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LATE QUATERNARY PLANT ZONATION AND CLIMATE IN SOUTHEASTERN UTAH

by

Julio L. Betancourt

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SIGNED: Julio L. Betancourt

APPROVAL BY RESEARCH ADVISORY COMMITTEE

This manuscript has been approved for submission on the date shown below:

Paul S. Martin

Owen K. Davis

Raymond M. Turner

James W. Cathey

Graduate Student Coordinator, or
Head of Deartment

Date 9/15/83

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ABSTRACT

Plant macrofossils from packrat middens in two southeastern Utah caves outline development of modern plant zonation from the late Wisconsin. Allen Canyon Cave (2195 m) and Fishmouth Cave (1585 m) are located along a continuous gradient of outcropping Navajo Sandstone that extends from the Abajo Mountains south to the San Juan River. By holding the site constant, changes in the floral composition for a plot of less than one hectare can be observed, even if sporadically, over tens of millennia. At Allen Canyon Cave, engelmann spruce-alpine fir forest was replaced by the present vegetation consisting of pinyon-juniper woodland on exposed ridgetops and cliffside stands of Douglas fir, ponderosa pine, and aspen. Xerophytic woodland plants such as pinyon, Plains prickly pear, and narrowleaf yucca arrived sometime in the middle Holocene between 7200 and 3400 B.P. At Fishmouth Cave, Utah juniper in Holocene middens replaced blue spruce, limber pine, Douglas fir, and dwarf and Rocky Mountain junipers in late Wisconsin samples.

Disharmonious associations for the late Wisconsin occur only at the lower site with the xerophytes Mormon tea, Plains prickly pear, and narrowleaf yucca growing alongside subalpine conifers. One possible explanation involves the late Wisconsin absence of ponderosa and pinyon pines from the Colorado Plateaus. Released from competition at their lower limits, subalpine conifers were able to expand into lower

elevations and mix with xerophytic plants found today in understories of pinyon-juniper and ponderosa pine woodlands. Quantitative climatic estimates are derived for the late Wisconsin by applying vertical lapse rates for temperature and precpitation to the amount of vegetation depression. The Fishmouth Cave sequence indicates a minimum lowering of 850 m for blue spruce, limber pine, and dwarf juniper. A depression of at least 700 m for engelmann spruce and alpine fir is suggested for the Allen Canyon locality. Use of conservatively low lapse rates for stations below 2080 m yields a 3-4^{o}C cooling from present mean annual temperature and 35 to 60 percent more rainfall than today. Steeper lapse rates associated with more mountainous terrain suggest a 5^{o}C lowering in temperature and up to 120 percent increase over modern precipitation.

INTRODUCTION

Elevational plant zonation is by tradition the interpretative framework used in paleobotanical studies of the Southwestern United States. Early emphasis was placed on the amount of lowering for vegetation zones during Wisconsin cooling. Pollen studies such as that by Maher (1961) focused on upper treeline movement in the San Juan Mountains, while Wright et al. (1973) examined unequal lowering or "telescoping" of various zones in the Chuska Mountains on the Arizona-New Mexico border. In recent years, the pendulum has swung to recognize that Pleistocene zonation is often without modern analog. Consequently, changes along the elevational gradient are now being scrutinized from the individualistic rather than Clemensian point of view. The individualistic approach has gained impetus in Southwestern paleoecology with the advent of packrat (Neotoma spp.) midden analysis, allowing great taxonomic and geographic precision for discerning past changes in the elevational range of individual plants. Along these lines, a major focus has been to reveal disharmonious plant associations in Wisconsin time (Cole, 1981; Spaulding, 1981).

In high relief areas of western North America, steep gradients in plant zonation are often related to pronounced vertical variations in climate. Though no causal relationship has been demonstrated, it is assumed that mountain belts do in part explain the vertical distribution of plants. Quantitative estimates of past climates can be

achieved by applying present vertical lapse rates of precipitation and temperature to the amount of change in the elevational range of a plant. During the late Wisconsin, plants now limited to upper elevations expanded down to the surrounding lowlands. Prime examples include pinyon-juniper woodland in the Chihuahuan and Sonoran Deserts (Van Devender and Spaulding, 1979) and depressions of up to 1000 m for Utah juniper (Juniperus osteosperma) and limber pine (Pinus flexilis) in the Mohave Desert (Spaulding, 1981). Because rainfall increases and temperatures generally decrease with elevation, application of vertical lapse rates to characterize lowering of plant zones suggests both a cooler and wetter climate for the late Wisconsin of the western deserts.

Another way of deriving climate from the fossil plant record is suggested by the horizontal zonation of both plants and climate. During the late Wisconsin, the range of several plants expanded or contracted by several degrees in latitude. Notable examples are the southern expansion of Joshua tree (Yucca brevifolia) into the Sonoran Desert (Van Devender, 1973) or the restriction of Colorado pinyon (Pinus edulis) to the northern Chihuahuan Desert (Van Devender et al., in press). These records are interesting because range boundaries often coincide with steep atmospheric gradients separating well-defined air masses. The northern and southern limits of the Canadian boreal forest coincide with the summer and winter position of the arctic front (Bryson, 1966). Mitchell (1976) notes that of 73 tree species widely distributed in the western U.S., almost half reach their northern or southern limits between 40^{o} and 44^{o}N latitudes. North of this

boundary, westerly flow from the Pacific Ocean predominates, while below the boundary flow is to the south, originating in an anticyclone over southern Nevada. Hypothetically, long-term displacement of this boundary would serve to either contract or expand the ranges of certain trees.

A critical area for tracing large-scale migration of plants relative to the development of modern plant zonation is encompassed in those portions of New Mexico, Arizona, Coloado and Utah collectively known as the Colorado Plateaus. The vertical zonation of plants is relatively homogenous throughout the mountain ranges and higher plateaus that hover above the lower much-dissected tablelands. This homogeneity enhances the extrapolation of regional patterns from a few, strategic fossil localities. The area is also an excellent laboratory for studying the effects of shifting air flow patterns on regional vegetation. Mitchell's (1976) winter boundary coincides with the northern edge of the Colorado Plateaus, while the monsoonal boundary as defined by Bryson and Lowry (1955) crisscrosses the area from southwest to northeast. Both boundaries figure prominently in the biogeography of the western U.S.

To date, packrat midden data from the Colorado Plateaus include a Holocene chronology from Chaco Canyon, New Mexico (Betancourt and Van Devender, 1981), late Pleistocene projections of lowland vegetation from the Chuska Mountain pollen sequence (Wright et al., 1973) compared with midden macrofossils from adjacent Canyon de Chelly, Arizona (Betancourt and Davis, in press), and gradient analysis of plant response to Pleistocene climates in the eastern Grand Canyon (Cole,

1981, 1982). Until now, no fossil packrat middens had been collected from the central portion of the Colorado Plateaus in southeastern Utah.

The present study grew out of overall efforts to evaluate the feasibility of radioactive waste disposal in the Paradox Basin of Utah. Management and disposal require consideration of geologic and hydrologic processes expected to supervene during the toxic life of the waste (DeBuchananne, 1974). Geohydrologic information is needed to predict potential transportation (by water) of radionuclides away from burial sites. One important parameter is the variability of past climate over relevant watersheds in time intervals comparable to the toxic life of the waste. Under contract with Woodward-Clyde Consultants of San Francisco, which was acting in behalf of the Office of Nuclear Waste Isolation, Battelle Memorial Institute, I undertook a midden study to reconstruct late Quaternary vegetation change, and, by inference, paleoclimatic variability for the central portion of the Colorado Plateaus.

The elevational gradient from the Abajo Mountains south along Comb Ridge to the San Juan River was chosen for geologic reasons. Large rock shelters containing middens of all ages are common in the local Navajo Sandstone (Glen Canyon Group; Jurassic). This sandstone outcrops continuously from 2560 to 1340 m as a consequence of deformation by the igneous intrusion which formed the Abajo Mountains. A brief reconnaissance of the 1220 m gradient produced two midden sequences from late Wisconsin times to the present in rock shelters at 1585 m and 2195 m elevation. Vertical lapse rates for both precipitation and temperature were derived from 18 climatic stations in southeastern Utah

and are used to reconstruct climate at the fossil localities and elevational analogs for late Wisconsin plant assemblages. The midden record from southeastern Utah is also harnessed to generate new ideas about the historic development of vegetation patterns on the Colorado Plateaus.

METHODS

Packrat foraging for food and construction usually produces representative collections of the local flora. Because of predator pressure, packrats are tethered to within 100 m of their houses (Raun, 1966; Bleich and Schwartz, 1975; Stones and Hayward, 1968). Seemingly amorphous piles of plant and other material seal passageways and interior chambers from predators and serve to buffer daily or seasonal extremes in temperatures. The outer crust of the houses and the floors of the passageways are often hard-packed with feces and crystallized urine (amberat). During times of high atmospheric humidity, the amberat rehydrates and permeates the lattice work of an abandoned house. This process combines with gradual collapse of the structure to create the indurate masses referred to as middens. Packrat feces, urine and plant material dropped en route to the house may also produce middens in perch areas or trails along the walls of caves and rock shelters. Stratified deposits may form when packrats continue to build atop older middens. Problematical stratigraphy results when packrats build along the sides or even below older middens.

There is currently little agreement on field and laboratory procedures for packrat midden analysis. Generally, I collect middens with an indurated mass of 0.5 to 2.0 kg. Outer weathering surfaces are removed and the sample is carefully whittled down to the desired sample size with hammer and chisel. An individual sample is isolated that

appears to represent a single depositional episode with a temporally discrete assemblage of plants. Samples are weighed prior to disaggregation in water (the amberat is water soluble), which may take from two to ten days depending on the sample. The organic residue is wet-screened through a 20 mesh (0.84 mm) soil sieve to remove dust and urine still adhering to plant parts.

The organic residue caught by screening is weighed after drying in an oven and often comprises from 10 to 20 percent of the mass of the indurated midden. Initial sorting involves removal of all fecal pellets. The dry organic residue minus the fecal pellets yields the mass of plant matrix to be analyzed, which usually accounts for 50 to 70 percent of the dry weight of the washed sample. This plant matrix is sieved into size classes and hand-sorted for identifiable fragments. On the average, individual middens yield from 20 to 30 kinds of plants.

Species representation is commonly expressed in terms of relative abundance, primarily because the original mass and number of unidentifiable fragments vary per kilogram of unwashed midden (Van Devender, 1973; Phillips, 1977; Spaulding, 1981). A relative scale of one to five (1 = rare; 2 = uncommon; 3 = common; 4 = very common; 5 = abundant) is commonly used. Recently, other means of expressing macrofossil abundances have been suggested. Cole (1981) employs the concentration of macrofossils for each species per kilogram of indurated sample. The main pitfall in this strategy is the sample-to-sample variability in the concentration of amberat, sediment, rocks, and fecal pellets. Spaulding (in press) shows the relative frequency of a given taxon as a percentage of the total number of identified

specimens, noting that often the numbers for a single taxon overwhelm the rest of the assemblage. This is avoided by subtracting the overrepresented taxon from the total number of identified specimens. Aside from the problem of comparing seeds and stems, this method is under the same constraints as pollen percentages (Davis, 1963), whereby the percentage of one pollen or macrofossil type is mutually dependent on other types in the sample. To avoid these problems, I prefer to divide the mass of the species by that of the plant matrix in a midden, to include unidentified portions. This permits comparisons of the abundances for a single species throughout a lengthy midden sequence and between contemporaneous middens at various localities.

Radiocarbon dating of packrat middens has been the subject of much debate. Wells (1976) advocates dating mixed debris from a thin layer of midden. Van Devender (1973) and Mead et al. (1979) recommend dating either a single fragment (e.g., a piece of wood) or a composite sample from one species. The species targeted for dating should be critical to paleoecological reconstructions. For instance, in a midden study aimed at determining the arrival of pinyon (Pinus edulis) on the Colorado Plateaus, direct dates on pinyon macrofossils circumvent potential problems with mixed assemblages or questionable stratigraphy. When no species from a single midden yields sufficient material for a radiocarbon determination (greater than 3 g), a date on some other fraction such as packrat pellets may be necessary. Although the cost may be prohibitive, multiple dates on a single midden are often necessary. This becomes crucial where a single midden assemblage is employed as the keystone of a sequence, marking a biochronologic event

or boundary. Multiple dates are also imperative in middens suspected of contamination. Spaulding (1981) reviews a series of middens with multiple dates, concluding that the dates were discordant at one standard deviation in 30 percent of the cases. However, in a number of the cases he examined, there was reason to doubt the first date based on questionable associations of plants in the assemblage. Confirmation of suspected contaminants, present only in trace amounts, will become routine with further development of accelerator dating.

Early midden research focused on the contrast between Wisconsin and modern vegetation. In the field, Wisconsin-age middens were easily recognized by the presence of plants now growing at much higher elevations or even different latitudes. For the user of midden data concerned with the historic continuum, the bias for Pleistocene middens produced many incomplete chronologies. The scant attention paid to younger middens partly reflected the sentiment that there had been little or no sequential change in Holocene vegetation. Recent midden studies in the Great Basin (Thompson and Hattori, in press), northern Chihuahuan Desert (Van Devender et al., in press) and the Colorado Plateaus (Betancourt and Van Devender, 1981) demonstrate that Holocene migration of plants in the West may be as dynamic as postglacial invasion north of the glacial border. I would argue that much of this movement continues today. Moreover, historical explanation for present vegetation patterns can only be gleaned from chronologies that trace development of local vegetation over long periods of time. I prefer to hold the site constant for each chronology by developing lengthy midden sequences from individual rock shelters or caves. Hence, the floral

composition for a plot of less than one hectare can be observed, even if sporadically, over thousands of years.

PHYSICAL SETTING

The Colorado Plateaus are characterized by flat-lying sedimentary rocks, modified locally by faulting, folding and igneous intrusions. The various "plateaus" are elevated from 1520 m to 3350 m. Elevations below 1520 m are limited to the canyon bottoms of the Colorado River and its numerous tributaries. The central portion of the Plateaus is occupied by the spectacular Canyonlands of southeastern Utah. A tableland of resistant Dakota Sandstone, known locally as the Great Sage Plain but nonetheless much dissected, separates the La Sal and Abajo Mountains from the principal ranges of the southern Rocky Mountains. The Great Sage Plain is bordered on the west by the Monument Upwarp, boasting scenic buttes (monuments) and steep escarpments of Triassic and Jurassic sandstones. The crest of the upwarp is poorly defined at Elk Ridge, while the Comb Ridge monocline forms the steeply downfolded eastern edge. The latter is delineated by a comb-like crest of Navajo Sandstone stretching 160 km from west of Kayenta, Arizona to the northeast base of Elk Ridge. The uplands in the area are defined by several laccolithic ranges, including the Ute, Henry, Navajo, La Sal, and Abajo mountains. At Navajo Mountain, the sedimentary rock has not eroded sufficiently to expose the igneous core, which outcrops at higher elevations in the other ranges. The higher peaks in the region are in the La Sal Mountains, rising up to 3877 m at Mount Peale (Gregory, 1938). Only the La Sal Mountains were

glaciated during the late Wisconsin interval (Richmond, 1962; Witkind, 1965).

Plant Zonation

Floristicaly, the La Sal and Abajo Mountains are considered outliers of the southern Rocky Mountains (Cronquist et al., 1972). There is also a close resemblance in the elevational range of plants. Below, I employ the zonal concept simply as an heuristic device without traditional ecological implications. In general, the upper elevational limits of each species occur on open, south-facing slopes, whereas the lower limits are usually defined on north-facing slopes or in mesic ravines. Alpine tundra is confined to the La Sal Mountains at elevations above 3660 m. Abajo Peak at 3660 m is the highest in the Abajo Mountains. From Mt. Linnaeus (3340 m) to the San Juan River (1340 m), plant zonation is as follows:

Engelmann spruce-alpine fir forest (3660-2896 m): Engelmann spruce (Picea engelmannii) and alpine fir (Abies lasiocarpa) are the dominant species of forests above 2896 m. Engelmann spruce is usually the more abundant as well as the taller of the two species in mixed stands. The herbaceous cover in closed stands is mostly depauperate due to the accumulation of duff and debris (Daubenmire, 1943). Dense, spruce-fir stands are common mostly on steep, northerly exposures. Subalpine meadows cover extensive areas on the more gentle slopes. Common shrubs include currant (Ribes spp.), dwarf juniper (Juniperus communis), elderberry (Sambucus racemosa), blackberry (Rubus idaeus), snowberry (Symphoricarpus oreophilus), russet buffaloberry (Shepherdia

canadensis), and boxleaf (Pachystima myrsinites). Limber pine (Pinus flexilis) is limited to dry, rocky exposures although it occasionally occurs within the spruce-fir forest. Aspen (Populus tremuloides) frequently occurs at the base of steep, south-facing exposures (Ellison, 1954) and is most common in the lower part of the zone.

Douglas fir-white fir-blue spruce zone (3048-2438 m): the mixed conifer forest at these elevations is usually dominated by Douglas fir (Pseudotsuga menziesii), which has a broad elevational range. Douglas fir is distributed from the spruce-fir zone in the Abajo Mountains down to 1830 m in Natural Bridges National Monument. White fir (Abies concolor) and Douglas fir share dominance on sheltered and north-facing slopes. Riparian forests at these elevations are dominated by blue spruce, white fir and aspen. Blue spruce often extends down to low elevations along the major canyon streams. Along upper Indian Creek on the north side of the Abajos, blue spruce can occur down to 2320 m. Xeric exposures in this zone are frequently occupied by limber pine at the higher elevations and ponderosa pine (Pinus ponderosa) on the lower slopes. Large portions of the exposed uplands may be clad in ponderosa pine forest at the lower elevations. Many of the understory shrubs in this mixed-conifer forest are the same as in the spruce-fir zone, with two important additions--Rocky Mountain maple (Acer glabrum) and seviceberry (Amelanchier utahensis).

Ponderosa pine-Gambel oak zone (2740-1830 m): This zone is dominated by ponderosa pine and the deciduous Gambel oak (Quercus gambelii). At higher elevations, extensive clones of Gambel oak apparently have developed from a single individual over a period of

several hundred years. Ponderosa pine may form thick stands on the broken slopes of the Abajos, or occur as parkland as on Elk Ridge near Bear's Ears. Douglas fir commonly occurs in this zone, particularly at the base of cliffs with northerly exposures. Gallery forests with an overstory of ponderosa pine extend down to 1830 m in Cottonwood Wash and its tributaries. The lowest stand of ponderosa pine in the study area in a riparian setting is at 1700 m near the source of Butler Wash on the east side of Comb Ridge. The ponderosa pine-Gambel oak zone shares many shrubby species with the lower pinyon-juniper woodland. Some of the common trees and shrubs include Rocky Mountain juniper (Juniperus scopulorum), mountain mahogany (Cercocarpus spp.), serviceberry, snowberry, kinnick-kinnick (Arctostaphylos uva-ursi), buckbrush (Ceanothus fendleri), squawbush (Rhus trilobata), bitterbrush (Purshia tridentata), water birch (Betula occidentalis), rabbitbrush (Chrysothamnus viscidifloris), and big sagebrush (Artemisia tridentata).

Pinyon-juniper woodland and big sagebrush parkland (2290-1650 m): The dominant vegetation type in the area is a woodland of Colorado pinyon (Pinus edulis) and Utah juniper (Juniperus osteosperma). The area in pinyon-juniper woodland greatly exceeds that of the other vegetation zones; half of San Juan County lies between 1830 m and 2130 m elevation. Pinyon may occur up to 9000 ft (2743 m) as on the summit of Bear's Ears on Elk Ridge. Scattered Utah junipers are not uncommon below 1520 m. In this zone, pure stands of big sagebrush often cover wide expanses, especially in the shallow divides at the heads of drainages and generally where soils are relatively deep but lack a

well-developed calcic layer. Common shrubs in the pinyon- juniper woodland and sagebrush parkland include sevicebery, single-leaf ash (Fraxinus anomala), roundleaf buffaloberry (Shepherdia rotundifolia), mountain mahogany, rabbitbrush, snakeweed (Gutierrezia spp.), cliffrose (Cowania mexicana), Mormon tea (Ephedra spp.), yuccas (Yucca spp.), and prickly pear (Opuntia polyacantha).

Desert shrub zone (1650-1340 m): In the study area, this zone is more or less compressed due to the relatively high elevation of the San Juan River. Almost pure stands of blackbrush (Coleogyne ramosissima) occur on the sandy slopes west of Comb Wash, its upper limits overlapping the lower limits of Utah juniper. Typical stands in lower Road Canyon west of Comb Ridge are interspersed with galleta grass (Hilaria jamesii), Indian ricegrass (Oryzopsis hymenoides), snakeweed, and Mormon tea. Sand dunes in this zone are frequently vegetated by sand sagebrush (Artemisia filifolia), single-leaf ash, and sand oak (Quercus undulata). In the lower parts of the zone, shadscale (Atriplex confertifolia) is common though seldom occurs in pure stands. Other common shrubs at these elevations include several saltbushes (Atriplex spp.), buckwheats (Eriogonum spp.), and greasewood (Sarcobatus vermiculatus). The latter is the principal phreatophyte in the zone and dominates the lower courses of Cottonwood, Butler and Comb washes.

Climate

Probably the most useful scheme to describe air flow patterns over southeastern Utah is provided by Mitchell (1976), who uses equiva-

lent potential temperature to determine seasonal locations of air mass boundaries over the western United States. Mitchell notes a winter pattern from November through March and a summer pattern from June through September, with April, May and October as transitions between the two modes. Two equivalent potential temperature gradients, one in winter and the other in summer, traverse northern and southeastern Utah, respectively (Mitchell, 1976; Fig. 3).

The winter gradient across northern Utah (ca. 41^{o}N lat.) coincides with a convergence zone. Flow below the boundary is southerly, originating in the anticyclone over southern Nevada. To the north, the flow is westerly from the Pacific Ocean. Several times during winter the anticyclone breaks down and allows storm tracks from the northern Pacific Ocean Aleutian Low to shift southward. This mechanism is responsible for most of the winter precipitation in southeastern Utah. The winter gradient separates cold, polar air from warmer sub-tropical air. The summer gradient, commonly called the monsoon boundary, runs diagonally from western Arizona, across southeastern Utah and northwestern Colorado, into the Great Plains. During mid to late summer (July, August, and September), the area east of the boundary is under the influence of the Bermuda High over the Atlantic Ocean, while to the north, westerly flow from over the Pacific ocean predominates. Flow around the western end of the Bermuda High produces incursions of moist air over the southeastern part of the western United States. These incursions are responsible for the distinct summer rainy season over much of the Southwest. The subtropical moisture originates both from the Gulf of Mexico (Bryson and Lowry, 1955) and from the Gulf of

California (Hales, 1974). Both the winter and summer gradients have been linked to jet stream patterns. The winter gradient has been related to the tropospheric polar jet stream (Reed, 1979; Mullen, 1979), whereas the monsoonal pattern is linked to the subtropical jet stream (Bryson and Lowry, 1955).

Secular trends in the climate of the Southwest suggest that the two patterns, though occurring in different seasons, are in direct opposition throughout the year (Sellers, 1960). This has broad implications for any consideration of past climates in southeastern Utah, particularly if trends of longer duration (on the order of several millennia) are caused by major shifts in the position of the jet streams. Generally, a southerly displacement of the polar jet stream produces a cooling trend; a warming trend is associated with a shift to the north. In the last 100 years, a warming trend occurred prior to 1940 and temperatures have been decreasing since that time in the northern hemisphere (Miles, 1978). Nielson and Wullstein (in press) have examined the two trends as manifested in June and July latitudinal precipitation profiles along the gradient from Logan, Utah (42^{o}N lat.) to Flagstaff, Arizona (35^{o}N lat.). During the cooling trend, the monsoon withdraws to the south and its peak intensity shifts from July to August. Frequency patterns of early and late winter frontal systems occur approximately one month later than usual, significantly increasing June precipitation (late spring cyclonics from the north). June precipitation decreases from north to south along the gradient, opposite the trend for July. During warming trends, Nielson and Wullstein (in press) note an increase in July precipitation to the

north, due to radial expansion of the Bermuda High. In Arizona, Sellers (1960) notes that September precipitation from a Pacific source is closely related to the precipitation for the preceding winter and that increases are favored by a southward displacement of the middle latitude storm track. Heavy September precipitation in Arizona is mostly related to tropical disturbances in the Pacific Ocean. The conditions favorable for high September precipitation are not favorable for July precipitation.

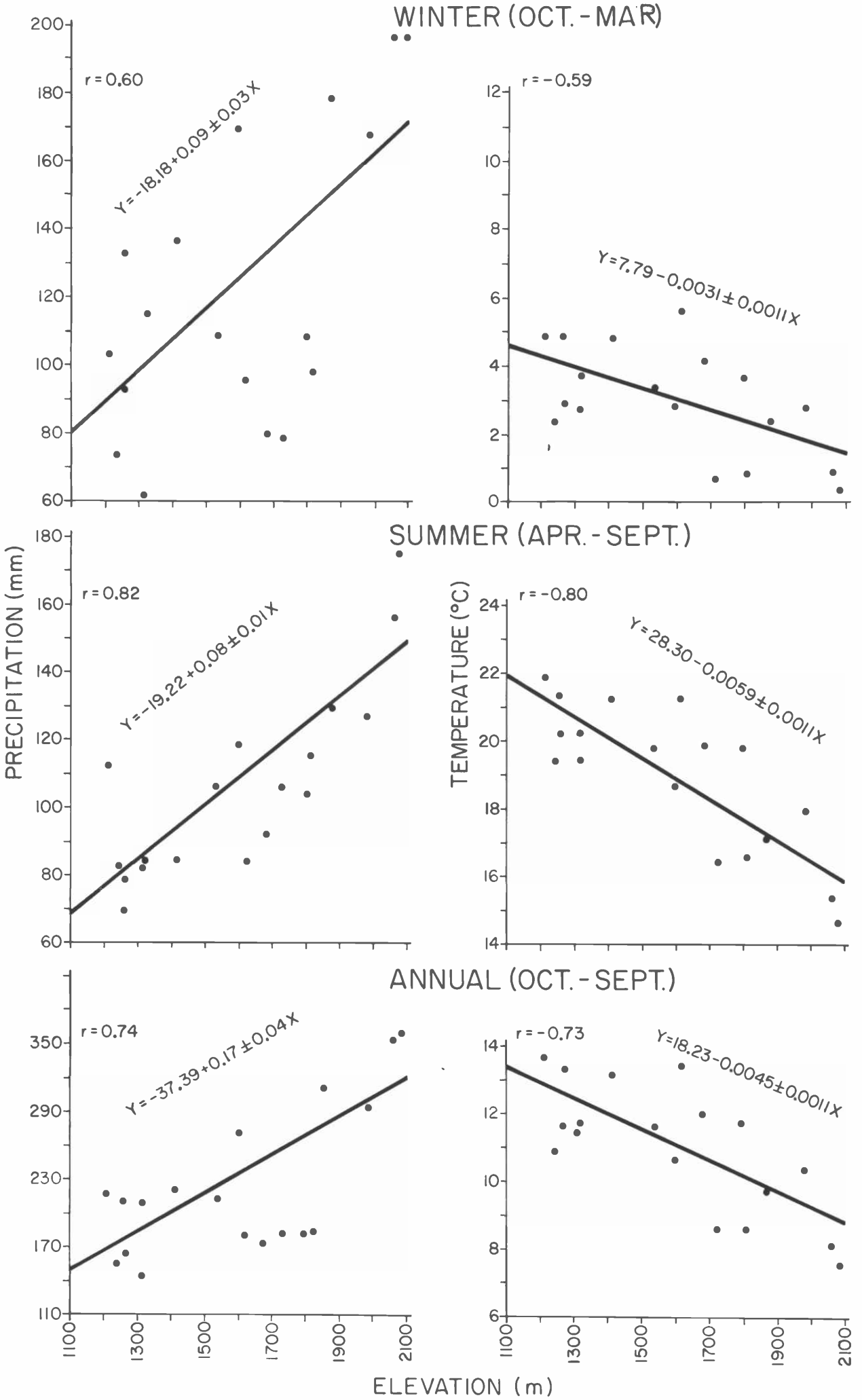
For southeastern Utah a southward displacement of the polar jet stream might result in increased winter precipitation, a decrease in midsummer precipitation, cooler summer temperatures, and a higher incidence of spring freezes. Possible increases in June and September precipitation may also be related to what Gifford et al. (1976) refer to as the Southern Utah Low. This is a high altitude low pressure system that today produces widespread precipitation in May and October, during the transition from winter cyclonic to summer anticyclonic circulation patterns. A northward shift of the jet stream (contraction of the polar vortex) might result in higher annual temperatures, a decrease in winter moisture, an increase in midsummer precipitation, and a relative dry late spring and foresummer.

As in other parts of the West, temperature and precipitation are greatly influenced by elevation in southeastern Utah. In general, air temperatures decrease and precipitation increases with elevation. In the Intermountain West, both relationships are largely linear for every month of the year (Price and Evans, 1937; Baker, 1944; Lull and Ellison, 1950; Williams and Peck, 1962; Houghton, 1979). Vertical

Table 1. Climatic stations and years of records used to calculate vertical lapse rates for temperature and precipitation in southeastern Utah.

Station	Elevation	Latitude	Longitude	Temperature-- Years of Record Used	Precipitation-- Years of Record Used
Moab	1209 m	38°36'N	109°36'W	1962-1967, 1969-1971, 1973-1976, 1978-1979	1961-1980
Green River	1241 m	39°00'N	110°10'W	1961-1972, 1975	191-1980
Dewey	1256 m	38°48'N	19°18'W	1970, 1973-1978, 1980	1968-1975, 1977-1980
Mexican Hat	1256 m	37°09'N	109°52'W	1961, 1963, 1966-1968, 1970-1971, 1973-1980	1961-1968, 1970-1980
Hanksville	1313 m	38°22'N	110°43'W	1961-1980	1961-1980
Bluff	1315 m	38°17'N	109°33'W	1962-1966, 1968-1980	1961-1980
Aneth Plant	1409 m	37°15'N	109°20'W	1966, 1968-1980	1966-1980
Hovenweep	1597 m	37°23'N	109°05'W	1961-1974, 1976-1980	1961-1980
The Canyonlands-- The Needle	1536 m	38°09'N	109°45'W	1966-1970, 1972, 1974, 1979-1980	1966-1980
Monument Valley Mission	1615 m	37°09'N	110°13'W	1964, 1966-1967, 1969-1970, 1972, 1974, 1979-1980	1963-1980
Capitol Reef National Monument	1676 m	38°17'N	111°16'W	1968-1980	1968-1980
Castle Dale	1725 m	39°13'N	111°01'W	1961-1968, 1971-1980	1961-1980
Canyonlands-- The Neck	1798 m	38°27'N	109°50'W	1966, 1968-1972, 1976-1980	1966-1980
Ferron	1807 m	39°05'N	111°08'W	1961-1969, 1971, 1973, 1976-1980	1961-1980
Blanding	1868 m	37°37'N	109°28'W	1961-1980	1961-1980
Natural Bridges	1981 m	37°37'N	109°59'W	1967, 1969-1977k 1979-1980	1966-1980
Cedar Point	2060 m	37°43'N	109°05'W	1964-1980	1961-1980
Monticello	2079 m	37°52'N	109°18'W	1961-1980	1961-1980

Figure 1. Linear regressions that express the relationship between temperature and precipitation with elevation from 18 climatic stations in southeastern Utah.


WINTER (OCT.-MAR)
r = 0.60
Y=-18.18+0.09±0.03X
r = -0.59
Y=7.79-0.0031±0.0011X
SUMMER (APR.-SEPT.)
PRECIPITATION (mm)
r = 0.82
Y=-19.22+0.08±0.01X
TEMPERATURE (°C)
r = -0.80
Y=28.30-0.0059±0.0011X
ANNUAL (OCT.-SEPT.)
r = 0.74
Y=-37.39+0.17±0.04X
r = -0.73
Y=18.23-0.0045±0.0011X
ELEVATION (m)

lapse rates for temperature and precipitation in winter (Oct.-Mar.), summer (Apr.-Sept.), and the hydrological year (Apr.-Sept.) were reconstructed from the last 20 years of record at 18 stations between 1209 and 2079 m in southeastern Utah (Table 1, Fig. 1). These lapse rates may be unusually low because the elevational range of the stations is small and they are all located in areas of relatively low relief below the base of the mountains. An annual lapse rate of $-0.59^{o}C/100$ m is recorded for the nearby San Juan Mountains of southwestern Colorado (Barry and Bradley, 1976), a higher figure than the $-0.45^{o}C/100$ m obtained for southeastern Utah. The regression equations for precipitation (Fig. 1) also grossly underestimate annual precipitation in the mountains. The Soil Conservation Service maintains two rain gauges near the lower limits for Engelmann spruce-alpine fir forest in the Abajo Mountains Camp Junction (2804 m) and Buckboard Flat (2865 m). Mean annual precipitation averaged over the past 20 years is 720 mm for Camp Junction and 790 mm at Buckboard Flat. The regression equations using data from lower elevations predict from 440 to 450 mm at these two sites, underestimating real precipitation by about 40 percent. The lapse rate for precipitation between Monticello (2079 m) and Buckboard Flat (2865 m) is ca. 52 mm/100 m or 3 times steeper than the average rate calculated from the 18 stations below the base of the mountains. The steeper rate is comparable to the 41 mm/100 m cited for the Wasatch Plateau of central Utah, using data from an elevational range of 1690 to 3110 m (Lull and Ellison, 1950).

Obviously, mountainous terrain has a greater physical effect on storm systems than the lesser plateaus. A significant difference lies in the steeper rates of increase for winter precipitation at higher elevations (above 2130 m). One explanation might involve seasonal variations in the type, areal extent, and direction of storm systems relative to the network of stations. In winter, convergent- type storms are subject to orographic uplift over a wide area. The paths of convective storms during summer are highly erratic and the precipitation-elevation relationship is partly a function of a station's location along the path of an individual storm (Lull and Ellison, 1950). An equally important factor is the temperature at the site of the precipitation. On cloudy days in winter, there may be no rainfall at the lower elevations but snow is prevalent with the onset of freezing temperatures in the mountains.

The regression equations from Fig. 1 are used later to predict climate at the elevations of fossil localities and the modern analogs for late Wisconsin assemblages. The lower lapse rates associated with the 18 lowland stations should provide minimum estimates for the lower temperature and higher precipitation inferred for the last Wisconsin. The potential error in underestimating the steeper lapse rates in mountainous terrain is taken into account.

RESULTS

Two large rock shelters along the Comb Ridge-Abajo Mountains gradient (Fig. 2) yielded midden sequences spanning the last 13,000 years. Fishmouth Cave (37°25'45"N, 109°39'W; 1585 m) is located on the east side of Comb Ridge, about 20 km northwest of Bluff. Allen Canyon Cave (37°47'30"N, 109°35'30"W; 2095 m) was spotted from the main road that skirts the base of Mt. Linneaus some 20 km northwest of Blanding.

Fishmouth Cave (Fig. 3) is a large shelter (75 m wide, 75 m deep, and up to 40 m high) that is plainly visible from several vantage points along the monoclinal valley of Butler Wash. The shelter has been visited by several notable geologists and archeologists, but is mentioned only briefly in the literature. The inscription "Hyde Exploring Expedition, R.W., 1894" on the back wall refers to a visit from Richard Wetherill, an adventurous rancher financed by the Expedition to reconnoiter prehistoric ruins in southeastern Utah. Prudden (1903: 275) describes the cave briefly from Wetherill's correspondence. A photograph of the cave also appears in Gregory's (1938, Plate 23Ai) classic treatise on the geology of southeastern Utah.

Vegetation on slopes adjoining Fishmouth Cave can be described as juniper grassland. The lower edge of the pinyon-juniper woodland is but a few kilometers north along Comb Ridge and barely 50 m higher in elevation. Riparian vegetation along the deeply entrenched channel of

Figure 2. The central portion of the Colorado Plateaus showing location of fossil localities discussed in text.

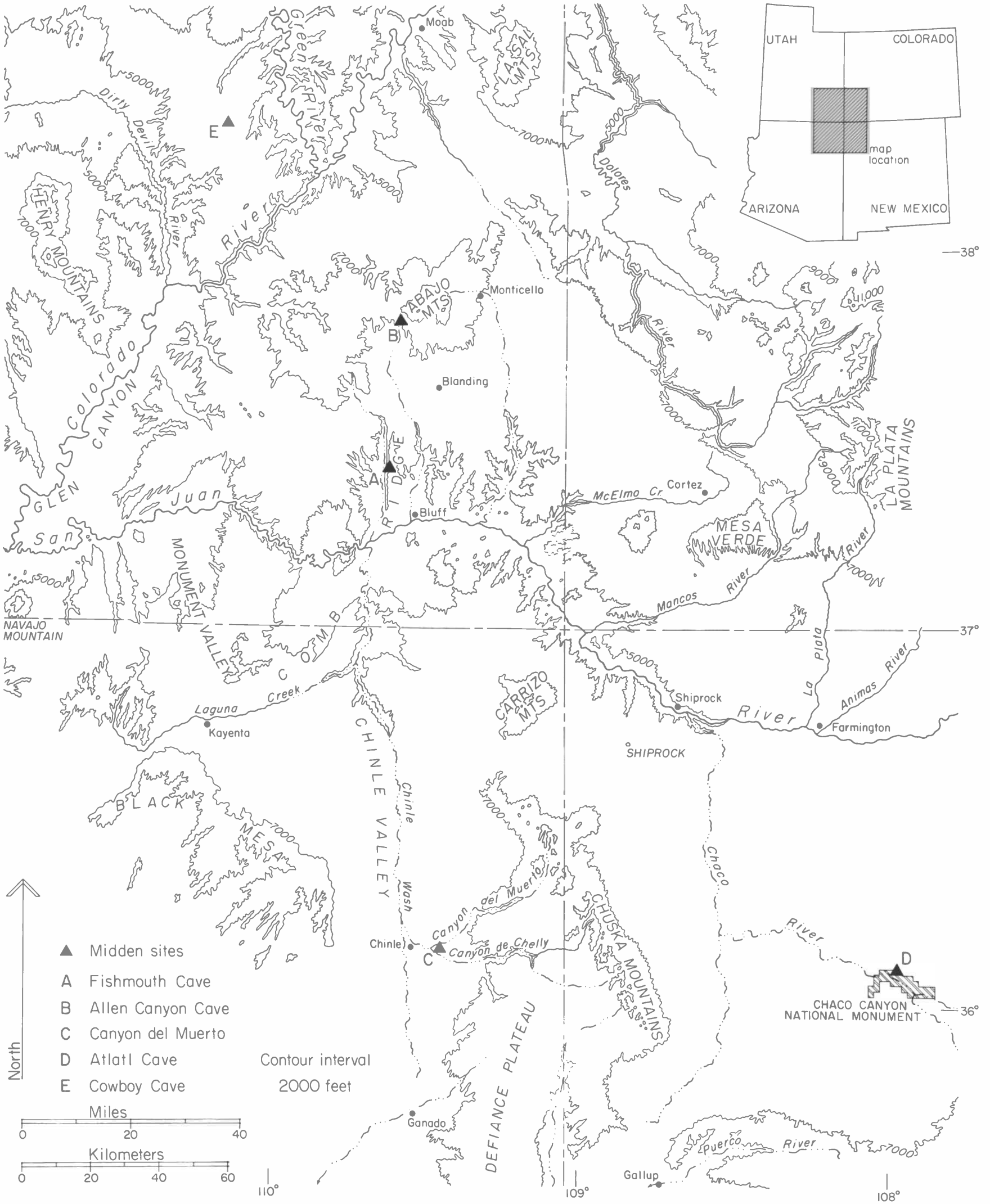
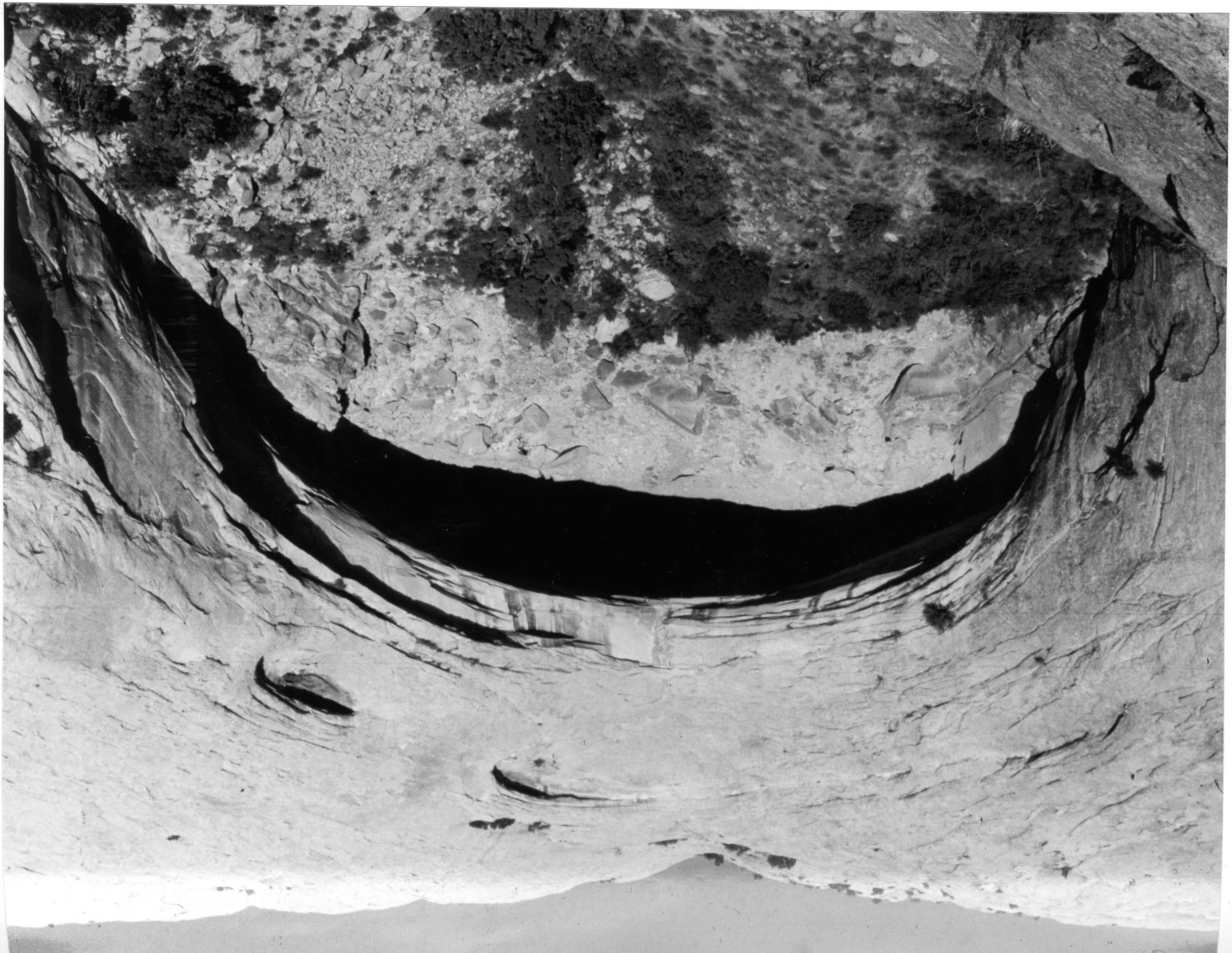

UTAH
COLORADO
ARIZONA
NEW MEXICO
map location
Moab
Green River
LA SAL MTS
Dirty Devil River
HENRY MOUNTAINS
Colorado River
GLEN CANYON
San Juan River
MONUMENT VALLEY
NAVAJO MOUNTAIN
Laguna Creek
Kayenta
BLACK MESA
CHINLE VALLEY
Chinle Wash
Chinle
CARRIZO MTS
Shiprock
SHIPROCK
La Plata River
Animas River
Farmington
Dolores River
ABAJO MTS
Monticello
Blanding
RIDGE
Bluff
McElmo Cr.
Cortez
MESA VERDE
Mancos River
LA PLATA MOUNTAINS
Canyon del Muerto
CHUSKA MOUNTAINS
Canyon de Chelly
Chaco River
CHACO CANYON NATIONAL MONUMENT
DEFIANCE PLATEAU
Ganado
Puerco River
Gallup
A
B
C
D
E
38°
37°
36°
109°
110°
108°
5000
7000
9000
11,000
North
▲ Midden sites
A Fishmouth Cave
B Allen Canyon Cave
C Canyon del Muerto
D Atlatl Cave
E Cowboy Cave
Contour interval
2000 feet
Miles
0 20 40
Kilometers
0 20 40 60

Figure 3. View of Fishmouth Cave from ridge to the southeast, showing plant community directly in front of shelter. -- The larger trees and shrubs include Utah juniper (Juniperus osteosperma), single-leaf ash (Fraxinus anomala), Utah serviceberry (Amelanchier utahensis), and squawbush (Rhus trilobata).



Butler Wash is dominated by Fremont cottonwood (Populus fremontii), narrowleaf cottonwood (Populus angustifolia), and tamarisk (Tamarix pentandra). Impenetrable thickets of young tamarisks choke the confluence of Butler Wash and the ravine leading out from the cave. Other common plants in the confluence area are willows (Salix spp.), greasewood (Sarcobatus vermiculatus), rabbitbrush (Chrysothamnus nauseosus), Russian thistle (Salsola kali), fourwing saltbush (Atriplex canescens) and summer cypress (Kochia spp.). Table 2 lists plants found within 100 m of the cave entrance. Slope exposure near the cave entrance is to the northeast.

Allen Canyon Cave (Fig. 4) is a slightly smaller shelter located on the north side of a ridge of Navajo Sandstone separating Allen Canyon from an unnamed tributary in the area of Bayles Pasture. Both drainages have their sources on the west slopes of Mt. Linneaus, eventually flowing into South Cottonwood Wash, which closely parallels Butler Wash en route to the San Juan River. Mt. Linneaus 6.4 k distant) and the spruce-fir forest near its summit are neatly framed by the arched ceiling when one looks out from the cave. On the exposed ridge above the shelter, pinyon pine and Utah juniper predominate with scattered ponderosa pine. Along the base of the cliffs, the dominant tree is Douglas fir with aspen groves located in pockets of deeper soils. On the gentle slope leading down to the level valley is a dense stand of Rocky Mountain maple (Acer glabrum), interspersed with Gambel oak, water birch (Betula occidentalis), and elderberry (Sambucus sp.). Table 3 lists plants growing on the northwest-facing slope in front of Allen Canyon Cave.

Table 2. Plant list from within 100 m of Fishmouth Cave.

AGAVACEAE
- Yucca angustissima Engelm. - narrowleaf yucca

ANACARDIACAE
- Rhus trilobata Nutt. - squawbush

ASCLEPIADACEAE
- Asclepias asperula (Decme.) Woodson - milkweed

BORAGINACEAE
- Cryptantha jamesii (Torr.) Payson - catseye
- Lappula redowskii (Hornem.) Greene - stickseed

CACTACEAE
- Opuntia phaeacantha Engelm. - variable prickly pear
- Opuntia polyacantha Haw. - Plains prickly pear

CHENOPODIEACEAE
- Atriplex canescens (Pursh) Nutt. - fourwing saltbush
- Ceratoides lanata (Pursh) J. T. Howell - winterfat

CLEOMACEAE
- Cleome serrulata Pursh - Rocky Mountain beeweed

COMPOSITAE
- Artemisia ludoviciana Nutt. - white sage
- Artemisia tridentata Nutt. - big sagebrush
- Aster sp. - aster
- Brickellia californica (Torr. & Gray) Gray - brickellbush
- Chrysothamnus nauseosus (Pall.) Britt. - rabbitbush
- Gutierrezia sarothrae (Pursh) Britt. & Rusby - snakeweed
- Heterotheca villosa (Pursh) Shinners - golden aster
- Lygodesmia grandiflora (Nutt.) T. & G. - skeleton plant
- Xanthium strumariuml L. - cocklebur

CRUCIFERAE
- Stanleya pinnata (Pursh.) Britton - desert plume

CUPPRESSACEAE
- Juniperus osteosperma (Torr.) Little - Utah juniper

ELAEGNACEAE
- Shepherdia rotundifolia Parry - roundleaf buffaloberry

Table 2 -- Continued

EPHEDRACEAEA
Ephedra viridis Cov. - Mormon tea

FAGACEAE
Quercus gambelii Nutt. - Gambel oak

GRAMINEAE
Bouteloua barbata Lag. - sixweeks grama
Bouteloua curtipendula (Michx.) Torr. - sideoats grama
Bromus tectorum L. - cheatgrass
Hilaria jamesii (Torr.) Benth. - galleta
Oryzopsis hymenoides (Roem. & Schut.) Ricker - Indian ricegrass
Sitanion hystrix (Nutt.) J. G. Smith - bottlebrush

JUNCACEAE
Juncus sp. - rush

LEGUMINOSAE
Astragalus sp. - milkvetch
Melilotus albus Desr. - white sweet clover

MALVACEAE
Sphaeralcea sp. - globemallow

OLEACEAE
Fraxinus anomala Torr. - single leaf ash

ONAGRACEAE
Oenothera hookeri T. & B. - evening primrose
Oenothera neomexicana (Small) Munz. - evening primrose

POLEMONIACEAE
Ipomopsis aggregata (Pursh) Spring. - shooting star

POLYGONACEAE
Eriogonum corymbosum Benth. - wild buckwheat
Eriogonum inflatum Torr. & Frem. - desert trumpet
Eriogonum alatum Torr. - winged buckwheat

RANUNCULACEAE
Clematis ligusticifolia Nutt. - virgin's bower

ROSACEAE
Amelanchier utahensis Koehne - serviceberry
Cercocarpus intricatus S. Wats - littleleaf mountain mahogany

Table 2 -- Continued

SALICACEAE
Salix exigua Nutt. - coyote willow
Populus fremontii Wats. - Fremont cottonwood
SCROPHULARIACEAE
Castilleja linariaefolia Benth. ex. DC. - Indian paintbrush
Cordylanthus wrightii Gray ex Torr. - birdbeak
ULMACEAE
Celtis reticulata Torr. - netleaf hackberry

Figure 4. View of Allen Canyon Cave from the unentrenched valley of an unnamed tributary of Allen Canyon. -- The larger trees in front of the shelter are Douglas fir (Pseudotsuga menziesii) and ponderosa pine (Pinus ponderosa). A grove of aspen (Populus tremuloides) occupies the foreground. Scattered ponderosa pine trees occur in pinyon-juniper woodland on the ridge top.

30

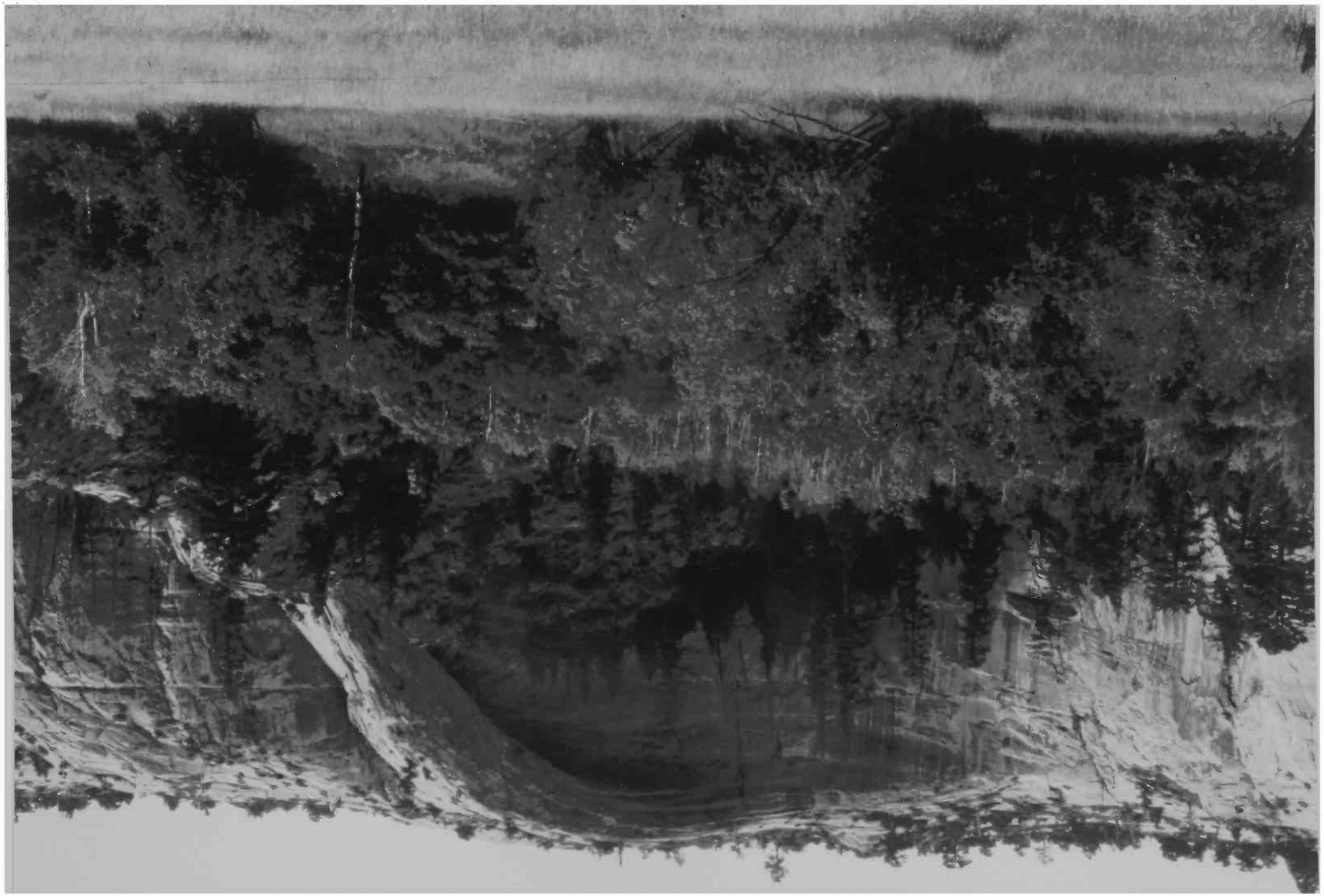


Table 3. Plant list from within 100 m of Allen Canyon Cave.

ACERACEAE
Acer glabrum Torr. - Rocky Mountain maple

AGAVACEAE
Yucca angustissima Engelm. - narrow leaf yucca

ANACARDIACEAE
Rhus radicans L. var. *rydbergii* (Small) - poison ivy
Rhus trilobata Nutt. - squawbush

BETULACEAE
Betula occidentalis Hook. - water birch

BORAGINACEAE
Cryptantha sp. - catseye
Hackelia pinetorum (Greene) Johnst. - stickseed

CACTACEAE
Opuntia polyacantha Haw. - Plains prickly pear

CAPRIFOLIACEAE
Sambucus sp. - elderberry

CELESTRACEAE
Pachystima myrsinites (Pursh) Raf. - mountain lover

CHENOPODIACEAE
Chenopodium sp. - goosefoot

COMPOSITAE
Antennaria sp. - pussytoes
Artemisia ludoviciana Nutt. - white sage
Aster sp. - aster
Brickellia grandiflora (Hook.) Nutt. - large-flowered thoroughwort
Chrysothamnus viscidiflorus (Hook.) Nutt. - rabbitbrush
Solidago missouriensis Nutt. - goldenrod
Tragopogon dubius - goatsbeard

CRUCIFERAE
Stanleya pinnata (Pursh) Britton - desert plume

CUPPRESSACEAE
Juniperus osteosperma (Torr.) Little - Utah juniper
Juniperus scopulorum Sarg. - Rocky Mountain juniper

ERICACEAE
Arctostaphylos uva-ursi (L.) Spreng. - kinnick-kinnick

Table 3 -- Continued

FAGACEAE
Quercus gambelii Nutt. - Gambel oak

GRAMINEAE
Festuca sp. - fescue
Muhlenbergia sp. - muhly

HYDROPHYLLACEAE
Phacelia sp. - phacelia

HYPNACEAE
Hypnum cuppressiforme Hedw. - moss

LESKEACEAE
Thuidium abietinum (Brid.) BSG - moss

LILIACEAE
Allium sp. - wild onion

ONAGRACEAE
Oenothera neomexicana (Small) Munz - evening primrose

PINACEAE
Pinus edulis Engelm. - Colorado pinyon
Pinus ponderosa var. scopulorum Engelm. - ponderosa pine
Pseudotsuga menziesii (Mirb.) Franco - Douglas fir

POLEMONIACEAE
Ipomopsis aggregata (Pursh) Spengl. - skyrocket

POLYPODIACEAE
Cheilanthes sp. - lipfern

ROSACEAE
Amelanchier utahensis Koehne - Utah serviceberry
Cercocarpus intricatus Wats. - little leaf mountain mahogany
Holodiscus dumosa (Nutt.) Heller - shrubby creambush
Prunus virginiana L. - western chokecherry
Rubus sp. - blackberry

SALICACEAE
Populus tremuloides Michx. - aspen

SAXIFRAGACEAE
Ribes aureum Pursh. - golden currant

Eight middens (a total of 16) were collected from 40 to 50 middens scattered on the floor and talus of each cave. All middens were briefly inspected and samples were collected to represent the total variability in plant macrofossil assemblages. Based on field examination of midden surfaces and preliminary lists of plant macrofossils, I anticipated that both sequences encompassed the interval from late Wisconsin to present. Table 4 lists the weight statistics for all middens, showing surprisingly little variation in the percentage of organic residue saved during washing or the concentration of fecal pellets per unit mass.

A total of 21 radiocarbon samples were used to determine the age of the 16 middens (Table 5). The material dated includes Douglas fir wood, needles, and buds, limber pine needles and seeds, Utah juniper twigs and seeds, and packrat pellets. At Fishmouth Cave, the midden sequence spans the interval from 12,770 to 2260 B.P. The Allen Canyon series encompasses the period from 11,310 to 1820 B.P. At both localities the oldest samples (greater than 9000 B.P.) were all found on the steep talus toward the front of the shelter. Younger middens are most common on roof fall and ledges deeper inside the shelter. This pattern is partly the result of natural exfoliation from the interior walls. As the back walls recede, old roof falls are buried by progressively younger ones. Outcrops of the oldest roof falls occur toward the front of the shelter. If a threshold slope has been reached on the steep talus, the downslope waste of the younger material may continue to expose the outcrop of older roof fall. The high incidence of rock slides may discourage packrats from occupying the front talus,

Table 4. Weight statistics of middens from Fishmouth Cave (FC) and Allen Canyon Cave (AC). -- All weights in grams.

Midden Number	Indurated Weight (i)	Washed Weight (w)	w/i (%)	Neotoma Pellets (p)	p/w (%)	Plant Matrix (w-p)
FC #1	993.6	162.5	16.35	75.6	46.52	86.9
FC #2*	-	178.00	-	163.3	58.74	114.7
FC #3	1312.6	236.8	18.04	112.4	47.47	124.4
FC #4	842.1	123.6	14.68	54.4	44.01	69.2
FC #5	842.1	182.9	21.72	70.2	38.38	112.7
FC #6	1181.2	201.6	17.07	51.4	25.50	150.2
FC #7	1125.8	247.0	21.94	103.1	41.74	143.9
FC #9	879.8	108.7	12.36	46.4	42.69	62.3
MEAN	1025.3	192.6	17.45	84.6	43.13	108.0
AC #1	916.1	166.6	18.19	72.5	43.51	94.1
AC #2	868.0	114.2	13.16	54.7	47.90	59.5
AC #4**	1951.7	98.7	5.06	32.4	34.58	66.3
AC #5	1105.6	110.6	10.00	39.7	35.90	70.9
AC #6	952.1	69.4	7.29	25.6	36.89	43.8
AC #7	1724.8	175.3	10.16	54.3	30.97	121.0
AC #8	1178.9	181.6	15.40	82.0	45.15	99.6
AC #9	1081.1	128.4	11.88	55.6	43.30	72.8
MEAN	1222.1	130.6	11.39	52.1	39.78	78.5

* Loose, unindurated deposit collected in niche created by boulders on talus slope.

** Uriniferous sample collected directly below ledge where modern packrats continue to perch today. Crystallized urine was denser than in the other samples from this locality.

Table 5. Radiocarbon dates on packrat (Neotoma) middens from Fishmouth (FC) and Allen Canyon (AC) caves, San Juan Co., Utah. -- All dates are calculated on the Libby half-life of 5568 years.

Midden	Age	Lab. No.	Material Dated
FC #1	12,770 ± 140	BETA-5582	Pinus flexilis needles and seeds
FC #2	10,360 ± 80	BETA-5761	Neotoma fecal pellets
FC #2	9340 ± 290	BETA-5762	Pseudotsuga menziesii needles, twigs, and buds
FE #3	10,540 ± 180	BETA-5757	"
FC #3	2790 ± 100	BETA-5758	Juniperus osteosperma twigs and seeds
FC #5	9700 ± 110	BETA-5763	"
FC #4	6100 ± 100	BETA-5759	"
FC #7	3740 ± 70	BETA-5584	"
FC #6	3550 ± 60	BETA-5764	"
FC #9	2260 ± 90	BETA-5765	"
AC #7	11,310 ± 200	BETA-5756	Pinus flexilis needles
AC #9	10,070 ± 70	BETA-5767	Neotoma fecal pellets
AC #1	10,030 ± 330	BETA-5760	Pseudotsuga menziesii needles, twigs, and buds
AC #1	9660 ± 140	BETA-5589	P. menziesii wood
AC #1	10,030 ± 200	DIC-2598	" (same branch as BETA-5589)
AC #8	10,140 ± 190	A-3120	Neotoma fecal pellets
AC #8	7530 ± 200	BETA-5588	Pseud otsuga menziesii needles, twigs, and buds
AC #2	7200 ± 90	BETA-5586	Neotoma fecal pellets

Table 5. -- Continued

AC #6	3400 ± 60	BETA-5583	"
AC #5	3000 ± 70	BETA-5585	"
AC #4	1820 ± 50	BETA-5766	"

forcing them to gentler grades toward the back and sides of the shelter.

Cole and Mayer (1982) discuss a similar pattern for caves in the Redwall Limestone of the eastern Grand Canyon, where the oldest middens are preserved nearest the cave entrances. Their model involves rapid retreat of the cliff face, rather than exfoliation of the interior walls, as influencing the age and spatial distribution of middens. The effect of roof falls as a burying agent may not apply in the relatively narrow caves of the Redwall Limestone. Increasing darkness with depth may be a deterrent to packrat activity beyond the entrance area in the Grand Canyon caves, so that midden preservation is affected mostly by cliff retreat and not by roof collapse.

Multiple dates were used to test the temporal integrity of four of the midden assemblages. The rationale for redating these assemblages is as follows.

FC #2 is the only loose, unindurated midden collected from either of the two localities. Because the macrofossils from FC #2 were not encased in hardened urine since the time of deposition, at least low levels of contamination were anticipated. Initial sorting of the midden revealed no anomalies. Nonetheless, we independently dated Douglas fir needles (9340 B.P.) and packrat fecal pellets (10,360 B.P.). These dates are within the 1,000 year uncertainty recommended by Klein et al. (1982) to account for cosmic ray flux in samples older than 8000 B. P. Based on the lack of Utah juniper in this sample, which first appears in FC #5 at 9700 B.P., FC #2 is assigned the older date of 10,360 $\pm$ 80 B.P.

FC #3 is an indurated midden which contains a mix of Utah and Rocky Mountain juniper associated with limber pine and Douglas fir. No other middens from this locality record these junipers. Older assemblages only have Rocky Mountain juniper, while samples younger than 9700 B.P. contain Utah juniper, which is at the site today and is the most likely candidate for contamination in older middens. While it is conceivable that FC #3 represents a time when both junipers grew at the site, independent dates on Douglas fir (10,540 $\pm$ 180 B.P.) and on Utah juniper (2790 $\pm$ 100 B.P.) failed to bear this out. Because of the great discrepancy between the two dates, this sample was excluded from further analysis.

AC #1 is an early Holocene assemblage, where I suspected no contamination but wished to test potential differences between dates from a single wood fragment and a composite sample of specimens from the same species, in this case Douglas fir. The two dates overlap at two standard deviations. An equal portion of the same Douglas fir branch was dated by a second C-14 facility with comparable results.

Redating of AC #8 was the most problematical. An initial date of 7350 $\pm$ 100 B.P. suggests that limber pine, spruce, and other montane elements persisted until the middle Holocene. Another midden (AC #2) nearby lacks these elements and records the arrival of several new taxa at 7200 $\pm$ 90 B.P. Two lines of reasoning suggest that the 7530 B.P. date is incorrect. Primarily, AC #8 is similar in macrofossil composition to AC #1 and AC #9, which dated at ca. 10,000 B.P. Also, the difference in assemblages between AC #8 and AC #2 is so great, yet the age differences so negligible, that these middens either mark an

abrupt vegetation change or one or both of the dates are incorrect. I chose to redate AC #8, anticipating a new date of ca 10,000 B.P. I accept the second date of 10,140 ± 190 B.P. and reject the first date of 7530 ± 200 B.P. To accept the latter would require explaining a 2,000 year lag time between similar vegetation changes at Fishmouth Cave and the Allen Canyon locality.

At both rockshelters, low levels of contamination were anticipated because middens spanning several millennia occur side by side across the large floor areas. Unindurated middens of considerable age (e.g., FC #2) provide loose plant material for construction of much younger houses. For this reason, traces of Douglas fir (1 or 2 needles) are likely contaminants in FC #6 and FC #9. The same might be true for the single limber pine needle in FC #4. At the Allen Canyon locality, a single limber pine needle was in AC #2 and is considered anomalous to the rest of the assemblage. A single Utah juniper twig in AC #9 may represent a younger contaminant.

Seven middens from Fishmouth Cave yielded a total of 67 taxa, with an average of 21 taxa per sample (Table 6). At the Allen Canyon locality, 73 taxa were identified from eight middens, with a mean of 25 taxa per sample (Table 7). The number of taxa per midden does not appear to be a function of sample size, at least not in a positive sense. The Spearman rank-difference correlation coefficient was computed for the paired observations of number of taxa and the mass of the plant matrix. Surprisingly, a high negative correlation (rho = -0.652) was obtained. Table 11 shows that the negative correlation arises from my inherent bias to collect larger samples from middens with extralocal

Table 6. Plant macrofossils and their relative abundances in fossil packrat middens from Fishmouth Cave, San Juan Co., Utah. -- 1 = Rare; 2 = Uncommon; 3 = Common; 4 = Very Common; 5 = Abundant; ? = Possible Contaminant.

Species	Common Name	12,770 ± 140 FC#1	10,360 ± 80 9380 ±290 FC#2	9700 ± 110 FC#5	6100 ± 100 FC#4	3740 ± 70 FC#7	3350 ± 60 FC#6	2260 ± 90 FC#9
TREES, SHRUBS AND SUCCULENTS								
cf. Alnus	alder			2				
Amelanchier utahensis	Utah serviceberry		4	2	2	2	2	2
Artemisia tridentata-type	sagebrush			3			2	
Atriplex canescens	fourwing saltbush			2	2		2	2
Atriplex sp. (not A. canescens)								3
Ceanothus cf. fendleri	buckbrush					1		
Celtis reticulata	netleaf hackberry			2				
Ceratoides lanata	winterfat				2		2	
Cercocarpus intricatus	littleleaf mountain mahogany			3	3	2	2	2
Cercocarpus montanus	alderleaf mountain mahogany	2	2					
Chrysothamnus sp.	rabbitbush	2						
Cornus stolonifera	red osier dogwood	4	1	1				
Coryphantha sp.								1
Cowania mexicana	cliffrose							3
Ephedra viridis	Mormon tea				3			
Ephedra sp.	Mormon tea	2		2		3	3	3
Fraxinus anomala	singleleaf ash						2	1
Gutierrezia sarothrae	snakeweed			1		1	2	3

Table 6 -- Continued

Species	Common Name	12,770 ± 140 FC#1	10,360 ± 80 9380 ±290 FC#2	9700 ± 110 FC#5	6100 ± 100 FC#4	3740 ± 70 FC#7	3350 ± 60 FC#6	2260 ± 90 FC#9
Juniperus communis	dwarf juniper	3						
Juniperus osteosperma	Utah juniper			5	5	5	5	5
Juniperus scopulorum	Rocky Mountain juniper	4	3					
Opuntia polyacantha	Plains prickly pear	2	3	3	3	2	2	3
Picea pungens	blue spruce	2						
Pinus edulis	Colorado pinyon					3		
Pinus flexilis	limber pine	5	3		1?			
Pseudotsuga menziesii	Douglas fir	5	5	3	3		1?	1?
Prunus sp.	chokecherry		1					
Purshia tridentata	bitterbrush							1
Quercus gambelii	Gambel oak		4	2	2			
Rhus trilobata	squawbush		2	1	3	2	3	2
Rosa woodsii	rose	2						
Shepherdia rotundifolia	buffaloberry							1
Sclerocactus sp.	sclerocactus				1			
Yucca angustissima	narrowleaf yucca	1		3	1	2	2	
HERBS								
Artemisia ludoviciana	white sage	1	2	2				2
Astragalus	milkvetch	1						
Brickellia sp.	brickellbush				1			2

Table 6 -- Continued

Species	Common Name	12,770 ± 140 FC#1	10,360 ± 80 9380 ± 290 FC#2	9700 ± 110 FC#5	6100 ± 100 FC#4	3740 ± 70 FC#7	3350 ± 60 FC#6	2260 ± 90 FC#9
Chenopodium sp.	goosefoot		2					
Cirsium sp.	thistle	2						
Cryptantha sp.	catseye					1		2
Euphorbia sp.	spurge			1		1		
Helianthus sp.	sunflower	2		2	2			2
Heterotheca villosa	golden aster					2		
cf. *Hymenoxys*	hymenoxys							1
cf. *Ipomopsis*	gilia	1		1				1
Lappula redowskii	stickseed	1						1
Lepidium sp.	peppergrass				1			2
Plantago sp.	Indian plantain			1				
Polygonum sp.	knotweed	1						
Sphaeralcea sp.	globemallow		1					
Thuidium abietinum	moss					1		
GRASSES								
Agropyron sp.	wheatgrass			1				
Agropyron cf. *smithii*	wheatgrass							1
Andropogon scoparius	little bluestem					1		
Bouteloua barbata	sixweeks grama				1		1	
Bouteloua curtipendula	sideoats grama			1				1

Table 6 -- Continued

Species	Common Name	12,770 ± 140 FC#1	10,360 ± 80 9380 ± 290 FC#2	9700 ± 110 FC#5	6100 ± 100 FC#4	3740 ± 70 FC#7	3350 ± 60 FC#6	2260 ± 90 FC#9
Echinochloa crusgallii	barnyard grass				1			
Enneapogon desvauxii	spike pappusgrass						1	
Festuca ovina	fescue			1			1	1
Hilaria jamesii	galleta				1	1		
Hordeum cf. pusillum	little barley							1
Koehleria cristata	crested wheatgrass							1
Muhlenbergia cf. pungens	pungent muhly						1	
Munroa squarrosa	false buffalograss							1
Oryzopsis hymenoides	Indian ricegrass	2			4	3	3	1
Poa cf. fendleriana	muttongrass			2			2	1
Number of taxa (N) = 67		N=20	N=13	N=24	N=20	N=16	N=20	N=32

Table 7. Plant macrofossils and their relative abundances in fossil packrat middens from Allen Canyon Cave, San Juan Co., Utah. -- 1 = Rare; 2 = Uncommon; 3 = Common; 4 = Very Common; 5 = Abundant; ? = Possible Contaminant.

Species	Common Name	11,310 ± 200 AC#7	10,140 ± 190 AC#8	10,070 ± 70 AC#9	10,030 ± 200 10,030 ± 330 9660 ± 140 AC#1	7200 ± 90 AC#2	3400 ± 60 AC#6	3000 ± 70 AC#5	1820 ± 50 AC#4
TREES, SHRUBS AND SUCCULENTS									
Abies lasiocarpa	subalpine fir	4	1		2				
Acer glabrum	Rocky Mountain maple	2	2	1	2	1			
Amelanchier utahensis	Utah serviceberry	1	2	1		2	2	2	2
Arctostaphylos cf. uva-ursi	kinnick-kinnick			1			2	2	2
Cercocarpus montanus	alderleaf mountain mahogany								1
Cercocarpus intricatus	littleleaf mountain mahogany				1	2	2	2	3
Cornus stolonifera	red osier dogwood	2	2	2	2	2	1		2
Coryphantha sp.	coryphantha			3					
Gutierrezia sarothrae	snakeweed						1		
Juniperus communis	dwarf juniper	4	2		3	3	2		
Juniperus osteosperma	Utah juniper				1?	2	3	3	2
Juniperus scopulorum	Rocky Mountain juniper					2	1	2	
Opuntia polyacantha	Plains prickly pear						1	3	3
Pachystima myrsinites	boxleaf	2	2	3	2	2	2	3	
Picea engelmannii	Englemann spruce	5		2					

Table 7 -- Continued

Species	Common Name	11,310 ± 200 AC#7	10,140 ± 190 AC#8	10,070 ± 70 AC#9	10,030 ± 200 10,030 ± 330 9660 ± 140 AC#1	7200 ± 90 AC#2	3400 ± 60 AC#6	3000 ± 70 AC#5	1820 ± 50 AC#4
Picea pungens	blue spruce		2		2				
Pinus edulis	Colorado pinyon						5	5	4
Pinus flexilis	limber pine	5	4	3	4	1?			
Pinus ponderosa	ponderosa pine		1	2	1	5	2	2	2
Prunus sp.	chokecherry							1	
Pseudotsuga menziesii	Douglas fir	2	5	5	5	4	4	4	4
Purshia tridentata	bitterbrush			1				2	
Quercus gambelii	Gambel oak		1			2	1	2	1
Rhus radicans	poison ivy					1		1	
Rhus trilobata	squawbush					2	2	2	
Rosa sp.	rose			1		1			
Rosa woodsii	rose	2	2		2				
Rosa cf. nutkana	rose			1					
Rubus sp.	blackberry	3	2	2	2	2		1	
Sambucus racemosa	elderberry	2		2	1				
Shepherdia canadensis	russet buffaloberry	3	3	3	3				
Yucca angustissima	narrowleaf yucca						2	1	1
HERBS AND MOSSES									
Amaranthus sp.	pigweed							1	1

Table 7 -- Continued

Species	Common Name	11,310 ± 200 AC#7	10,140 ± 190 AC#8	10,070 ± 70 AC#9	10,030 ± 200 10,030 ± 330 9660 ± 140 AC#1	7200 ± 90 AC#2	3400 ± 60 AC#6	3000 ± 70 AC#5	1820 ± 50 AC#4
Antennaria sp.	pussytoes					2			
Artemisia frigida	estafiata							2	
Artemisia ludiviciana	Mexican sage						1	2	
Aster sp.	aster		1	1					1
Centaurea sp.	starthistle					3			
Cirsium sp.	thistle			1					
Clematis sp.	virgin's bower					1			
Cryptantha sp.	catseye					1	2	1	
Eriogonum sp.	wild buckwheat					1			
Equisetum hyemale	scouring rush				1				
cf. Helenium	sneezeweed								1
Helianthus sp.	sunflower						1	1	
Heterotheca sp.	golden aster	2	1	1		1	2	1	1
Hypnum cupressiforme	moss	1	1			1		1	
Lithospermum sp.	stoneseed					1	1		2
Lupinus sp.	lupine						2		
Physalis sp.	groundcherry								2
Polygonum sp.	knotweed	2	2	1				1	1
Potentilla sp.	cinquefoil	1							
Ranunculus sp.	buttercup					2	2		2

Table 7 -- Continued

Species	Common Name	11,310 ± 200 AC#7	10,140 ± 190 AC#8	10,070 ± 70 AC#9	10,030 ± 200 10,030 ± 330 9660 ± 140 AC#1	7200 ± 90 AC#2	3400 ± 60 AC#6	3000 ± 70 AC#5	1820 ± 50 AC#4
Selaginella sp.	selaginella						1	1	
Thalictrum fendleri	meadowrue	2	1						
Thuidium abietinum	moss	1					1	1	
GRASSES									
Agropyron sp.	wheatgrass							1	1
Agropyron cf. smithii	wheatgrass	1							
Brachiaria arizonicum	brachiaria					1			
Bromus anomalus	nodding brome	1	1						
Bouteloua gracilis	blue grama			1		1			
Deschampsia caespitosa	tufted hairgrass	1		2					
Festuca ovina	sheep fescue	1							
Hilaria jamesii	galleta						1		
Koeleria cristata	crested wheatgrass	2						2	1
Muhlenbergia sp.	muhly			1					
Muhlenbergia arsenei	muhly							1	
Oryzopsis hymenoides	Indian ricegrass						1	2	2
Panicum sp.	panic grass			1		1			

Table 7 -- Continued

Species	Common Name	11,310 ± 200 AC#7	10,140 ± 190 AC#8	10,070 ± 70 AC#9	10,030 ± 200 10,030 ± 330 9660 ± 140 AC#1	7200 ± 90 AC#2	3400 ± 60 AC#6	3000 ± 70 AC#5	1820 ± 50 AC#4
Poa cf. fendleriana	muttongrass	2	1			3	1	2	2
Sitanion-type	squirreltail					1			
Stipa comata	needle and thread grass								1
Trisetum spicatum	spike trisetum	1							
Total number of taxa (N) = 73		26	22	23	16	30	27	33	25

plants combined with a tendency for the oldest samples to yield low numbers of taxa. In the time series for the Allen Canyon locality, a strong trend emerges when the ratios for number of taxa to mass of the plant matrix are compared (Table 8). In the four oldest samples (late Pleistocene-early Holocene), this ratio ranges from 0.17 to 0.32. In the youngest four samples (mid to late Holocene), the values range from 0.38 to 0.62. This trend is not apparent at Fishmouth Cave.

At Allen Canyon one is tempted to infer an increase for species diversity in the plant community during the middle and late Holocene. Species diversity in modern subalpine communities (late Pleistocene and early Holocene assemblages) is generally lower than for pinyon-juniper woodland or stands of Douglas fir-ponderosa pine (middle and late Holocene assemblages from). This observation is substantiated for modern vegetation on the northern Colorado Front Range (Peet, 1978; Figs. 1 and 4). Other explanations might be equally viable and would only demonstrate the difficulty in interpreting the number of taxa identified from packrat middens. Particularly relevant is the notion that the number of taxa is also a function of my own ability to identify plant parts. Greater familiarity with understory plants in pinyon-juniper woodland than in subalpine forest might produce a pattern similar to that noted for the Allen Canyon sequence.

A total of 106 plant taxa were identified from the fifteen middens reported in Tables 6 and 7. Of these, 34 are shared by both the Fishmouth Cave and Allen Canyon sequences. In the majority of cases positive identification was accomplished by matching the macrofossil to modern voucher specimens at the Laboratory of Paleoenviron-

Table 8. Comparisons of number of taxa (N) to plant matrix (w-p) in fossil packrat middens from Fishmouth Cave (FC) and Allen Canyon Cave (AC), southeastern Utah.

Midden	Age	N	w-p (g)	$\frac{N}{w\text{-}p}$
FC #1	12,770 ± 140	20	86.9	0.23
FC #2	10,360 ± 80 9380 ± 290	13	114.7	0.11
FC #5	9700 ± 110	24	112.7	0.21
FC #4	6100 ± 100	20	69.2	0.29
FC #7	3740 ± 70	16	143.9	0.11
FC #6	3550 ± 60	20	150.2	0.13
FC #9	2260 ± 90	32	62.3	0.51
AC #7	11,130 ± 200	26	121.0	0.21
AC #8	10,140 ± 190	22	99.6	0.22
AC #9	10,070 ± 70	23	72.8	0.32
AC #1	10,030 ± 200 10,030 ± 330 9600 ± 140	16	94.1	0.17
AC #2	7200 ± 0	30	59.5	0.50
AC #6	3400 ± 60	27	43.8	0.62
AC #5	3000 ± 70	33	70.9	0.47
AC #4	1820 ± 50	25	66.3	0.38

mental Studies and the Herbarium, University of Arizona. I was unable to identify a number of macrofossils from each midden. Some of these are distinctive and may be identified in the course of future work.

Separations within a few genera require further explanation. Blue spruce (Picea pungens) and Engelmann spruce (P. engelmannii) can be separated on the internal anatomy of the needles. Needles from each midden were immersed in water for about 1 week to soften. Thin sections were prepared, mounted on slides, and viewed through a compound microscope at various magnification. All spruce needles from the two sequences can be relegated to either blue or Engelmann spruce. They are separated from other species by the 4-angled or square cross-sections of the needles, and the presence and position of the resin ducts (Durrell, 1916). The two species were further distinguished on the relative size and position of the resin ducts. Blue spruce has relatively small resin ducts (less than one-fourth the size of the vascular bundle) touching the epidermis at the lateral angles. Engelmann spruce has large resin canals (greater than half and up to three-fourths the size of the vascular bundle) touching the epidermis at the sides. The distinction is important in comparing Fishmouth Cave (blue spruce only) with Allen Canyon (both), or the late Pleistocene (Engelmann spruce only) to the early Holocene (both) at Allen Canyon.

Three species of junipers (Juniperus communis, J. scopulorum, and J. osteosperma) are present in both midden sequences. Dwarf juniper, a circumpolar species that occurs in subalpine forests of the Abajo and La Sal Mountains, is the easiest to identify. The most common macrofossils are the broad, needle-like leaves or scales, often

twisted so that the dorsal surface bears a white band of stomata. Scale-like leaves of Rocky Mountain juniper and Utah pine are separated on the presence of minute teeth along the scale margins in Utah juniper and the presence of an elliptic resin gland on the dorsal surface of Rocky Mountain juniper scales. The gland in Utah juniper scales is deeply embedded in the mesophyll and is seldom visible on the surface (Vasek, 1966). Some difficulty may arise in distinguishing Utah juniper from its close relative, one-seed juniper (J. monosperma), which also has denticulate margins on the scales. However, the resin gland is often visible in one-seed juniper scales.

Fir (Abies) is represented in the Allen Canyon sequence by alpine fir. Alpine fir can be distinguished from white fir on the basis of external morphology of the needles. Alpine fir has relatively short needles (less than 3 cm) with a retuse or notched tip, while white fir has longer needles (greater than 3 cm) with rounded to acute tips. Although it was not necessary to cross-section the needles, the position of the resin ducts may be the most reliable way to tell the two species apart. In white fir, the resin ducts are external (located contiguous to the epidermis), while in alpine fir they occur in the area of the mesophyll away from the epidermis (Durrell, 1916).

The needles of ponderosa and limber pine were identified on the basis of external morphology. The strong serrations on needles originating from fascicles of three are diagnostic of ponderosa pine. AC #1, AC #9 and AC #2 produced strongly serrated needles from fascicles of two that could be referrable to lodgepole (P. contorta) or ponderosa pine on the basis of external morphology (W. B. Critchfield,

pers. comm.). However, in all three samples these specimens are clearly outnumbered by needles from fascicles of three. The Rocky Mountain race of ponderosa pine (P. ponderosa var. scopulorum) occasionally produces fascicles of two, whereas fascicles of three in lodgepole pine are known only at its northernmost stations in the Yukon (Critchfield, 1980). We thus refer all the strongly serrated needles in the middens to ponderosa pine.

Needles lacking strong serrations on the margins and originating from fascicles of five are identified as limber pine. They are distinguished from the bristlecone pines (P. longaeva and P. aristata) by having both dorsal and ventral stomata (bristlecone pine needles lack dorsal stomata) and needle length (less than 4 cm, for bristlecone and from 4 to 10 cm for limber pine) (Harlow, 1931). There is greater difficulty in separating needles of limber pine from its close relative, southwestern white pine (P. strobiformis). Southwestern white pine has discernible serrations (but weak, compared to ponderosa pine) and dorsal stomata limited to one or a few partial rows. Limber pine lacks serrations, or they are minute and sparse, and two or more rows of stomata are present on the dorsal surface of the needles (Steinhoff and Andersen, 1971). A few of the needles in the Allen Canyon series resemble Southwestern white pine, yet the nearest stands are in the Sangre de Cristo Mountains of northern New Mexico and the White Mountains of east-central Arizona. All the needles from the Fishmouth Cave and Allen Canyon series are assigned here to limber pine, which occurs today in the Abajo Mountains.

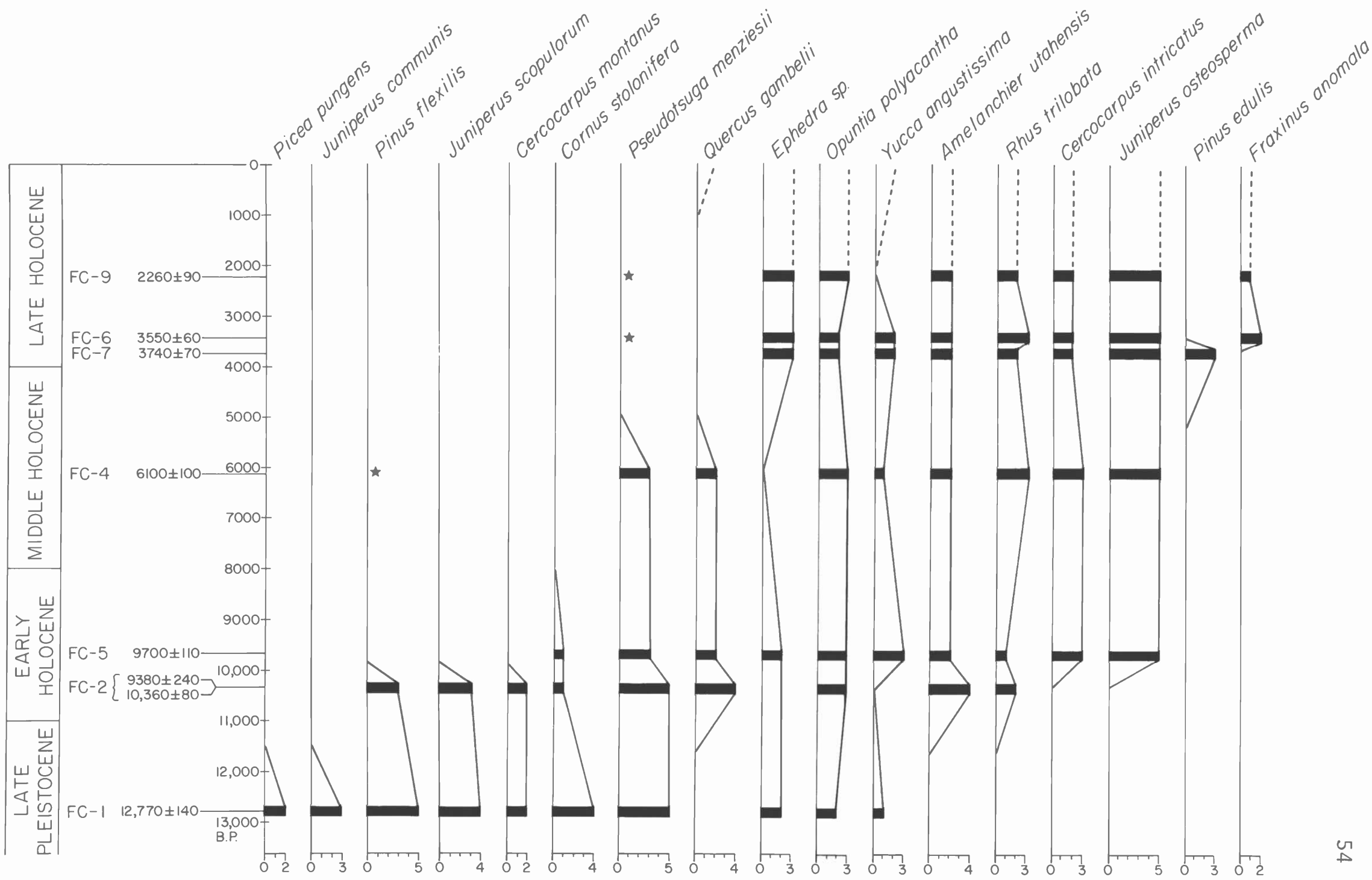
Fishmouth Cave Sequence

The sequence for Fishmouth Cave (Fig. 5) spans vegetation changes from assemblages dominated by limber pine and Douglas fir (latest Pleistocene) to modern ones dominated by Utah juniper (see Table 12). FC #1, dated at 12,770 B.P., is the single Pleistocene midden from this locality. Trees and shrubs abundantly represented from this sample include Pinus flexilis, Pseudotsuga menziesii, Cornus stolonifera, Juniperus communis, J. scopulorum, Cercocarpus montanus, and Rosa woodsii. None of these are at the site today and the assemblage does not occur locally at elevations lower than 2438 m, representing a minimum displacement of ca. 850 m. Three of the plants with relatively stable records from latest Pleistocene to the present are Ephedra sp., Opuntia polyacantha, and Yucca angustissima.

Two early Holocene middens (FC #2 and FC #5) from Fishmouth Cave record vegetation changes during the Pleistocene-Holocene transition. No longer at the site are Picea pungens, Juniperus communis, and Rosa woodsii. The older sample (FC #2) resembles the late Pleistocene midden in that it contains Pinus flexilis, Juniperus scopulorum, and Cercocarpus montanus. The younger midden (FC #5) may signal the initial development of modern vegetation; it lacks Pinus flexilis, Juniperus scopulorum, and Cercocarpus montanus and is in turn dominated by Juniperus osteosperma. Dated at 9700 B.P., FC #5 may represent the first arrival of J. osteosperma in the area of Fishmouth Cave. Macrofossils of Quercus gambelii were found only in the two early Holocene middens and a middle Holocene sample (FC #4). A marked decrease in Pseudotsuga menziesii is noted from FC #1 to FC #4 (Table

Figure 5. Seriated chronosequence of select plant macrofossils and their relative abundances in fossil packrat middens from Fishmouth Cave, San Juan County, Utah. -- Sample points are joined by a straight line not to imply a continuous stratigraphic record, but to accentuate differences between samples. Asterisks indicate probable contaminants.

FISHMOUTH CAVE, SAN JUAN CO., UTAH
37°25'45" N, 109° 39' W
ELEV. 1585 m (5200 ft)



9). Aside from Quercus gambelii and Juniperus osteosperma, plants that first appear in the early Holocene include Amelanchier utahensis, Rhus trilobata, and Cercocarpus intricatus. The latter three species have relatively stable records for the rest of the Holocene.

The middle and late Holocene middens from Fishmouth Cave approximate the modern flora with a few notable exceptions. The middle Holocene sample differs from the late Holocene in that it contains Pseudotsuga menziesii and Quercus gambelii. Single needles of Pseudotsuga in FC #6 and FC #7 are probable contaminants from older middens. Quercus gambelii occurs today as a riparian tree in the ravine in front of the shelter, but beyond the collecting range of packrats. During the early and middle Holocene, Gambel oak probably grew on the exposed slope immediately in front of the shelter.

The two oldest late Holocene middens (FC #7 and FC #6) are characterized by high percentages of juniper macrofossils, at least double what they are in other middens from Fishmouth Cave (Table 9). This may reflect a local increase in the density of junipers. The only record of pinyon (Pinus edulis), which is not at the site today, is FC #7 (3740 B.P.). This record may reflect limited expansion of pinyon south along Comb Ridge, at a time when the density of junipers is also increasing in the immediate vicinity of Fishmouth Cave.

The youngest sample from Fishmouth Cave (FC #9; 2260 B.P.) is peculiar for a number of reasons. The greatest number of taxa from Fishmouth Cave is recorded in this midden (N = 32). One of the dominants, Cowania mexicana, appears in no other sample. FC #9 also contains the only records of Shepherdia rotundifolia and Purshia

Table 9. Weight percentages for select plant taxa in fossil packrat middens from Fishmouth Cave (FC) and Allen Canyon Cave (AC), San Juan Co., Utah. -- Weight percentages obtained by dividing the total weight of macrofossils from one species by the total weight of the plant matrix in the midden (see Table 3), and then multiplying by 10. T = Trace Fossils, one or two items of insufficient weight, possible contaminants.

Fishmouth Cave	12,770 ± 140 FC #1	10,360 ± 80 9,380 ± 290 FC #2	9700 ± 110 FC #5	6100 ± 100 FC #4	3740 ± 70 FC #7	3550 ± 60 FC #6	2260 ± 90 FC #9
Pinus edulis					0.16		
Opuntia polyacantha	0.16	0.40	1.15	0.31	0.13	0.21	0.99
Juniperus osteosperma			8.47	12.19	21.49	26.49	7.81
Quercus gambelii		0.47	T	0.89			
Pseudotsuga menziesii	10.24	7.20	1.11	0.50		T	T
Pinus flexilis	12.38	0.50		T			
Juniperus scopulorum	0.28	2.10					
Juniperus communis	0.48						

Allen Canyon Cave	11,130 ± 200 AC#7	10,140 ± 190 AC#8	10,070 ± 70 AC#9	10,030 ± 200 10,030 ± 330 9600 ± 140 AC#1	7200 ± 90 AC#2	3400 ± 60 AC#6	3000 ± 70 AC#5	1820 ± 50 AC#4
Opuntia polyacantha						T	0.33	0.31
Pinus edulis						5.34	3.25	2.11
Juniperus osteosperma				T	0.19	2.23	1.53	0.12
Pinus ponderosa		T	0.22	T	5.04	0.06	0.14	0.06
Pseudotsuga menziesii	0.14	3.49	1.54	6.05	1.98	1.43	1.18	1.87
Juniperus communis	1.00	0.02		0.25	0.20	0.11		
Pinus flexilis	4.49	2.30	1.27	1.79	T			
Picea sp.	5.61	0.09	0.16	0.09				
Abies lasiocarpa	1.98	T		0.03				

tridentata. The weight percentages for Juniperus osteosperma and Opuntia polyacantha closely resemble those for FC #5 (9700 B.P.).

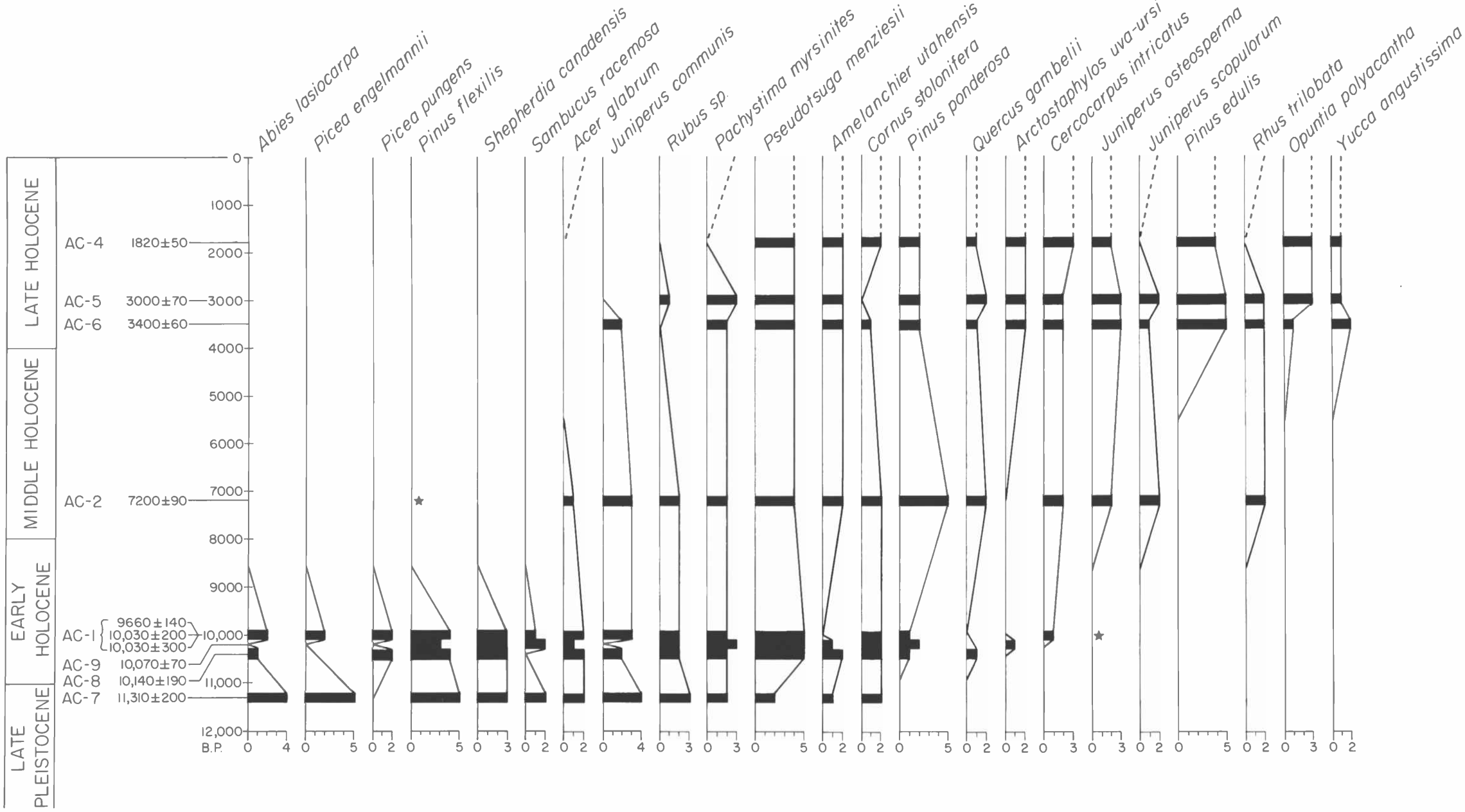
Allen Canyon Cave Sequence

The rich macrofossil record from Allen Canyon Cave (Fig. 6) spans the last 11,300 years, with the vegetation at the site ranging from spruce-fir forest to stands dominated by Pseudotsuga menziesii, Pinus ponderosa, and Pinus edulis. A number of plants appear throughout the entire sequence. These include Pseudotsuga menziesii, Pachystima myrsinites, Amelanchier utahensis, and Cornus stolonifera. Two mosses, Hypnum cupressiforme and Thuidium abietinum occur sporadically throughout the sequence starting with the oldest sample. Both mosses, which have very large ecological amplitudes (Haring, 1961), grow directly in front of the shelter today. The Allen Canyon sequence is characterized by major and rapid change in the overstory and remarkable stability in the understory of the cliffside communities.

The latest Pleistocene sample (AC #7: 11,310 B.P.) is dominated by Picea engelmannii, Pinus flexilis, Abies lasiocarpa, and Juniperus communis. Pseudotsuga menziesii is a relatively unimportant plant in this assemblage (Table 9). This sample also contains a few specimens of Bromus anomalus, Trisetum spicatum, and Deschampsia caespitosa, which are common grasses in subalpine to alpine meadows. The assemblage from AC #7 suggests a modern analog at ca. 2896 m at the lower limits of engelmann spruce-alpine fir forest.

Figure 6. Seriated chronosequence of select plant macrofossils and their relative abundances in fossil packrat middens from Allen Canyon, San Juan County, Utah. -- Sample points are joined by a straight line not to imply a continuous stratigraphic record, but to accentuate differences between samples. Asterisks indicate probable contaminants.

ALLEN CANYON CAVE, SAN JUAN CO., UTAH
37°47'30" N, 109°35'30" W
ELEV. 2195 m (7200 ft)



The three early Holocene middens (AC #8, AC #9, AC #1) were all dated at ca. 10,000 B.P. and record significant changes from the late Pleistocene. Table 12 shows an enormous reduction in the weight percentages for Picea spp., Abies lasiocarpa, and Juniperus communis. Pinus flexilis also decreases by a factor of three whereas there is a 10- to 40-fold increase in the abundance of Pseudotsuga menziesii. One of the more interesting developments is the replacement of Picea engelmannii by the lower elevation P. pungens, indicating an upward shift in vegetation zones. Shepherdia canadensis, Acer glabrum, and Sambucus racemosa retain their importance from the late Pleistocene. Significant new arrivals include Pinus ponderosa, Quercus gambelii, and Cercocarpus intricatus. A single Juniperus osteosperma twig in AC #1 may be a contaminant from younger material in the shelter. With a few exceptions, the early Holocene assemblages from the Allen Canyon locality resemble the late Wisconsin midden from Fishmouth Cave. Differences include the presence of Ephedra sp., Yucca angustissima, and Opuntia polyacantha at the lower site, and the richer assemblage of understory shrubs (Shepherdia canadensis, Acer glabrum, Pachystima myrsinites, and Rubus sp.) at the higher site.

The single middle Holocene sample (AC #2) indicates a major turnover in the local flora between 10,000 and 7200 B.P. Judging from the chronology at Fishmouth Cave, this change may have happened between 9000 and 10,000 B.P. Plants that drop out of the record completely include Abies lasiocarpa, Picea spp., Pinus flexilis (see comments below), Shepherdia canadensis, and Sambucus racemosa. The single Pinus flexilis needle may be a contaminant from an early Holocene midden (AC

#1) just a few meters away on the floor of the shelter. New arrivals at Allen Canyon Cave are Juniperus osteosperma, J. scopulorum, and Rhus trilobata. Surprisingly, the dominant in the late Holocene middens, Pinus edulis, is absent from AC #2. Instead, this midden contains from 20 to 40 times as much P. ponderosa as any of the early and late Holocene middens (Table 12).

Three middens (AC #6, 3400 B.P.; AC #5, 300 B.P.; and AC #4, 1820 B.P.) record the mmodernization of the local flora. Between 7200 and 3400 B.P., Acer glabrum drops out of the sequence. It occurs today alongside Populus tremuloides in the steep drainage just below the shelter. Probably within the last few millennia, this drainage eroded upstream, leaving the shelter perched 50 m above moist, riparian habitats where Acer glabrum thrives. The increased vertical distance from the mouth of the shelter to the steep headcut may explain the absence of Acer glabrum in the latter part of the sequence. Records for Juniperus communis, J. scopulorum, and J. osteosperma are quite variable during the late Holocene. All three occur in the oldest of the three middens (AC #6). J. communis is missing from the two youngest middens (AC #5 and AC #4), which contain both J. scopulorum and J. osteosperma. The most recent sample only has J. osteosperma. New plants that arrive in the late Holocene include Pinus edulis, Opuntia polyacantha, Yucca angustissima, and Oryzopsis hymenoides. The appearance of these plants in the Allen Canyon sequence may signal the middle Holocene expansion of xeric woodlands at higher elevations.

BIOGEOGRAPHIC AND PALEOCLIMATIC CONSIDERATIONS

A relatively high number of endemic plants (70) has been reported for the Colorado Plateaus (Welsh, 1978). According to Reveal (1979), this is the result of historical stability and isolation due to imposing physiographic barriers of mountains and high plateaus. Two corridors that may have permitted plant migration are the relatively low divide between the San Juan and Rio Grande Rivers and the Dixie Corridor between the Grand Canyon and the Utah Plateaus. Reveal (1979) believes that in the Great Basin, Pleistocene compression of low vegetation zones between the base of the mountains and pluvial lakes on the valley floors extirpated many low-elevation plants. Holocene retreat of the shorelines of the Holocene exposed large areas for plant colonization, particularly by halophytes. Because there were no large pluvial lakes on the Colorado Plateaus, Reveal (1979) maintains that the existing vegetation was not significantly pushed out of the area during the Pleistocene.

There are several problems with Reveal's interpretation for the high number of endemics on the Colorado Plateaus. I have already demonstrated a minimum lowering of 700-850 m for subalpine trees along the Abajo Mountains-Comb Ridge gradient. Late Pleistocene records of Picea pungens, Pinus flexilis, and Juniperus communis down to 1585 m suggest that both the pinyon-juniper woodland and the modern desert-scrub zones were displaced far to the south and west. I seriously

doubt that either zone existed upstream of the confluence (1040 m) of the San Juan and Colorado Rivers. The high number of endemic species of milkvetches (Astragalus sp.), mostly from low elevations, gives the appearance that the majority of endemic plants are today restricted to desert elevations. However, almost half of the endemics on the Colorado Plateau now occur above 1980 m. The decrease in area with elevation translates into a greater density of endemics at higher than lower elevations (Welsh, 1978). Pleistocene lowering of montane communities probably increased the area occupied by these higher-elevation endemics. Elevations above 2130 m, mostly clad in spruce-fir forest and alpine tundra, would have served as effective bariers to the migration of plants now occurring at intermediate elevations. In southeastern Utah, many of today's low-elevation endemics probably grew alongside subalpine and montane conifers, or in Artemisia steppe, during the late Wisconsin. Postglacial competition with new arrivals better adapted to xeric conditions may have forced endemics either upslope or to poorer substrates (e.g., Mancos Shale) where competition is less intense.

Similar lowering of vegetation zones has been documented elsewhere on the Colorado Plateaus. At Cowboy Cave (1770 m) in nearby Wayne County, cave sediments dated to between 11,000 and 13,000 B.P. yielded macrofossils of both Picea pungens and P. engelmannii (Spaulding and Peterson, 1980; species determination by O. K. Davis). During the full-glacial period (21,000-15,000 B.P.) in the eastern Grand Canyon, several conifers, including Pseudotsuga menziesii, Juniperus communis, Abies concolor, Picea engelmannii, and Pinus

flexilis expanded 600-1000 m below their modern ranges (Cole, 1982). At 1700 m in Canyon de Chelly, northeastern Arizona, a packrat midden dated at 11,900 B.P. contains *Picea pungens*, *Pinus flexilis*, *Juniperus communis*, and *Pseudotsuga menziesii* (Betancourt and Davis, in press). *Pinus flexilis* no longer occurs in the nearby Chuska Mountains, which rise just slightly above 2740 m.

Depression of these montane and subalpine elements resulted from relaxation of the limiting factors in effect at their lowest elevations, mainly drought and possibly competition. At the lower limits of a plant, high temperatures and deficient soil moisture produce transpirational stress for established individuals and reduce the potential for germination and seedling establishment. Relaxation of these controls can be accomplished most readily by lowering summer temperatures and/or increasing precipitation for critical times of the year. Table 10 compares modern climates at Fishmouth and Allen Canyon caves with climates for their late Wisconsin analogs at higher elevations. The reconstructed values for the elevations of the caves (1585 m and 2195 m) are probably reasonable estimates. Because the regressions (Fig. 1) include only stations below 2080 m, predicted climates for higher elevations should be taken as minimum estimates based on unusually low vertical lapse rates. Using these conservatively low rates, calculations based on elevational analogs represent roughly 35 to 60 percent more rainfall than today. For comparison, I recalculated the precipitation-elevation regressions to include data from Camp Jackson (2804 m), Buckboard Flats (2865 m), and La Sal Mountains (2865 m). Application of the higher lapse rates

Table 10. Precipitation and temperature predicted from elevations of Fishmouth Cave, Allen Canyon Cave, and the modern elevational analogs for late Wisconsin midden assemblages at the two sites. -- Linear regression equations used to calculate these values are presented in Figure 2. The elevational analog approach ignores possible shifts in the seasonal distribution of rainfall. Such shifts may in effect alter environmental lapse rates. Annual means are for the hydrological year (October-September) with winter means from October to March and summer from April to September.

	Fishmouth Cave	Modern analog for FC #1	Percent Increase in ppn or Cooling in ^{o}C	Allen Canyon Cave	Modern Analog for AC #7	Percent Increase in ppn or Cooling in ^{o}C
Elevation (m)	1585	2438	--	2195	2896	--
Winter ppn (mm)	124	201	62%	179	242	35%
Summer ppn (mm)	108	176	62%	157	212	35%
Annual ppn (mm)	232	377	62%	336	452	35%
Winter T (^{o}C)	3	0	$3^{o}C$	1	-1	$2^{o}C$
Summer T (^{o}C)	19	14	$5^{o}C$	15	11	$4^{o}C$
Annual T (^{o}C)	11	7	$4^{o}C$	8	5	$3^{o}C$

suggests a 50 to 120 percent increase over modern rainfall. The difference between the predictions for Allen Canyon Cave as opposed to Fishmouth Cave does not necessarily imply that rainfall increased more at lower than at higher elevations. I posit that the lower limits of engelmann spruce-alpine fire were in Cottonwood Wash down to 1830 m (a 60 percent increase using the lower lapse rates).

Seasonal lapse rates (and thus annual lapse rates) may be quite different today than during the late Wisconsin. For the middle Holocene, Davis et al. (1980) incurred a change in seasonal lapse rates to explain unequal displacement of spruce and fir in the White Mountains of New Hampshire. Most reconstructions of late Pleistocene climate in the western United States call for increases in winter rainfall (Van Devender and Spaulding, 1979; Spaulding et al., in press). Though not yet demonstrated with historical data, the steeper lapse rates probably occur in winter when snowfall is disproportionately high at upper elevations. Judging from the absence of plants that respond primarily to summer moisture, late Wisconsin summers might have been much drier than today. Hence, the seasonal breakdown of predicted values in Table 10 should be taken as a first approximation that considers the seasonal relation of precipitation with temperature in respect to effective moisture at the various elevations. This analog approach suggests a $4^{o}C$ cooling of mean annual temperatures during the late Wisconsin at Fishmouth Cave and a lesser $3^{o}C$ lowering for the Allen Canyon locality. The more significant differences are in summer temperatures ($4-5^{o}C$) as opposed to winter ($1-2^{o}C$). At Fishmouth Cave, the presence of Opuntia polyacantha and Yucca angustissima in the late Wisconsin assemblage

suggests that the winters were moderate. Neither occurs today above 2740 m in the Abajo Mountains or other local ranges. Also, neither species appears in the Allen Canyon sequence until 3400 B.P. If we can assume that Opuntia polyacantha and Yuca angustissima are rare where mean annual temperature dips below 6°C, the estimated value for 2740 m, it is unlikely that annual temperatures were lowered by much more than 5°C. A regional cooling greater than this (with little or no increase in rainfall) is proposed by several authors to explain Wisconsin depressions of 1000 m for orographic snowline, cryogenic deposits, and timberlines (Brakenridge, 1978; Galloway, 1970).

There are several pitfalls to the elevational analog approach. By definition, a depression in vegetation zones implies both increases in precipitation and decreases in temperature. Theoretically, observed depressions can be explained through increases in effective soil moisture induced by (1) increased rainfall alone, (2) cooler temperatures alone or (3) some combination of the two. Planting of spruce in suburban landscapes of Denver and Albuquerque (both at ca. 1585 m elevation) gives the first tenet some credibility. Brakenridge (1978) illustrates the second example by citing a latitudinal analog for junipers found in packrat middens from the Sonoran and Chihuahuan Deserts. These same junipers grow at similar elevations along the Snake River Plain of southern Idaho, where precipitaton is the same or less, but temperature is 8°C cooler than the fossil sites (see objections by Wells, 1979). The third possibility, involving both parameters, is the most difficult to model. Environmental lapse rates

combine along elevational gradients to produce rates of change in effective moisture and thus, the advantage of elevational analogs.

The estimates derived from the southeastern Utah data differ from paleoclimatic reconstructions derived from packrat midden sequences in the Great Basin. The midden record shows that Pinus flexilis and P. longaeva expanded down to low elevations (1525-2070 m) throughout the Great Basin. These are the only two subalpine conifers present today in the central and southern Great Basin. Displacement of Picea engelmannii and Juniperus communis have been documented at the more northerly sites, while records of Pseudotsuga menziesii and Abies concolor are present only in the eastern and southern Great Basin (Thompson and Mead, 1982). The moisture requirements for Pinus longaeva and P. flexilis are considerably less than for other subalpine and montane conifers. Expansion of P. longaeva and P. flexilis in the absence of other mesophytic conifers has been used to imply cold and dry conditions for the Great Basin (Thompson and Mead, 1982). Conversely, mesophytic conifers such as Picea spp., Abies spp., and Pseudotsuga menziesii were able to expand down to low elevations on the Colorado Plateaus. The two paleoclimatic reconstructions are not necessarily at odds, since they aproximate the present east-to-west gradient in increasing aridity.

In both the Great Basin and the Colorado Plateaus, depressions of subalpine conifers may have been enhanced by a lack of competition with conifers prevalent today in lower montane forests and xeric woodlands. North of 36^{o}N latitude, macrofossil evidence for Pinus edulis, P. monophylla, and P. ponderosa is scanty for the Pleistocene. P.

monophylla occurred at ca. 11,600 B.P. (1850 m) in the Sheep Range of southern Nevada (36°30'N) (Spaulding, 1981). Isolated Pleistocene records of pinyon occur in the western Grand Canyon: the unconsolidated packrat layer at Rampart Cave (535 m); a packrat midden dated at 12,650 B.P. from 635 m elevation (Phillips, 1977), and another midden dated at 16,580 B.P. from the Cave of the Early Morning Light at 1300 m elevation (Van Devender and Spaulding, 1979). Aside from these records, pinyon is missing from over 70 Pleistocene middens collected between 425 and 2050 m throughout the Grand Canyon (Van Devender and Mead, 1976; Van Devender et al., 1977; Phillips, 1977; Mead, 1981; Mead and Phillips, 1981; Mead, 1983; Cole, 1982). Cowboy Cave (1770 m) has also yielded pinyon macrofossils of possible Pleistocene age, though the chances for contamination from rodent burrowing in the cave sediments are high. Traces of P. edulis were identified at Cowboy Cave from Unit 1b dated to between 13,000 and 11,000 B.P. (Spaulding and Peterson, 1980). Significantly, pinyon was not found in the overlying Units II and III dated to between 8700 and 6400 B.P. Aside from the trace amounts in Unit I, pinyon first appears in sediments associated with a date of 3600 B.P. (Hewitt, 1980). The Pleistocene record from Cowboy Cave is equivocal until a direct date on pinyon can be obtained.

The only Wisconsin-age macrofossils of Pinus ponderosa anywhere in the Southwest are from the Santa Catalina Mountains of southern Arizona (Thompson and Van Devender, 1982). P. ponderosa and P. edulis arrive at Chaco Canyon, New Mexico (1920 m) between 9500 and 8300 B.P. (Betancourt et al., in press). P. ponderosa is recorded at the Allen Canyon locality as early as 10,140 B.P., and P. edulis occurs only in

samples younger than 7200 B.P. For the Colorado Plateaus, the present distributions of both species were probably achieved during the Holocene. P. edulis probably migrated into the Plateaus from Pleistocene woodlands in the Chihuahuan Desert (Van Devender et al., in press). It remains unclear whether P. ponderosa migrated from the south with the onset of postglacial conditions or simply expanded from small populations in local mountain ranges. The absence of P. ponderosa and P. edulis in the Pleistocene may have facilitated low elevation expansion of other montane and subalpine conifers, primarily through competitive release. This may ultimately explain the disharmonious association of subalpine conifers with xerophytic plants common today in ponderosa pine and pinyon-juniper woodlands.

The late Wisconsin, absence of P. ponderosa and P. edulis from the Plateaus is climatically significant. Pearson (1950) notes that regeneration of P. ponderosa is sporadic because favorable distribution of summer rainfall must be combined with a productive seed year. Its reproductive success in the Southwest depends largely on the predictability of abundant summer rainfall. Once established, the seedlings are capable of withstanding drought, with soil moisture content near or even below wilting point, enabling them to survive at lower altitudes than other associated conifers (Fowells and Kirk, 1945). P. edulis and Quercus gambelii, the latter a frequent associate in pinyon-juniper woodlands and ponderosa pine forests, presently terminate their northern ranges at ca. 41^{o}N latitude. Neilson and Wullstein (in press) suggest that the northern limits of both species result from low rates of reproduction and seedling survival due to the greater frequency of

spring freezes and summer droughts with increasing latitude. Macrofossils of Quercus gambelii first appear in the Allen Canyon and Fishmouth Cave localities during the early Holocene. A midden of similar age from Canyon de Chelly, northeastern Arizona, contains no oak pollen (Betancourt and Davis, in press). However, both macrofossils of Q. gambelii and oak pollen have been identified from a late Wisconsin dung layer in a cave (1340 m) along the Waterpocket Fold, about 100 km west of Comb Ridge (O. K. Davis, pers. comm.). These data imply that Q. gambelii may have been restricted to lower elevations at the northern edge of its late Wisconsin range.

Another interesting species that is missing from the late Wisconsin at Fishmouth and Allen Canyon Caves is Juniperus osteosperma. This juniper is a common element in Pleistocene middens from 2070 m down to 425 m in the Grand Canyon (Cole, 1982; Phillips, 1977). Its arrival at Fishmouth Cave ca. 9700 B.P. probably signals its Holocene expansion north and east of the Grand Canyon. A similar expansion of its close relative J. monosperma probably occurred north and west of the Chihuahuan Desert into the eastern portion of the Colorado Plateaus. The modern ranges of the two overlap along a strip from east-central Arizona into western Colorado. During the late Wisconsin both the northern and eastern limits of Juniperus osteosperma were probably in the vicinity of the Grand Canyon. Juniperus monosperma probably did not range far north of 34^{o}N latitude in New Mexico (Van Devender et al., in press). Expansion of J. osteosperma might have been rapid, with midden records as early as 10,000 B.P. from the Pryor Mountains in Montana (J. I. Mead, pers. comm.). The oldest record of

J. monosperma from Chaco Canyon is 8300 B.P. (Betancourt et al., in press).

For the Wisconsin, range contractions to the south may be related to a southerly displacement of the polar jet stream and Mitchell's (1976) "winter" boundary. Such a displacement has been proposed by a number of authors from paleovegetation data (Van Devender and Spaulding, 1979), general circulation models (Bryson and Wendland, 1967), and modern plant distributions (Neilson and Wullstein, in press). In southeastern Utah, a southerly displacement of the jet stream and mid-latitude storm track would result in greater winter and less summer precipitation, cooler summer temperatures and a higher incidence of spring freezes than today. If the reasoning of Bryson and Wendland (1967) is to be followed, large decreases in winter temperatures were prevented by the presence of the North American ice sheets. They argue that the high plateaus of ice blocked incursions of cold, low level Arctic air from entering the United States. Air flow from the ice caps would have been mostly katabatic, producing mild winters over the North American continent.

The early Holocene on the Colorado Plateaus appears to have been a time of rapid changes in vegetation. At Fishmouth Cave, two major shifts in the flora occurred in quick succession. Between 12,770 and 10,000 B.P., both Picea pungens and Juniperus communis dropped out of the sequence, with Pinus flexilis and Juniperus scopulorum following suit soon after 10,000 B.P. New arrivals in the early Holocene of Fishmouth Cave included Quercus gamgelii and Juniperus osteosperma. At Allen Canyon Cave, again there were two shifts during the early part of

the sequence. Picea engelmannii and Abies lasiocarpa retreated to higher elevations between 11,300 and 10,000 B.P., leaving Pinus flexilis and Pseudotsuga menziesii as the dominants. The initial change towards the modern flora at the site occurred between 10,000 and 7200 B.P. A similar change happened between 9500 and 8300 B.P. at Chaco Canyon, which is intermediate in elevation (1920 m) between the two sites. At all three sites, plants associated with summer precipitation and relatively high annual temperatures (Quercus gambelii, Pinus ponderosa, Pinus edulis, Juniperus monosperma, J. osteosperma, etc.) began arriving at ca. 10,000 B.P. Pinus edulis is not recorded at either Fishmouth or Allen Canyon caves until the late Holocene, but this may result from location of the sites at the lower and upper ends of modern pinyon-juniper woodland.

The timing of these rapid vegetation changes during the early Holocene in southern Utah is very similar to the Swan Lake pollen and macrofossil records on the Idaho-Utah border (Bright, 1966). Both records are interpreted as representing a progressive decrease in effective moisture, either due to warmer temperatures and/or reduced rainfall, for the latest Pleistocene. However, effective moisture during the early Holocene is interpreted as being higher than today. During the latter part of the period there appears to have been a change in the seasonal distribution of rainfall, signalling the onset of monsoonal conditions for the Colorado Plateaus. The use of elevational analogs may not apply, since a major reorganization of vegetation zones occurred during this period. These results are interesting in light of the general circulation model recently proposed

for 9000 B.P. (Kutzbach, 1981; Kutzbach and Otto-Bliesner, 1982), and location of the southeastern Utah sites along the present monsoonal boundary. The model uses increases in solar radiation for June-July-August in 9000 B.P. to power land-ocean temperature contrasts and intensified monsoonal circulation. Paleoclimatic data from Africa and Asia closely agree with the model's prediction for intensified summer monsoons during the early Holocene, but the model has not been applied to North America because of difficulties in assessing the role played by the ice sheets.

There is general agreement that global temperatures were warmer during the middle Holocene (ca. 8000-4000 B.P.) than today. In the western U. S., a great deal of controversy has revolved around whether this period was drier or wetter than now. The argument seems to be over the relative amounts of summer precipitation. The concept of a hot-dry "Altithermal" (7500-4000 B.P.) was formulated by Antevs (1955) from work in the northern Great Basin, which is beyond monsoonal influences. Widespread application of the Altithermal concept across the western U. S., regardless of regional variability in climate, has been called into question. Martin (1963) first argued that warmer conditions might enhance the effectiveness of the summer monsoons south and east of the Great Basin. Although considerable data have since been applied to this issue, the controversy remains unresolved.

Warmer temperatures for the middle Holocene have been suggested from modern distributions of relic hybrids between Quercus gambelii and Q. turbinella (Cottam et al., 1959). The deciduous Q. gambelli is better adapted to cold winter temperatures than the evergreen Q.

turbinella. Leaves of the hybrid remain until late fall, long after Q. gambelii has dropped its leaves. I agree with Cottam et al. (1959) that neither oak could have persisted in north-central Utah during the Wisconsin glaciation. Both species probably expanded into this area during the middle and late Holocene, with the hybrid isolated from Q. turbinella with decreasing temperatures during the Neoglacial. A similar expansion and contraction in the range of Pinus edulis and P. monophylla may account for ecotonal hybrids north and west of the present range of P. edulis (Lanner, 1974).

In general, the records from both Allen Canyon and Fishmouth Cave indicate greater effective moisture during the middle and early part of the late Holocene (before 3000 B.P.). At Fishmouth Cave, the extralocal and mesophytic Pseudotsuga menziesii occurs in a sample dated at 6100 B.P., but I cannot ascertain that it is not a contaminant from older deposits. Around 3700-3500 B.P., pinyon-juniper woodlands might have expanded into lower elevations along Comb Ridge, as indicated by high macrofossil percentages for Juniperus osteosperma and macrofossils of the extralocal Pinus. edulis. At Allen Canyon Cave, the pattern is similar. P. ponderosa achieved by far its highest macrofossil percentages in a midden dated at 7200 B.P. A sample dated at 3400 B.P. contains the youngest macrofossils of the extralocal J. communis. J. scopulorum appears in all middle and late Holocene middens except the youngest at 1820 B.P., which only contains the more xerophytic J. osteosperma. The arrival of Pinus edulis, Opuntia polyacantha and Yucca angustissima in the late Holocene may also denote a greater aridity for the site than during the middle Holocene. At

both sites, the youngest middens (1800-2200 B.P.) best approximate the modern floras. The midden record from southeastern Utah suggests that the modern elevational range of local plants was not achieved until very recently.

SUMMARY

Packrat midden sequences from two caves record vegetation changes from the late Wisconsin through late Holocene in the central portion of the Colorado Plateaus. The two sites are separated vertically by 610 m in elevation along a more or less continuous gradient of Navajo Sandstone from Comb Ridge into the Allen Canyon country of the Abajo Mountains. Fishmouth Cave (1585 m) is located in Utah-juniper grassland just below and south of pinyon-juniper woodland. Allen Canyon Cave (2195 m) occupies an area intermediate between mesa top pinyon-juniper woodland and cliffside stands of Douglas fir, ponderosa pine, and aspen. The midden sequences trace the development of modern plant zonation from the much-displaced vegetation of the late Wisconsin. Local environmental lapse rates are used to calculate the differences between late Wisconsin and modern climates. The similar intervals encompassed at each site allow simultaneous views of vegetation change at low and intermediate elevations. Comparison with other midden sites from the Colorado Plateaus and adjacent areas yields a rough sketch of past regional biogeography. The distributions of several important plants are related to changes in the position of air mass boundaries over northern and southern Utah.

The late Wisconsin record calls for minimum elevational depressions of 700-850 m for subalpine and upper montane plants. At Allen Canyon Cave, spruce-fir forest dominated by Abies lasiocarpa,

Picea engelmannii, Pinus flexilis, and Juniperus communis was depressed from its lower limits today at ca. 2896 m to 2195 m. Picea pungens, Pinus flexilis and Juniperus communis occur in the late Wisconsin midden from Fishmouth Cave, suggesting an elevational analog above 2438 m. The analog approach predicts a 3-4°C cooling from present mean annual temperatures. Records of Opuntia polyacantha and Yucca angustissima at Fishmouth Cave argue against late Wisconsin cooling exceeding 5°C. Mean annual precipitation is estimated at from 35 to 60% greater than today. Potential error is recognized in the use of elevational analogs to reconstruct quantitative climatic estimates is recognized. The analog approach dictates both increases in precipitation and decreases in temperature to produce greater effective moisture. Concentration of climatic stations at lower elevations, for instance, means that the steeper rates of temperature decrease and precipitation increase in the upper mountain belts are ignored. The minimum estimates for climatic change are probably reasonable considering that depression of subalpine and upper montane conifers was probably enhanced by the absence of Pinus ponderosa and P. edulis.

The early Holocene at the two sites appears to represent a major reorganization in local plant communities. Beginning ca. 10,000 B.P., several plants now dominant in the area began to arrive. These include Pinus ponderosa, Quercus gambelii, and Juniperus osteosperma. Pinus edulis was a rather late arrival (in the middle Holocene), but this may reflect the location of the two sites at its upper and lower limits. In nearby Chaco Canyon, New Mexico, this pygmy conifer arrived sometime between 9500 and 8300 B.P. Pinyon probably arrived in the

middle of its elevational range between 10,000 and 8,000 B.P. and failed to fully expand its present elevational range until the middle and late Holocene. A case is made for the early Holocene climate to involve a northward displacement of the polar jet stream and middle latitude storm track following its southerly position during the late Wisconsin. The upward migration of subalpine and upper montane elements coupled with the arrival of plants formerly displaced to the south is interpreted to mean increased summer as well as mean annual temperatures, a decreasing frequency of spring freezes, and a shift from winter to summer-dominant rainfall. The present monsoonal boundary began to approach its present position between 10,000 and 8000 B.P. A model calling for increased summer temperatures and intensified summer monsoons during the middle Holocene is suggested by the midden records. Greater effective moisture than present is inferred at both sites. The modern vegetation at the sites is not fully in place until ca. 2000 B.P.

Based on these new data from southeastern Utah, I envision the scope of future midden studies on the Colorado Plateaus to be as follows. A network of midden localities should be established at the southern end of the Plateaus to delineate the late Wisconsin northern limits of such hallmark plants as ponderosa pine, pinyon pine, one-seed juniper, and Gambel oak. Midden sequences from the northern part of the Plateaus in north-central Utah and northern Colorado can be used to determine the arrival times at the northernmost stations for these species. Holocene rates of migration can thus be extrapolated. It is also possible that several of these plants expanded beyond their

present northern limits as a consequence of a warming trend during the middle Holocene. This is directly testable with development of new midden sequences at critical localities. Data from Fishmouth and Allen Canyon caves also point up an interesting possibility that plants migrating into an area arrive first into the middle of their elevational range. A lag time of several millennia may separate the first arrival of a species and local expansion into its full elevational range.

Quantitative estimates of climatic change are a desirable, if sometimes untenable, aspect of paleoecology. Specifically, strategies such as the use of elevational analogs are fraught with the inability to independently estimate changes in temperature or precipitation. Many of the arguments based on shifts in the elevational range of plants can be reduced to fluctuations in effective moisture. That is, greater effective moisture results from either lowered temperatures, increased rainfall, or some combination of both. One approach is to develop ways of assessing temperature changes independent from rainfall. The temperature signal from ratios of stable isotopes ($^{18}O/^{16}O$; $^{13}C/^{12}C$; D/H) in meteoric water suggests one possibility that is currently being tested. In general, isotope ratios in meteoric water reflect the temperature at the site of precipitation (the lower the temperature the smaller the isotopic ratio). Natural systems which record variations in these ratios through time should preserve a record of past temperature fluctuations. One such system is represented in plants (Epstein et al., 1976). Conversion of cellulose from plant macrofossils to water and measurement of its isotopic composition

should yield an assessment of temperature for the specific fossil locality. Measurement of isotopic ratios from packrat midden macrofossils is already underway. Arnold (1979) demonstrates that the approach is viable for isotope ratios in juniper from Sonoran Desert middens. A more recent experiment with a lengthy sequence of middens from the Great Basin show an even greater sensitivity (Siegel, 1983). In the near future, we anticipate that single-site sequences, such as are described here for Fishmouth and Allen Canyon Caves, will be specifically targeted for the measurement of stable isotopic ratios and reconstruction of paleotemperature curves, independent from precipitation.

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