with limber pine. Subsequently, by 8000 cal. yr BP, dominants include Utah juniper, ponderosa pine and squawbush.

At Fishmouth Cave (1585 m elevation) and Fallen Arches (1460 m elevation) on the west slope of Comb Ridge, modern vegetation is Utah juniper, Utah serviceberry (*Amelanchier utahensis*), singleleaf ash, buffaloberry (*Shepherdia rotundifolia*), and blackbrush (Betancourt, 1990). At Fishmouth Cave, IS 2 vegetation consisted of limber pine, Douglas fir, Rocky Mountain and common juniper, with small amounts of blue spruce. At Fallen Arches, an assemblage dated at 23,400 cal. yr BP was dominated by limber pine, with smaller amounts of Rocky Mountain juniper and Douglas fir. This midden also contained the xerophytes four-wing saltbush and littleleaf mountain mahogany, which are either contaminants or would indicate a community with few or no modern analogues. By 15,500 cal. yr BP, there was an increase in Rocky Mountain juniper and a reduction in xerophytes. At nearby Cottonwood Cave (1390 m elevation), a relatively wet and deep alcove, an IS 2 assemblage was dominated by blue spruce with only traces of limber pine and Douglas fir. Between 18,700 and 15,000 cal. yr B.P., the assemblage shifted to dominance by limber pine, with lesser amounts of blue spruce, Douglas fir and Rocky Mountain juniper; by 14,000 cal. yr BP there was no blue spruce at the site. This sequence suggests gradual drying of the springs in the alcove. At all three sites, the transition to IS 1 occurred between 12,500 and 11,000 cal. yr BP, with the replacement of conifers with Gambel oak, Utah juniper, and mountain mahogany. A similar transition from full- to late-glacial as on Comb Ridge was also recorded on the Waterpocket Fold in the Glen Canyon area. Long Canyon Cave records a transition from a midden dominated by sagebrush and traces of Utah juniper and no other conifers (20,700 cal. yr BP), to a midden dominated by blue spruce and western birch (*Betula occidentalis*; 18,000 cal. yr BP) (Betancourt, 1990). The latter assemblages match late-glacial deposits from Bechan Cave (1310 m), just 5 km southeast of the Long Canyon Cave locality (Davis et al., 1984).

4. Regional paleoenvironmental reconstruction

In our paleoenvironmental reconstructions we rely primarily on paleobotanical data from the southern

Colorado Plateau, and on sites that have long, near-continuous records. We summarise the records discussed above in a series of temporal snapshots of the region. Fig. 8d shows the modern elevational distribution of vegetation on the southern Colorado Plateau.

Although the late- and middle-Wisconsin glacial history is virtually unknown, the highest elevations on the Colorado Plateau were probably ice-covered for much of IS 3 and 2. Permanent ice is not found today on the Colorado Plateau. Late-Wisconsin glaciers originating on Brian Head on the Markagunt Plateau (Fig. 1) terminated at ca. 3080 m elevation; radiocarbon dates of $14,400 \pm 850$ ^{14}C yr BP (Mulvey et al., 1984) and $13,020 \pm 690$ ^{14}C yr BP (Anderson et al., 1999) document minimum ages of recession. Less than 100 km to the northeast lie the Aquarius, Fish Lake and Thousand Lake plateaus, whose <3350 m (11,000 ft) summits were ice-covered for much of the Wisconsin (Flint and Denny, 1958). Late-Wisconsin moraines in the La Sal Mountains of southeastern Utah extended downward to between 3131 and 3240 m (10,270–10,630 ft) elevation (Richmond, 1962). In the White Mountains, late-Wisconsin glaciers descended to between 3200 and 2990 m (10,500–9800 ft) (Merrill and Péwé, 1977), while on the San Francisco Peaks, 'later Wisconsin age' deposits (Péwé and Updike, 1976) terminate between ca. 2800 m (9200 ft) and 2620 m (8600 ft), depending upon aspect. Recession ages are unavailable for the White Mountains, the San Francisco Peaks, the La Sal Mountains, and the south-central Utah Plateaus. Protalus ramparts between 2560 and 2800 m on Navajo Mountain probably formed near the orographic snowline along seasonal snow banks above timberline (Blagbrough and Breed, 1967).

4.1. IS 3 (27,500–50,000 cal. yr BP)

Information on the IS 2 and 3 vegetation above ca. 2800 m is presently unavailable. However, pollen data from Walker, Hay and Dead Man lakes suggest that during IS 3, high-elevation pines (perhaps bristlecone or limber) mixed with Engelmann spruce and subalpine fir to create an open forest, perhaps with sagebrush growing in the forest openings, at ca. 2700 m elevation (Fig. 8a). If the record from Potato Lake is typical of similar altitudes on the southern Colorado Plateau, an open forest of Engelmann spruce, white fir and Douglas fir, with sagebrush, occupied much of the Mogollon Rim country. Calculated average summer temperatures were ca. 3–4ºC lower during IS 3 than at present (Table 2; Anderson, 1993).

Table 2
Estimated changes in temperature at Potato Lake, Arizona, during IS 2 and 3 (from Anderson, 1993).

	Temperature change (ºC) relative to modern Isotope Stage (IS) 3	Isotope Stage (IS) 2
Annual	−2.9 to −4.3	−5.2
Summer	−3.8 to −5.7	−7.0
Winter	−2.1 to −3.1	−5.8

Our knowledge of the vegetation in the ca. 1600–2100 m elevational range is minimal. At present, depositional basins that might preserve pollen and plant macrofossils are rare, and an appropriate suite of packrat midden sites has yet to be identified. A single midden of IS 3 age from Canyonlands National Park (ca. 1700 m) in Utah documents the occurrence of Rocky Mountain juniper, limber pine and Douglas fir (Mead and Agenbroad, unpublished), matching many of the IS 2 records above 1400 m on the Plateau. The absence of ponderosa pine macrofossils from both IS 2 and 3 middens on the Plateau is perplexing. Climatic explanations range from an absence of fine fuels and low fire frequency to cold late summers truncating both tree growth and recruitment (Betancourt, 1990; Anderson, 1993).

At elevations below ca. 1500 m (to at least 450 m), a juniper–desertscrub association existed over much of the area studied to date. Both Utah and single-seed junipers were present, with sagebrush, prickly-pear cactus, agave, and, in the lowest elevation samples, saltbush. Virtually all of these data come from sites within the Grand Canyon; several middens contain plant associations which are unique to this low-elevation corridor (Cole, 1990). However, two IS 3 middens from Canyonlands National Park confirm the widespread occurrence of Utah juniper with prickly-pear cactus at ca. 1500 m elevation (Mead and Agenbroad, unpublished).

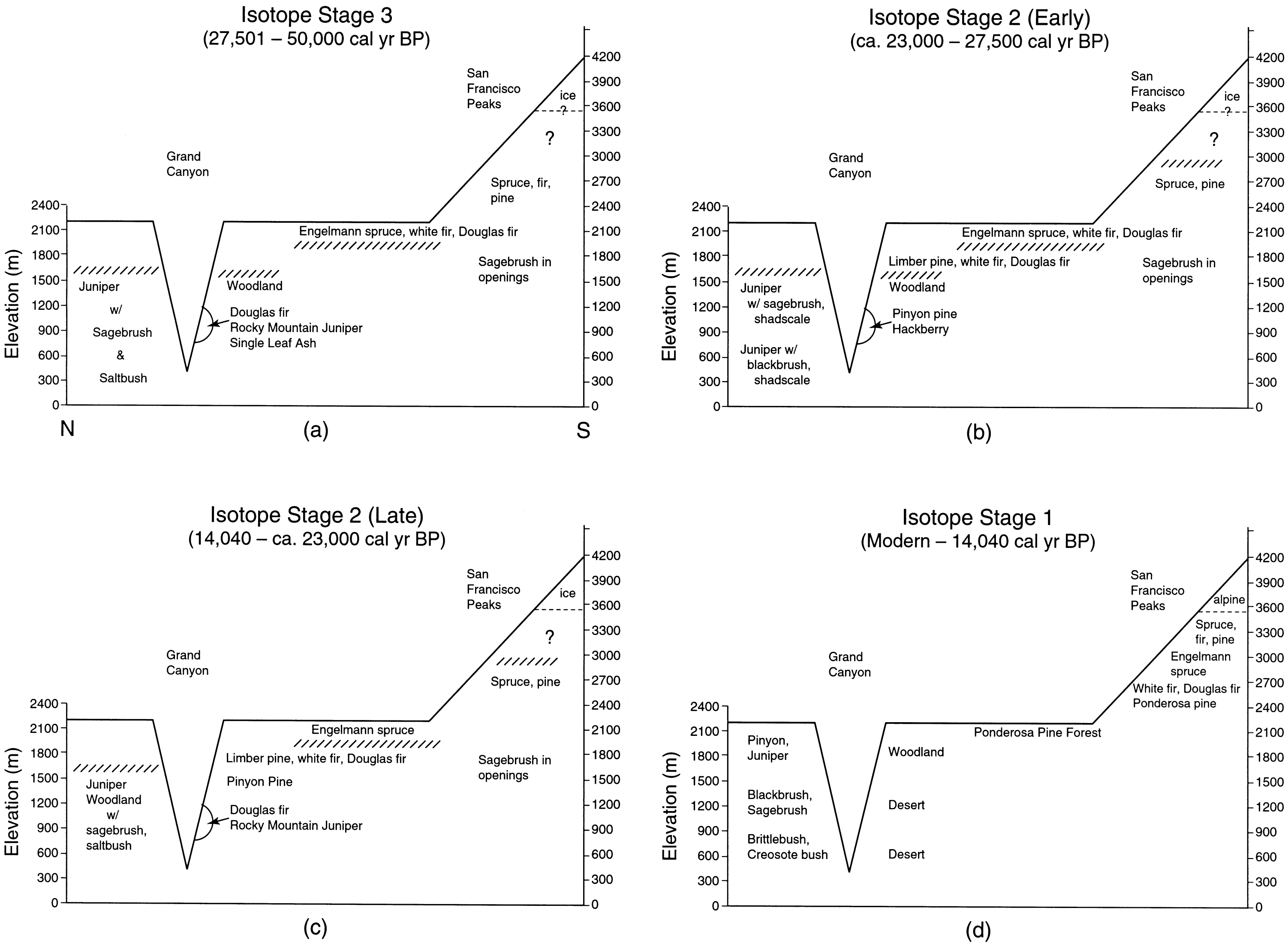


Fig. 8. Inferred elevational distribution of vegetation on the southern Colorado Plateau, in a line running from the Grand Canyon to the San Francisco Peaks (see Fig. 1 for locations): (a) inferred vegetation for Marine Oxygen Isotope Stage (IS) 3 (27,501–50,000 cal. yr BP); (b) inferred vegetation for early Marine Oxygen Isotope Stage 2 (23,000–27,500 cal. yr BP); (c) inferred vegetation for late Marine Oxygen Isotope State 2 (14,040–23,000 cal. yr BP); (d) inferred vegetation for Marine Oxygen Isotope Stage 1, and the modern environment (present–14,040 cal. yr BP).

4.2. IS 2 (14,040–27,500 cal. yr BP)

Considerably more information is available for IS 2. Greater site density, particularly at lower elevations, allowed Betancourt et al. (1990b) to draw a preliminary map of the late-Wisconsin vegetation of the southwest, including the Colorado Plateau. No direct data on alpine vegetation exist for the area, but alpine vegetation probably occurred as high-elevation islands in a broad area stretching along the northwest margin of the Colorado Plateau — from the Markagunt, Paunsaugunt and Aquarius plateaus in the southwest, through the Wasatch Plateau to the flanks of the Uinta Mountains. Alpine islands would have been of greater size in the north and west than on the southern or eastern portions of the Plateau, due to smaller mountain mass in the latter areas.

Surrounding alpine islands was the high-elevation boreal forest, which, during the earliest phase of IS 2, remained mostly unchanged from IS 3 (Fig. 8b). A nearly continuous boreal forest may have existed on the northwestern plateaus, with the La Sal and Abajo Mountain boreal assemblages connected or nearly so to boreal forests extending westward from the Rocky Mountains. Much smaller islands of high-elevation forest probably occurred in the Chuska and White Mountains of New Mexico and Arizona, respectively. The Mogollon Rim area of central Arizona also supported spruce–fir and mixed-conifer forests.

Early in IS 2, however, colder conditions prevailed (Fig. 8b). IS 2 at Hay Lake is characterised by elevated spruce and grass pollen, with declines in pine. At Walker Lake, non-arboreal pollen types are more important than before, with maximum spruce and fir abundance between 22,000 and 24,000 cal. yr BP. After ca. 22,000 cal. yr BP at Potato Lake the high-elevation mixed-conifer forest is converted to Engelmann spruce (Fig. 8c). IS 2 witnessed the maximum elevational depression of species during the Wisconsin, from these data estimated to range from a minimum of 570 m to 900 m. Anderson (1993) suggested that the vegetation changes at Potato Lake amounted to apparent elevation changes of at least 800 m during IS 2. Elevational lowerings of this magnitude correspond to average annual temperatures up to ca. 5.2°C colder for IS 2 (Table 2).

Even more sites occur within the ca. 1600–2100 m elevation range. For example, in the Grand Canyon a mixed-conifer forest (‘montane conifers’ of Betancourt et al. (1990b)) that included limber pine, white fir and Douglas fir occupied these elevations. Common associates included Utah juniper, and an understorey of sagebrush, rosaceous shrubs, agave and prickly-pear cactus. Sites from the core of the Colorado Plateau record similar assemblages, confirming the widespread distribution of the above species at these elevations, and documenting a minimal elevational depression of 600 m. Douglas fir and white fir expanded down to at least 1500 m in the eastern Grand Canyon (Cole, 1990), while limber pine, Douglas fir and Rocky Mountain juniper occurred at similar elevations in the central Plateau (Betancourt, 1990). Utah juniper, which dominated the low elevations of the Grand Canyon, probably had its northeasternmost populations on low-elevation limestone sites as far upstream as the mouth of the Green River, and Bluff, Utah on the San Juan River. Today, Utah juniper extends as far north as the Pryor Mountains on the Wyoming–Montana border.

Mixed-conifer assemblages are absent from sites below 1400 m. Instead, Utah and single-seed junipers mixed with sagebrush and shadscale, as well as Mormon tea and others. Junipers dominated the vegetation even at the lowest elevation sites, ca. 450 m, with additional desert-scrub species of blackbrush and shadscale. Single-leaf ash grew commonly around Rampart Cave (Phillips, 1977; Mead and Phillips, 1981).

The transition from IS 2 to IS 1 (ca. 14,000 cal. yr BP; Fig. 8c) witnessed major reorganisations of the vegetation on the southern Colorado Plateau. At 3278 m near Brian Head on the Markagunt Plateau, an open sagebrush steppe with Engelmann spruce was converted to spruce forest. Species of the mixed-conifer forest retreated upslope to attain their near-modern elevational distributions (ca. 2600–2200 m). Ponderosa pine quickly became established across middle-elevations of the southern Colorado Plateau between ca. 1980 and 2200 m (Anderson, 1989), with pinyon–juniper woodlands occupying lower plateaus at ca. 1600–2100 m (Betancourt, 1990). At lower elevations in the Grand Canyon, desertscrub communities succeeded juniper woodlands (Cole, 1990), while further north in central regions of the Plateau, sagebrush and other shrubs occupied extensive valley bottoms between mesas (Betancourt, 1990) (Fig. 8d).

5. Paleoclimatology of the middle and late Wisconsin

Several studies have advanced quantitative estimates of paleotemperatures and precipitation trends during IS 2 and 3 for the southern Colorado Plateau. Based upon lapse rates and modern analogues, Anderson (1993) estimated that mean annual temperatures (MAT) during IS 3 were ca. 3–4ºC cooler than today, while the mean annual temperature during IS 2 was ca. 5ºC colder. Using the distribution of dominant plant species in packrat middens, work of Betancourt (1984) in southeastern Utah suggested that late-Wisconsin MAT were 3–5ºC lower than modern, and annual precipitation was 35–60% greater than today; he also reconstructed warm-season temperatures at least 6.3ºC cooler than today. Taking a different approach, Phillips et al. (1986) reconstructed Late Pleistocene ($>30,000$ ^{14}C yr BP) temperatures and precipitation from deuterium ratios in dated groundwaters from the San Juan Basin, east of the Chuska Mountains. Stable isotope analysis of Pleistocene-age waters suggested colder mean annual temperature (5–7ºC) and perhaps greater winter precipitation than today. Noble-gas concentrations in the same groundwaters suggested MAT 5.5ºC colder than today (Phillips et al., 1986; Stute et al., 1995). More recently, Smith and Betancourt (1998) used packrat body size estimated from fecal pellet diameter and modern calibration of body size/environmental temperatures to suggest that both July and January temperatures may have been 6–10ºC colder on Comb Ridge and other sites on the Colorado Plateau.

In the Great Basin to the west, pollen and plant macrofossils record similar vegetation changes and lowered temperatures during the Late Pleistocene. Though transitions are poorly dated, dominant IS 3 pollen taxa (an integrative record representing vegetation of ca. 125,000 km^2) from Great Salt Lake Core ‘C’ are *Artemisia*, Cheno-am, *Picea*, *Pinus*, and *Juniperus*, suggesting a juniper-steppe at elevations that today support greasewood (*Sarcobatus*) steppe (Spencer et al., 1984). Subsequent expansion of spruce and fir pollen suggested even colder conditions during IS 2. Similar stratigraphies from additional Great Salt Lake cores (Davis, 1998; Davis and Moutoux, 1998) verify these results. Plant remains in packrat middens from Bonneville Basin locations suggested to Rhode and Madsen (1995) that IS 2 summer temperatures were ca. 6ºC lower than today.

Using deuterium/hydrogen ratios in cellulose from plant remains in Snake Range (eastern Nevada) packrat middens, Siegal (1983; reported in Thompson, 1990) determined that IS 3 temperatures were at least 2.5ºC lower, and IS 2 temperatures were at least 4.1ºC lower than at present (see also Long et al., 1990). However, paleoclimatic interpretation of deuterium and other isotopes in plant cellulose remains problematical (Pendall et al., 1999)

The paucity of data from all but the southern portion of the Colorado Plateau for the middle Wisconsin suggests that our reconstructions are more speculative, but similarities between the paleofloras of both IS 2 and 3 argue for the persistence of similar climatic patterns. Paleovegetation and lake-level data summarised by COHMAP Project Members (1988) and Thompson et al. (1993) produced paleoclimatic maps for North America during IS 2. These indicators also confirm greater effective moisture during the late Wisconsin than at present.

The COHMAP simulations (Kutzbach et al., 1993) produced IS 2 climatic conditions very different from today. The size and location of the Laurentide Ice Sheet produced considerable changes in atmospheric circulation over North America. Anticyclonic circulation caused easterly winds with cold dry conditions in the Pacific northwest. The jet stream was diverted ca. 20ºS latitude of its present position in January (to ca. 30ºN latitude; Thompson et al., 1993; Bartlein et al., 1998), and was still evident in July, though less prominent. Simulated onshore upper-level winds were also stronger along the west coast, essentially mimicking present conditions further north today. For the southwest and Colorado Plateau, these conditions produced colder winters and summers than at present, and greater winter precipitation.

Monsoonal flow would have been inhibited by (1) the southerly position of the jet stream in summer, blocking the development of a high pressure over the midcontinent; (2) a heavy spring snowpack over the Plateau and the southern Rockies preventing summertime heating and thermally induced low pressure upstream; and (3) lower sea level in the Gulfs of

Mexico and California, and a colder tropical ocean. Despite these physical reasons for inhibited monsoonal flow, isotopic evidence from tooth enamel suggests a preponderance of C_4 grasses in the diets of IS 2 and 3 herbivores, primarily in southern Arizona and southern New Mexico (Connin et al., 1998). These data are paralleled by relatively enriched soil carbonates in alluvial deposits in southern Arizona and southern New Mexico, also indicative of dominance by summer-flowering C_4 grasslands (Liu et al., 1996; Monger et al., 1998). Fossil teeth and soil carbonates have not been examined for the Colorado Plateau, so it remains unclear as to the northward extent of the C_4 grasslands, and by inference summer rainfall. Connin et al. (1998) suggest that summer rainfall in southern Arizona and southern New Mexico could have several explanations besides monsoonal circulation. The most probable alternative explanation is the steering of Pacific tropical storms and/or frontal systems by a jet stream also displaced to the south (35°N) in summer.

In the 12,000 ^{14}C yr BP (= 14,000 cal. yr BP) simulation, reduction in size of the Laurentide Ice Sheet allowed for (1) the northward shift of the jet stream, and (2) weakening of the glacial anticyclone. In addition, summer insolation was near its maximum, allowing surface temperatures in both winter and summer to increase. Consequently, the associated surface storm tracks moved northward. The continuation of a stronger-than-present westerly circulation caused precipitation levels to remain higher than at present (Thompson et al., 1993).

5.1. Millennial-scale variability

At the scale of 10^3 years, the Greenland ice-core record documents more than 20 abrupt, millennial-scale warming events during the last glacial period, referred to as 'Dansgaard–Oeschger interstadials' (Dansgaard et al., 1993). Warming apparently occurred within decades, followed by gradual return to glacial conditions over hundreds of years. These 2000 to 3000-year oscillations occur in series (referred to as Bond cycles), in which the amplitude increases until an unusually cold phase is succeeded by unusual warmth. The extreme cold swings are recorded as major ice-rafting events (coarse debris) in North Atlantic deep-sea sediments, so-called Heinrich events (Heinrich, 1988; Bond et al., 1993). In addition, minor ice-rafting cycles synchronous with the cold phase of the Dansgaard–Oeschger temperature shifts have now been identified in glacial sediment from the North Atlantic (Bond and Lotti, 1995). The cause of Dansgaard–Oeschger events, Bond cycles, and Heinrich events are not well understood, but may result from transient changes in boundary conditions including surging of continental ice sheets, reversals in ocean thermohaline circulation, short-term increases in atmospheric CO_2, and solar variability. Originally thought to be restricted to Greenland and the North Atlantic, evidence for Dansgaard–Oeschger and Heinrich events now is proposed for key areas in North America, including offshore sediments along the Pacific margin (Kennett and Ingram, 1995; Thunnell and Mortyn, 1995; Behl and Kennett, 1996), mountain glaciation (Clark and Bartlein, 1995; Phillips et al., 1996) and lake levels in the western U.S. (Allen and Anderson, 1993; Benson et al., 1996; Benson et al., 1997; Oviatt, 1997), and pollen variations in lake sediments from Florida (Grimm et al., 1993), a region teleconnected to the tropical Pacific and the southwestern U.S. via the subtropical jet stream.

The long records of biological change from the southern Colorado Plateau provide an opportunity to examine the biological consequences of millennial-scale variability. Though the timing of Heinrich events varies somewhat between authorities (Bond et al., 1993; Broecker, 1994), we accept the following calendar ages for Heinrich events 0 to 5: H0 = 12,500 cal. yr BP; H1 = 17,100 cal. yr BP; H2 = 24,500 cal. yr BP; H3 = 29,500 cal. yr BP; H4 = 38,000 cal. yr BP; and H5 = 50,000 cal. yr BP (based upon the median of several reported ages; P. Bartlein and C. Whitlock, pers. commun., 1996). Despite ample evidence for rapid global-scale changes during the last glacial period, involving the climatically important Pacific Ocean, the midden vegetation record for the American southwest appears relatively monotonous (Van Devender et al., 1987; Betancourt et al., 1990a; Thompson et al., 1993). Part of this has to do with the nature of the midden record. While acknowledging the poor temporal resolution of the midden record, we note that there are basically no wholesale reversals in floral assemblages. Either the midden record skips over each Heinrich event, or

Heinrich events did not produce climatic reversals sufficiently dramatic to change vegetation. Nevertheless, we exclude middens and focus on the more continuous lake records. We also acknowledge that the existing dating schemes for the southern Colorado Plateau lake records are less than optimum for detailed correlations.

The record from Potato Lake spans Heinrich events H0 to H3 (Fig. 4). The pollen assemblage encompassing H3 time differs significantly from that for H2, H1 or H0, which are similar to each other. Whereas the pollen for H3 shows high sagebrush and lowered spruce and white pine percentages, the spectra for H2 to H0 show lowered sagebrush, with somewhat higher spruce, white pine and fir. The difference between vegetation assemblages is largely precipitation, with the former indicating cold, dry, and the latter cold, wetter conditions.

The Walker Lake record shows a somewhat different pattern. Event H4 falls within a period of nondeposition, probably when the lake dried completely (Fig. 5). However, events H3, H2 and H1 all show high sagebrush and pine, with low spruce/fir, and grass percentages. These assemblages suggest cold, dry conditions at the time of deposition.

Pollen spectra from Hay Lake (Fig. 6) show no consistent pattern for arboreal species, associated with Heinrich events. However, each Event is associated with elevated percentages of sagebrush pollen. The interpretation advanced from these data is that Heinrich events are associated with drier episodes on the Colorado Plateau. The data from Dead Man Lake are equivocal, although high sagebrush pollen percentages are associated with H1.

The records from several additional long, continuous sedimentary sequences immediately upwind from the Colorado Plateau provide equivocal comparisons between the North Atlantic and Colorado Plateau records. Sediments from the Santa Barbara Basin in the California borderlands document sedimentological and paleontological changes over the last ca. 160,000 years. Foraminiferal assemblages suggest that surface water temperatures during much of IS 2–4 were ca. 7–8°C cooler than today (Kennett and Venz, 1995), resulting from changes in oceanic circulation. Though sedimentary evidence links periods of laminated sedimentation in the Basin (warmer interstadial conditions) to North Atlantic Dansgaard–Oeschger cycles for 19 of 20 events since ca. 60,000 years ago (Behl and Kennett, 1996), only one Heinrich event — the Younger Dryas (= H0) — is recorded unambiguously (Kennett and Ingram, 1995). Increased deposition of warm-water planktonic forams is associated with ages of H3 and H5, while few warm-water forms are associated with H0, H1, H2 and H4 (Kennett and Venz, 1995). Fluctuations in pollen assemblages do not show repeated patterns associated with ages of known Heinrich events (Heusser, 1995). Similarly, Owens Lake, California, pollen (Litwin et al., 1997), and diatom (Bradbury, 1997a,b) data are equivocal with respect to D-O cycles and Heinrich events over the last ca. 50,000 years, though detailed analysis of oxygen isotope, total inorganic carbon and pollen stratigraphies from Owens Lake (Benson et al., 1997, 1998) suggest millennial-scale glacier fluctuations in the Sierra, and a strong teleconnection between the southwest and the North Atlantic for H0.

However, falling-lake events in Pleistocene Lake Bonneville apparently correspond with Heinrich events H1 and H2, suggesting drier conditions immediately upwind from the Colorado Plateau at those times (Oviatt, 1997). Until higher-resolution studies of existing and new paleoecological records from the southern Colorado Plateau are performed, our understanding of the nature of the strength and duration of teleconnections between the southwest and the North Atlantic will remain vague.

6. Discussion and conclusions

The Colorado Plateau is a distinct physiographic region with complex terrain, from near sea-level to over 3850 m elevation. Situated between the Rocky Mountains and the Great Basin, and split by a major river corridor (Colorado River), the Plateau serves as a key connection between the largest interior mountain system in North America, and regions to the west and southwest. Understanding the paleoenvironments of the Plateau will contribute to our knowledge not only of plant and animal biogeography of western North America, but also of the important climatic processes affecting the southwest.

The southern Colorado Plateau and the Colorado River corridor contain the heaviest concentration of paleobotanical sites studied to date on the Plateau. Additional sites should be identified from the northern third of the Plateau (Fig. 1). Further, the southern portion of the Plateau contains more identified sites with IS 3 data than on the north, and our efforts should be concentrated on identifying potential localities which will help us understand the middle Wisconsin in the north. Since old lakes are rare within the area, our best hope in this dry region may be to identify deep cave profiles, or detailed packrat midden series, that will extend our knowledge to the outer limits of radiocarbon dating.

One of the significant paleoclimatic unknowns for the southern Colorado Plateau is the importance of summer precipitation during IS 2 and IS 3 (the southwestern or Mexican monsoon (Shafer, 1989; Mock, 1996; Higgins et al., 1997)). Paleobotanical evidence from sites on the southern Colorado Plateau can assist in our understanding of its development. During the last glacial, the southern position of the jet stream, a cooler tropical ocean, and a heavy spring snowpack over the Plateau and Southern Rockies probably conspired to suppress monsoonal flow. Instead, seasonality of precipitation appears to have been dampened, with the majority of moisture embedded in this southerly displaced winter storm track. Several authors (e.g., Anderson, 1989, 1993; Betancourt, 1990) have suggested that the rapid migration of ponderosa pine (*Pinus ponderosa*) across the southern Colorado Plateau at the beginning of IS 1 signaled the development of the summer precipitation maximum, perhaps related to the summer insolation maximum, which peaked at ca. 9000 years ago (Kutzbach and Webb, 1993). Further study of the modern distribution and former geographic ranges of species, such as ponderosa pine and C_4 grasses, will help track the history of the summer monsoon (Connin et al., 1998).

Evidence for millennial-scale variability (e.g., Dansgaard–Oeschger cycles, Heinrich events) on the Colorado Plateau is at present equivocal. At least one continuous sedimentary record from areas upwind from the Plateau appears to show variations in climatic parameters on millennial scales, but others do not. On the southern Colorado Plateau, changes in the pollen assemblages contemporaneous with Heinrich events recorded elsewhere suggest drier conditions at some, but not all, sites. It is possible that correlations are hampered by problems in dating of the profiles. The nature of the packrat midden record, 'snapshots' of local vegetation with up to several millennia between middens, force us to rely more heavily on continuous sedimentary records, and such long records are in short supply.

Nevertheless, one of the hallmarks of the midden record of the southwestern U.S. is the apparent persistence of vegetation patterns, with no dramatic reversals, during IS 2 and 3. One hypothesis is that millennial-scale variability noted elsewhere in the world was simply not enough to shift plant distributions 300 m or more along elevational/climatic gradients. However, there exist critical gaps in midden coverage, for example 1600–2000 m, where millennial-scale variability might have shifted ecotonal boundaries, specifically the lower limits of spruce–fir forests on the Colorado Plateau.

Of greater certainty is our estimate of average climatic parameters for the southern Colorado Plateau. Between-site consistency suggests that the mean depression of late-Wisconsin temperature was at least 5°C, while the mid-Wisconsin was somewhat warmer at only 2.5–4°C colder than today.

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