SMITHSONIAN CONTRIBUTIONS TO THE EARTH SCIENCES • NUMBER 33

Great Basin Aquatic Systems History

Robert Hershler, David B. Madsen, and Donald R. Currey
EDITORS

Smithsonian Institution Press
Washington, D.C.
2002

ABSTRACT

Hershler, Robert, David B. Madsen, and Donald R. Currey, editors. Great Basin Aquatic Systems History. *Smithsonian Contributions to the Earth Sciences,* number 33, 405 pages, 190 figures, 21 tables, 2002.—The 14 papers collected herein treat diverse aspects of the aquatic history of the Great Basin of the western United States and collectively attempt to summarize and integrate portions of the vast body of new information on this subject that has been acquired since the last such compilation was published in 1948. In the first section, four papers (Lowenstein, Negrini, Reheis et al., Sack) focus on physical aspects of Great Basin paleolake histories, whereas a fifth paper (Oviatt) summarizes the contributions to the study of Bonneville Basin lacustrine history made by two early giants of the field, Grove Karl Gilbert and Ernst Antevs. In the second section, four papers synthesize perspectives on Great Basin aquatic history provided by diatoms and ostracods (Bradbury and Forester), fishes (Smith et al.), aquatic insects (Polhemus and Polhemus), and aquatic snails (Hershler and Sada), whereas a fifth (Sada and Vinyard) summarizes the conservation status of the diverse aquatic biota that is endemic to the region. In the final section, three papers integrate terrestrial biotic evidence pertaining to Great Basin aquatic history derived from pollen from cores (Davis), floristics (Wigand and Rhode), and the mammal record (Grayson), whereas a fourth (Madsen) examines the relationship between Great Basin lakes and human inhabitants of the region. Although diverse in scope and topic, the papers in this volume are nonetheless linked by an appreciation that integration of geological, biological, and anthropological evidence is a necessary and fundamental key to a mature understanding of Great Basin aquatic systems history.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Annals of the Smithsonian Institution.* SERIES COVER DESIGN: Volcanic eruption at the island of Krakatau in 1883.

Library of Congress Cataloging-in-Publication Data

Great Basin aquatic systems history / Robert Hershler, David B. Madsen, and Donald R. Curry, editors.
p. cm. — (Smithsonian contributions to the earth sciences ; no. 33)
Includes bibliographical references.
1. Limnology—Great Basin. 2. Paleolimnology—Great Basin. I. Hershler, Robert. II. Madsen, David B. III. Currey, Donald R. IV. Series.

QE1 .S227 no. 33
[QH104.5.G68]
550 s—dc21
[551.48'0979]

2002026685

♾ The paper used in this publication meets the minimum requirements of the American National Standard for Permanence of Paper for Printed Library Materials Z39.48—1984.

Contents

Page

LAKE HISTORIES

AQUATIC BIOTIC PERSPECTIVES

NON-AQUATIC BIOTIC AND HYDROCLIMATIC PERSPECTIVES

Great Basin Vegetation History and Aquatic Systems: The Last 150,000 Years

Peter E. Wigand and David Rhode

ABSTRACT

The Great Basin was seen by early settlers as a terrifying barrier to be crossed on the way to the golden promise that was California. Although the region was visited by fur trappers and mountain men in the 1820s and 1830s, it was not until the 1840s that the European pathfinders and empire builders tarried to explore the woodland-covered mountains and playa-bottomed valleys of the Great Basin. Mormon farmers and spirited miners settled this wild land, uprooting the native people who had lived there for millennia. As the region opened to European settlement, evidence of a long and complex environmental history was discovered and explored. But as recently as 50 years ago our knowledge of Late Quaternary lake histories and climates was minimal, and our knowledge of the dynamics of Pleistocene and Holocene vegetation was virtually nonexistent. Our understanding has advanced dramatically in the last half century, with advances in analyses of pollen, woodrat middens, and tree rings. A substantial pollen and plant macrofossil database has been assembled, spanning tens of thousands to hundreds of thousands of years, such that our knowledge of Late Quaternary vegetation history in the Great Basin rivals that of any other region in the world. These data, coupled with the long-term lake histories deduced from the basins of the Lahontan, Bonneville, Chewaucan, and Owens-to-Death Valley lake systems, permit detailed examination of late Pleistocene vegetation dynamics in relation to aquatic system history. By examining proxy records from the various subregions of the Great Basin and the northern Mojave Desert, we have compiled a compelling picture of past climate and the vegetation and hydrologic responses during the last 50,000–150,000 years.

Peter E. Wigand, Quaternary Sciences Center, Desert Research Institute, 2215 Raggio Parkway, Reno, Nevada 89512, USA. David Rhode, Earth and Ecosystem Sciences, Desert Research Institute, 2215 Raggio Parkway, Reno, Nevada 89512, USA.

Reviewers: Owen K. Davis, Department of Geosciences, University of Arizona, Tucson, Arizona 85721-0077, USA; David B. Madsen, Environmental Sciences, Utah Geologial Survey, Salt Lake City, Utah 84114, USA; P. Peterson, Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560-0166 USA; G. Spaulding, Dames and Moore, 7180 Pollock Drive, Suite 200, Las Vegas, Nevada 89119, USA.

Introduction

Our understanding of Late Quaternary biological history in the Great Basin, particularly its vegetation history, has advanced substantially in the half century since the publication of works by Antevs (1948) and by Hubbs and Miller (1948). By that time evidence derived from the interpretation of modern biogeographic indicators such as disjunct taxa and isolated hybrid populations had led to the recognition that Pleistocene glaciopluvial episodes and mid-Holocene warming wrought substantial shifts in vegetation zones, but even the barest outlines of these shifts remained uncertain. In 1948 the number of Late Quaternary fossil plant localities studied in the Great Basin was negligible (Deevey, 1949). Laudermilk and Munz (1934, 1938) had analyzed late Pleistocene pollen and plant fragments from dung balls of the Shasta ground sloth (*Nothrotheriops shatensis*), found in Gypsum and Rampart Caves along the lower Colorado River just outside the southern margins of the Great Basin. Plant remains had been recovered from other cave sites (e.g., Smith Creek Cave; Thompson, 1984) but these were as yet unstudied. Only two Late Quaternary pollen sequences from within the Great Basin—Chewaucan and Warner marshes in south-central Oregon—had been analyzed by Ernst Antevs' colleague Henry Hansen (Hansen, 1947). These pollen records, in combination with knowledge of the northern European climatic sequence (Blytt-Sernander) (Iversen, 1973:13–14), were instrumental in Antevs' formulation of his tripartite Neothermal climatic scheme (Antevs, 1948). Another early pollen locality, Tsegi Canyon in northeastern Arizona (Sears, 1937), lay well beyond the Great Basin's southeastern edge. Use of tree ring analysis to provide clues of the Holocene climates driving vegetation changes was still in its descriptive stage, and chronologies were still relatively limited in length (Hardman and Reil, 1936; Antevs, 1938; Schulman, 1956). The revolution in reconstruction of vegetation and climate history of arid areas, brought about by the recognition of the potential of packrat middens as a fossil record (Betancourt et al., 1990), was still nearly a decade and a half in the future. Indeed, a half century ago, we had more direct information about Tertiary floras in the

Great Basin and adjacent regions than we did about Late Quaternary vegetation history (La Motte, 1936; Axelrod, 1939, 1944, 1948; Brown, 1949).

Today our much-improved understanding of late Pleistocene terrestrial vegetation history can be usefully compared with the history of Great Basin aquatic and landscape systems, with detailed human and faunal records, and, most fundamentally, with global and regional climate reconstructions. The advances in our understanding of Great Basin vegetation history come from three main sources: (1) millennia-long tree ring records, (2) pollen and plant macrofossils recovered from lake, marsh, and dry cave settings, and (3) plant materials obtained from ancient woodrat nests (Figure 1). In addition, studies of plant macrofossils and tree ring series provide information regarding plant physiology through study of anatomical features (e.g., Van de Water et al., 1994) and stable isotopic signatures (Siegal, 1983; Feng and Epstein, 1994; Van de Water et al., 1994; Wigand, 1995; Jahren, 1996). The potential of future molecular and genetic studies of these remains (e.g., Hamrick et al., 1994; Poinar et al., 1998) will offer additional information regarding phylogeography and the response of plant populations to changes in past climate.

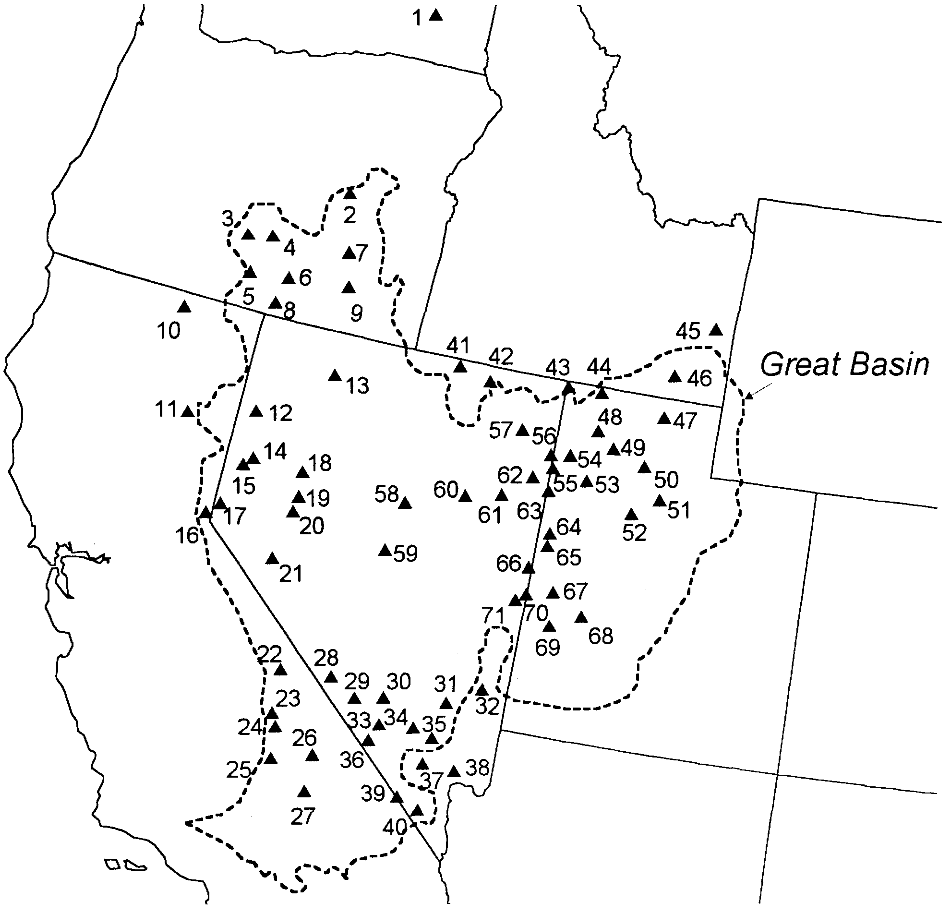

FIGURE 1.—Map of the western United States showing the Great Basin and localities, as discussed in the text, from which tree ring records, pollen and plant macrofossils, and plant materials from ancient woodrat nests were obtained. 1, Wildcat Lake; 2, Craddock Meadow; 3, Summer Lake (Ana River, Bed and Breakfast); 4, Alkali Lake Valley; 5, Chewaucan marsh; 6, Bicycle Pond; 7, Diamond Pond; 8, Warner Lake; 9, Steens Mountain (Fish Lake, Wildhorse Lake); 10, Lava Beds; 11, McCoy Flat; 12, Smoke Creek Desert; 13, Jackson Range; 14, Pyramid Lake; 15, Painted Hills; 16, Lake Tahoe; 17, Little Valley; 18, Lovelock Cave; 19, Carson Sink (Lead Lake); 20, Hidden Cave; 21, Walker Lake; 22, White Mountains (Methusaleh Walk); 23, Alabama Hills; 24, Owens Lake; 25, Little Lake; 26, Warm Sulphur Springs; 27, Searles Lake; 28, Eureka Valley; 29, Cofer Spring; 30, Eleana Range; 31, Lower Pahranagat Lake/Pahranagat Range; 32, Meadow Valley Wash; 33, Specter Range/Spotted Range/Little Skull Mountain; 34, Pintwater Range (Pintwater Cave); 35, Sheep Range; 36, Ash Meadows/Owl Canyon; 37, Tule Springs; 38, Gypsum Cave; 39, Sandy Valley; 40, McCullough Range; 41, Owyhee River Valley; 42, Jarbidge Mountains (Mission Cross Bog); 43, Grouse Creek Range (Swallow Shelter); 44, Raft River Mountains (Curelom Cirque); 45, Grays Lake; 46, Swan Lake; 47, Bear River (Cutler Dam formation); 48, Crescent Spring/Hogup Cave; 49, Lakeside Range (Homestead Cave, Gillespie Hills); 50, Great Salt Lake; 51, Snowbird Bog; 52, Onaqui Range (Devils Gate); 53, Knolls; 54, Silver Island Canyon; 55, Wendover (Danger Cave, Leppy Overhang, Triple Barrel); 56, Pilot Range (Raven Cave); 57, Pequop Range (Icicle Cave); 58, Potato Canyon Bog; 59, Gatecliff Shelter; 60, Ruby Marsh; 61, Cherry Creek Range; 62, Goshute/Toano Range (Top of the Terrace, Marblehead Mine); 63, West Bonneville Basin (Bonneville Estates, Twin Peaks, Pristine Shelter); 64, Indian Farm Canyon; 65, Granite Canyon; 66, Northern Snake Range (Council Hall Cave, Smith Creek Cave, Arch Cave, Ladder Cave, Old Man Cave); 67, Confusion Range; 68, Cricket Mountains; 69, Wah Wah Range; 70, Garrison; 71, Southern Snake Range.

Our intention in this paper is not to summarize everything that we currently know about vegetation history in the region, but rather to highlight major vegetation patterns and changes that reveal underlying climate trends and variability throughout the Great Basin.

ENVIRONMENTAL SETTING

The Great Basin of western North America is a region of dramatic topographic relief and striking vegetation transitions over short distances. Lying between the Sierra Nevada/Cascade mountain chain on the west and the Wasatch Front on the east, the Great Basin comprises a great mosaic of diverse habitats. Great Basin climate reflects the effects of both the heterogeneous topography and the varying impact of three major air mass systems that intersect over it (Houghton, 1969; Houghton et al., 1975).

Pacific: a regime dominated by maritime polar air masses. These moist cool air masses from the Pacific Ocean produce cool, wet winters, and their absence in summer makes the growing season hot and dry. Plant species such as Sierran white fir (*Abies concolor* var. *lowiana* (Gordon) Lemmon) and whitebark pine (*Pinus albicaulis* Engelm.) depend upon the reliable winter rainfall that this air mass provides. These species extend into the Great Basin from the west and northwest, dotting mountain tops that lie in the path of the Pacific storm tracks.

Gulf: a regime dominated by maritime and continental tropical air masses. These warm, moist air masses entering the southwestern United States from either the Gulf of Mexico or the Gulf of California produce hot, moist summers with midsummer torrential rainfall (originating during convective storms) and warm, dry winters. Plants, such as creosote bush (*Larrea tridentata* (Sessé & Moc. ex DC.) Cov.), and perhaps singleleaf piñon pine (*Pinus monophylla* Torr. & Fremont), that favor warmer winter temperatures and summer rainfall extend into this area from the southern desert, except in places where winter or summer temperatures are too harsh.

Polar: a regime dominated by continental polar and arctic air masses. These cold, dry continental air masses from the North American interior extend into the Great Basin from the northeast during the winter. Such air mass system "outbreaks" restrict the plant species able to grow within the area of greatest influence to those with physiological limits tolerant of cold, dry winters coupled with periodic drought (e.g., limber pine, *Pinus flexilis* James).

Movements of these air systems, and their effects on local and regional climate, are reflected in changes in hydrology, erosion/deposition processes, and vegetation. Displacement of winter and summer storm tracks and the variations in penetration of the summer monsoon are all affected by the realignment of these pressure systems through time. Because movements of these three large air masses reflect changes in global circulation and are potentially revealed in the climatic proxy data of the Great Basin, changes in a large portion of the earth's climate system may be monitored through time.

In addition to the effects of these air masses, Great Basin climates and vegetation are further complicated by topography. The effect of topographic diversity in the Great Basin on the distribution of precipitation has resulted in the formation of a multiplicity of habitats within close proximity, thus fostering rich biotic diversity (Billings, 1951). Elevational changes in plant distributions can be dramatic in response to the orographic effect of north–south-trending mountain chains that lie across the paths of Pacific storms or, conversely, that funnel summer monsoonal rainstorms northward. Finally, the overriding rain shadow effect of the Sierra Nevada mountains to the west exerts a massive impact upon rainfall distribution in the Great Basin. The rising of these mountains that began during the Pliocene and accelerated during the course of the Pleistocene accentuated this effect (Axelrod and Raven, 1985; Axelrod, 1990; Thompson, 1991).

VEGETATION RESPONSE TO CLIMATE CHANGE

During the Late Quaternary most changes in vegetation communities occurred in response to climate change. Vegetation changes observed in the Great Basin have included large-scale latitudinal shifts of plant taxa that typically occurred in the south and east as well as the primarily altitudinal shifts that characterized the central and northwestern Great Basin. Smaller scale shifts in abundance of major taxa within plant associations have characterized the entire region during both low- and high-magnitude climate changes. Differences in the response of vegetation to variation in climate result from several factors. Primary among these factors are the magnitude and duration of the new climatic regime to which individual plant species are adjusting. Secondary are the variable effects of topographic relief in the formation of microhabitats, each with its own microclimate. Third in importance is the distance to source areas from which plant species would have to expand during climatic transitions.

The climatic sensitivity of vegetation in the Great Basin lies in the physiological characteristics of its species. As a result of millions of years of adaptation to arid and semiarid conditions—even before the Great Basin was formed (Tidwell et al., 1972)—many of the plants that grow in this region are opportunistic. They have evolved to quickly take advantage of increased precipitation. Many species respond to wetter conditions through increased pollen and seed production and rapid vegetative growth. Because the annual production of biomass is linearly related to effective annual precipitation (Walter, 1954), biomass production in arid and semiarid environments is a sensitive indicator of changing climate. Such changes can be measured directly today through satellite imagery and historically through repeat photography (Hastings and Turner, 1965). Increased productivity is evidenced in the fossil record by wider tree and shrub growth rings, greater needle and leaf size, and copious production of pollen. Therefore, even relatively brief episodes of greater rainfall that resulted in increased pollen production may be evidenced in high-frequency pollen records as sudden rises in pollen influx.

Plant adaptations favoring rapid migration are aided by Great Basin topography. Many plants disperse their pollen and seeds with the wind, favoring rapid dispersal of propagules. Seeds of some plants are ingested or held in specialized organs by certain animals, then carried great distances to favorable locations where they may germinate and grow (e.g., Clark's nutcracker (*Nucifraga columbiana*) and whitebark pine). Because of the steep relief of Great Basin mountain ranges, species can move the equivalent of several degrees of latitude by moving vertically only a few hundred meters. The north–south-aligned mountain ranges of the Great Basin also serve as corridors (at various elevations) that facilitate the north–south movement of plant and animal species in response to the vagaries of climate. (Intervening valleys may impede east–west movement between mountain ranges, however.) As a consequence, the potential lag time between climatic input and plant response to reach a new equilibrium may be much less in the Great Basin than it is in areas of reduced topographic relief, where plants must move hundreds of kilometers latitudinally to reach a new environmental equilibrium.

VEGETATION CHANGE, THE HYDROLOGIC RECORD, AND CYCLES OF EROSION AND DEPOSITION

In the Great Basin, rates of erosion and deposition are usually closely tied to climate. The low rainfall and high evaporation rates that characterize much of the Great Basin today support a relatively sparse vegetation cover that leaves much of the ground surface exposed to the erosive effects of rainfall. Areas with greater rainfall have relatively greater ground cover offering more protection against erosive processes. Great Basin plant communities respond to increased rainfall through greater foliage production by extant plants and through establishment of extra local plant species. Eventually, increased biomass provides a better buffer to increases in rainfall and reduces the amount of water reaching streams and lakes. Sudden increases in rainfall (either during a single event or during the course of a year) can overwhelm the ability of relatively sparse vegetation cover to assimilate the excess. This is almost immediately reflected in increased runoff and accumulation of water in the playa lakes, the sinks of Great Basin fluvial systems. If increased effective precipitation continues, the increase in the biomass of existing plants and the establishment of new plants providing cover (or protection) for previously exposed ground will eventually reduce the rate of sediment movement. A return to sparser vegetation cover will mark the return to lower effective precipitation and greater erosion potential. Thus, monitoring changes in sediment deposition rates in streams and lakes, directly through historical records and prehistorically through paleoecological studies, can provide excellent proxy data of climate-induced vegetation change.

THE NATURE OF THE DATA

The natural distribution of paleobotanical data sets is constrained to a large degree by moisture differences within the Great Basin. Low amounts of effective precipitation have favored the preservation of certain kinds of proxy data. Plant macrofossils preserved in dry cave deposits and woodrat middens provide intermittent records of local vegetation spanning tens of thousands of years. Wood from long-dead trees, preserved by the dry conditions that often characterize upper tree lines in the Great Basin, provides continuous evidence of climatic variation spanning the Holocene. A few lakes and desert springs provide long and often complex sedimentary records that can span thousands to hundreds of thousands of years. High organic production in some of these areas has resulted in rapid rates of deposition, and the records are particularly valuable for the examination of high-frequency pollen and the macrofossils of local aquatic plants. These records can be compared with tree ring data to generate longer, more detailed records of regional climate and vegetation response.

In general, the number of well-preserved palynological records decreases to the south (reflecting the greater rarity of lakes and marshes), and the number of woodrat midden localities decreases to the north (reflecting increasingly wetter conditions that favor dissolution of the protective urine coating of the nests). Tree ring series are taken mainly from near the tree line in the higher mountains of the margins of the Great Basin, most commonly in the southern half of the Basin. Fortunately, recent field studies are alleviating some of these problems of data scarcity.

Integration of currently available paleobotanical proxy data reveals Great Basin vegetation dynamics in great detail for the last 4 Ka (thousand years ago) and more coarsely for the last 35 Ka. Earlier than 40 Ka, only a few pollen or midden records are available (e.g., from the Summer Lake/Chewaucan Lake basin in the northwest, Owens Lake in the west, Searles Lake in the south, and the Bonneville Basin in the east). For the period after 40 Ka, data obtained from pollen records are supplemented by evidence obtained from ancient radiocarbon-dated woodrat middens. Several high-resolution pollen records in the northwestern Great Basin and the northern Mojave Desert provide excellent coverage of both terrestrial and aquatic vegetation history from 6 Ka to the present. Ostracodes and diatoms from the northern Mojave Desert record are being used to reconstruct regional groundwater histories as well. In the Lahontan and Bonneville Basins, vegetation history inferred from middens and pollen records can be correlated with well-dated Late Quaternary lake histories.

In general, evidence of the relocation of semiarid and subalpine woodlands is most obvious for the late Pleistocene/early Holocene transition, especially in the woodrat midden record of the Great Basin and northern Mojave Desert mountain ranges (Van Devender et al., 1987). These records show that during the Pleistocene, woodland species often grew as much as 1000 m (and in a few instances >1000 m) below their present-day elevation. Substantial shifts in woodland species, however, have occurred during the Holocene as well. During the middle Holocene, some tree species were displaced by perhaps as much as 500 m above where they are found today, especially in the western and northwestern Great Basin. Downward displacement of semiarid woodland by as much as 150 m appears to have occurred several times late Holocene.

Changes in the distribution of individual shrub species and changes in the composition of shrub communities have also been dramatic during the late Holocene. This is most obvious in the southern Great Basin and the northern Mojave Desert but also has occurred in the northern Great Basin. Changes are most obvious in woodrat midden records of lowland and intermediate elevations, but some less obvious changes in shrub communities are also apparent in the few pollen records of the Great Basin. Because the plant communities of the northern and northwestern Great Basin are situated well away from major vegetation formation boundaries, they do not appear to be as dynamic as do those of southern Nevada that currently lie on the boundary between the Great Basin and the Mojave Desert. However, as the paleobotanical evidence described below will show, this perception is more apparent than real.

These various factors have differentially shaped the vegetation history of three broad regions of the Great Basin: (1) the northwest (Lahontan Basin and adjacent mountain ranges), (2) the south (southern Great Basin and northern Mojave Desert), and (3) the northeast (Bonneville Basin and adjacent mountain ranges). Late Quaternary vegetation histories of these three regions are discussed separately below. In these discussions, chronological estimates are based on uncalibrated radiocarbon years, unless otherwise noted. Chronological divisions (e.g., the Wisconsin/Holocene break) follow general vegetation and geomorphic patterns within each separate region.

Northern and Western Great Basin

LATE PLEISTOCENE (~250 TO 12.5 KA)

Mifflin and Wheat (1979) indicated that the Great Basin rivaled the Minnesota of today as a land of lakes during the Pleistocene. The Holocene remnants of these Pleistocene lakes in the northern and western Great Basin were visited by European fur trappers, including Peter Skene Ogden, as early as the 1820s (Davies et al., 1961). Several lakes, including Pyramid Lake, were described by J.C. Frémont during his explorations of the West during the 1840s (Frémont, 1845). The first study of pluvial Lake Lahontan was made by I.C. Russell (1885), who described two lake phases indicated by lower and upper lacustral clays. Morrison (1964, 1965, 1991) and Morrison and Frye (1965) further defined the lake's history using such picturesque formation names as the Eezta (early Wisconsin or earlier), the Sehoo (late Wisconsin), and the Fallon (Holocene). They correlated these lakes with stades of the Wisconsin glaciation or other Late Quaternary episodes of cooler, wetter climate. Since then, Davis (1978) and Benson et al. (1987, 1990, 1992, 1997) have further narrowed the chronology and details of lake history. These understandings serve as a backdrop for reconstruction of the vegetation history of the region.

PRE–LATE WISCONSIN (>35 KA).—A growing body of research in the northern and western Great Basin is clarifying the relationships among past climate history, lake and marsh history, and vegetation change (Mehringer, 1985, 1986). Two long pollen records that include more than just the Holocene—Summer and Owens Lakes (respectively: Cohen et al., 2000; Smith and Bischoff, 1997)—are available from the region, not including a series of pollen cores from the southern Cascades near Klamath Lake (Adam et al., 1995). Although the proxy record of past climate is far from complete, the general pattern suggests that high lakes may be more closely linked to the onsets and declines of glacial episodes in the region than to the glacial maxima.

The Summer Lake basin of south-central Oregon currently lies on the transition between the pine woodlands of the eastern slope of the Cascades and the sagebrush (*Artemisia* spp.) steppe of the northern Great Basin. Three pollen localities from the Summer Lake basin span much of the last 250 Ka (Cohen et al., 2000). The Summer Lake records include the lower two-thirds of oxygen isotope stage (OIS) 6, all of OIS 4 and OIS 3, and the lower portion of OIS 2 as defined by Pisias et al. (1984) and Shackleton and Opdyke (1973). There also seem to be a few samples from the top dating to OIS 1. Shifts in the dominance of mixed montane conifers, cold steppe shrubs, and desert scrub species record the varying effects of precipitation and temperature and their changing seasonal influence. Greater abundance of fir (*Abies* spp.) and spruce (*Picea* spp.) pollen in a sediment column taken from the Ana River Canyon indicates that climate in the northern Great Basin was more mesic during the OIS 6 section (~170–220 Ka) than during OIS 4 and OIS 2 (Cohen et al., 2000). Unfortunately, an erosional episode (or episodes) removed much of the sediment that accumulated during the end of OIS 6 and much of OIS 5. Therefore, we do not have a good indication of the nature of vegetation and lake history in the Summer Lake basin during the latter portion of OIS 6 or at the beginning of OIS 5. Indices of drought (based upon a ratio of the pollen of dry- to that of wet-loving plant species) and temperature (based upon spore abundance) reflect much greater climatic variability during OIS 6 than in later stages (Figure 2). After the relatively brief cool, wet episode of OIS 4 (about 70 Ka), OIS 3 climates were relatively cool and dry and apparently comparably stable. The dominance of sagebrush and saltbush (*Atriplex* spp.) shrub communities during this stage suggests that plant communities on the valley floors were not much different than they are today. The Summer Lake paleoenvironmental records (Ana River, Wetlands Levee, and Bed and Breakfast localities; see Negrini et al., 2000; Negrini, 2002 (this volume)) are all truncated at about 22 Ka just as conditions were becoming cooler and wetter (the beginning of OIS 2 conditions). The nature of effectively wetter climatic episodes differs throughout the record.

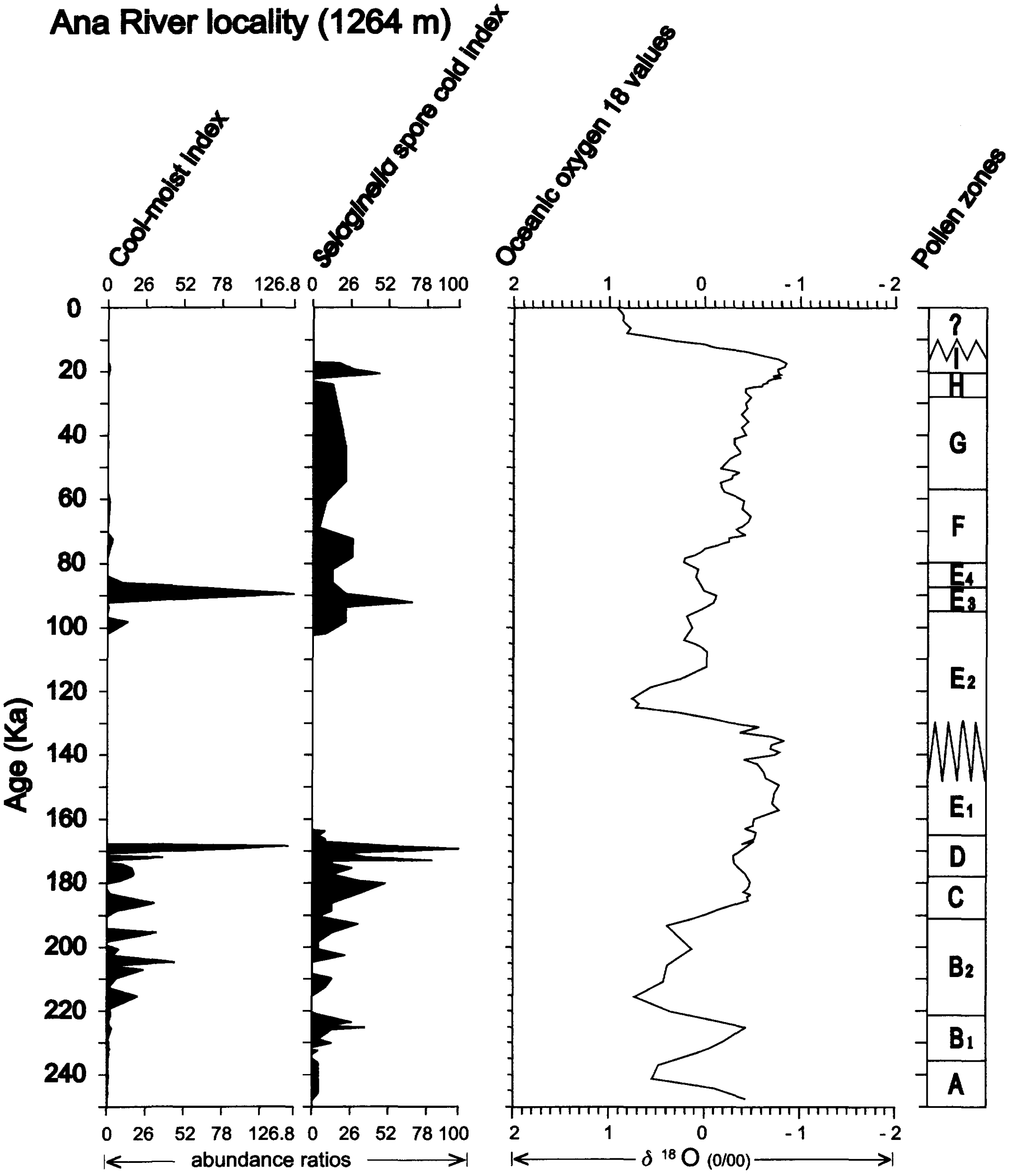

FIGURE 2.—Comparison of moisture and temperature indices from the Ana River in Summer Lake basin, south-central Oregon (elevation, 1264 m), with the oceanic ^{18}O curve (Martinson et al., 1987). The cool-moist index (or rather, "drought" index) was generated by setting relative abundances of conifer pollen against those of saltbush and greasewood pollen; values represent a ratio of pollen from the dry-loving species to that of the wet-loving species (moister is to the right on the x-axis). The temperature index is a measurement of the relative abundance of spike moss (*Selaginella densa*) spores (to the right is colder). A combination of radiocarbon and paleomagnetic dating techniques was used to obtain ages (Ka = thousands of years ago).

Glacial maxima appear to have been characterized by extremely cold temperatures and relatively little rainfall. The maxima of the interstades seem to have been typified by warmer temperatures and, in some cases, by substantial drought. The transitions generally were typified by moister conditions and varied only in whether they were warmer or cooler. Records for both Summer Lake and Owens Lake indicate that cool, wet periods resulted in the regional expansion of conifers, but these expansions occurred during the initial and terminal (transitional) stages of glacial stades. Once the glacial stage approached its climax, temperature (extremely cold conditions) became more important than moisture as a control for vegetation. Therefore, the transitional periods between warm, dry climates and cool, dry climates were the most amenable for the expansion of forests and woodlands. Marsh expansion and algae productivity also was greatest during these periods. When lake levels were high, the extent of marsh area in the Summer Lake basin was restricted by the steep gradients of the mountains on the north, west, and south margins. Marsh expansion was most extensive at the shallow north end of the basin during periods of intermediate-depth lakes, when the water table would have been close to the surface. Today the northern fringing marsh is artificially maintained by levees constructed by the U.S. Fish and Wildlife Service. The levees result in high water table conditions in the northern part of the Summer Lake basin—conditions that mimic those of the intermediate-depth lakes found locally during the Pleistocene and the moist periods of the Holocene. Marsh areas during shallow-lake periods would have been severely restricted to areas immediately surrounding stream entries at lake edges or around spring seeps.

This climatic pattern also appears to be reflected in the Owens Lake pollen record (Woolfenden, 1993, 1997). A ratio of juniper (*Juniperus* sp.) pollen to *Ambrosia*-type pollen reflects the effect of Late Quaternary climatic conditions on vegetation; this ration clearly indicates that periods of greater juniper pollen were warmer and periods of *Ambrosia*-type pollen were cooler (Woolfenden, 1997, fig. 17). Although wetter than those of today, Owens Lake climates >35 Ka were relatively dry. More closely spaced samples at Owens Lake revealed greater detail in the record, but major transitions to a warmer, drier climate at 120 Ka, and to a cooler, wetter climate at 70 Ka are clear in the records from Owens Lake and the Summer Lake basin. Dugas (1998) recorded a highstand of pluvial Lake Malheur northeast of Summer Lake between 80 and 70 Ka based on the occurrence of water-deposited Pumice Castle tephra. Gehr (1980) dated mollusk shells from a beach ridge indicating a highstand of pluvial Lake Malheur at 32 Ka, and Dugas (1998) presented additional dates that Gehr obtained on shells that confirm this age from other beach ridge positions. In addition, the occurrences of indicator species reflect the warm conditions of the interglacial and even, to some extent, the interstades for the last 150 Ka. At Owens Lake, oak (*Quercus* sp.) and walnut (*Juglans* sp.) pollen were more common during the last interglacial and the interstades (Woolfenden, 1997, fig. 8). In the record from the Ana River, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) is the indicator.

PRE–FULL GLACIAL (35 TO 26 KA).—Terrestrial conifer pollen evidence from the Bed and Breakfast and Wetlands Levee localities at Summer Lake (Figure 3) and from woodrat midden strata west of Pyramid Lake indicates that cooler, wetter conditions prevailed from 34 to 30 Ka. Haploxylon pines in this area primarily prefer a cooler and/or wetter climate pines whereas diploxylon pines generally prefer a warmer and/or drier climate. This shift was heralded by an expansion of juniper (Figure 2) and sagebrush. Increased regional abundance of grass together with retreat of saltbush and greasewood (*Sarcobatus* sp.) are indicated (Figure 3). Slight differences between the Wetlands Levee and the Bed and Breakfast records may reflect differences in both sample spacing and distance from shore within the basin. Dramatically reduced productivity of the eutrophically adapted algae *Botryococcus* at the Bed and Breakfast locality, indicates colder water temperatures during this period (Figure 3). A return to drier conditions at ca. 29.6 Ka is indicated by a decrease in fir and spruce and an increase in saltbush (Cohen et al., 2000). A major drought from 28 to 26 Ka is flanked by regionally correlatable grass expansions in the woodrat midden pollen record at Pyramid Lake as well as in the sediments of Summer Lake (Figures 3, 4). This drought is evidenced by saltbush expansion and is reflected in lowered lake levels throughout the northwestern Great Basin (Negrini and Davis, 1992).

In the north-central Great Basin, subalpine and/or tundra species of juniper (prostrate or creeping juniper, *Juniperus horizontalis* Moench, and common juniper, *J. communis* L.) appear in a woodrat midden from the Owyhee River Valley, dating from about 27 Ka (Wells, 1983). Their appearance in a woodrat midden dating to this period of drought (Benson et al., 1990; Negrini and Davis, 1992) suggests that the period may have been not only dry but cold as well.

The pollen records from Summer Lake and McCoy Flat (a valley floor site along Pine Creek, west of Eagle Lake on the eastern fringe of northern California's Modoc Plateau), and the woodrat midden records from around the pluvial Lake Lahontan basin, indicate that juniper occasionally was locally abundant between 50 and 12 Ka in the northwestern Great Basin (Figures 5, 6). This occasional juniper pollen, which differs somewhat in appearance from juniper pollen typically found in the sediments of Summer Lake and McCoy Flat during most of the Late Quaternary, might be that of common and/or prostrate juniper. This might indicate colder, more tundra-like or alpine-like conditions.

Woodlands dominated by Utah juniper (*J. osteosperma* (Torr.) Little), as evidenced by the presence of Utah juniper twiglets dating to ~34 Ka in woodrat middens, were growing at least as far north as the shores of pluvial Lake Lahontan (Wigand and Nowak, 1992; Nowak et al., 1994a, 1994b). Comparison of juniper with other species in the pollen and macrofossil records from the region indicates that juniper expansions occurred during cool, moist periods of climate before and after the glacial maxima.

LAST GLACIAL CYCLE (26 TO 12.5 KA).—Effectively moister climate after 24.5 Ka, coincident with renewed growth of pluvial Lake Lahontan, encouraged the spread of Utah juniper woodlands and allowed whitebark pine to intrude into scattered localities as low as 1380 m in elevation (Wigand and Nowak, 1992). Slopes currently dominated by saltbush scrub were

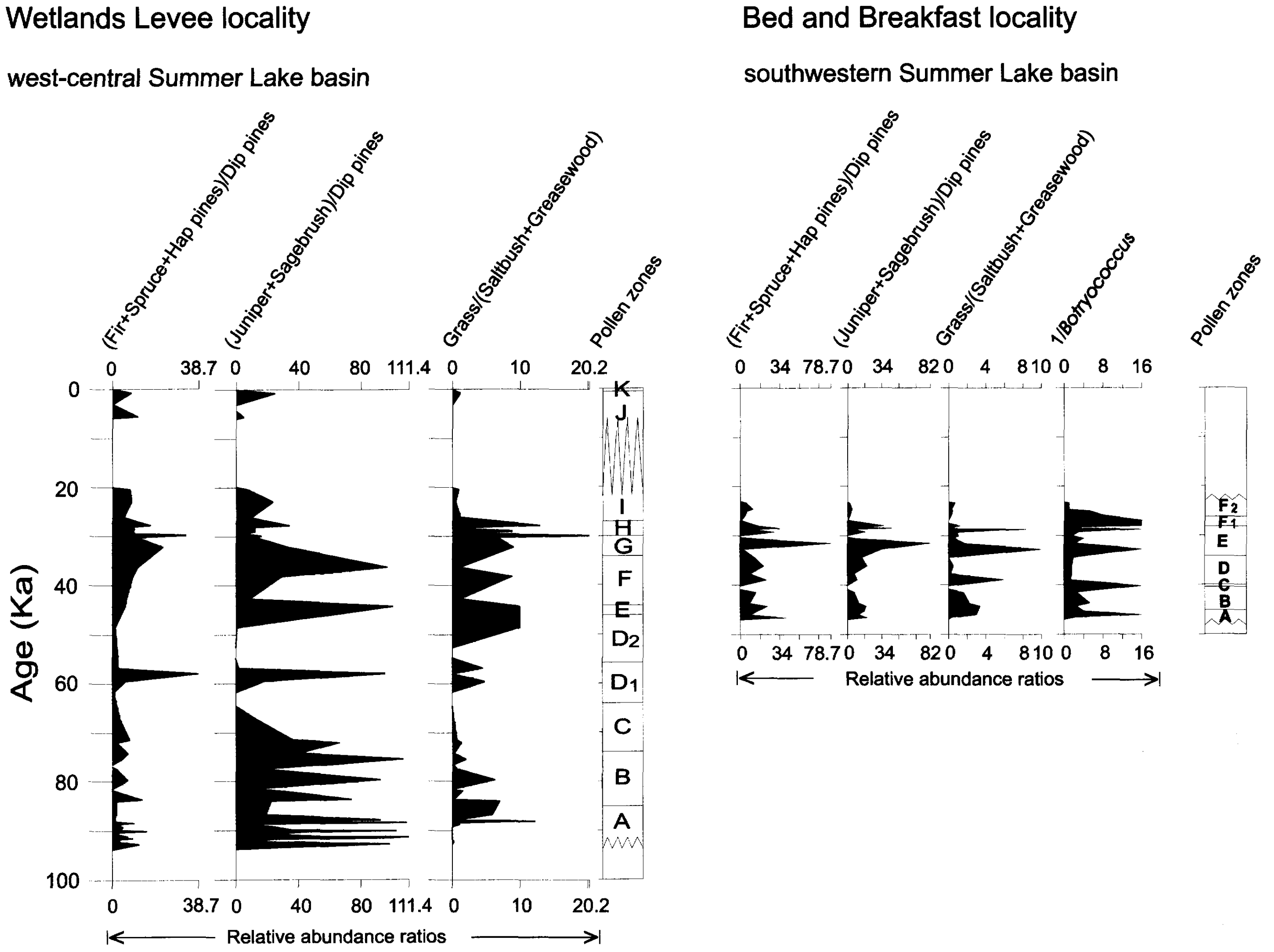

FIGURE 3.—Ratios of the abundances (x-axis) of selected major pollen types from the Wetlands Levee and Bed and Breakfast localities in the Summer Lake basin, south-central Oregon, by date (years before present, B.P.). Increases in the ratio of (fir + spruce + haploxylon (Hap) pine)/diploxylon (Dip) pine indicates cooler, moister conditions. Increases in the ratio of (juniper + sagebrush)/Dip pine herald the expansion of juniper woodland. Increased regional moisture is indicated with increases in the ratio of grass/(saltbush + greasewood). Dramatically reduced productivity of the algae *Botryococcus* is revealed by plotting the inverse of its abundance, 1/*Botryococcus*. All ratios indicate moister conditions to the right and drier conditions to the left.

characterized then by sagebrush steppe and by occasional perennial seeps lush with fewflower spikerush (*Eleocharis quinqueflora* (F.X. Hartmann) Schwarz) (Wigand and Nowak, 1992). Utah juniper macrofossils that were found in a woodrat midden dating to 20,460 ± 990 years B.P. (before present; laboratory no. Beta-41919), located just above the highest shoreline of pluvial Lake Lahontan on the western margin of the Carson Sink, reflect the peak of pre–glacial maximum expansion of juniper well beyond its current limits (Wigand and Nowak, 1992). This period corresponds to the rapid rise of pluvial Lake Lahontan at the beginning of the last glacial cycle (Benson et al., 1997, fig. 4). By 20 Ka the onset of much cooler, drier glacial maximum conditions led to a decline in Utah juniper, disappearance of whitebark pine from the midden record, and expansion of mixed sagebrush and shadscale (*Atriplex confertifolia* Torr. & Fremont) desert scrub communities (Nowak et al., 1994a). Approximately 23 and 12 Ka, during the wetter periods leading up to and following but not during the glacial maximum, whitebark pine occurred along the western margin of the Lahontan Basin, more than 1000 m lower than its current eleva-

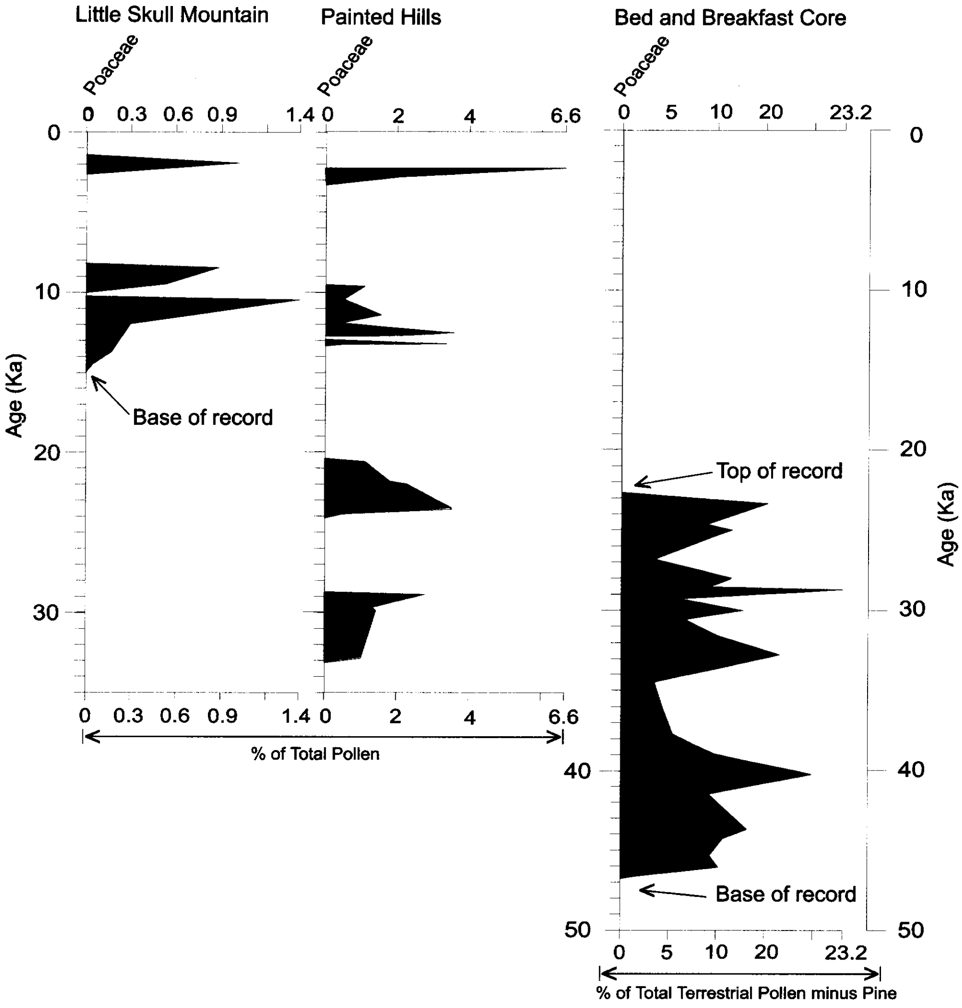

FIGURE 4.—Comparison of Late Quaternary relative abundances (as percentages) of grasses (Poaceae) in lacustrine core sediment from the Bed and Breakfast locality in Summer Lake basin, Oregon, with the relative grass percentages from the woodrat midden pollen records obtained from Painted Hills west of Pyramid Lake, west-central Nevada, and from Little Skull Mountain in the northern Mojave Desert, southern Nevada, by date (years before present, B.P.). The pollen record from Pyramid Lake was obtained from a single stratified woodrat midden, whereas the Little Skull Mountain record was from several adjacent woodrat middens.

tion (Wigand and Nowak, 1992; Nowak et al., 1994a, 1994b). This provides an indication of just how cold the glacial maximum may have been in northwestern Nevada. Estimates of the temperature difference for the onset and decline of the glacial maximum, based upon the current temperature limits of whitebark pine in the area today, indicate that the mean annual temperature (MAT) was at least 7° C colder during the onset and decline of the glacial maximum. Considering that woodland in this region disappeared during the glacial maximum because conditions were so cold, the MAT may have been 1°–2° C colder still.

The harsh (much colder and drier) conditions during the glacial maximum around 18 Ka also may have severely restricted semiarid woodland. Juniper even may have been locally or regionally extinct in the northwestern Great Basin. Utah juniper appears to have been present before and after the glacial maximum along the western shore of pluvial Lake Lahontan (Wigand and Nowak, 1992; Nowak et al., 1994a, 1994b). After the glacial maximum, woodrat midden data indicate that western juniper (*Juniperus occidentalis* Hook.) was present in places along the shores downwind of pluvial Lake Lahontan, where it may benefitted from "lake effect" (Thompson et al., 1986). Absence of woodrat midden strata and the scarcity of pollen records dating to the glacial maximum preclude making definite inferences regarding the distribution of juniper on the landscape. Greater shrub dominance, however, in both the

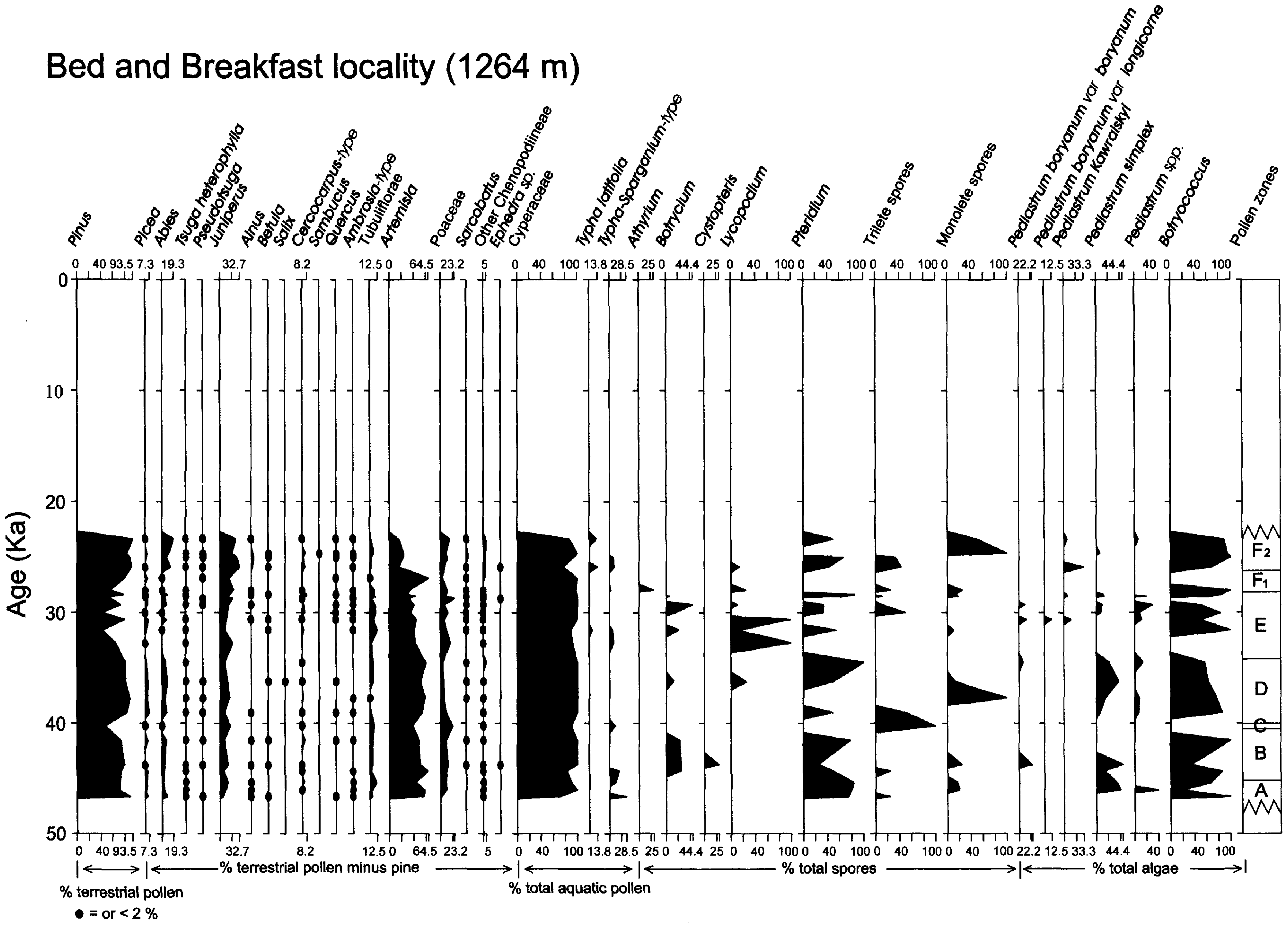

FIGURE 5.—Relative percentage diagram of major pollen, spore, and algae types from the Bed and Breakfast locality, Summer Lake basin, Oregon (elevation, 1264 m). Dates are based upon paleomagnetic age assignments. A bullet (•) on a line indicates a constituent value of ≤2%. Pollen zones are from Cohen et al., 2000.

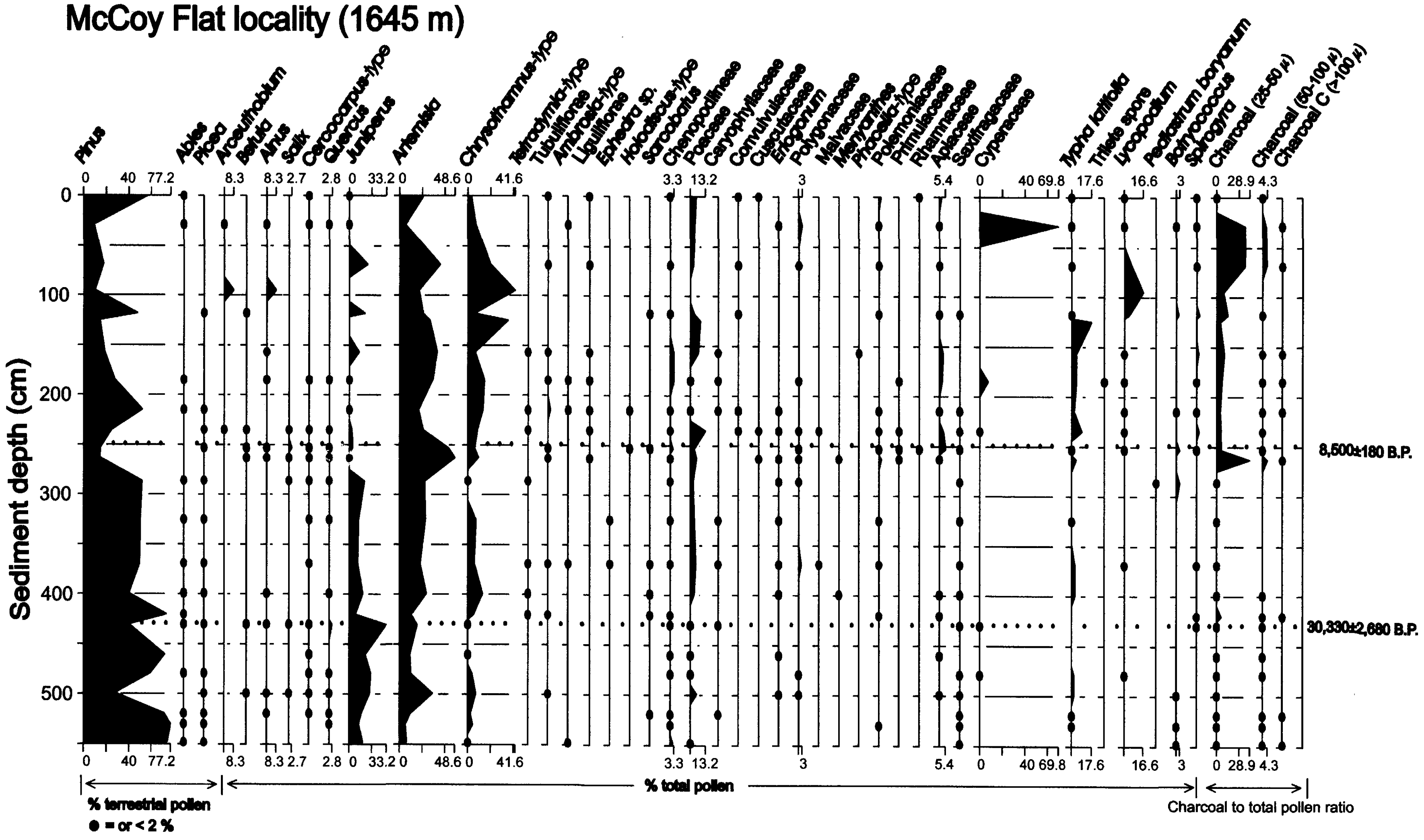

FIGURE 6.—Relative percentage diagram of major pollen, spore, and algae types and charcoal from McCoy Flat (elevation, 1645 m), Pine Creek drainage, west-central Eagle Lake basin, northern California, plotted with respect to sediment depth. Radiocarbon dates in the right margin are years before present (B.P.). A bullet (•) indicates a value of ≤2%.

pollen and macrofossil samples from woodrat midden strata immediately before and after the glacial maximum suggests that juniper may have been relatively scarce, probably occupying protected locations. On the other hand, shrub communities dominated by sagebrush, and at times saltbush, characterized extensive portions of the northwestern Great Basin (Wigand and Nowak, 1992). These data suggest that it was either too dry or too cold (or both) for juniper woodland to survive in the northern Great Basin during the last glacial maximum.

Relatively warmer, wetter conditions after the glacial maximum led to dramatic increases in sagebrush-dominated communities, and limited reexpansion of whitebark pine as well (Wigand and Nowak, 1992; Nowak et al., 1994a). Findings of Utah juniper in woodrat middens dated to 12,260 ± 140 years B.P. (Beta-47203) and 11,980 ± 110 years B.P. (Beta-47204) at the highest strandline on the eastern shore of the Carson Sink reflect reexpansion of semiarid woodland after the glacial maximum. By 12.5 Ka (concurrent with the final late-Pleistocene highstands of pluvial Lake Lahontan (Benson et al., 1990, 1992); see Negrini, 2002) mesic plant communities, reflecting lake effect and orographic forcing of rainfall along the eastern shore of pluvial Lake Lahontan, contrasted sharply with more xeric plant communities to the west (Wigand and Nowak, 1992).

The pollen record from a large woodrat midden west of Pyramid Lake that spans the last 34 Ky (thousand years) suggests substantial differences between climates at the onset (~24 Ka) and at the end (~12 Ka) of the last glacial cycle (Wigand and Nowak, 1992; Figure 7). Despite the expansion of whitebark pine during both periods (evidenced by the presence of macrofossils in the midden), the substantially greater abundance of sagebrush pollen and the appearance of mountain mahogany (*Cercocarpus* sp.) in the macrofossil record of the latter period suggest cooler temperatures and less precipitation 12.5 Ka than ~24 Ka. In part this could also reflect greater variability in climate, as suggested by the deep-water tufa record from Pyramid Lake (Pelican Point) (Benson et al., 1995; Benson et al., 1996).

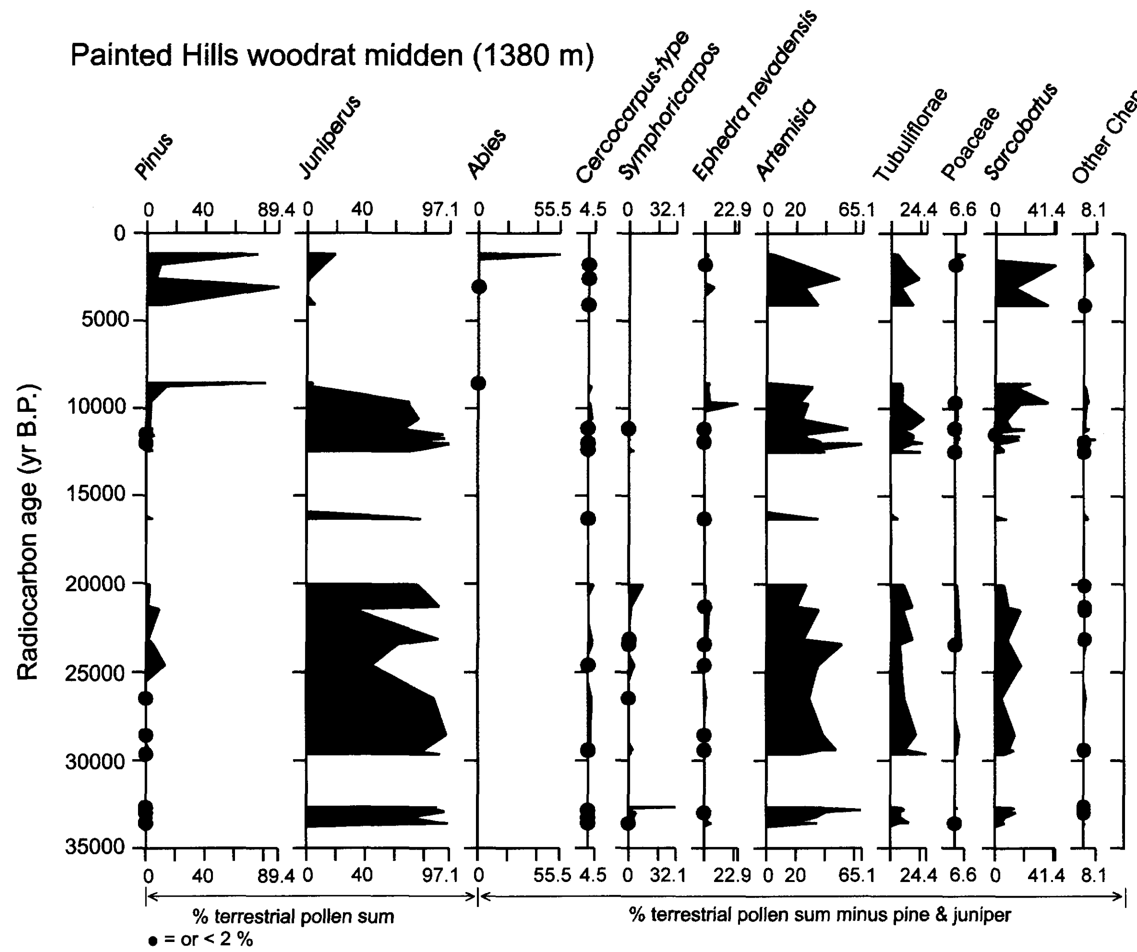

FIGURE 7.—Relative percentage diagram of major pollen types from a single stratified woodrat midden near Pyramid Lake, western Nevada (elevation, 1380 m). Dates are radiocarbon-based. A bullet (•) indicates a value of ≤2%.

LATEST PLEISTOCENE/EARLY HOLOCENE (12.5 TO 8 KA)

This period is characterized by often incredibly diverse plant communities that contained species typical of the cooler conditions of the glacial period along with pioneering plant species that heralded the Holocene. Mehringer (1985) noted several characteristics that tied many of these plant communities together during this time, especially at the higher elevations and in the more xeric areas of the northern Great Basin. This includes (1) a treeless sagebrush steppe, often with abundant grass; (2) common occurrence of russet buffaloberry (*Shepherdia canadensis* (L.) Nutt.), occasionally juniper (probably common juniper), and more rarely spruce and fir; (3) combinations of pollen types such as *Rumex–Oxyria, Bistorta, Polemonium, Eriogonum,* and *Koenegia* that indicate subalpine or alpine plant communities; and (4) abundance of the spores of cold-climate plants such as *Selaginella densa, S. selaginoides, Botrychium,* and *Lycopodium*. For example, the pollen record from 2250 m at Fish Lake near Steens Mountain, Oregon, reflects the substantially colder conditions of the transition from the late Pleistocene to the early Holocene. The pollen record is dominated by sagebrush (*Artemisia*) and grass (Poaceae), which are representative of a cool, moist steppe (Mehringer, 1985). It also contains juniper pollen, which may signal the movement of common juniper from its lower elevation distribution during the Pleistocene to its new Holocene position high atop the mountain (Mehringer, 1985). By 9.7 Ka the last glacial ice remnants disappeared from the high, southeast-facing cirque basin near the top of Steens Mountain that became Wildhorse Lake (2560 m). Common juniper was probably established in the surrounding subalpine grassland that had replaced the snow and ice of the Pleistocene (Mehringer, 1985, 1986). The departure of ice from this basin and initiation of the lake may record, in part, the impact of the early Holocene thermal maximum.

The 9000-year-long pollen record from Bicycle Pond in the Warner Valley, south-central Oregon, indicates that the current lower limit of western juniper on the west-facing slope of Hart Mountain was probably dominated by a grassy, sagebrush steppe 9 Ka (Figure 8). Juniper, though present then, was less abundant than today. Although scattered pine trees may have occurred in nearby canyons, pine woodland probably lay where it does today: around the tops of the mountains lying west of the Warner Valley and in the west-facing canyons and on the east slope of Hart Mountain. The aquatic pollen record suggests that throughout the Pleistocene, Bicycle Pond was fed by a seasonal stream and springs that flowed from the layered basalts that composed the mountain above it. Bicycle Pond is cradled by a steep-sided, Pleistocene landslide basin that restricts littoral plant growth to a narrow margin. The well-drained slopes behind the littoral margin support a grassy, sagebrush steppe, which extends a couple of hundred meters to the floor of the Warner Valley. Grass pollen values that were higher in the early Holocene than today reflect a wetter environment then; and abundant sedge pollen (Cyperaceae) from that period indicates that the marsh around Bicycle Pond was much more extensive then than it is today and reflects substantial early Holocene spring activity.

At lower elevations, the early Holocene expansion of sagebrush steppe vegetation is matched by expansion of saltbush-dominated desert scrub vegetation before the fall of Mazama ash (see Chenopodiineae values in Figure 8). The climax of saltbush scrub vegetation before and after the fall of Mazama ash is clearly evident in the pollen records from the Warner and Chewaucan valleys analyzed by Hansen (1947). Analysis of pollen from sediments in the Alkali Lake Valley in south-central Oregon, undertaken by one of the authors (Wigand), indicates that marshes (abundant sedge pollen) were present in the valley floor until ~9.5 Ka but disappeared soon after to be replaced by saltbush-dominated shrub communities. Gehr (1980) and Dugas (1998) recorded a series of radiocarbon dates between 9.6 and 7.4 Ka on mollusks from beach ridges and charcoal that indicated multiple pluvial highstands of Lake Malheur including some within five meters of its overflow into the Snake River drainage at Malheur Gap. The latter of these lakes may have been considerably lower. Mehringer and Cannon (1994) recorded a wet episode in the Fort Rock Basin, dating to around the fall of Mazama ash. In any case, generally drier conditions resulted in the establishment of saltbush communities by the time that Mazama volcanic ash fell in the region.

The pollen record from Fish Lake indicates that sagebrush steppe had expanded, becoming denser during the climatic warming of the early Holocene on Steens Mountain (Mehringer, 1985, 1986). This climaxed shortly before the fall of Mazama volcanic ash.

Further south in northwestern Nevada, the persistence of Utah juniper during the early Holocene at lower elevations (below where it occurs today) ended ~9.5 Ka. Radiocarbon (^{14}C) dates for Utah juniper of 9640 ± 110 years B.P. (Beta-46256) and 9700 ± 90 years B.P. (Beta-46255) record the last time that it appeared during the early Holocene beyond its current distribution west of the Lahontan Basin. These dates correspond directly with the last dates on lithoid tufa that Benson et al. (1995) obtained from Pyramid Lake (Pelican Point), suggesting that retreat of juniper and dramatically lowered lake levels are contemporaneous and coincide with high northern hemisphere solar radiation during the early Holocene (Kutzbach and Guetter, 1986; Kutzbach et al., 1993). In areas more distant from the current margin of the semiarid woodland, juniper may have disappeared as much as a thousand years earlier.

Radiocarbon dates for Utah juniper from woodrat middens on the southwest margin of the Smoke Creek Desert, northwestern Lahontan Basin, suggest that it disappeared from that area by 10.3 Ka. A cluster of these dates ranging from 10,830 ± 100 years B.P. (Beta-47200) to 10,340 ± 210 years B.P. (Beta-35814) are the last from that area until a late-Holocene reexpansion of juniper.

As juniper was disappearing from areas it occupied during the Pleistocene, it was expanding northward into new areas. The

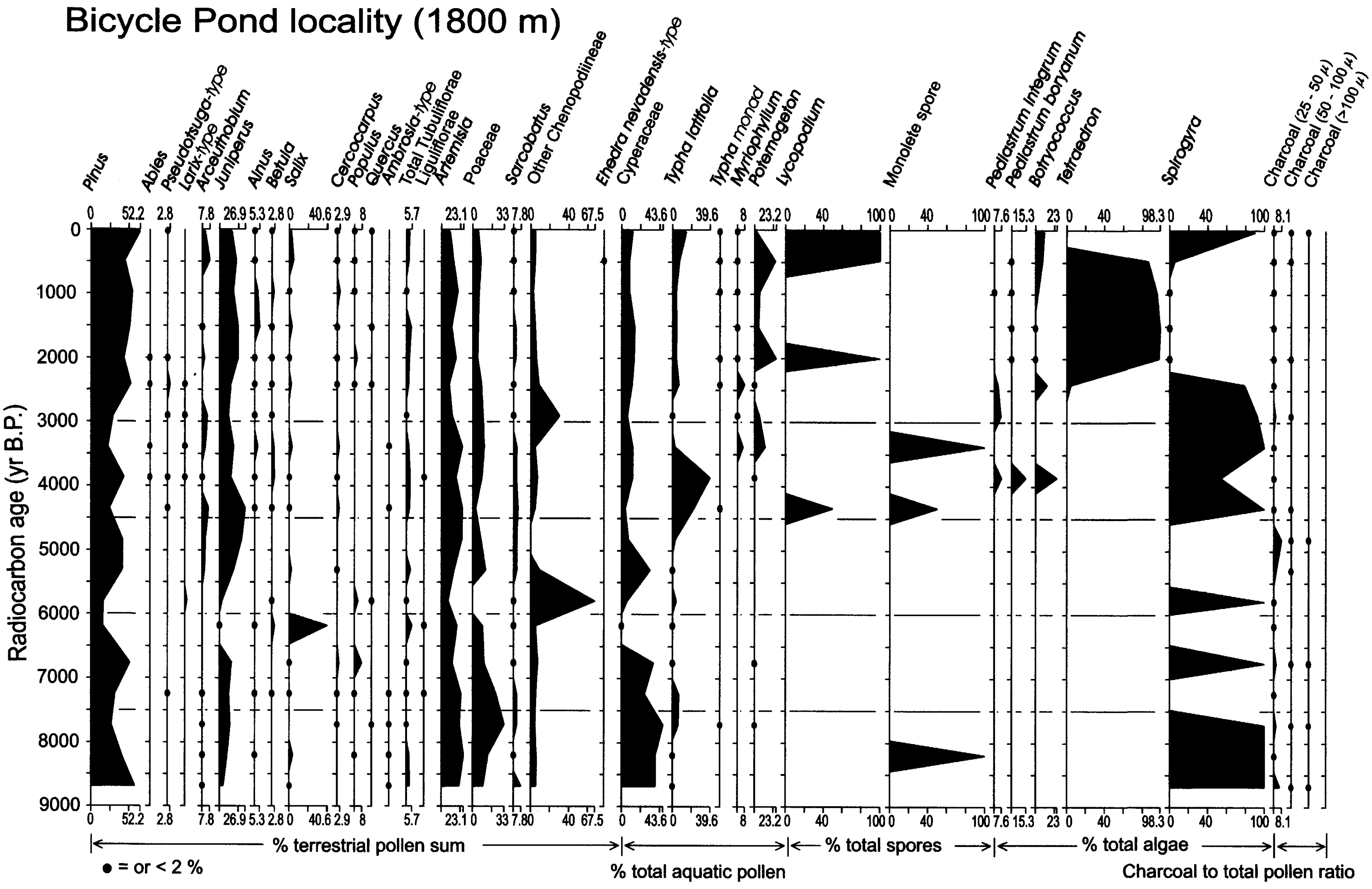

FIGURE 8.—Relative percentage diagram of major pollen, spore, and algae types and charcoal from Bicycle Pond, Warner Valley, south-central Oregon (elevation, 1800 m). Samples were dated based on a deposition rate curve generated from a polynomial fit on three radiocarbon-based dates. A bullet (•) indicates a value of ≤2%.

presence of semiarid juniper woodland in the northwestern Great Basin by ~8.5 Ka is evidenced by juniper pollen values in pollen records from McCoy Flat in northern California and from Bicycle Pond on the west slope of Hart Mountain in the Warner Valley, south-central Oregon (Figures 6, 8). This is further corroborated by directly dated Utah juniper twigs from woodrat middens in the Jackson Range of northern Nevada with a date of 8490 ± 90 ^{14}C years B.P. (Beta-64360). Although we know from the pollen records mentioned above that juniper occurred in south-central Oregon, no macrofossils have been recovered that indicate the species. This is the earliest species identification for the area.

The pollen record from Hidden Cave in the Carson Sink also reflects the early Holocene decline of woodland and expansion of desert shrub vegetation at the expense of sagebrush steppe (Wigand and Mehringer, 1985). Although the high lakes had disappeared from the Lahontan Basin by 11.0 Ka, cattail (*Typha*) pollen in Hidden Cave sediments indicates that extensive marshes remained until about 9.6 Ka (Wigand and Mehringer, 1985, fig. 36). The pollen record indicates that dramatic regional decline in pine and sagebrush and equally dramatic increases in greasewood characterized this period. The ongoing effects of regional drought at low elevations are reflected in the fourfold increase in Chenopodiineae (primarily saltbush) pollen in Hidden Cave sediments by ~9.0–8.0 Ka, levels that would characterize the remainder of the Holocene. Additional evidence of desiccation of the lake basin is indicated in analysis of the sediments from the cave.

Statistical parameters of grain size analysis of Hidden Cave sediments conducted by P.J. Mehringer, Jr. (see Wigand and Mehringer, 1985), in the late 1970s indicate that between 7.5 and 5.5 Ka the energy of colluvial processes was declining as the energy of early Holocene storms was waning (Figure 9). However, eolian processes (indicated by more-positive skewness of sediments) were increasingly more active during this period of transition in the Lahontan Basin (Figure 9). Although the colluvial contribution to transportable sediment was declining during this transitional period, the regional reduction in plant cover

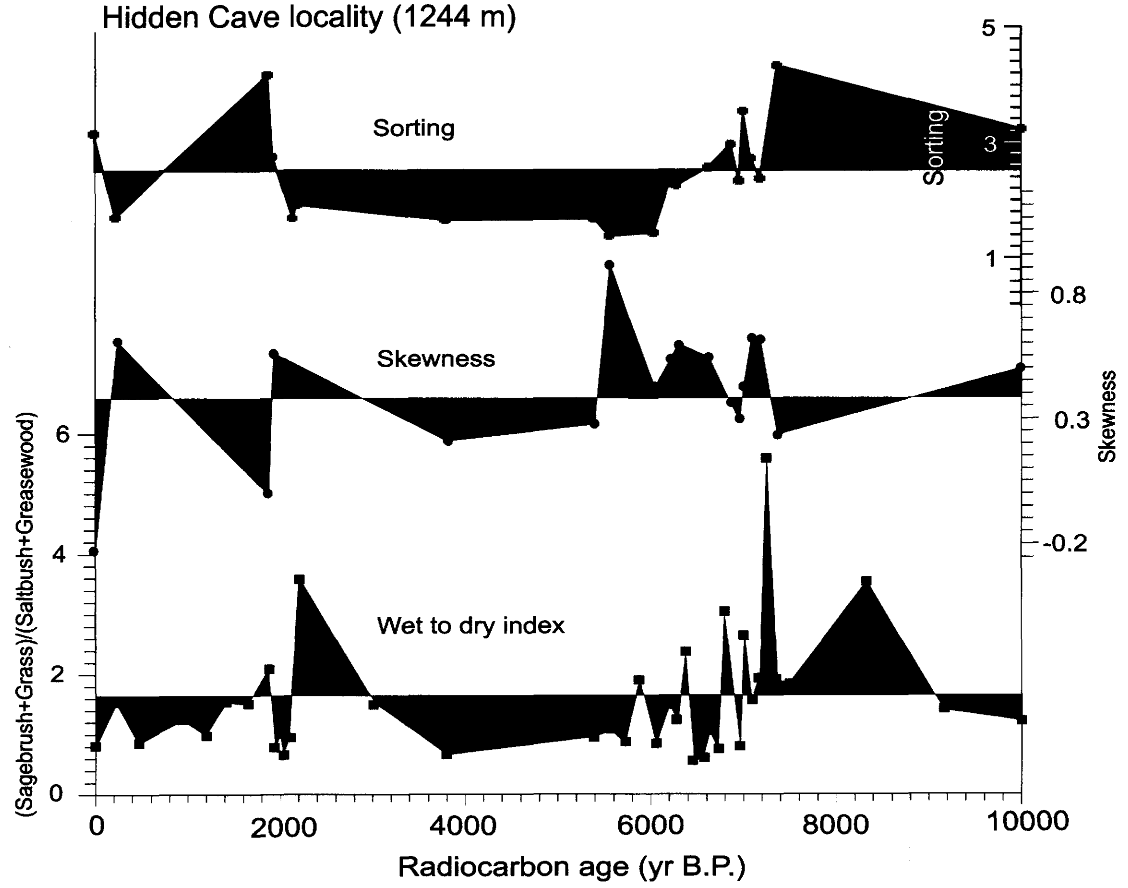

FIGURE 9.—Wet-to-dry index, (sagebrush + grass pollen)/(saltbush + greasewood pollen), generated with sediment pollen data from Hidden Cave in the Carson Sink, Nevada, compared with the skewness and sorting of Hidden Cave sediments; the latter two are statistical parameters derived from grain-size analysis and can be related to understandings of erosional and depositional processes. Skewness is used as a measure of eolian activity, and sorting is used as a measure of the amount of energy in the medium that moved sediment. "Up" on the drought index indicates wetter climate, up on the skewness index indicates greater eolian activity, and up on the sorting index indicates greater energy in the medium that was moving sediment. Sample dates were based on deposition rates extrapolated from radiocarbon dates (Davis, 1985).

density in response to drought was exposing large areas to eolian erosion (Figure 9). The pollen record from Lovelock Cave (Byrne et al., 1979) corroborates these trends. The general correspondence between the Hidden Cave and Lovelock Cave pollen records is close.

Preliminary pollen analyses of human fecal material, removed from the 9400-year-old Spirit Cave burial site in the Carson Sink of west-central Nevada, corroborate the environmental reconstruction (Wigand, 1997a). (The cave contained the partially mummified body of a man, the Spirit Cave Man, 5'2" tall and about 40–50 years old.) The fecal material was composed almost entirely of the remains of small fish (Eiselt, 1997). However, a very low pollen background in the samples may have mirrored the regional pollen rain. The pollen may have found its way into the fecal material through residues present on plants eaten by the early Nevadan or may have entered through the stomachs of the fingerlings that were ingested. Fish may have eaten the pollen as it floated on the water surface of the marsh during flowering time (suggested by P.J. Mehringer, Jr.). This pollen record is statistically identical to pollen of the same age recovered from nearby Hidden Cave (Wigand, 1997a). It reflects a saltbush-dominated environment with evidence for persistent marshes and eolian habitats. Comparison of the drought index from Hidden Cave with one produced from the Hogup Cave pollen record analyzed by Kelso (1970) indicates that this was a regional pattern at low elevations across the northern Great Basin (Figure 10).

Today the McCoy Flat area comprises a mosaic of mixed-conifer-forested, Late-Tertiary/early Pleistocene volcanic cones that rise above a lattice of wide, low-grade stream valleys dominated by sagebrush steppe. The pollen record from McCoy Flat indicates that by the early Holocene a regional decline in pine and juniper woodland corresponded to an increase in steppe dominated by sagebrush and rabbitbrush (*Chrysothamnus*-type pollen) (Figure 6). An increase in grass values at this time, corresponding to the increase seen at Bicycle Pond and in

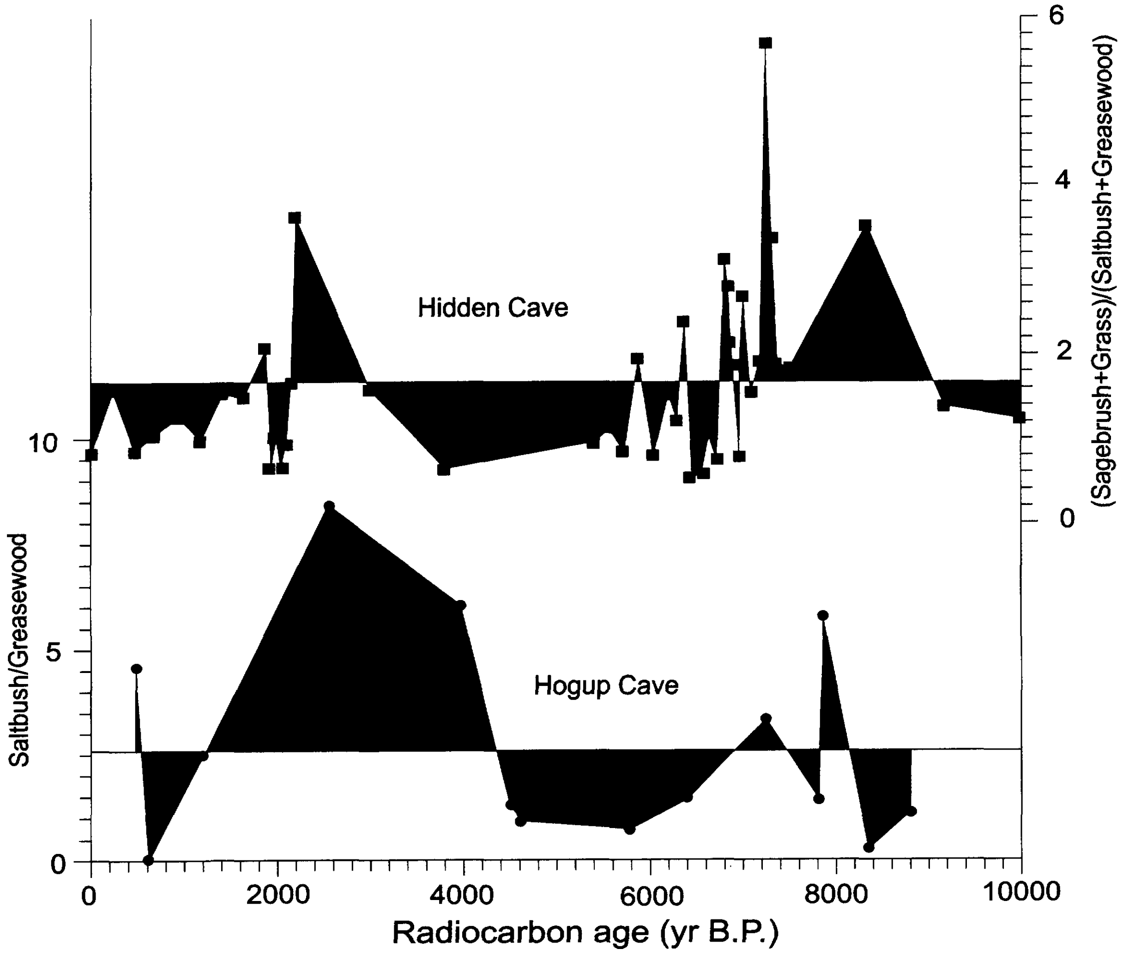

FIGURE 10.—A comparison of two drought indices generated from pollen analyses of sediments obtained from Hidden Cave in the Lahontan Basin, Nevada (Wigand and Mehringer, 1985), and Hogup Cave in the Bonneville Basin, Utah (Kelso, 1970). Up indicates wetter climate. Differences between the two records primarily reflect sample spacing and error introduced through extrapolation of sample ages from radiocarbon-based dates.

the midden pollen record from Pyramid Lake, may reflect a regional response to increased rainfall in late spring or early summer, an increase also hinted at in vegetation records further south and east in the Great Basin. Increased cattail pollen in the record may simply reflect decreased competence of the local stream, which was now filling the deep channel cut that had characterized Pine Creek during the Pleistocene.

MIDDLE HOLOCENE (8 TO 5.5 KA)

The McCoy Flat and Bicycle Pond records indicate that by the beginning of the middle Holocene the retreat of juniper woodland and the expansion of sagebrush steppe had reached a climax (Figures 6, 8). Both of these records also indicate that saltbushes (Chenopodiineae pollen) were regionally more important than they had been before. The decline of grass in the McCoy Flat record reflects the middle-Holocene drought.

At Steens Mountain, the Fish Lake pollen record indicates that sagebrush steppe became the dominant vegetation at elevations lying above the juniper woodland zone (Mehringer, 1985). Sagebrush pollen to grass pollen ratios from Fish Lake indicate that the climate that typified the period between 8.8 and 5.6 Ka was the driest to occur there during the Holocene (Mehringer, 1986). The Wildhorse Lake record evidences the arrival of sagebrush steppe by ~8 Ka (Mehringer, 1986). It was to remain dominant at these elevations until about 3.8 Ka. In southern Oregon, dry pluvial lake basins are indicated by dune deposits dated to this period, including ones in the Catlow Valley at Skull Creek (Mehringer and Wigand, 1986), Fort Rock Valley (Mehringer and Cannon, 1994), and the Malheur Valley (Dugas, 1998).

The all-pervasive drought of the middle Holocene is reflected in the dearth of paleobotanical records throughout the northern Great Basin at low elevations and especially around the Lahontan Basin. The almost continuous midden record that exists in the Painted Hills on the west shore of Pyramid Lake is interrupted for almost 4000 years, from ~8 to 4 Ka (Wigand and Nowak, 1992). Juniper macrofossils disappear from woodrat middens lying 200 m above the early and late-Holocene lower elevational limits of juniper evidenced in the woodrat midden record. This suggests that juniper retreated upward in elevation by at least 200 m or more above its current distribution during the middle Holocene.

The Hidden Cave pollen record indicates dominance of saltbush shrub communities in the margins of the Lahontan Basin (Wigand and Mehringer, 1985). Statistical parameters generated from the grain size analysis of Hidden Cave sediments indicate that transport of sediment through eolian (less positive skewness) and colluvial (better sorting) processes in the Carson Sink had declined substantially (Figure 9). The near absence of evidence of high-energy colluvial transport may have resulted from the rarity of high-energy storms in the Lahontan Basin. Reduced colluvial transport despite the reduced vegetation cover indicates that rainfall was at a minimum, especially during the summer. The dramatic reduction in eolian activity may be attributable to the depletion of transportable materials in the basin. Because colluvial and fluvial activity was at a minimum, there was a reduction in the material that would have been available for eolian transport. A comparison of the Hidden Cave drought index with one generated from the pollen record of Kelso (1970) from Hogup Cave in northwestern Utah suggests that widespread drought characterized much of the northern Great Basin (Figure 10). Pyramid Lake may have reached its lowest level at this time (Born, 1972).

Woodrat midden evidence from the White Mountains on the California–Nevada border indicates that middle-Holocene drought displaced semiarid woodlands upward in elevation by as much as 300–500 m (Jennings and Elliot-Fisk, 1993). Taken together with the evidence from the Lahontan Basin, it appears that this displacement may have characterized large portions of the western Great Basin (Wigand and Nowak, 1992).

Upward woodland displacement in this area coincides with the age of drowned trees found 10–15 m below the modern surface of Lake Tahoe. These trees became established in the Tahoe Basin during periods of intense, long-duration drought ~6.5 Ka (Lindström, 1990). Throughout the northern Great Basin lakes and marshes desiccated and pollen of drought-tolerant salt desert species increased substantially (Wigand, 1987; Mehringer and Wigand, 1990). At Diamond Pond south of Lake Malheur in south-central Oregon, greasewood pollen reached levels of 80% of the terrestrial pollen, whereas currently it makes up less than ~20% of the modern pollen record. These changes coincided with dramatically reduced evidence of the activities of Native American populations (Grayson, 1993). This is consistent with a decline in foraging resources and corroborates the severity of this drought (Aikens, 1986).

EARLY LATE HOLOCENE (5.5 TO 2 KA)

Beginning ~5.4 Ka, the extreme drought of the middle Holocene came to an end. Temperatures remained warm, but pollen and macrofossil data indicate gradually increasing annual precipitation punctuated by periodic increases in rainfall abundance (Davis, 1982; Mehringer, 1986; Wigand, 1987). A brief, extremely dramatic climatic event that can be correlated from the Columbia Plateau of eastern Washington to the spring deposits of Ash Meadows in the northern Mojave Desert effectively signals the end of the middle Holocene in the intermountain West.

Evidence for this panregional event begins in the north at Wildcat Lake in eastern Washington. At 5.4 Ka, the deposition of reworked Mazama ash in the lake sediments suddenly ended (Peter J. Mehringer, Jr., pers. comm. to Wigand, 1978). This indicates that vegetation density on the landscape became great enough to prevent the resuspension of the volcanic ash either by wind or water. This increase in vegetation density probably directly reflects a dramatic shift toward greater rainfall.

At Diamond Pond in south-central Oregon there was a shift from dry-climate pollen assemblages to much more mesic assemblages (Wigand, 1987). Just after 5.4 Ka, pollen spectra that previously had been dominated by as much as 80% greasewood pollen were instead characterized within a few decades by as much as 40% sagebrush pollen. Although a shift back toward drier climate occurred during the next 1400 years, the conditions that characterized the period before 5.4 Ka never reoccur.

This event is also noted in the Tahoe Basin on the west-central margin of the Great Basin, where montane forests were so rapidly submerged beneath the cold waters of Lake Tahoe at 5.5 Ka that they had no opportunity to decay (Martin Rose, pers. comm. to Wigand, 1995). An 8000-year-long tree ring record of a bristlecone pine (*Pinus longaeva* D.K. Bailey) from Methuselah Walk in the White Mountains reveals this same rapid shift in climate that ended a period of drought that may have lasted as long as 1500 years (Graybill et al., 1994). The paleolimnological record from Walker Lake, the southernmost subbasin of ancient pluvial Lake Lahontan, indicates that the Walker Lake basin, which had been a dry playa, was refilled by ~4.7 Ka (Bradbury et al., 1989). This probably resulted from wetter conditions at this time, but it also may have been caused by a shift in the course of the Walker River from the Carson Basin to the Walker Basin. This shift, however, also may have resulted from changes in the Walker River alluvial process precipitated by a change in climate.

The shift to wetter conditions at ~5.5 Ka had other ramifications as well. It initiated the reexpansion of woodlands and montane forests. The earliest evidence of western juniper reported in its historic range of northeastern California and eastern Oregon are twigs from ancient woodrat middens at Lava Beds, California (5.4 Ka), and Diamond Craters, Oregon (4 Ka) (Mehringer and Wigand, 1987, 1990).

Just east of the Tahoe Basin, a 3.5 meter core (unpublished) recovered from a bog north of Little Valley, Nevada, revealed responses of both local montane forest and regional semiarid woodland and sagebrush steppe to climate change since ~6.3 Ka, when the pond formed (Figure 11). Little Valley is on the east slope of the Sierra Nevada near the lower edge of the montane forest. Across the valley to the east lie the piñon- and juniper-dominated ranges of the Great Basin. Cluster analysis of the Little Valley core pollen reflects the shift from dry middle-Holocene conditions to more mesic late-Holocene conditions. Local sagebrush predominance between 6.3 and 5.6 Ka (Zone I) indicates relatively more xeric conditions than any of the succeeding periods. A retreat of sagebrush and an increase in pine and juniper initiated a period of more mesic climate between 5.6 and 4 Ka (Zone II) (Figure 11). Sedges probably dominated the margins of the pond during both periods. Two more mesic periods occurred between 5.6 and 4 Ka, when fir may have first expanded into the valley from above. This period corresponds with the drowning of low-lying trees in the Tahoe Basin by rising lake levels. Between 4 and 1.9 Ka (Zone III), major downward expansions of fir (both red fir, *Abies magnifica* A. Murr., and white fir, *A. concolor* (Gordon & Glend.) Lindl. ex Hildebr.) into Little Valley occurred (Figure 11). Abundant sedge pollen at this time records filling of the pond and generation of sedge peat. In addition, alder (*Alnus*), birch (*Betula*), and willow (*Salix*) pollen evidences the establishment of these taxa in mesic communities in Little Valley. This period was clearly cooler and more mesic than those that preceded or followed it. Local fire severity seems to have increased substantially between 5.6 and 4 Ka, perhaps in response to the greater availability of fuel. After 3 Ka, fire severity appears to have declined substantially.

Expansions of juniper woodland into areas at elevations lower than where it is currently found in the northern Great Basin are recorded in the Diamond Pond juniper pollen record and by western juniper macrofossils from woodrat middens in Diamond Craters east of Diamond Pond (Wigand, 1987; Mehringer and Wigand, 1990). Expansion of western juniper woodland into the lower elevation sagebrush steppe began about 4.5 Ka (Wigand, 1987). The rate of juniper woodland expansion increased dramatically ~3.7 Ka and again 2.7 and 2.3 Ka. Except for two lapses, western juniper woodland remained near this lower elevational limit (~150 m below its current extent) until about 1.9 Ka (Wigand, 1987; Mehringer and Wigand, 1990). Broad Neopluvial expansion of pine in the woodlands on the northernmost boundary of the Great Basin is recorded in the Craddock Meadow, Oregon, pollen record (Wigand, 1989). Further south a pollen record from Potato Canyon Bog in Grass Valley, central Nevada, also shows evidence of expansion of semiarid woodland during this period (Madsen, 1985). Three episodes (~3.7, 2.7, and ~2.3 Ka) of fir expansion at Little Valley (Figure 11) mirror the episodes of moister climate revealed at Diamond Pond as well. Together these data reflect a pattern of forest and woodland expansion that occurred throughout the entire northern and western Great Basin.

These episodes are characterized not only by the expansion of both forests and woodlands, but also by a regional rise in the water table and a reexpansion of lakes and marshes (Wigand, 1987; Grayson, 1993). Even the record from Walker Lake indicates deep lake levels between 4 and 2.9 Ka (Bradbury et al., 1989, fig. 11). Although lake levels had fallen by 2.2 Ka, the absence of dated samples between 2.9 and 2.2 Ka leaves lake level elevation during that period in question. In general, climates in the northern Great Basin during the Neoglacial or Neopluvial from 4 to 2 Ka were cooler and substantially wetter, with winter precipitation dramatically increased relative to summer precipitation (Davis, 1982; Wigand, 1987).

Although macrofossils indicate the presence of western juniper at lower elevations than its current distribution, juniper pollen values from Diamond Pond indicate that juniper woodlands at the lower elevations during this Neopluvial expansion were less dense than those currently found in the area (Wigand, 1987). Recent analyses of $\delta^{13}C$ in western juniper twigs and Utah juniper twigs from ancient woodrat middens indicated that water stress—either as a result of drought or frequent freezing

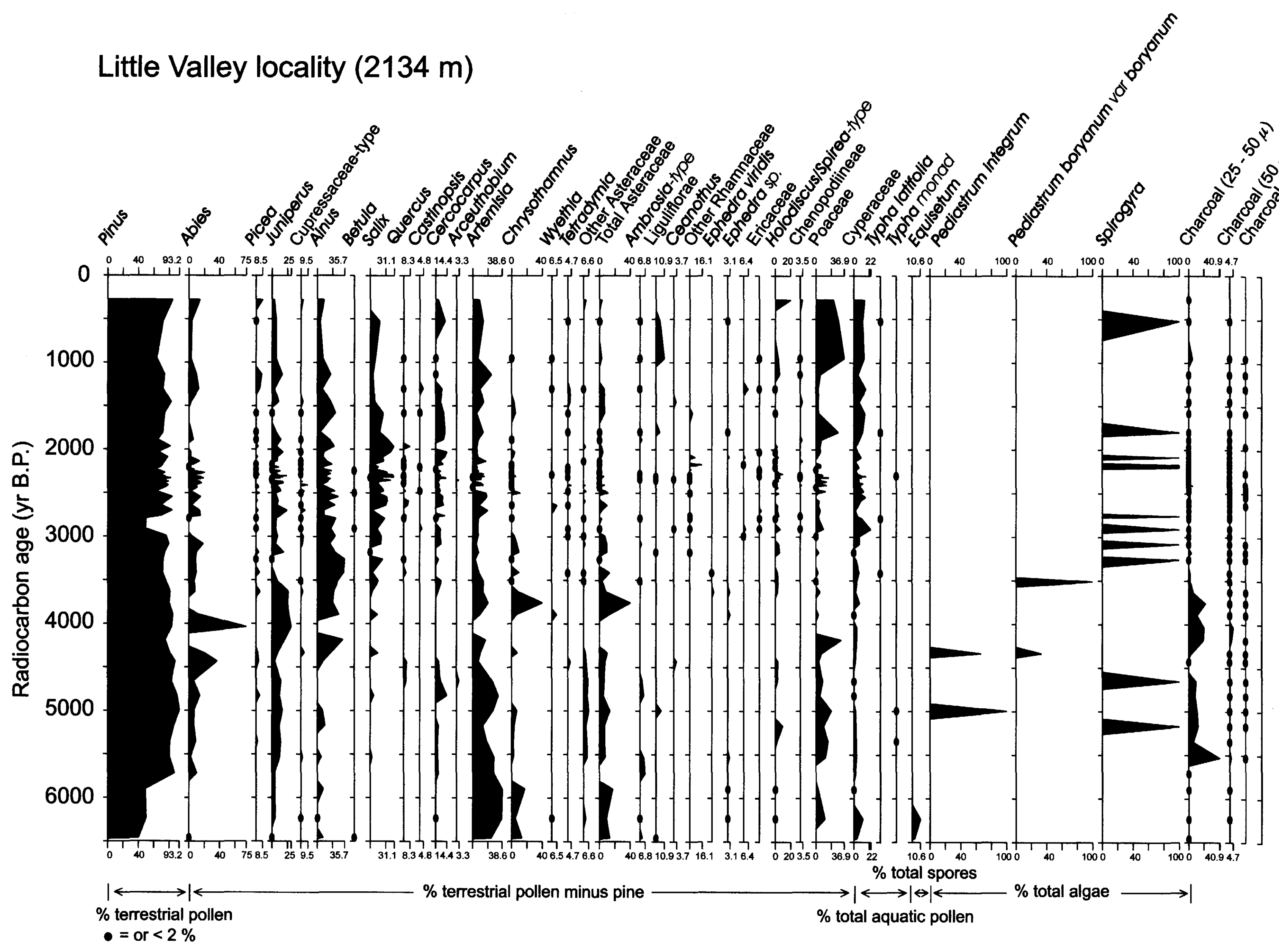

FIGURE 11.—Relative percentage diagram of major pollen, spore, and algae types and charcoal from Little Valley, Nevada (elevation, 2134 m), on the east slope of the Sierra Nevada east of Lake Tahoe. Samples were dated based on a deposition rate curve generated from a polynomial fit on seven radiocarbon-based dates. A bullet (•) indicates a value of ≤2%.

during the growing season—typically affected the condition of juniper during the Neopluvial (Wigand, 1995).

Intermediate-elevation juniper woodland was at least as thick or thicker than it is today (Davis, 1981). Based upon modern studies, the more mesic conditions of the Neopluvial brought on by a combination of increased rainfall and lowered summer temperatures probably resulted in closer spacing of trees and more foliage near the middle elevational distribution of juniper (Fritts and Xiangdig, 1986; Miller and Wigand, 1994).

Juniper pollen values at Fish Lake on Steens Mountain indicate that although a late middle-Holocene upward elevational shift in juniper occurred when conditions were still warm but increasingly wet, lower juniper pollen values during the succeeding Neopluvial period suggest that the upper tree line of juniper dropped in elevation (Mehringer, 1985, 1987; Mehringer and Wigand, 1987). The colder temperatures that seem to have characterized this period probably limited juniper expansion at higher elevations.

Periodic increased abundance of grasses relative to sagebrush and saltbushes during this period indicate that the broad areas lying around Diamond Craters, which today are dominated by desert scrub vegetation, may have been characterized by a grassy, sagebrush steppe. A dramatic reduction in desert shrub vegetation was also caused by marshland expansion into areas previously dominated by greasewood and saltbushes (Wigand, 1987; Mehringer and Wigand, 1990). This pattern probably characterized much of the northern and western Great Basin.

Increased abundance of grass pollen coincident with woodland expansion also mirrors the presence of a vigorous herbaceous understory and of occasional fire episodes. Three very pronounced grass pollen increases at Diamond Pond are closely tied to preceding charcoal events between 4 and 2 Ka and are evidence of dramatic local grass expansion after fire (Miller and Wigand, 1994). Although climatic conditions favored juniper growth at middle elevations and expansion at lower elevations during this period, the charcoal recovered from Diamond Pond cores evidences frequent drought-driven local and regional fires. The fuels that accumulated from the abundant herbaceous understory promoted fire and probably helped maintain the low density of the lower elevational juniper woodlands—the point in its distribution where juniper would be stressed the most when droughts occurred (Wigand, 1987; Miller and Wigand, 1994). Periodic, regional megadroughts resulted in extensive fires that characterized both the lower and middle elevational distribution of juniper woodland in the Great Basin during the Neopluvial (Wigand, 1987).

MIDDLE LATE HOLOCENE (2 TO ~1 KA)

After the Neoglacial ~1.9 Ka, the Great Basin climate generally became warmer and drier (Davis, 1982; Wigand, 1987; Wigand and Rose, 1990; Wigand and Nowak, 1992). Juniper pollen values in the northwestern Great Basin declined dramatically relative to shrubs and grasses (Wigand, 1987). In addition, the shift in the ratio of coarse to fine charcoal when compared with the changes in the dominant vegetation type at Diamond Pond clearly reflect the change from juniper woodland to shrub steppe fuels (Wigand, 1987).

At Fish Lake an increase in big sagebrush pollen relative to grass pollen reflects decreased grass in response to drier conditions and was probably characteristic of the upper sagebrush zones of the northern Great Basin (Mehringer, 1987). An increase in desert scrub vegetation, indicated by increasing saltbush and greasewood pollen at Diamond Pond, provides additional evidence for increasing local and regional aridity, particularly between 1.9 and 1 Ka (Wigand, 1987). Pollen and macrofossils of aquatic plant species at Diamond Pond, Oregon, indicate that water levels had dropped substantially since the Neoglacial (Wigand, 1987).

At Little Valley, the pollen record from 1.9 Ka to the present (Zone IV) exhibits local retreat of fir, alder, birch, and willow indicating more xeric conditions (Figure 11). Increased grass and retreat of juniper during this period may reflect the shift to increased summer rainfall seen elsewhere in the northern Great Basin and also in the southern Great Basin and northern Mojave Desert (see below). Pine increases may relate to the regional expansion of piñon pine evidenced in woodrat middens between 1.5 and 1.1 Ka (and again after 0.4 Ka) (Wigand, 1997b; and see below).

An unpublished pollen record from Lead Lake in the Carson Sink records terrestrial and aquatic vegetation dynamics for the central Great Basin during the last 2200 years. The major trend for the last two millennia has been the decline in greasewood while marsh species became more dominant. The decline of greasewood is matched by increases in pine, sagebrush, and grass (Figure 12). Higher values of broadleaf cattail (*Typha latifolia* L.) and narrowleaf cattail (*Typha angustifolia* L.), indicating shallow marsh conditions, occurred between ~2.2 and 1.5 Ka. The abundance of cattail (primarily broadleaf cattail) relative to sedge between 2.2 and 1.9 Ka probably reflects influxes of fresher water than before into the marshes. These episodes correspond to wetter events indicated in the Diamond Pond record as well (Wigand, 1987). Increasing pondweed (*Potamogeton* sp.) pollen values beginning ~1.9 Ka and decreasing dramatically after ~0.8 Ka reflect slightly deeper water conditions. Renewed abundance of narrowleaf cattail after 0.8 Ka indicates renewed expansion of marsh in the Carson Sink. Ratios of the more abundant pollen types reflect these trends more clearly (Figure 13). The decline of juniper relative to sagebrush probably reflects warmer, drier conditions following the end of the Neopluvial. Increasing sagebrush relative to saltbush is the result of marsh expansion into areas previously occupied by saltbush communities. The predominance of emergent aquatic plants relative to littoral plant species indicates slightly deeper water conditions in the marsh between 1.9 and

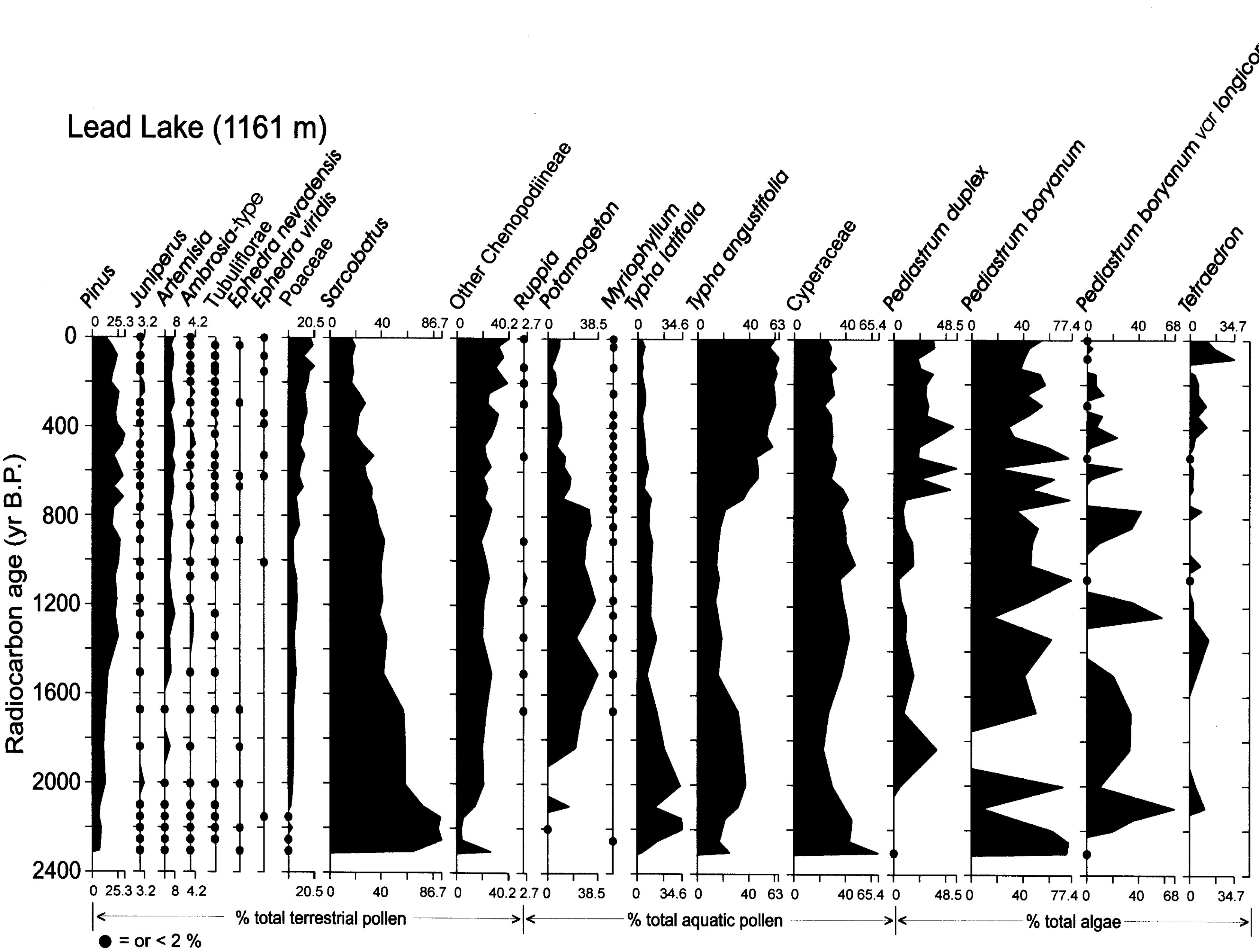

FIGURE 12.—Relative percentage diagram of major terrestrial and aquatic pollen and algae types from Lead Lake, Carson Sink, west-central Nevada. Samples were dated based on a deposition rate curve generated from a polynomial fit on three radiocarbon-based dates. A bullet (•) indicates a value of ≤2%.

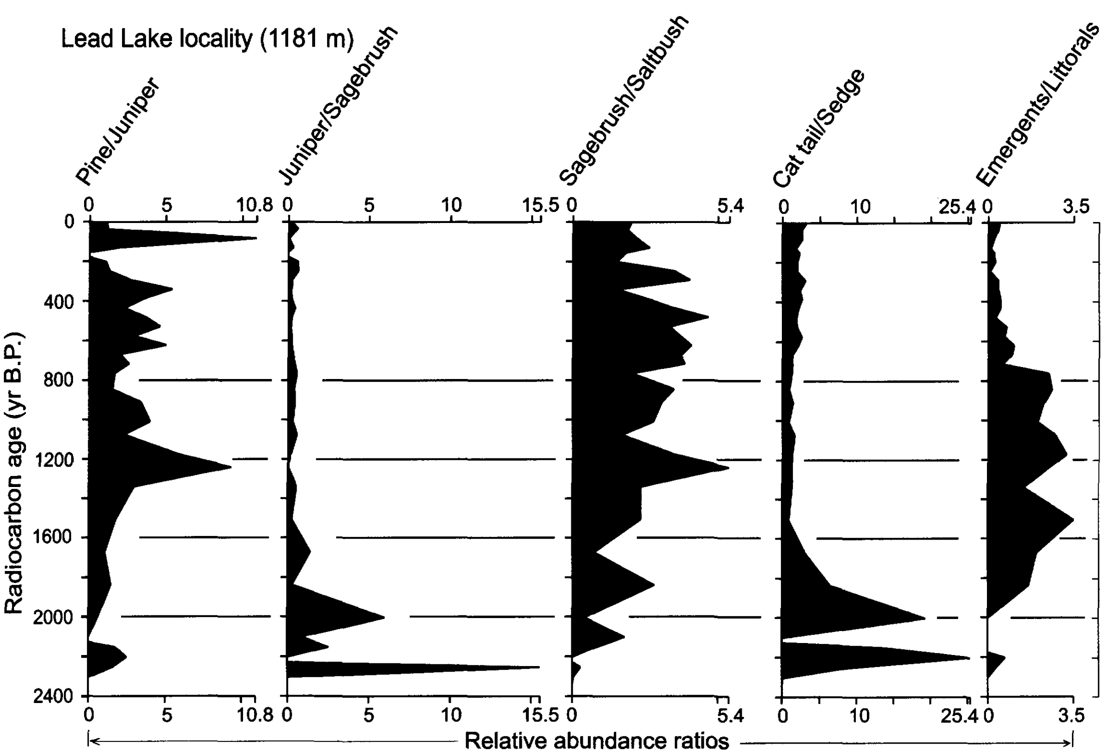

FIGURE 13.—Abundance ratios of major pollen types from Lead Lake, Carson Sink, Nevada. Samples were dated based on a deposition rate curve generated from a polynomial fit on three radiocarbon-based dates.

0.8 Ka (Figure 13). Deeper water at this time does not mean that climate was wetter. Other evidence (see below) suggests that, although annual precipitation remained relatively unchanged, a shift toward more rainfall in summer resulted in the persistence of deeper water conditions into the warm season, when high evaporation rates would normally have shrunken the marsh or dried it out. Increased abundance of pine relative to juniper between 1.4 and 0.9 Ka indicate that piñon pine became an important part of the semiarid woodland in the northwestern Great Basin at this time. Although piñon pine may have entered the area earlier, the woodrat midden evidence indicates that it became much more abundant upon the landscape. Macrofossils of piñon pine from woodrat middens throughout the Lahontan Basin indicate that it expanded both northward in latitude and downward in elevation (Wigand et al., 1995) (Figure 14).

This rapid change in piñon pine distribution was primarily triggered by increased rainfall throughout the summer, which

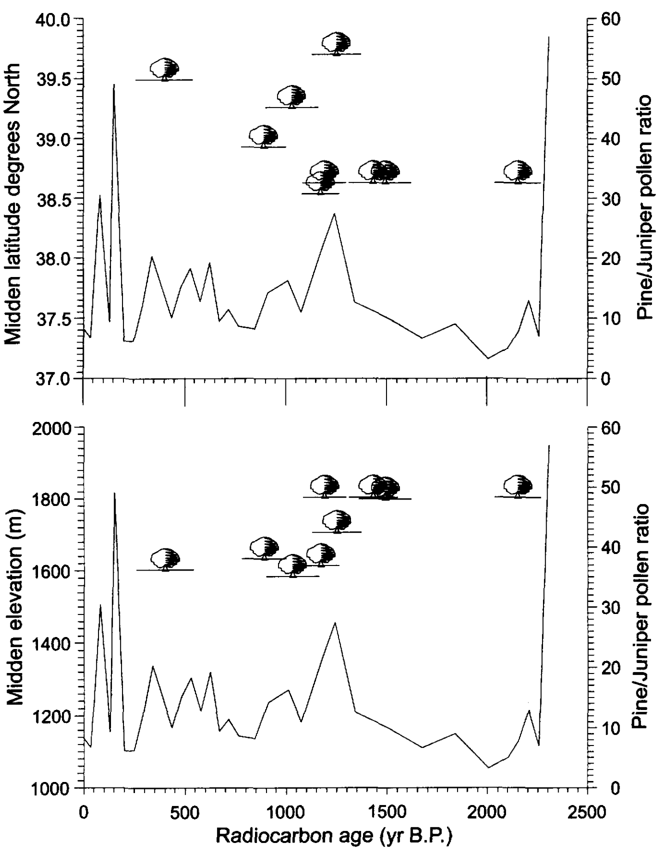

FIGURE 14.—Ratios of pine to juniper pollen (tree symbols) from Lead Lake plotted against (top) the latitudinal distribution and (bottom) the elevational distribution of directly dated juniper twigs (solid lines) from woodrat middens in the Reno, Nevada, area of the Lahontan Basin. Northward expansion of piñon pine during the last 1500 years is evident; and lower elevational distribution of juniper during the last 1500 years also is indicated. Samples were dated based on a deposition rate curve generated from a polynomial fit on three radiocarbon-based dates.

encouraged seedling establishment. However, this expansion probably would not have been possible without the milder winters that followed the end of the Neopluvial after 1.9 Ka. The pollen record from Lead Lake indicates that a contraction in semiarid woodland occurred in the area after ~1 Ka (Figure 13). This is borne out by the reduced numbers of woodrat middens in the area containing piñon pine and juniper (Figure 14).

At Diamond Pond in the Harney Basin of south-central Oregon, an early post-Neoglacial expansion of grass between 1.9 and 1.0 Ka overlaps with the piñon pine expansions seen at Lead Lake (Wigand, 1987; Wigand, 1997b). Western juniper, which during most of the record from Diamond Pond had varied in concert with grass, did not increase in abundance with grass during this period, indicating the occurrence of summer-shifted rainfall as well. That this expansion of grass was regional in nature is demonstrated by the dramatic increase of bison (*Bison* spp.) remains in archaeological sites of the northern intermountain West. Radiocarbon dates plotted with standard deviations on bison remains from archaeological sites in the northern Great Basin (Marwitt, 1973) and the plateau of eastern Washington (Schroedl, 1973) show remarkable coincidence with this period of grass expansion (Wigand, 1997b, fig. 10).

A substantial increase in juniper pollen values ~1 Ka in the northern Great Basin at Diamond Pond, coincident with local increased abundance of woodrat middens containing western juniper macrofossils, evidences a renewed expansion of woodland in the north and the end of grass abundance (Wigand, 1987; Mehringer and Wigand, 1990). This corresponds to increased large versus small charcoal values, indicating both a change in fuel type as well as more frequent fires as fuels accumulated in response to wetter climate (Wigand, 1987; Wigand et al., 1995). Dugas (1998) indicated that higher lake stands may have occurred in the Malheur Basin ~1 and ~0.8 Ka.

THE LAST MILLENNIUM IN THE NORTHERN AND WESTERN GREAT BASIN (<1 KA)

Evidence of severe drought and resultant fire in the northern, central, and southern Great Basin between ~0.9 and 0.5 Ka, confirmed by Sierran and Great Basin tree ring studies, coincide with a decline of the woodland (Holmes et al., 1986; Wigand, 1987; Wigand and Rose, 1990). The drought of the middle of the millennium is recorded in the expansion of saltbushes in the northern Great Basin and in evidence that Diamond Pond reached some of its lowest levels since the middle Holocene (Wigand, 1987). Reexpansion of marsh at Lead Lake evidences regional drying of the western Great Basin after 0.8 Ka (Figures 12, 13). Charcoal evidence from the cores at Little Valley indicates that fire frequency increased considerably after about 0.6 Ka (Figure 11). Destruction of the lower margin of the woodland appears as a sudden gap in the woodrat midden evidence of northern Nevada for this period (Wigand and Nowak, 1992; Figure 14). Stine (1990) reported that extended droughts were terminated about 0.9, 0.6, and 0.35 Ka by brief wet events.

The "Little Ice Age," a pattern of stronger winter precipitation and cooler temperatures beginning 300 to 400 years ago, terminated the droughts of the middle portion of the millennium and initiated a gradual reexpansion of juniper woodland in the northern Great Basin (Mehringer and Wigand, 1990). Further south in the central and southern Great Basin, increasing pine pollen values relative to juniper pollen values indicated that piñon pine benefited more from the shift toward mesic climate conditions (Wigand and Nowak, 1992; Wigand, 1997b). By the time Europeans first entered the area, climate-initiated reexpansion of Great Basin woodlands was well underway. In the northern Great Basin, increased occurrence of pine in the pollen record at Lead Lake during the last 0.15 Ka corresponds to the 2.5-fold increase in areal coverage of piñon pine after the Little Ice Age, as recorded in stand establishment records (Tausch et al., 1981).

The pollen record at Diamond Pond indicates increasing aridity since the end of the Little Ice Age. Juniper woodland retreated and sagebrush steppe advanced (Wigand, 1987). Grasses seem to have become less abundant throughout the region. A decrease in water depth in Diamond Pond reflects a regional drop in the water table in the Harney Basin (Wigand, 1987; Mehringer and Wigand, 1990). Lower frequency fluctuation of juniper pollen values in the early 1800s contrasts with the recent sharp increases since the middle 1900s (Mehringer, 1987; Mehringer and Wigand, 1990). Increased variability, in part, reflects a real expansion in woodland, but also it may reflect reduced sediment compaction. Fewer years are represented in each of the one-centimeter-high samples at the top of the core than in samples from lower down in the cores. As a result, interannual variability of pollen production in response to weather variation from year to year is not being averaged as much as it was lower in the record. This gives the impression of greater climatic variability when compared with earlier periods.

The post–Little Ice Age trend toward lower effective precipitation brought on by warmer mean annual temperatures combined with the spread of woodlands should have increased the potential for fire in the Great Basin. Despite increased drought stress on the trees in this semiarid region, the occurrence of fire decreased. This contradicts the prehistoric pattern of massive fires that typified periods when Great Basin woodlands were subjected to drought conditions—i.e., the end of the Neoglacial (Wigand, 1987).

Decreased fire frequency may have occurred, in part, because conditions were dry enough to keep the production of light fuels (i.e., grasses and forbs and even shrubs) low. On the other hand, Peter Skene Ogden noted abundant evidence of fires set by Native Americans in the Harney and Malheur lakes region during the middle 1820s (Davies et al., 1961). A decline in fire frequency as Native American populations declined and were displaced may have enabled the expansion of semiarid woodlands at the time of European settlement. Livestock grazing may also have played a role in decreased fire frequency through the reduction of fine fuels (see discussion in Miller and Wigand, 1994). Grazing may also have played a role in juniper expansion through seed dissemination and encouragement of shrubs that provided nursery areas for juniper seedling establishment.

Prehistorically, climate change was the primary factor affecting the expansion of semiarid woodlands. Droughts and resultant disturbance phenomena such as insect infestations, disease, and fire all contributed to periodic retreat of these woodlands. Since the arrival of Europeans, both climate change and human action have substantially affected woodland distribution. Drier climates during this century have resulted in increased physiological stress on plant communities. Fire suppression practices and the use of insecticides have disrupted normal cycles of disturbance phenomena such as fire, insect infestation, and disease. The resulting fuel build-up has increased the potential for intense, widespread fires.

Periods of wetter climate around 1910, the early 1940s, the late 1960s to early 1970s, and the early 1980s have served to briefly revitalize juniper woodlands in the northern Great Basin (Mehringer and Wigand, 1990). However, if droughts similar to those of the early 1990s are near the climatic norm for the last millennium, as Graumlich (1993) suggested from Sierran tree ring records, we can expect continued retrenchment of semiarid woodlands to higher elevations, with a reduction in perennial grasses and expansion of sagebrush and annual grasses.

Southern Great Basin and Northern Mojave Desert

Paleobotanical records from the southern Great Basin and the northern Mojave Desert consist primarily of data obtained from plant macrofossils collected from ancient woodrat middens. The Tule Springs pollen record (Mehringer, 1967), however, and a record from Death Valley (undergoing analysis) promise to extend length to our record of vegetation history and to cover gaps in the Late Quaternary record not covered by woodrat midden evidence. Other sources of climatic evidence, such as the stable isotope records from Devils Hole (Winograd et al., 1988, 1992, 1997) and Death Valley (Li et al., 1996; Ku et al., 1998), provide evidence of past climates but tell us nothing of Late Quaternary vegetation dynamics. Thus far, only the record from Browns Room at Devils Hole (Szabo et al., 1994) can successfully be compared with vegetation dynamics in the northern Mojave Desert.

If pollen preservation is adequate in the Death Valley core, that record promises to extend our paleobotanical history of the northern Mojave Desert by at least 190 Ky (Li et al., 1996; Ku et al., 1998). Currently, however, a few woodrat middens and perhaps some pollen samples from Tule Springs provide our only indication of vegetation in the area from before about 35 Ka.

PRE–LATE WISCONSIN (>35 KA)

Profile I at Tule Springs apparently contains pollen spectra dating to before 35 Ka (Mehringer, 1967, fig. 31). The profile documents a cool, wet event dating to more than 37 Ka. This may actually be one of the two periods of wetter climate indicated in the Browns Room record dating to either ~40 or ~45 Ka, or it may be an earlier event (Szabo et al., 1994, fig. 4). The episode is characterized by both pine and fir expansion. Neither the age nor the duration of this event can be determined, but it seems to document the same kind of vegetation pattern that is seen in later pluvial episodes. The pollen record indicates that desert shrub communities dominated by saltbushes characterized low elevations. Juniper and sagebrush pollen suggests that juniper woodland, possibly mixed with pine, was also common. As cooling progressed, the contribution of pine pollen to the record became overwhelming. This resulted, in part, from the increased area that was available for pine to expand into as its habitat was displaced down the mountainsides (see Mehringer's (1967) discussion of the impact upon pollen abundance by the displacement of species along the area elevation curve). Fir pollen became more abundant than that of juniper. This may have resulted from poor preservation of juniper pollen, but values of about seven percent suggest a substantial increase in fir regionally. Pollen from juniper and sagebrush indicates that juniper woodland was still widespread. The decrease in pine and fir values and the disappearance of juniper near the top of the profile seem to signal a return to a drier climate. This pattern is repeated throughout the late Pleistocene in the northern Mojave Desert.

Unfortunately, most woodrat middens dated to before 35 Ka have multiple dates and reflect substantial mixing of materials of many ages. Typical of this problem are middens from the Eleana Range (Spaulding, 1985). This mixing may be an indication that climatic conditions since the initial formation of these woodrat middens have been wet enough to cause re-solution of the crystallized urine cementing them.

LATE PLEISTOCENE (~35 TO 12.5 KA)

Woodrat midden studies during the last 30 years have enabled identification to the species level of the likely contributors of both pine and fir pollen from the Tule Springs pollen record. It is clear that in the southern Great Basin and the northern Mojave Desert, expansions and contractions of limber pine and white fir (possibly Rocky Mountain white fir, *Abies concolor* var. *concolor*) record periods of wetter climate during the cooler, drier spans of the late Pleistocene (Figures 15, 16). Originally recorded in the pollen record obtained from Tule Springs (Mehringer, 1967), they have been corroborated and refined by the substantial woodrat midden record that has been accumulated (Mehringer and Ferguson, 1969; Spaulding, 1977, 1981, 1985, 1994; Forester et al., 1996).

The woodrat midden record indicates that during much of the last glacial cycle between 33 and 11 Ka, limber pine formed a

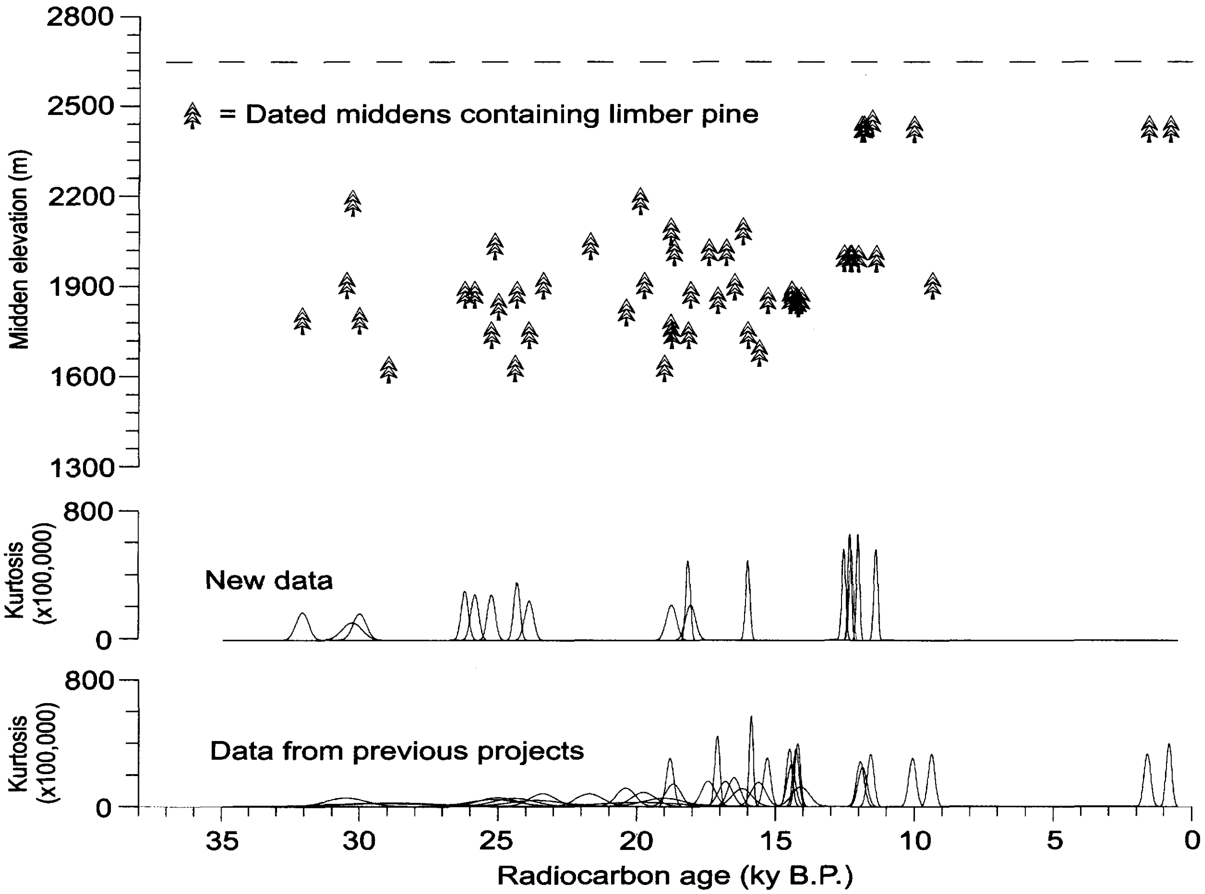

FIGURE 15.—Elevational distribution of limber pine, as ascertained with macrofossils from ancient woodrat middens in the northern Mohave Desert, by radiocarbon age. (Top) Our own and previously published data from middens containing limber pine (tree symbols) in a 200 km radius around Yucca Mountain; the dashed line is the approximate lower elevational distribution limit of limber pine in the Sheep Range today. (Middle, Bottom) Radiocarbon dates on limber pine for this study (middle) and for other studies (bottom) plotted as a normal distribution at three standard deviations around the mean. For these kurtosis plots, the normal distributions are a measure of radiocarbon date precision—i.e., the more pointed the distribution curve, the more precise the date is; and the flatter the curve, the less precise the date is.

subalpine woodland that occasionally extended down to at least 1600 m in elevation, ~1000 m below where it grows today in the Sheep and Spring Ranges of southern Nevada (Table 1; Figure 15). This is roughly equivalent to the period of highest water table in Browns Room at Devils Hole (Szabo et al., 1994). Limber pine macrofossils appear in the midden record of ~33–30 Ka, 26.5–23 Ka, 21–14 Ka, and 13–11 Ka. White fir occasionally appeared in this woodland also. At those times it certainly grew along the bases of cliffs and in canyons (where woodrat middens are preserved), but whether conditions were moist enough for it to grow on exposed slopes is uncertain. Periods of downward translocation of white fir are centered at ~35–32 Ka, 26.5–21 Ka, 16–14 Ka, and 13–12 Ka (Table 2; Figure 16). Limber pine disappears from the midden record between 35 and 33 Ka and between 23 and 21 Ka, leaving white fir as the only tree species present.

Late Pleistocene climates can be extrapolated by using modern analogue temperature and precipitation requirements for limber pine and white fir. Limber pine favors cool, dry continental conditions with rainfall distributed relatively evenly during the year; it is drought tolerant. White fir favors cool, moist conditions with a winter peak in rainfall, but it often survives in canyons where shallow groundwater is available to it. In either case, white fir expansion indicates moister conditions. Rocky Mountain white fir appears to survive under cooler and drier conditions than does Sierran white fir. The seasonal distribution of rainfall appears to vary considerably as well where Rocky Mountain white fir grows. The modern analogue climates of these two species suggest the following climatic scenario for the late Pleistocene.

The wettest periods were those when limber pine disappeared from the woodland record. These appear to coincide

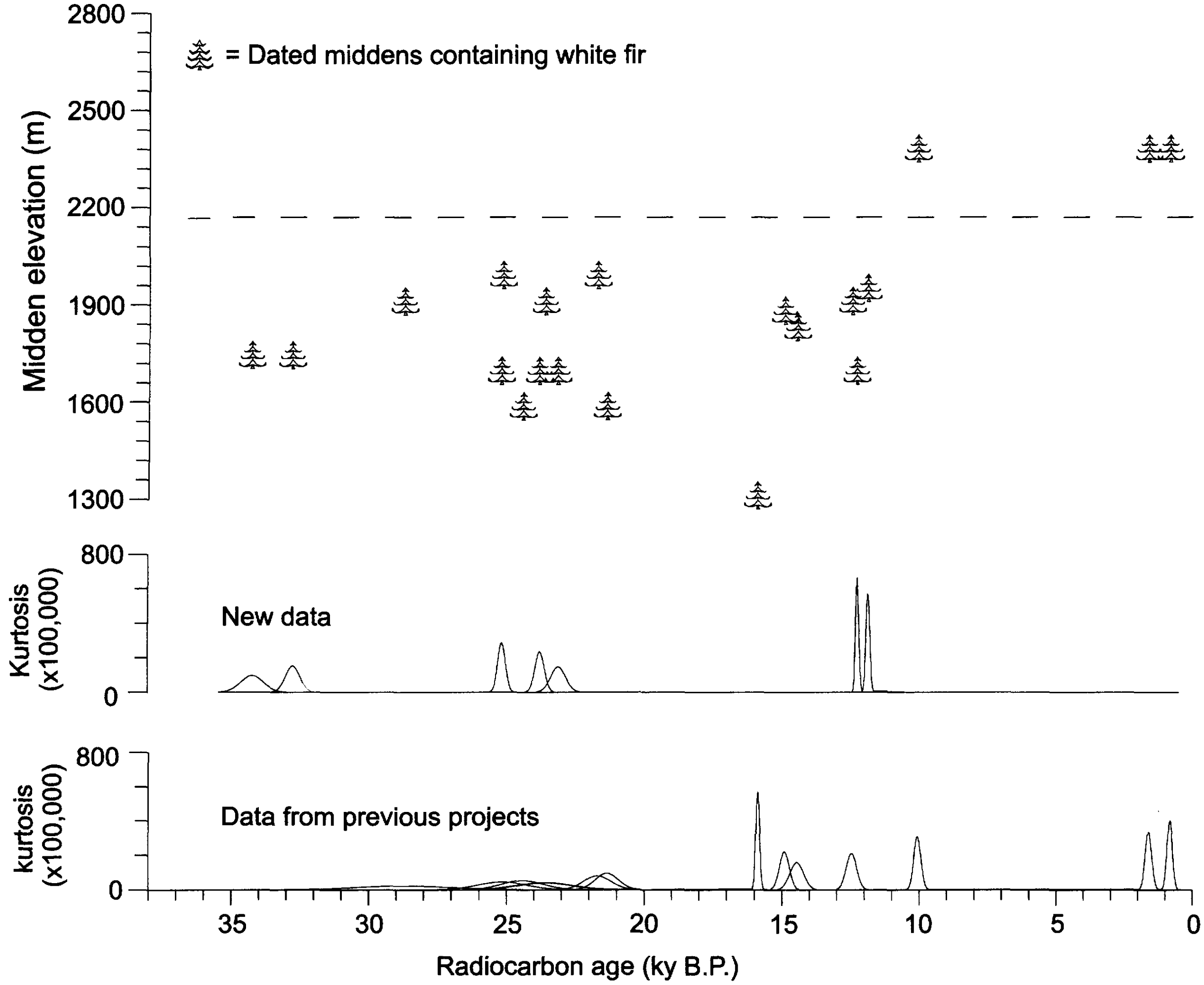

FIGURE 16.—Elevational distribution of white fir, as ascertained with macrofossils from ancient woodrat middens in the northern Mohave Desert, by radiocarbon age. (Top) Our own and previously published data from middens containing white fir (tree symbols) in a 200 km radius around Yucca Mountain; the dashed line is the approximate lower elevational distribution limit of white fir in the Sheep Range today. (Middle, Bottom) Radiocarbon dates on white fir for this study (middle) and for other studies (bottom) plotted as a normal distribution at three standard deviations around the mean. See Figure 15 caption for explanation of these kurtosis plots.

with the onset (23–21 Ka) and demise (16–14 Ka and 13–12 Ka), but not the climax, of the late glacial maximum. An earlier cold/wet period centered between ~35 and 33 Ka apparently corresponds to one noted in the pollen records from the Summer Lake basin and from the Pyramid Lake midden (see middle Holocene above in "Northern and Western Great Basin"). The pollen record from Profile II at Tule Springs records increased pine and fir corresponding with the pre–glacial maximum episodes (Mehringer, 1967, fig. 32). Such episodes suggest that Pacific air masses played a greater role in the climates of southern Nevada at that time. Conversely, periods of cold, dry continental climates (continental polar and Arctic air mass predominance) occurred from 16 to 21 Ka and from 29 to 32 Ka based on the absence of white fir in communities with abundant limber pine.

Our knowledge of the modern mean annual precipitation (MAP) requirements of key plant species together with changes in their distribution during the Pleistocene—as revealed in the plant macrofossil data from woodrat middens in southern Nevada (and northern Nevada)—indicate rapid shifts toward wetter winter precipitation patterns lasting from about one century to as long as one to two millennia. The MAP ranges for modern analogue plant species suggest a Pleistocene MAP range between 380 and 635 mm at elevations between 1500 and 2000 m (Forester et al., 1996). This is roughly an increase of 50%–90% above the current range of 200–250 mm.

TABLE 1.—Lower elevational occurrences of limber pine (*Pinus flexilis*) within a 200 km radius of Yucca Mountain, Nevada, as revealed in the current study (in **bold**), from lowest to highest elevation. Midden data analyzed by other investigators are Fortymile Canyon (Spaulding, 1994), Sheep Range (Spaulding, 1981), Eleana Range (Spaulding, 1985), Potosi Mountain (Mead et al., 1978), and Clark Mountain (Mehringer and Ferguson, 1969). All sites are in Nevada unless noted otherwise (NTS = Nevada Test Site).

Locality; midden no.	Radiocarbon age (years)	Laboratory no.	Material dated	Elevation (m)
Fortymile Canyon, NTS; FMC-11A (1)	15,870 ± 70	QL-4223	Fecal pellets	1310
Sheep Range; Penthouse 2(1)	28,960 ± 2,000	A-1773	Utah juniper	1580
Sheep Range; Willow Wash 4C(1)	24,400 ± 760	A-1751	Utah juniper	1585
Sheep Range; Willow Wash 4C(2)	19,020 ± 750	UCR-729	Utah juniper	1585
Sheep Range; Basin Canyon 1	15,610 ± 260	WSU-1856	Utah juniper	1635
Pahranagat Range; PR230594ARM1(1)	**16,010 ± 80**	**BETA-74775**	**Limber pine**	**1695**
Pahranagat Range; PR230594ARM1(1)SSIDE	**18,160 ± 80**	**BETA-86066**	**Limber pine**	**1695**
Pahranagat Range; PR110688PEW3(2)	**18,765 ± 180**	**BETA-32405**	**Limber pine**	**1695**
Pahranagat Range; PR230594ARM1(2)	**23,890 ± 160**	**BETA-74772**	**Limber pine**	**1695**
Pahranagat Range; PR110688PEW3(3)	**25,250 ± 140**	**BETA-86063**	**Limber pine**	**1695**
Double Cave, Pahroc Range; DC180595JPB1(1)	**32,070 ± 230**	**BETA-86031**	**Limber pine**	**1743**
Double Cave, Pahroc Range; DC180595JPB1(2)	**30,000 ± 240**	**BETA-86105**	**Limber pine**	**1743**
Sheep Range; Flaherty Mesa 1	20,390 ± 340	WSU-1864	Utah juniper	1770
Sheep Range; Wagon Canyon 2	25,000 ± 710	A-1656	Utah juniper	1790
Eleana Range, NTS; ER-3(14)	14,200 ± 100	USGS-1266	Limber pine	1800
Eleana Range, NTS; ER-2(4)	14,090 ± 320	A-2927	Limber pine	1810
Eleana Range, NTS; ER-2(4)	15,300 ± 130	USGS-875	Limber pine	1810
Eleana Range, NTS; ER-2(5)	14,260 ± 110	USGS-874	Limber pine	1810
Eleana Range, NTS; ER-2(6)	14,500 ± 110	USGS-885	Limber pine	1810
Eleana Range, NTS; ER-2(10)	17,100 ± 90	USGS-1069	Limber pine	1810
Ribbon Cliffs, Nellis Air Force Base; RC250588LCP11	**18,075 ± 180**	**BETA-32407**	**Limber pine**	**1829**
Ribbon Cliffs, Nellis AFB; RC060795PEW41A	**24,330 ± 110**	**BETA-86080**	**Limber pine**	**1829**
Ribbon Cliffs, Nellis AFB; RC060795PEW41B	**26,210 ± 130**	**BETA-86082**	**Limber pine**	**1829**
Ribbon Cliffs, Nellis AFB; RC060795PEW41C	**25,850 ± 140**	**BETA-86084**	**Limber pine**	**1829**
Potosi Mountain, Spring Range; Potosi Mtn 2C2	14,430 ± 150	LJ-4005	Limber pine	1830
Sheep Range; Eyrie 3(1)	16,490 ± 220	WSU-1853	Utah juniper	1855
Sheep Range; Eyrie 1(3)1	23,380 ± 490	WSU-1864	Utah juniper	1860
Sheep Range; Eyrie 1(3)2	9,370 ± 120	WSU-1863	Utah juniper	1860
Sheep Range; Eyrie 5(2)	30,470 ± 740	WK-168	Utah juniper	1860
Sheep Range; Eyrie 5(3)	19,750 ± 450	WK-167	Fecal pellets	1860
Clark Mountain, California; CM-1	23,600 ± 980	I-3557	Twigs	1910
Clark Mountain, California; CM-2	28,720 ± 1,800	I-3648	Twigs	1910
Stockade Wash, NTS; STW220594ARM113	**11,400 ± 60**	**BETA-86123**	**Limber pine**	**1950**
Stockade Wash, NTS; STW220594ARM114	**12,040 ± 60**	**BETA-86088**	**Limber pine**	**1950**
Stockade Wash, NTS; STW220594ARM111	**12,290 ± 70**	**BETA-74777**	**Limber pine**	**1950**
Stockade Wash, NTS; STW220594ARM112U	**12,340 ± 60**	**BETA-86121**	**Limber pine**	**1950**
Stockade Wash, NTS; STW220594ARM112	**12,550 ± 70**	**BETA-74779**	**Limber pine**	**1950**
Sheep Range; Deadman 1(1)	17,420 ± 250	LJ-3707	Limber pine/bristlecone pine	1970
Sheep Range; Deadman 1(2)	16,800 ± 250	WSU-1860	Utah juniper	1970
Sheep Range; Deadman 1(4)	18,680 ± 280	WSU-1857	Utah juniper	1970
Sheep Range; South Crest 1(4)2	21,700 ± 500	LJ-2840	Limber pine/bristlecone pine	1990
Sheep Range; South Crest 1(3)	25,140 ± 900	A-1669	Utah juniper	1990
Sheep Range; Spires 2(1)	18,800 ± 130	USGS-199	Fecal pellets	2040
Sheep Range; Spires 2(2)	16,200 ± 350	A-1875	Limber pine/bristlecone pine	2040
Cliff Springs, Belted Range, NTS; CS0909900GHH11	**30,270 ± 360**	**BETA-64355**	**Limber pine**	**2133**
Clark Mountain, California; CM-2	19,900 ± 1,500	GAK-1987	Limber pine/bristlecone pine	2140
Sheep Range; Hidden Forest 3A	1,600 ± 120	A-1742	Utah juniper	2380
Sheep Range; Hidden Forest 3B	820 ± 100	WSU-2046	Rocky Mountain juniper	2380
Sheep Range; Hidden Forest 3C(1)	10,060 ± 130	LJ-3729	Limber pine/bristlecone pine	2380
Sheep Range; Hidden Forest 3C(2)	11,940 ± 140	LJ-3730	Limber pine/bristlecone pine	2380
Sheep Range; Hidden Forest 3C(3)	11,860 ± 160	LJ-3728	Limber pine/bristlecone pine	2380
Sheep Range; Hidden Forest 1	11,570 ± 120	LJ-4046	Limber pine/bristlecone pine	2400

TABLE 2.—Lower elevational occurrences of white fir (*Abies concolor*) within a 200 km radius of Yucca Mountain, Nevada, as revealed in the current study (in **bold**), from lowest to highest elevation. Midden data analyzed by other investigators are from Fortymile Canyon (Spaulding, 1994), Sheep Range (Spaulding, 1981), Potosi Mountain (Mead et al., 1978), and Clark Mountain (Mehringer and Ferguson, 1969). All sites are in Nevada unless noted otherwise.

Locality; midden no.	Radiocarbon age (years)	Laboratory no.	Material dated	Elevation (m)
Fortymile Canyon, Nevada Test Site; FMC-11A (1)	15,870 ± 70	QL-4223	Fecal pellets	1310
Sheep Range; Willow Wash 4A	21,350 ± 420	WSU-1858	Utah juniper	1585
Sheep Range; Willow Wash 4C(1)	24,400 ± 760	A-1751	Utah juniper	1585
Pahranagat Range; PR230594ARM1(1)	**12,280 ± 60**	**BETA-74776**	**White fir**	**1695**
Pahranagat Range; PR110688PEW3(2)	**23,150 ± 270**	**BETA-32404**	**White fir**	**1695**
Pahranagat Range; PR230594ARM1(2)	**23,820 ± 170**	**BETA-74773**	**White fir**	**1695**
Pahranagat Range; PR110688PEW3(3)	**25,200 ± 140**	**BETA-86064**	**White fir**	**1695**
Double Cave, Pahroc Range; DC180595JPB1,1	**32,790 ± 260**	**BETA-86032**	**White fir**	**1743**
Double Cave, Pahroc Range; DC180595JPB1(2)	**34,260 ± 410**	**BETA-86106**	**White fir**	**1743**
Potosi Mountain, Spring Range; Potosi 2C L	14,450 ± 250	A-1778	White fir	1830
Potosi Mountain, Spring Range; Potosi 2A (2)	14,900 ± 180	LJ-4004	Miscellaneous	1880
Clark Mountain, California; CM-3	12,460 ± 190	I-3690	Piñon pine	1910
Clark Mountain, California; CM-1	23,600 ± 980	I-3557	Twigs	1910
Clark Mountain, California; CM-2	28,720 ± 1,800	I-3648	Twigs	1910
Stockade Wash, Nevada Test Site; STW220594ARM111	**11,890 ± 70**	**BETA-74778**	**White fir**	**1950**
Sheep Range; South Crest 1(4)2	21,700 ± 500	LJ-2840	Limber pine/ bristlecone pine	1990
Sheep Range; South Crest 1(3)	25,140 ± 900	A-1669	Utah juniper	1990
Sheep Range; Hidden Forest 3B	820 ± 100	WSU-2046	Rocky Mountain juniper	2380
Sheep Range; Hidden Forest 3A	1,600 ± 120	A-1742	Utah juniper	2380
Sheep Range; Hidden Forest 3C(1)	10,060 ± 130	LJ-3729	Limber pine/ bristlecone pine	2380

Shifts from the dominance of xeric climate shrub species to Utah juniper during the Pleistocene at elevations from ~700 to 1500 m record precipitation increases ranging between 33% and 66%, a gain of 50–100 mm above current values (Forester et al., 1996). Whereas today's MAP is only 150 mm, the Pleistocene MAP was at least 200 mm or as high as 255 mm at elevations between ~700 and 1500 m.

Other evidence for these wetter episodes is provided by the accumulating database of radiocarbon dates on spring deposits in the northern Mojave Desert. Dates from the Las Vegas Valley, Corn Creek Dunes, Three Lakes Valley, and Indian Springs Valley indicate several episodes of late Pleistocene and early Holocene spring activity (Quade et al., 1995, 1998). Quade et al. (1995) suggest that based upon the radiocarbon dates at Corn Creek Dunes there may be three distinct phases of discharge: an early set centered around or prior to 31 Ka, a second set from ca. 25 to 14 Ka, and a third set from 14 to 8 Ka. As more dates accumulate, these episodes may become more constrained and may match the vegetation data more closely. To the southeast in the Lake Mojave basin, a series of lakes—some lasting for as many as 2000 years and others lasting only a few hundred—span the period between ~22 and ~11.5 Ka (Brown et al., 1990, fig. 8). These may, in part, correspond to the precipitation events seen in the record from southern Nevada; however, these lakes reflect climatic conditions in transverse ranges, which may have experienced a quite different sequence of rainfall history because of their proximity to the Pacific Ocean.

These occasional wet episodes are set against the major portion of the Pleistocene between 35 and 12 Ka, which was dominated by more continental conditions characterized by cold-dry climate about 1.33 times wetter than today (Forester et al., 1996). Based upon a comparison of the temperature requirements of Rocky Mountain and Sierran white firs versus limber pine, the onset and decline of the late glacial maximum may have been 2°–6° C warmer than its climax.

Precipitation gradients increased substantially during the Pleistocene. The MAP was approximately 133% of what it is today at ~750 m in elevation, based upon the displacement of Utah juniper (Wells and Jorgensen, 1964; Wells and Berger, 1967; Forester et al., 1996). Limber pine displacement indicates that MAP was approximately 190% of what it is today at ~1500 m (Forester et al., 1996). If the increase in regional MAP had been regular, the percent of increase should be the same at all elevations. However, the difference in MAP between these two elevations during the Pleistocene reveals that precipitation was ~50% greater at 1500 m than it was at 750 m. Lack of woodrat midden data above 2000 m for the Pleistocene prevents extrapolation of precipitation values to higher elevations. This reconstructed rainfall gradient indicates a dramatically enhanced orographic precipitation effect during the late Pleistocene in southern Nevada.

TABLE 3.—A general sequence of climate and mean annual precipitation (MAP) for southern Nevada from ca. 35 to 12 Ka.

Radiocarbon date (Ky B.P.)	Relative climate	Estimated MAP (mm)
~35–33	Very wet, cool	560–635
33–26.5	Dry, cooler	406–457
26.5–23	Wet, cool	457–560
23–21	Very wet, cool	560–635
21–16	Dry, cold	406–457
16–14	Wet, cool	457–560
14–13	Dry, cooler	406–457
13–12	Wet, cool	457–560

By using the MAPs derived from the vegetation data summarized above, a general sequence of climate is generated for the period from ~35 to 12 Ka for southern Nevada (Table 3). This applies only for elevations around 1500 m. At elevations around 750 m, estimates should be about 50% of those at 1500 m. Above 2000 m, absence of data prevents estimation. Climate designations in Table 3 are only relative.

At lower elevations, desert shrub communities dominated by saltbushes, rabbitbrush (*Chrysothamnus* spp.), mormon tea (*Ephedra* spp.), and other shrubs appear to have prevailed through much of the late Pleistocene (Spaulding, 1985, 1990, 1994; Wells and Woodcock, 1985). Investigations in the Pintwater Cave area, north of the Spring Range in southern Nevada, revealed shrub community dominance with intermittent incursions of Utah juniper for most of the last 34 Ky. A brief appearance of Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) in the area of the cave after ~34 Ka (numerous seeds in the cave sediments) suggests cooler, wetter climates at that time than later in the Pleistocene. Similar climatic conditions seem to have allowed Rocky Mountain juniper to exist on the east shore of pluvial Owens Lake between 23 and 17.5 Ka (Koehler and Anderson, 1994). The cool temperatures generated in the Owens Valley by the nearby Tioga glacial advance may have provided conditions suitable for the survival of Rocky Mountain juniper far from its current upper-elevation distributions.

EARLY HOLOCENE (12.5 TO 8 KA)

In southern Nevada, replacement of subalpine woodland dominated by limber pine with juniper-dominated semiarid woodland at intermediate elevations preceded the disappearance of low-elevation juniper woodland by desert scrub (Spaulding, 1977, 1981; Wigand et al., 1995). Although woodrat midden records indicate that piñon pine appeared in several areas around southern Nevada including the Pahranagat Range well before 8.5 Ka, it seems to have been a much less important component of early Holocene semiarid woodlands than was juniper (Spaulding, 1985, 1990; Thompson, 1990; Wigand et al., 1995). However, records from the north-central and eastern Great Basin (Thompson and Hattori, 1983; Thompson and Kautz, 1983; Wells, 1983; Madsen and Rhode, 1990; Thompson, 1990) confirm piñon pine's rapid northward expansion.

Despite evidence of warming climates in the southern Great Basin, the persistence of juniper woodland outliers after 9.5 Ka may reflect occasional wetter and/or cooler periods of climate that aided their persistence. At Little Skull Mountain on the southern edge of the Nevada Test Site, juniper persisted until 10.5 Ka but disappeared from the record by 10 Ka (Wigand, unpublished data). By 9.5 Ka, however, it reappeared in the woodrat midden macrofossil record at Little Skull Mountain. Organic mats (residues) dating primarily from 10.2 to 8.6 Ka also reflect these episodes of moister climate (Quade et al., 1998, especially fig. 5). Based upon the vegetation during this span of time, the rainfall from two different climatic regimes may have been responsible for formation of the black mats. Climates may have been considerably cooler from 11.2 to 10.2 Ka than from 12 to 11.5 Ka, resulting in reduced evaporation rates and greater effective precipitation. Climates were warmer from 10.2 to 8.6 Ka, and from 9.5 to 8.6 Ka the summer rainfall may have increased considerably.

Evidence of a shift to summer seasonal rainfall during the warm portion of the latter early Holocene between 9.5 and 9 Ka is provided by the appearance of netleaf hackberry (*Celtis laevigata* var. *reticulata* (Torr.) L. Benson) seeds in the paleobotanical record of southern Nevada. Hackberry seeds (endocarps) have been recovered from woodrat middens located on the xeric southeast slope of Little Skull Mountain (Wigand et al., 1994), from middens in the Sheep Range north of Las Vegas (Spaulding, 1990), and from the Sandy Valley (Spaulding, 1994), and several hundred seeds were recovered from the sediments of Pintwater Cave (Jahren et al., 2001). Today it occurs in canyons, seeps, and washes at elevations of 500–1700 m. Hackberry ranges from the southern Sierra Nevada foothills and the San Bernardino Mountains in the southwestern United States and northern Mexico into the southern plains to Kansas, with outliers in Washington (Benson and Darrow, 1981; Krajicek and Williams, 1990). In southern Nevada it is found associated with a spring near Pahroc Spring in the Pahroc Range, in one locality in Fortymile Canyon on the Nevada Test Site, and in canyons at the southern end of the Spring Range. The appearance of hackberry remains in middens suggests it grew at the bases of cliff faces or in arroyo bottoms, areas that are currently too dry to support it, and reveals a pattern of greater regional abundance of the tree between 9.5 and 9 Ka.

These reconstructed climatic conditions compare well with evidence of increased spring discharge found by Quade et al. (1998) that apparently may correspond to incursions of monsoon rains during the thermal maximum (Spaulding, 1985; Spaulding and Graumlich, 1986). In particular, well-developed black mats, which Quade et al. (1998) describe from the valleys surrounding the Spring Range, dating to between 9.5 and 8.6 Ka probably reflect the period of increased summer monsoon activity. Additional evidence of episodes of the incursion of moisture during this period are the intermittent lakes that appear in the Lake Mojave basin (Silver and Soda Lake playas) at this time (Brown et al., 1990). The evidence indicates that as many as six lakes (with intervening drying) occupied the Lake Mojave basin between 11.5 and ~8.5 Ka (Brown et al., 1990, fig. 8). Therefore, during a period when other climate proxies indicate that conditions were much warmer and that mean annual rainfall was decreasing, a shift of rainfall toward the summer season coinciding with the early Holocene thermal maximum would explain the presence of perennial seeps, as evidenced by the latter period of black mat formation, the majority of which Quade et al. (1998) have dated to between 10.2 and 8.6 Ka.

In the Alabama Hills north of the Owens Lake basin, the termination of Pleistocene woodland occurred 9.5 Ka (Koehler and Anderson, 1995). This coincides with the disappearance of juniper woodland from outlier positions in the Lahontan Basin, as noted above, and also with the termination of lithoid tufa formation around the Lake Lahontan shoreline. This is also, as just noted, the beginning of the period of greater penetration of monsoon rainfall into southern Nevada. Together these data suggest a major northward displacement of regional climatic regimes at this time.

MIDDLE HOLOCENE (8 TO 5.5 KA)

As Spaulding (1990) indicated, the early Holocene vegetation assemblages of the northern Mojave Desert were, in most cases, unique and did not survive the middle Holocene. Pollen samples from Profile V in the Tule Springs record indicate a dramatic increase in low-spine (*Ambrosia*-type) pollen shortly after 8.5 Ka (Mehringer, 1967). This probably corresponds to the appearance of white burrobush (*Ambrosia dumosa* (Gray) Payne), one of the two codominants of the typical Mojave Desert creosote bush–white burrobush vegetation assemblage (Spaulding, 1990, fig. 9.13). According to the woodrat midden macrofossil record, creosote bush appears slightly later in the area (but see Grayson's (1993:200) discussion). Further west the appearance of these two species is even later (Spaulding, 1980). Unfortunately, pollen can not be used to document the presence or appearance of creosote bush because of its rarity in the pollen record. Both these species arrived as migrants from further south, but the climatic impetus for their arrival is unclear.

Truncation of the pollen record in Profile IV at Tule Springs sometime after 7.5 Ka corresponds with the beginning of a general absence of paleobotanic data spanning the next 2 Ka in the southern Great Basin and northern Mojave Desert (Mehringer, 1967). The dearth of vegetation data is probably a direct reflection of the impact of severe drought in the region. Springs and marshes dried and woodrats may have retreated into more favorable areas. Severe eolian erosion may have characterized parts of this period, because late-Holocene spring and marsh deposits in the northern Mojave Desert generally lie upon erosion surfaces that were formed during the middle Holocene (Mehringer and Warren, 1976; Mehringer and Sheppard, 1978; Wigand, 1997b). This suggests that vegetation cover may have been very sparse.

Only a few middens are dated to this period. One collection of middens from the McCullough Range southwest of Las Vegas is dominated by thermophilic (warm-temperature) plant species (Spaulding, 1991). These reflect the warm, dry conditions of the middle Holocene. Spaulding also suggested that no evidence exists for summer seasonality of rainfall between 6.8 and 5 Ka.

LaMarche (1974) suggested that upper tree line temperatures were considerably warmer during this period and that upper tree lines extended upward. Graybill et al. (1994) indicated extended periods of drought as well. These data suggest that the middle Holocene in the Great Basin was characterized by considerable warmer and drier conditions than currently exist in the Great Basin.

EARLY LATE HOLOCENE (5.5 TO 2 KA)

In the northern Mojave Desert there is a dramatic change in climate at this time. It is most clearly manifested in the sudden formation of peats that overlie erosional unconformities. Peats occurred at the base of the Little Lake record in the Owens River valley (Mehringer and Sheppard, 1978), in Ash Meadows south of the Nevada Test Site (Mehringer and Warren, 1976), and at the base of the Lower Pahranagat Lake cores in the White River valley northeast of Las Vegas (Wigand, 1997b). These peats attest to the sudden rejuvenation of springs in the region. Mesophilic plant abundance in woodrat middens of the McCullough Range began in strata dating to 5.5 Ka (Spaulding, 1991). A woodrat midden stratum in the southern Pahranagat Range dated to 5.6 Ka reveals a brief lowering in elevation of Utah juniper below its current elevational distribution (Wigand et al., 1995).

In southern Nevada, increased abundance of woodrat middens containing Utah juniper and piñon pine macrofossils evidence a major Neoglacial reexpansion and/or increase in density of piñon–juniper woodland beginning ~3.8 Ka (Wigand et al., 1995, fig. 4). This early phase of semiarid woodland expansion culminated about 2.3 Ka.

At Lower Pahranagat Lake, a pollen record analyzed back to 3.8 Ka with a resolution of a sample every 14 or so years provides a clear record of drought cycles for the northern Mojave Desert and the southern Great Basin (Figure 17; Wigand, 1997b). This record is correlatable with the White Mountain tree ring record of Graybill et al. (1994) (Figure 18). It provides an indication not only of relative increases in precipitation but also of shifts in seasonal distribution as well.

Wetter climate events of the Neoglacial are reflected in the record from Lower Pahranagat Lake, but two differences from the Neoglacial wet events in the Diamond Pond record of the Great Basin are evident. First, only two of the three major wet

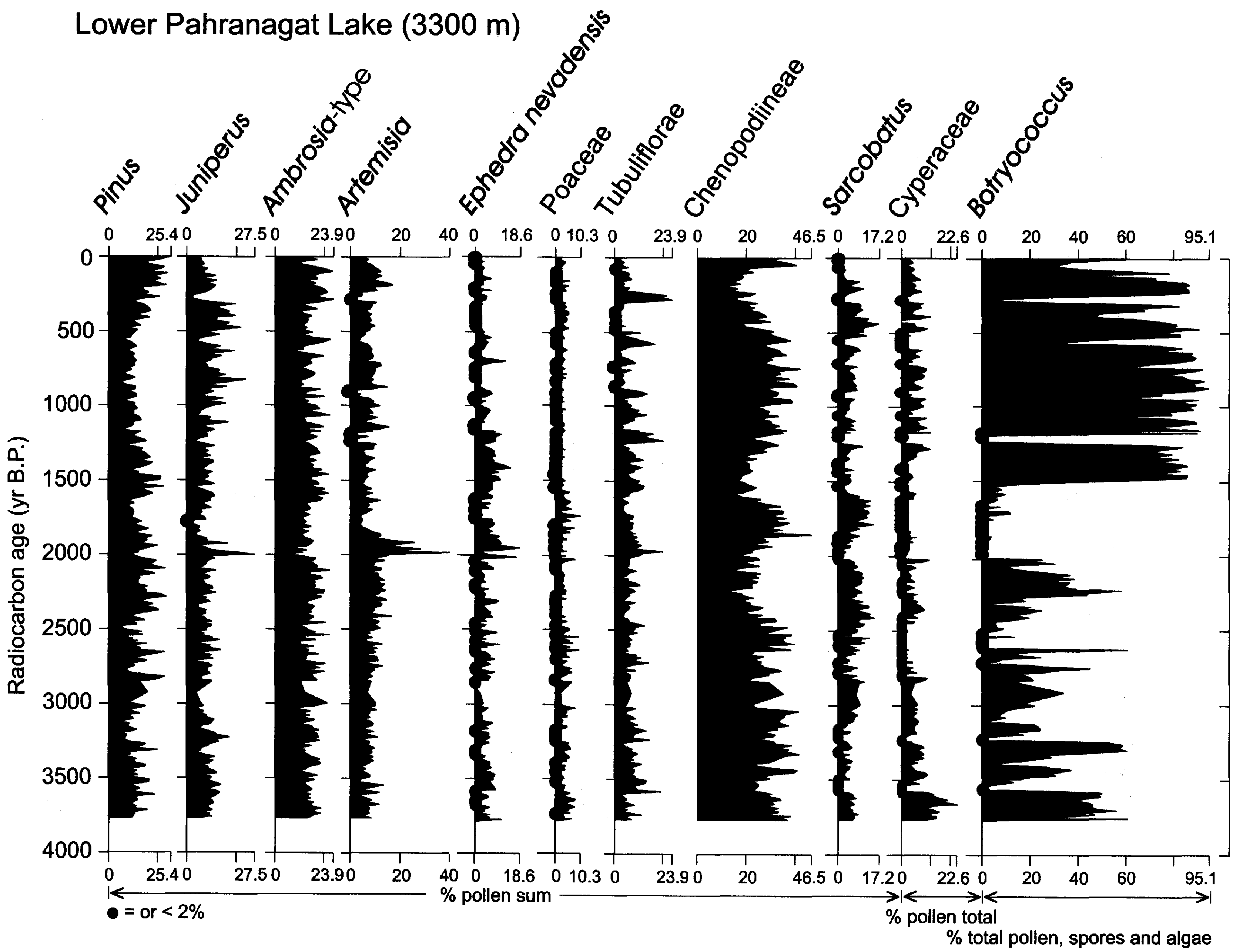

FIGURE 17.—Relative percentage diagram of major pollen and algae types from Lower Pahranagat Lake, White River valley, southeastern Nevada. Samples were dated based on a deposition rate curve generated from a polynomial fit on 24 radiocarbon-based dates. A bullet (•) indicates a value of ≤2%.

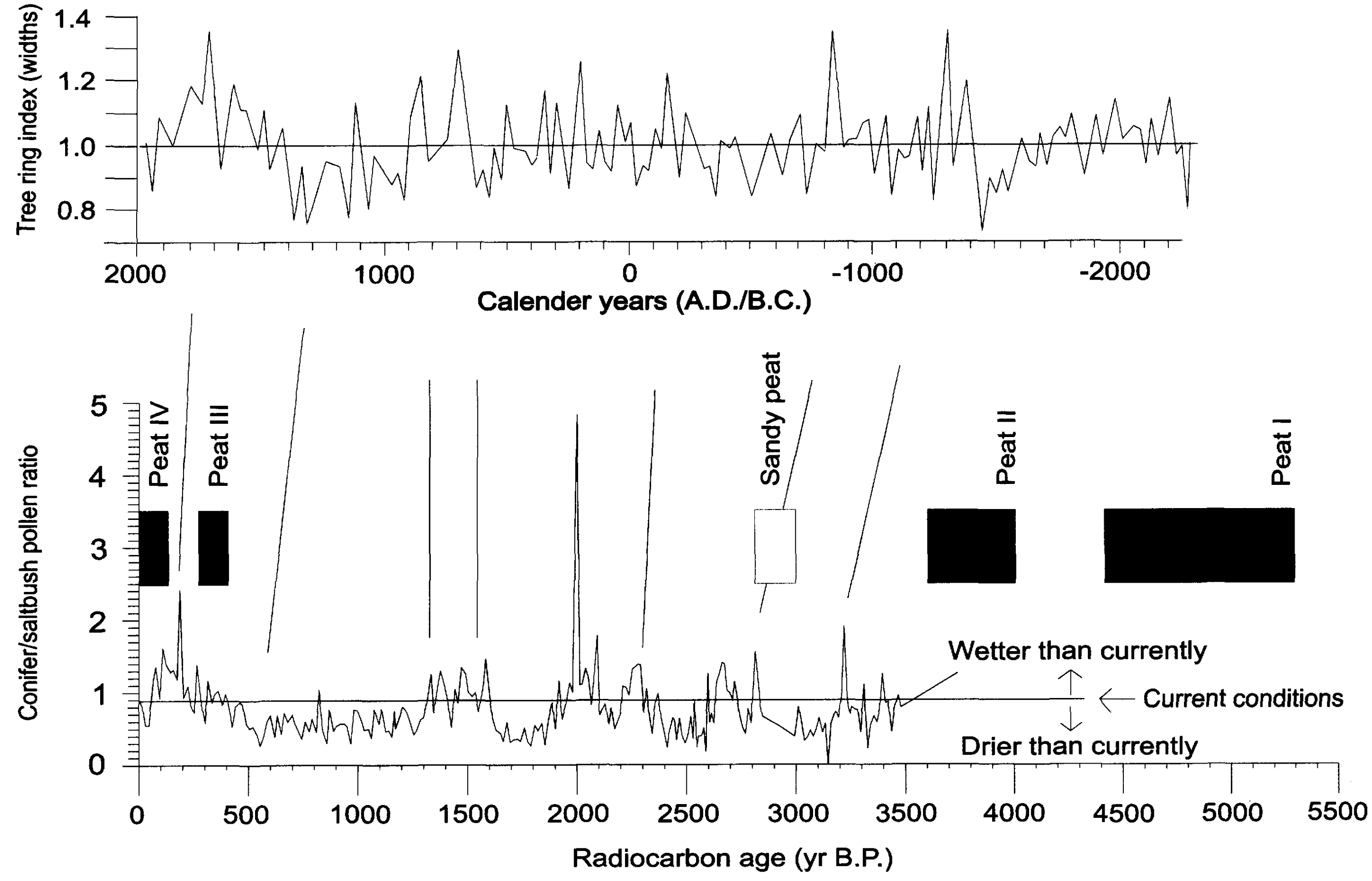

FIGURE 18.—Index of effective precipitation in the southern Great Basin and northern Mohave Desert for the last 4000 years, based on pollen, tree ring, and marsh peat proxy climate data. The conifer/saltbush pollen record of Lower Pahranagat Lake in the southern Great Basin (bottom), by radiocarbon date, is compared with the bristlecone pine tree ring record from the White Mountains (top), by calendar date (years A.D./B.C.) (Graybill et al., 1994). Straight lines between the two graphs indicate correlations in the records. Growth of peat strata in Ash Meadows, reported by Mehringer and Warren (1976), is also correlated with pollen ratios by radiocarbon date. The pollen ratio, (juniper + pine)/all Chenopodiineae, reflects regional precipitation. Increases in the ratio indicate wetter periods, primarily winter precipitation; decreases indicate reduced winter precipitation. The tree ring index also reflects regional precipitation, although temperature may also play a role. Wider ring widths (in millimeters) (up) correspond with greater precipitation; narrower widths (down) correspond with reduced precipitation.

periods (~3.7 and 2.7 Ka) seen in the Diamond Pond record appear in the Lower Pahranagat Lake record (Figure 17). Second, their magnitudes (Figure 18) are considerably lesser at Lower Pahranagat Lake than at Diamond Pond (Wigand, 1987). This may indicate that it was Pacific storm systems that were primarily responsible for these periods of wetter climate and that their impact was focused primarily upon the northern Great Basin and the Pacific Northwest, not the southern Great Basin or southwestern United States. Ely et al. (1993) indicated that, between 3.6 and 2.2 Ka, large floods are completely absent from their record of floods for the Southwest. As mentioned above, the winter-dominated storm pattern may not have been very strong in the southwestern United States, and therefore the pattern of winter storms and cyclones currently associated with heavy flooding may not have been important in the Southwest. Reduced heavy flooding episodes may also reflect the impact of a denser vegetation cover that grew in response to heavier, winter rainfall throughout the West during the Neoglacial from 4 to 2 Ka. On the other hand, the lack of large floods could reflect a southward displacement of monsoonal systems and the resulting reduction in torrential episodes that would cause heavy floods.

Enzel et al. (1989, 1992) indicated that a shallow lake stood for a brief period in the Soda and Silver Lake basins ~3.6 Ka. This corresponds to the strongest of the wet events proposed for Diamond Pond in the northern Great Basin (Wigand, 1987). This event may have initiated late-Holocene vegetation recovery that served to buffer runoff between 4 and 2 Ka in the southwestern United States.

A terminal Neoglacial increase in pollen of juniper and several shrub species in Lower Pahranagat Lake records a brief, though unparalleled, episode of more mesic climate (Figure

17). Because it is juniper and sagebrush that responded most dramatically, an interval of cooler, wetter climate with winter-dominated rainfall pattern seems to have occurred ~2 Ka that lasted about 150–200 years (Figure 17; Wigand, 1997b).

Reconstructed deposition rates of the Lower Pahranagat Lake record together with dramatic changes in relative pollen values indicate that, at times, the transition to wetter, or conversely drier, conditions often took less than a decade or two (see the event 2 Ka in Figure 17). The local increase in effective precipitation needed to accomplish the observed changes in juniper abundance, based upon the difference in the minimal annual rainfall requirements between sagebrush (Mozingo, 1987) and Utah juniper (Leonard et al., 1987), must have been at least 10–20 millimeters per year at elevations around 1500 m. Reduced evaporation rates caused by reduced mean annual temperature probably played a substantial role in increasing effective precipitation.

LATE LATE HOLOCENE (2 KA TO PRESENT)

Severe drought marked by the expansion of saltbushes and greasewood signaled the end of the Neoglacial in southern Nevada (Figure 17). LaMarche (1974) sees a dramatic rise in tree lines at this time that lasted for the next 300 years. Increased grass abundance during this period suggests that summer-shifted rainfall characterized this episode of dry climate (Figure 17).

At Lower Pahranagat Lake, additional increases in juniper pollen, indicating greater effective precipitation resulting from increased winter precipitation and/or reduced evaporation rates from cooler temperatures, occurred ~1.5, 0.9, 0.7, and after 0.5 Ka (Figure 17; Wigand, 1997b). In fact juniper pollen values had their last climax about 0.3 Ka (during the Little Ice Age) and have since declined.

These periods roughly coincide to times when trees were drowned in the lake basins and stream valleys in the Mono Lake area, as indicated by Stine (1990). These episodes are mirrored in the marsh pollen records from Cofer Spring north of Beatty, Nevada (Wigand and Rose, 1990), and at Warm Sulphur Springs in the Panamint Valley (Smiley and Mehringer, n.d.). They coincide more roughly with the growth of peat layers in the latest dunes from Ash Meadows (Mehringer and Warren, 1976).

Episodic peat growth in Ash Meadows is probably promoted in part by increased surface discharge from the spring mounds that dot the area (Mehringer and Warren, 1976). The movement of local sand dunes, however, could also effect the growth of peat. Dunes occasionally divert watercourses that originate at the various spring mounds and that form ponds, which serve as the areas of peat formation. Peat formation corresponding with the wet event 5.5 Ka (which Quade et al., 1998, do not report) strongly suggests that the peats occurring at Ash Meadows correlate with higher spring discharge. Additional evidence for late-Holocene spring activity is provided by a few dates that Quade et al. (1998) reported for the Las Vegas Valley centered around 2.3, 1.4, and 0.6–0.5 Ka, periods that do not appear in the peat record at Ash Meadows.

There have been at least three substantial expansions of piñon pine as reflected in increases in pine pollen values in the Lower Pahranagat Lake record during the last 2 Ky (Figure 17; Wigand, 1997b, fig. 3). These pollen increases and the expansions of piñon pine reflect climatic conditions of a slightly different nature than those that occurred when juniper was expanding in southern Nevada. The most revealing of these expansions occurred between ~1.6 and 1.2 Ka (Wigand, 1997b, fig. 3). This period was characterized by minimal increases in juniper pollen values and began after a distinct period of increased grass pollen values. Analysis of woodrat midden data from the Pahranagat Range indicates that piñon pine expansion was regional. Contrasting the ecologies of juniper, piñon pine, and grass suggests that this climatic episode may have been a period of summer-shifted rainfall. Juniper, which favors winter precipitation, responded little during this period. Sagebrush, another plant favoring winter precipitation, did not respond during this period (Figure 17; Wigand, 1997b, fig. 4). The grass expansion evident just before the beginning of this period, at a time when saltbush (Chenopodiineae) and greasewood pollen values signal that a drier climate was prevalent, suggested the initiation of summer-shifted rainfall (Figure 17; Wigand, 1997b, figs. 4, 5). This pattern continued into the subsequent period of increased rainfall, which would have favored the establishment of piñon pine seedlings through the more reliable supply of moisture during hot summer months. LaMarche (1974) suggested that temperatures may have been slightly cooler during this period than in the periods after the Neoglacial.

Expansion of piñon pine in the Great Basin was further favored by the reduction in harshness of winter conditions after the Neoglacial ended about 2 Ka. Piñon pine is readily susceptible to winterkill during episodes of extreme cold. Even today its distribution in the northern Great Basin is characterized by stands on lower mountain ranges sheltered behind larger chains that effectively block the direct impact of winter storms. The regional nature of the climate changes reflected in the Lower Pahranagat Lake record is clearly documented by similar changes in contemporaneous records elsewhere in the Great Basin (see "Middle Late Holocene ..." and "The Last Millenium ..." sections, above in "Northern and Western Great Basin").

In southern Nevada, increases in saltbushes and greasewood in the pollen record of Lower Pahranagat Lake clearly reflect the strong drought conditions of this period (Wigand, 1997b). The transition from shallow lake to marsh conditions in Lower Pahranagat Lake about 1.2 Ka also may be linked in part to increasing drought. Three brief wet episodes ~0.9, 0.6, and 0.35 Ka correspond with those identified by Stine (1990). Pollen from the Lower Pahranagat record indicates that woodland may have retreated in some areas (Wigand, 1997b).

The pollen record from Lower Pahranagat Lake indicates that juniper woodland reexpanded ~0.35 Ka (corresponding to the beginning of the European "Little Ice Age") (Figure 17; Wigand, 1997b). Some marsh expansion occurred, and there was an increase in the algae *Botryococcus*, an indicator of eutrophic conditions (Figure 17). Together these suggest that southern Nevada climates were increasingly wet. However, pine values did not increase until near the end of this period after ~0.2 Ka. This may suggest that, although the period was characterized by wetter climates, winters may have been harsher, even in southern Nevada, thereby discouraging the establishment of piñon pine until temperatures began warming near the end of the period. Enzel et al. (1989) and Enzel et al. (1992) indicated that a shallow lake stood for a brief period in the Soda and Silver Lake basins ~0.39 Ka. This corresponds to the record for wetter climate from Lower Pahranagat Lake (Figure 17; Wigand, 1997b).

After the Little Ice Age, the prominence of pine in the woodlands of the southern Great Basin and northern Mojave Desert continued to grow as juniper seems to have declined (Figure 17; Wigand, 1997b, fig. 2). Saltbushes (Chenopodiineae in Figure 17; Wigand, 1997b, fig. 2) expanded dramatically with respect to sagebrush as well. This was followed by evidence that the creosote bush/white burrobush community (represented by *Ambrosia*-type pollen) expanded as saltbush communities contracted slightly. Although it appears that no major changes occurred in the abundance of sedges, a dramatic decline in *Botryococcus* suggests that the marshes were not as eutrophic, and instead, increased salinity may have effected marsh productivity. These changes reflected the drier conditions that developed after the end of the Little Ice Age. Most recently, wetter conditions have resulted in a regional resurgence of pine and renewed activity in the marsh, signaled by renewed *Botryococcus* abundance.

Bonneville Basin and Eastern Great Basin

The emerging picture of Late Quaternary vegetation change in the Bonneville Basin complements the well-known record of lake level fluctuations of Pleistocene Lake Bonneville and precursors (McCoy, 1981; Scott et al., 1983; Currey and Oviatt, 1985; Oviatt et al., 1987; Currey, 1990; Benson et al., 1992; Oviatt et al., 1992; Oviatt, 1997), the lesser-known Holocene history of Great Salt Lake (Currey et al., 1984), glacial records from the Wasatch Front (e.g., Richmond, 1964, 1986; Madsen and Currey, 1979; Scott, 1988), and nearby pollen localities (e.g., Bright, 1966; Beiswenger, 1991; Thompson, 1992). The Bonneville Basin provides a nearly ideal setting to examine long-term correlation between terrestrial vegetation patterns and regional aquatic history and to assess how these two systems both responded to climatic drivers. As Oviatt et al. (1992:239) sum up the situation, "by comparing chronologies from different proxy records, which show how different environmental systems responded to the same climatic factors, we can learn a great deal about the nature of late Pleistocene climates." We can also learn much about the strengths and weaknesses of the different proxy records.

The chronological framework used in this section generally follows the Lake Bonneville sequence outlined in Oviatt et al. (1992). The interglacial Holocene is herein assumed to follow the demise of Lake Gilbert at about 10 Ka (Benson et al., 1992). Temporal divisions within the Holocene follow the venerable tripartite scheme first outlined by Antevs (1948); these divisions are made as a matter of organizational convenience of a constantly fluctuating continuum and not to characterize distinctive or unified climatic or vegetational modes.

THE ILLINOIAN–SANGAMON GLACIAL–INTERGLACIAL CYCLE (150 TO 50 KA)

Several cores and pollen samples taken from lake sediments in the Bonneville Basin provide evidence of regional vegetation change prior to ca. 50 Ka (Eardley and Gvosdetsky, 1960; Martin and Mehringer, 1965; Eardley et al., 1973; Thompson et al., 1994; Davis, 2002 (this volume)). This period is beyond the limits of radiocarbon dating of organic materials, so dating uncertainties have prevented development of a detailed history of vegetation change. However, other dating methods (e.g., tephrochronology, paleomagnetism) allow general correlation of paleovegetation patterns with reconstructions of late Pleistocene lake history in the Bonneville Basin.

The last major deep-lake event before Lake Bonneville formed was the Little Valley lake cycle (Scott et al., 1983). Known deposits of this lake reach a maximum elevation of 1490 m, ~75–120 m below the maximum level of Lake Bonneville. The Little Valley cycle is broadly dated between 150 and 90 Ka, but it correlates with stage 6 of the marine oxygen isotope record (Shackleton and Opdyke, 1973; Pisias et al., 1984) as well as with the Illinoian glacial period, and it probably dates to between ca. 150 and 130 Ka (Scott et al., 1983). This lake cycle was followed by a long interglacial period during which lake levels were generally quite low. It was terminated by the Cutler Dam lake cycle, a relatively shallow lake (~1340 m in maximum elevation) that formed sediments called the Cutler Dam alloformation (Oviatt et al., 1987). Radiocarbon dates constrain the Cutler Dam lake to be older than 36 Ky (Oviatt et al., 1987), whereas luminescence dating places it at 59 ± 5 Ka (Kaufman et al., 2001), the latter being correlative with OIS 4.

Against this backdrop, the pollen evidence for this time period (Davis, 2002) suggests that, during the Little Valley lake cycle, vegetation on the margins of the Bonneville Basin consisted of sagebrush steppe and cold-dry-adapted pine woodland generally lacking junipers. Pine and montane conifers such as spruce and fir are suggested to have occurred some 500–1500 m lower in elevation in a mosaic of open woodland and shrub steppe rather than in closed-canopy forest.

During the subsequent interglacial period, the lake basin was filled approximately to the Gilbert level, covering the Great Salt Lake Desert at least to the vicinity of Wendover (Davis, 2002). High amounts of sagebrush and moderate quantities of chenopods indicate domination of sagebrush–saltbush steppe. The continued presence of moderate quantities of pine pollen and small amounts of pollen from other montane conifers suggests that climatic conditions remained fairly cool relative to today. Littoral marsh vegetation, including sedge and cattail, is represented in modest quantities, which suggests it occurred in favorable locations. A period of lake decline is estimated to have occurred about 70 Ka, based on the absence of pollen from the Wendover core. A short but distinctive episode corresponding to the Cutler Dam lake episode may be represented by high amounts of pine, sedge, and cattail pollen and low abundance of sagebrush and Chenopodiaceae-*Amaranthus* (Cheno-*Ams*) pollen at 1100 cm deep in the Knolls core and ~1200 cm deep in the Wendover core, estimated by Davis to have occurred approximately 80–70 Ka.

PRE–BONNEVILLE CYCLE, EARLY AND MIDDLE WISCONSIN (~50 TO 28 KA)

During this interval, the Bonneville Basin was characterized by generally low lake levels, at or below the level of the Gilbert shoreline (Scott et al., 1983; Oviatt et al., 1992; Davis, 2002). Paleovegetation records dating to the middle-Wisconsin interstadial period are still relatively sparse, restricted to a handful of very ancient packrat middens (Wells, 1983; Thompson, 1984), to pollen from a few lake cores and from cave sites (Martin and Mehringer, 1965; Mehringer, 1977; Spencer et al., 1984; Thompson, 1984; Davis, 2002), and to occasional isolated montane peat deposits or plant fragments in lacustrine sediments (e.g., Scott et al., 1983; Oviatt et al., 1987).

Packrat middens from the southern Bonneville Basin that date between 40 and 28 Ka indicate that montane settings supported coniferous woodlands dominated by bristlecone pine, with associates including sagebrush, rabbitbrush, snowberry (*Symphoricarpos* sp.), Utah juniper, and other mesophilic shrubs (Wells, 1983; Thompson, 1984). To the north, packrat middens dating to this interval are very scarce, but one locality, Top of the Terrace (Goshute Range), yields a series of midden samples that provide evidence of changing vegetation in upland settings before 28 Ka (Rhode, 2000a; Madsen et al., 2001; see Figure 19). Samples dating from older than about 50 Ka (infinite radiocarbon dates) show evidence of abundant Utah juniper, which is gone from the record by ca. 46 Ka and does not reappear until the late Holocene. By 46 Ka, upland meadow shrubs including sagebrush, currant (*Ribes* sp.), and shrubby cinquefoil (*Potentilla fruticosa* L.) replaced juniper woodland. Limber pine began to appear by ca. 41 Ka, and it became the dominant conifer through ca. 28 Ka (with one apparent decline ca. 30 Ka). Fernbush (*Chamaebatiaria millefolium* (Torr.) Maxim.), a montane woodland shrub of drier habitats, first appeared in large quantities by 36 Ka, similar to the distribution of limber pine. More mesophilic shrubs, however, declined in representation: cinquefoil disappeared from the record after 40 Ka, and currant was gone by about 34 Ka. In broad terms, the dominance of subalpine conifers (bristlecone pine in the south, limber pine in the north) and abundance of relatively dry upland shrubs at the expense of mesophiles suggests cold but dry conditions from 40 to 30 Ka. The midden record hints at substantial millennial-scale variation in vegetation content along dimensions of latitude and elevation, but the existing record and available dating techniques are insufficient to document these with clarity.

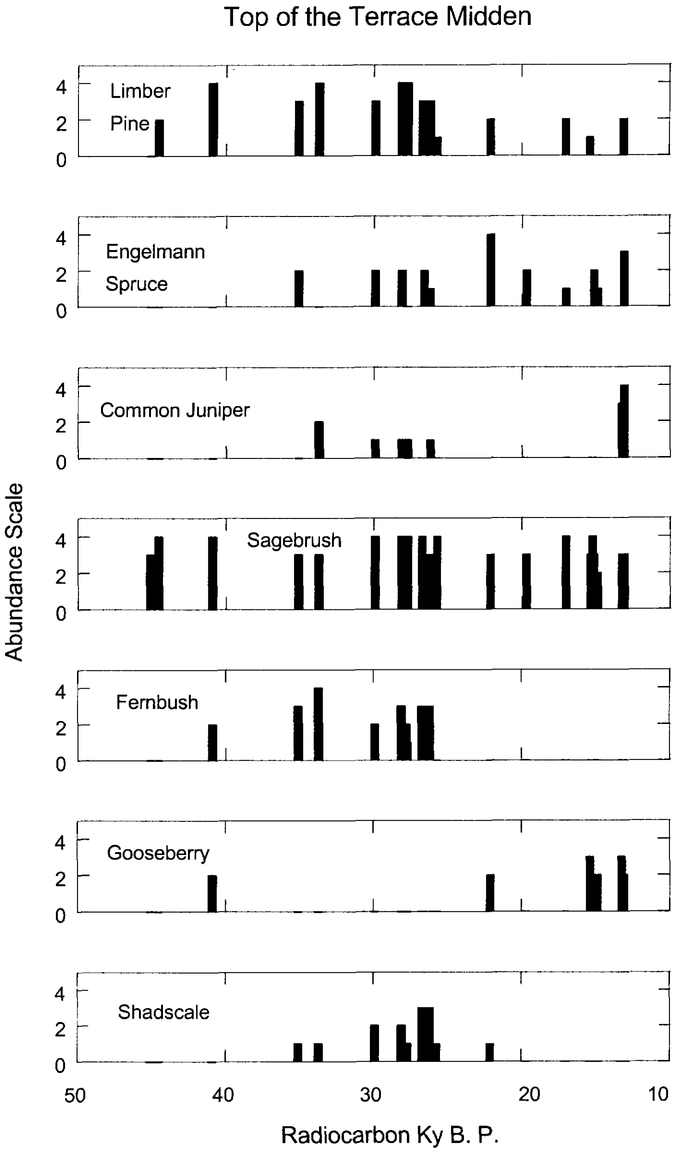

FIGURE 19.—Abundances of major plant constituents from selected radiocarbon-dated strata in the Top of the Terrace packrat midden, Goshute Range, eastern Nevada (Rhode, 1998). Radiocarbon dates are corrected for $^{13}C/^{12}C$ but are not calibrated. Abundance values follow an ordinal scale ranging from 0 (none) to 5 (abundant), as described by Rhode and Madsen (1995).

Pollen records from localities in and near the Bonneville Basin help to fill out this reconstruction of middle-Wisconsin-age vegetation. Pollen in Council Hall Cave (northern Snake Range) dating from ca. 40–30 Ka reflects montane vegetation dominated by pine and steppe shrubs including sagebrush, with conifers such as juniper, spruce, and fir represented in very small quantities. The presence of pollen of xerophytic shrubs such as chenopods and greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.) may indicate that these taxa dominated valley floors at the time (Thompson, 1984). Pollen from the sediment cores taken from near Wendover and Knolls contain high proportions of sagebrush, moderately high proportions of Cheno-*Ams*, and relatively low values of pine pollen prior to ca. 30 Ka (Davis, 2002). A basal date of the pollen record from Crescent Spring (Mehringer, 1977) is not available, but the sediments probably postdate ca. 28 Ka. Sediments from the Great Salt Lake Core C of Spencer et al. (1984) also postdate 30 Ka (Thompson et al., 1990). The basal units, which probably represent playa/playa edge deposits, are dominated by pollen of sagebrush and halophytic chenopods; pine pollen is lacking, although spruce, fir, and juniper pollen are present at low to moderate levels (Figure 20).

Further afield, the pollen sequence from Ruby Marsh, approximately 100 km west of the Bonneville Basin, indicates the presence of a shallow saline marsh/playa surrounded by sagebrush steppe (Thompson, 1984, 1992) from 40 to 28 Ka. Samples older than 30 Ka have the highest proportion of pine pollen of any in the 40,000-year record, but pine pollen is not abundant, indicating that pines were "probably present regionally, though not at the edge of the lake, and perhaps not in the southern Ruby Mountains" (Thompson, 1992:11). The very small amount of juniper pollen indicates that these conifers also were absent or rare.

Sagebrush steppe was the dominant lowland community on the Snake River Plain during this period, as indeed it was throughout the period from ca. 70 to 10 Ka (Bright and Davis, 1982; Mehringer, 1985; Davis et al., 1986; Beiswenger, 1991). Conifers were apparently limited to foothills and rocky terrain. Conifer pollen (mainly pine and spruce) increased slightly after 30 Ka, suggesting a slight increase in winter–spring moisture in a cold environment.

Together, these records point to cold but dry conditions before ca. 28 Ka in the eastern Great Basin. The climatic reconstruction based on vegetation data is consistent with the low lake levels that apparently characterized the Bonneville Basin prior to 28 Ka (Oviatt et al., 1992).

EARLY BONNEVILLE CYCLE, PRE–FULL GLACIAL (28 TO 20 KA)

Lake Bonneville began to rise about 30 Ka, slowly at first and rapidly after ca. 28 Ka; by 26 Ka the lake was roughly 100 m deep. The period from 26 to 20 Ka is marked first by continuing rise in lake level and subsequently by the Stansbury oscillation and development of the Stansbury Shoreline (Oviatt et al., 1990). According to Oviatt et al. (1990, 1992), the Stansbury oscillation represented a major change in hydrologic bud-

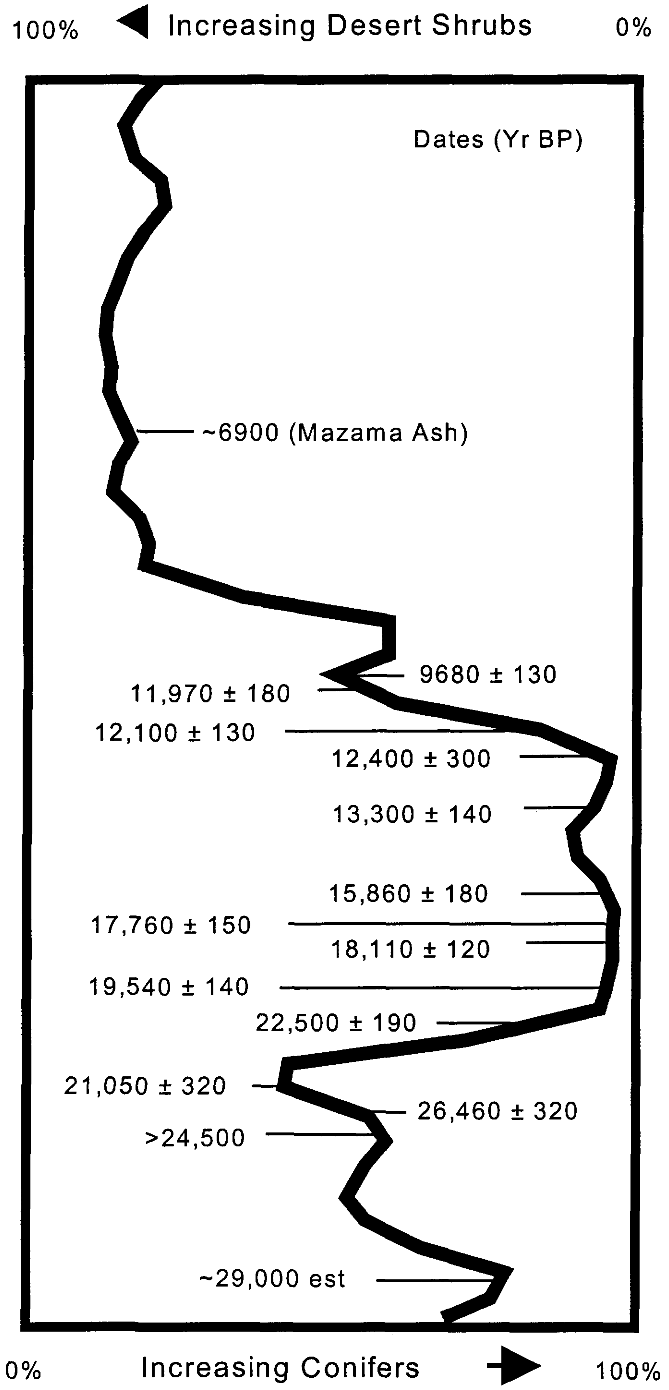

FIGURE 20.—Pollen ratios of xeric desert scrub/conifers for the last 30,000 years from Great Salt Lake Core C samples (Madsen and Kay, 1982; Spencer et al., 1984), with temporal controls in the right margin provided by Thompson et al. (1990). The curve shows relative percentages of Chenopodiaceae-*Amaranthus*+*Sarcobatus*+*Ambrosia*-type Asteraceae (scale at top) versus *Abies*+*Picea*+*Pinus*+*Pseudotsuga* (scale at bottom) and is smoothed by a weighted three-level moving average. (Modified from Madsen, 2000, fig. 4.)

get, though the climatic implications are still uncertain. Oviatt (1997) correlated this event with the termination of an ice-rafting (Heinrich) event in the northern Atlantic Ocean, suggesting a global-scale climatic cause.

The vegetation record dating to the millennia after 28 Ka shows continued dominance of bristlecone pine (without spruce or Utah juniper) in the southern Bonneville Basin, based on Council Hall Cave pollen (Thompson, 1984) and a couple of packrat midden samples (Wells, 1983). However, the interval between 28 and 18 Ka is poorly represented in the existing packrat midden record in the southern Bonneville Basin. Northward, at Top of the Terrace (Figure 19), several samples document that spruce increased in abundance while limber pine declined to low amounts (Rhode, 2000a; Madsen et al., 2001). Upper montane meadow plants such as currant and cinquefoil reappeared and expanded in abundance at the expense of fernbush; sagebrush maintained fairly consistent representation throughout. These vegetation changes suggest increasingly moist and cool conditions by ca. 22 Ka; however, the midden record for the period is more gap than record.

Fortunately, pollen and macrofossils in sediments and sediment cores provide more continuous, long-term records of vegetation change in the Bonneville Basin. The record from Crescent Spring (Mehringer, 1977) shows relatively low to moderate values of pine and spruce prior to ca. 24 Ka and relatively large values for sagebrush and Chenopodiineae, presumably shadscale and greasewood, reflecting widespread sagebrush–shadscale associations in valley bottoms, with pine and some spruce in uplands. A transition to deep, freshwater lake conditions occurred at ca. 24 Ka (Mehringer, 1985), with large increases in pine pollen, the appearance of spruce, and the decline of chenopods. Davis (2002) shows a very similar record for pollen taken from Wendover and Knolls. Pines may not have increased much in overall abundance on the landscape, but their pollen may have been concentrated and overrepresented by large lake effects. Chenopods, on the other hand, probably lost substantial habitat as rising levels of Lake Bonneville flooded valley bottoms and margins.

The Great Salt Lake Core C (Spencer et al., 1984; Thompson et al., 1990) indicates a similar transition to a fresh, deepwater lake by ca. 22.5 Ka, with greatly increased conifer pollen at the expense of sagebrush and xerophytic chenopods (Figure 20). A similar increase in lake level after 23 Ka is indicated in the lacustrine record from Ruby Marsh (Thompson, 1992), though pollen values suggest that sagebrush steppe continued to dominate the local landscape. Pollen from Grays Lake, in the uplands adjacent to the Snake River Plain (Beiswenger, 1991) shows that a pine/spruce woodland increased in abundance by ca. 30 to 26 Ka, intruding into what had been sagebrush steppe, and suggesting increasing moisture as well as continued cold temperatures. Finally, scattered occurrences of spruce and fir wood dating between 26 and 20 Ka are found in lake deposits on the east side of the Bonneville Basin (Scott et al., 1983), presumably indicating spruce/fir forests in the Wasatch Front. Wetter and cold conditions are indicated.

MIDDLE BONNEVILLE CYCLE, FULL GLACIAL (20 TO 14 KA)

During this interval Lake Bonneville rose abruptly from the Stansbury level—rapidly for the first 2000 years, then more slowly after 18 Ka—reaching the Bonneville highstand by ca. 15 Ka (Oviatt et al., 1992). Age estimates of glaciation in the Wasatch Range suggest the maximum extent of glaciation was between 20 and 18 Ka (Richmond, 1964, 1986; Madsen and Currey, 1979; Scott, 1988), at about the time Lake Bonneville was rising rapidly but a couple thousand years before the lake reached its highstand. The difference in timing between the age of the maximum extent of glaciation and the highstand of Lake Bonneville has been accounted for by the southward movement of the polar jet stream (Antevs, 1948; Benson and Thompson, 1987; COHMAP Members, 1988; Oviatt et al., 1990; Thompson et al., 1993). The rise of the lake was interrupted several times by substantial millennial-scale lake level declines (on the order of 50–100 m in depth). Oviatt (1997:155) has identified six "falling-lake events" ranging in age from 21 to 10 Ka that appear to be correlated with terminations of iceberg-rafting events in the northern Atlantic Ocean (Heinrich, 1988; Bond and Lotti, 1995). These events also appear to be correlated with glacial extent and climate changes in western North America (Allen and Anderson, 1993; Phillips et al., 1994; Clark and Bartlein, 1995). Oviatt (1997) suggested that these events may be related to latitudinal shifts in the polar jet stream that occurred several times during the late-Wisconsin interval in response to the topography of the continental ice sheet.

Vegetation records dating from the full glacial are somewhat more abundant than from the previous period. In the southern Bonneville Basin, packrat middens reveal that bristlecone pine continued to dominate, with additional representation of subalpine conifers including spruce, common juniper, Rocky Mountain juniper, and (rarely) limber pine; and shrubs including snowberry, spiny greasebush (*Glossopetalon spinescens* Gray), sagebrush, and (rarely) shadscale (Wells, 1983; Thompson, 1984). Pollen from Council Hall Cave contains large proportions of pine pollen with increasing spruce and decreasing abundance of juniper-type pollens and relatively stable amounts of sagebrush pollen. To the north, a midden sample dating to ca. 17 Ka at Top of the Terrace (Figure 19) shows an impoverished local flora, suggesting a tundra steppe dominated by sagebrush, some grass, and sparse cinquefoil, with rare occurrences of limber pine and spruce. This sample also contains several wetland plants, including bulrush (*Scirpus* sp.) and pondweed (*Potamogeton* sp.), as well as fish bones. It is highly unlikely that pondweed grew within the foraging radius of woodrats living at the midden locality. More likely is the possibility that seeds of aquatic plants were ingested by fish or waterfowl, which then became part of the diet of raptors, regurgitated in the shelter, and subsequently collected by woodrats. The seeds imply a nearby permanent body of water, probably Lake Waring in the valley below, but possibly also Lake Bonneville, east of the Goshute Mountains. Slightly younger samples from this midden locality document the reappearance of currant and an absence of limber pine.

Pollen from the Great Salt Lake Core C (Spencer et al., 1984) shows a continued dominance of spruce and pine during this period; the relative abundance of sagebrush and especially chenopod shrubs dropped substantially after ca. 22 Ka (Figure 20). In Ruby Valley, the large, freshwater Lake Franklin deepened to ~30 m from ca. 18 Ka until after 15 Ka, drowning what had been marshland (Thompson, 1992). Pollen from these sediments, however, shows relatively little change in the composition or abundance of sagebrush steppe vegetation surrounding the lake. It is likely that the lake resulted from reduced evaporation rate in a cold but relatively dry continental climate; increased precipitation likely would have resulted in more mesophilic shrubs and conifers in the region, which is not indicated in the pollen record.

In all, increasingly cold conditions are indicated after ca. 20 Ka; whether precipitation was substantially greater is less certain. Thompson and Mead (1982) noted that a steep vegetation gradient existed between the northern and southern Bonneville Basin (above the tree line in the north, below the tree line to the south), probably reflecting the distribution of growing-season temperatures and possibly also growing-season precipitation (dry in the north, more mesic in the south). The vegetation record is not yet sufficiently detailed or well dated to distinguish vegetation changes during the several falling-lake events reported by Oviatt (1997). Rapid fluctuations of pollen values in the Great Salt Lake Core C samples (Spencer et al., 1984) suggest that certain taxa (conifers and sagebrush) varied in abundance or that tree lines may have shifted in elevation in response to global-scale climatic changes during the full glacial (Figure 20).

LATE BONNEVILLE CYCLE, TERMINAL WISCONSIN (14 TO 10 KA)

Dating evidence summarized by Oviatt et al. (1992) and Benson et al. (1992) suggests that, after Lake Bonneville stabilized at the Provo level after the Bonneville Flood, the lake receded precipitously after 14 Ka, falling possibly to below modern levels by ca. 12 Ka, and marking the end of the Bonneville cycle. Subsequently, a large but much shallower lake rose to the Gilbert shoreline by around 10.9 Ka (possibly as early as 12 Ka), receding again by ca. 10 Ka. As Oviatt et al. (1992) noted, however, the timing of the recession from the Provo level is one of the least-known parts of the Bonneville lake cycle; dating of the Gilbert lake phase is little better (but see Oviatt et al., 2001). Recent dating efforts (Light, 1996; D.B. Madsen and C.G. Oviatt, pers. comm. to Rhode, 1996), as well as climate reconstructions from terrestrial vegetation data (Rhode and Madsen, 1995; see below), suggest that details of both the timing and magnitude of the post-Provo recession may need to be revised. Timing of the recession of Lake Bonneville also contrasts with the pluvial Lake Lahontan record, which indicates a deepening lake between 14.5 and 12.5 Ka (Benson et al., 1992), and with the evidence from the vegetation records in the northwestern Great Basin and the northern Mojave Desert, which suggests that this period was wetter than the glacial maximum (see "Last Glacial Cycle ..." above in "Northern and Western Great Basin" and see "Late Pleistocene ..." above in "Southern Great Basin and Northern Mohave Desert").

In contrast to the poorly dated recessional lake record, the terminal Wisconsin period is one of the best represented in the entire paleovegetation record, with many packrat middens and a couple of pollen sequences available (Madsen and Currey, 1979; Wells, 1983; Thompson, 1984; Rhode and Madsen, 1995). Several substantial vegetation changes occurred after 14 Ka. In the southern Bonneville Basin (Thompson, 1990), mesophilic shrubs tended to decline in abundance, and xerophytes or thermophilous shrubs took their place. Bristlecone pine remained common until shortly before 10 Ka. Spruce is no longer found in the record of this period, and several montane shrubs also drop out at particular localities. Limber pine increased substantially in frequency, especially after 11 Ka. Utah juniper and douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco) also began to appear in the south near the end of this period.

In the northern Bonneville Basin, numerous middens (Rhode and Madsen, 1995; Rhode, 2000a) document the presence of montane meadow vegetation comprising snowberry, currant, cinquefoil, sagebrush, and grass dating from ca. 14 to 13 Ka (Figure 21). From 13 to ca. 11 Ka, middens from relatively low elevations in the Bonneville Basin are dominated by limber pine, prostrate juniper, and sagebrush, and often contain remains of other montane shrubs. This evidence suggests that an extensive limber pine woodland (or mosaic of woodland and sagebrush steppe) dominated upper valley margins, while limber pine forest mixed with small numbers of spruce or fir apparently grew at higher elevations. Pollen data from Swan Lake, in the old Lake Bonneville overflow channel in southern Idaho, also show high values of limber pine and probably lodgepole pine (*Pinus contorta* Dougl. ex Loud.), along with spruce and fir, between 12 and 11 Ka (Bright, 1966). Pollen data from the Great Salt Lake Core C (Spencer et al., 1984; Thompson et al., 1990) show high relative abundance of pine and spruce until after 12.4 Ka, when sagebrush, greasewood, and Chenopodiineae rapidly increase. Pollen from Grays Lake (Beiswenger, 1991) documents a shift by ca. 12 Ka from a pine–sagebrush parkland reflecting cold, dry glacial conditions to a woodland/steppe mosaic, including spruce, pine, and sagebrush, suggesting cool but moister conditions. Subsequent postglacial warming resulted in the upslope retreat of spruce and pine and the expansion of sagebrush and xerophytic chenopods in the Grays Lake basin.

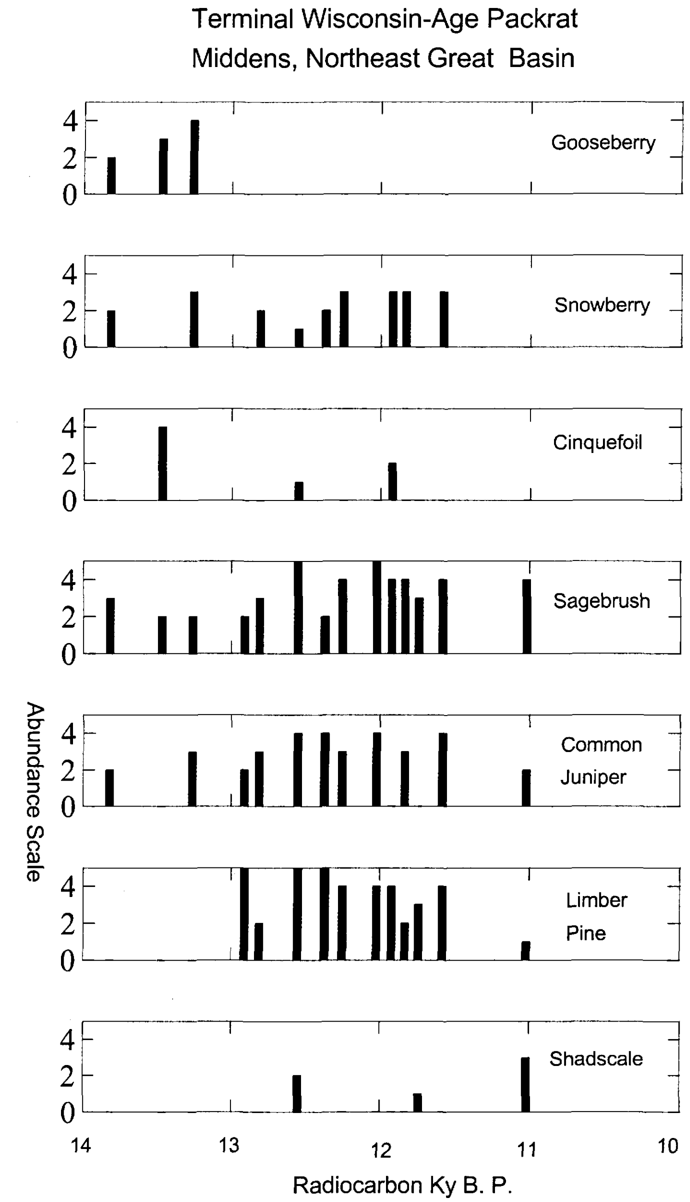

FIGURE 21.—Abundances of major plant constituents from selected radiocarbon-dated strata in packrat middens dating between 14 and 10 Ky B.P. in the northern Bonneville Basin (Rhode and Madsen, 1995). Radiocarbon dates are corrected for $^{13}C/^{12}C$ but are not calibrated. Abundance values follow an ordinal scale ranging from 0 (none) to 5 (abundant), as described by Rhode and Madsen (1995).

Together these records indicate warmer and possibly moister conditions ca. 14–12 Ka than during the full glacial, supporting montane meadows and woodlands in the north and more thermophilic woodland plants in the southern part of the Bonneville Basin. However, the climatic amelioration that occurred between 14 and 12 Ka was not so great as to prevent presently subalpine conifers from colonizing large areas at low elevations along the Bonneville highstand shoreline. Rhode and Madsen (1995) used the evidence that limber pine woodlands expanded substantially to the margins of the Bonneville Basin to suggest that growing season temperatures were ~6° C cooler than today. Insect assemblages from some of these middens also indicate substantially increased effective moisture relative to today (Scott Elias, pers. comm. to Rhode, 1998). In addition, the presence of fish bones in middens adjacent to the Great Salt Lake Desert and in Homestead Cave, in the Lakeside Range near Great Salt Lake, suggests relatively high lake levels perhaps as late as 11.5 Ka. Together, these biological data conflict with models of the decline of Lake Bonneville to below-modern levels at ca. 13–12 Ka (Benson et al., 1992; Oviatt et al., 1992).

By 12 Ka, the trend to drier conditions apparently strengthened. Pollen from Swan Lake indicates that spruce/pine woodlands were replaced by sagebrush steppe vegetation sometime between 11 and 10 Ka (Bright, 1966), possibly signaling cool but drier conditions during the Younger Dryas. The paleovegetation record from 11 to 10 Ka in the Bonneville Basin, however, is quite sparse at present. Middens dating to this interval are extremely scarce (Figure 21), and the Great Salt Lake C core (Spencer et al., 1984) is marked by a substantial temporal gap dating between ca. 12 and 9.6 Ka (Thompson et al., 1990) (Figure 20). What little data there are suggest a substantial reduction in pine woodlands and an increase in sagebrush–grass and shadscale associations, probably by 11 Ka and certainly by 10 Ka, reflecting the general trend of warming and drying. There is presently not enough evidence in the Bonneville Basin to show that vegetation changes occurring during the Gilbert lake cycle reflected enhanced moisture conditions, through either postulated Younger Dryas cooling (Benson et al., 1992) or increased summer monsoon precipitation (Currey, 1990; Oviatt et al., 1990).

EARLY HOLOCENE (10 TO 7 KA)

Early Holocene midden records are scarce by comparison with the terminal Wisconsin. The reason for the relative dearth of middens dating to the early Holocene remains unknown (Thompson, 1990), but it is possible that a continued warming and drying trend restricted *Neotoma cinerea* (bushy-tailed woodrat) habitat and population size. Fortunately, several pollen records from lacustrine settings exist for the Bonneville Basin and vicinity.

Comparison of vegetation patterns with the Holocene aquatic history of the Bonneville Basin also is hampered by lack of a well-known Holocene lake record for this Basin (Madsen et al., 2001). With the waning of Lake Bonneville after recession from the Provo level, lake level fluctuations became much smaller in scale. These smaller fluctuations are not as well dated as the lake events of the late Pleistocene (but see Currey and Madsen, 1974; Oviatt and McCoy, 1986), and some of the crucial evidence (for very low lake levels) is now under water and mostly inaccessible. It is known that lakes substantially larger than the present Great Salt Lake existed at several times during the Holocene (Currey et al., 1984). Evidence for an undated but probably early Holocene lake with a level somewhat below the Gilbert shoreline suggests a mesic interval (relative to today) some time between 10 and 7 Ka. Marsh deposits dated 10–9 Ka were identified recently in the vicinity of Wendover and near the Old River Bed channel (D.B. Madsen, pers. comm. to Rhode, 1998). Both marshes indicate greater surface water and a higher regional water table than what prevails today.

Woodrat midden records in the southern Bonneville Basin suggest that woodlands were dominated by newly immigrant Utah juniper and Rocky Mountain juniper, at least toward the end of the early Holocene; bristlecone pine, limber pine, and common juniper persisted in protected montane settings such as north-facing slopes (Thompson, 1990). The Council Hall Cave pollen record suggests that conifers were relatively scarce, whereas trees such as quaking aspen (*Populus tremuloides* Michx.), mountain mahogany, and chokecherry (*Prunus virginiana* L.) increased in abundance, and sagebrush and grass were common (Thompson, 1984). Cooler temperatures in the early Holocene apparently allowed mesophilic plants to grow at lower elevations than today (Thompson, 1990).

In the northern Bonneville Basin, the Great Salt Lake Core C pollen record (Spencer et al., 1984) shows that the abundance of pollen from xerophytic shrub communities relative to conifer woodlands was about the same 9.5 Ka as it was about 12 Ka, bridging the 2500-year-long unconformity in the core (Figure 20). Soon after 9 Ka, however, xeric desert scrub increased strongly at the expense of conifer woodlands.

Packrat middens (Rhode, 2000b; Madsen et al., 2001) also indicate that limber pine woodlands were replaced by more xerophytic sagebrush and shadscale scrub in lowlands by at least 9.5 Ka and probably a millennium earlier, as shadscale steppe continued to expand into the valley bottoms vacated by Lake Bonneville and Lake Gilbert (Figure 22). At the Leppy Overhang locality, a midden sample dating to 9.3 Ka contains remains of shadscale, horsebrush (*Tetradymia* sp.), and other arid desert shrubs, with no conifers represented. A sample dating to ca. 7.5 Ka at the same site is dominated by shadscale, with sagebrush, greasebush, rabbitbrush, Stansbury cliffrose (*Purshia stansburiana* (Torr.) Henrickson), desert snowberry (*Symphoricarpos longiflorus* Gray), and thornberry (*Lycium* sp.) also present. This locality had harbored limber pine woodlands at approximately 11.8–10.8 Ka (see "Late Bonneville Cycle ..." section above in "Bonneville Basin and Eastern Great Basin"). At the Twin Peaks locality, a midden sample that dates to 9.3 Ka is dominated by sagebrush, with shadscale as a relatively minor component. Limber pine, in association with common juniper, sagebrush, and buffaloberry, had occurred at the same locality some 3000 years before. The same contrast can be found in the modern vegetation at the two localities: sagebrush dominates at the Twin Peak locality, whereas the Leppy Overhang site is dominated by shadscale.

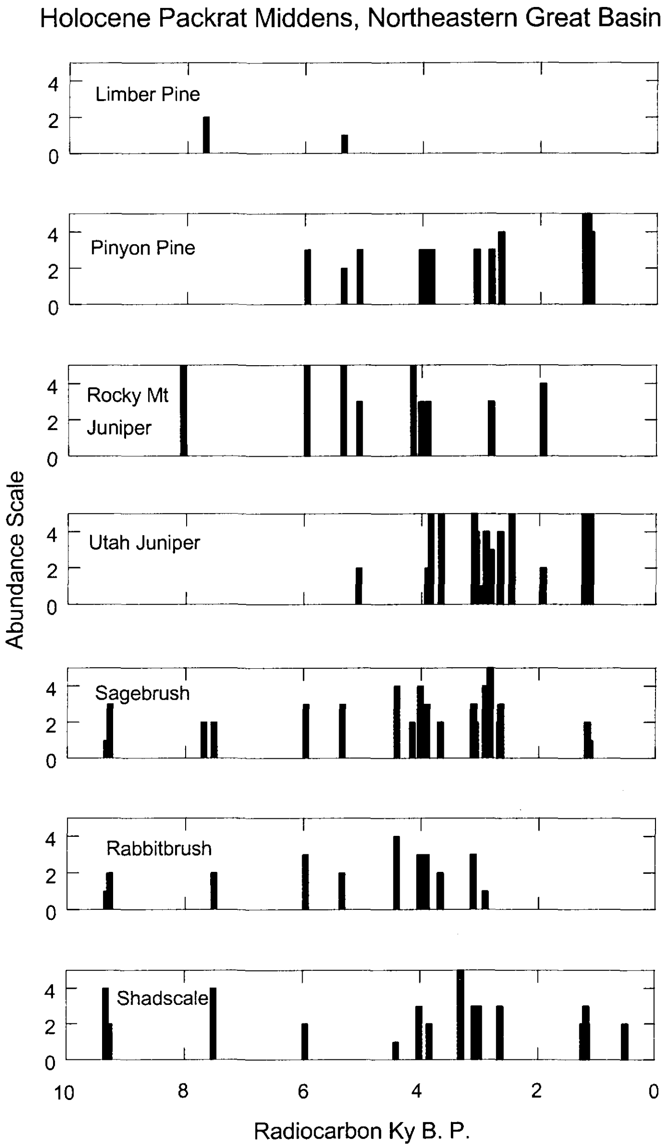

FIGURE 22.—Major plant constituents from selected radiocarbon-dated strata in packrat middens dating younger than 10 Ky B.P. in the northern Bonneville Basin (Rhode and Madsen, 1995; Rhode, 1998, and unpublished data). Radiocarbon dates are corrected for $^{13}C/^{12}C$ but are not calibrated. Abundance values follow an ordinal scale ranging from 0 (none) to 5 (abundant), as described by Rhode and Madsen (1995).

Several records suggest that climatic conditions during the early Holocene were cooler and/or moister than at present, at least before ca. 8.5 Ka. Thompson's (1984) midden data indicating a cooler, mesic early Holocene have been noted previously. Further north, a midden from the Cherry Creek Range dating to ca. 7.7 Ka shows that limber pine survived in sheltered upland settings below its present altitude. Limber pine nut hulls in Danger Cave, directly dating between 8 and 7 Ka, also suggest that populations of this now subalpine conifer grew at relatively lower elevations nearby (Rhode and Madsen, 1998). Limber pine retreated upslope to its scattered subalpine stations during the middle Holocene, as climates continued to warm and as thermophilous competitors migrated into the region. To the west, woodrat middens from near Gatecliff Shelter in the Toquima Range, central Nevada, are dominated by mesophilic trees and shrubs such as quaking aspen, serviceberry (*Amelanchier utahensis* Koehne), willow (*Salix* spp.), and Woods' rose (*Rosa woodsii* Lindl.), with sagebrush and rabbitbrush also present; conifers are rare or absent (Thompson and Hattori, 1983).

At Homestead Cave and the Lakeside Range in Utah, small mammal remains also indicate that the early Holocene was relatively cool and moist compared with conditions today (Grayson, 1998). Hackberry apparently was common in the outcrops around the cave and at lower elevations in the Lakeside Range from about 10 to 7 Ka (Hunt et al., 2000; Rhode, 2000b; Madsen et al., 2001). The climate today is too dry to support hackberry around Homestead Cave although it still occurs in the Lakeside Range (Albee et al., 1988) and is commonly found in the more massive and better-watered Oquirrh and Stansbury Mountains not far away. Hackberry prefers rocky substrates where it can absorb water trapped in cracks in outcrops (DeBolt and McCune, 1995). The presence of hackberry in the Lakeside Range during the early Holocene could have resulted from the more mesic conditions (perhaps summer precipitation) of the time, but it also could have resulted from a higher water table and more-saturated rock outcrops remaining from the Bonneville pluvial episode. The early Holocene hackberry in the Lakeside Range coincides with a similar increase in regional abundance of hackberry in southern Nevada, as noted above in the early Holocene section in "Southern Great Basin and Northern Mojave Desert."

Other regional vegetation records indicate substantial warming during the early Holocene, perhaps to temperatures warmer than today. The pollen record from Swan Lake (Bright, 1966) reveals a transition from sagebrush steppe to sagebrush/shadscale steppe ca. 9–8.5 Ka, reflecting increasing xericity through the early Holocene. A similar sequence occurred at Grays Lake (Beiswenger, 1991), where the transition is dated to ca. 8.5 Ka, and Ruby Marsh (Thompson, 1992), where the transition dates from 8.5 to 8 Ka. A decrease in the ratio of conifer pollen to all other pollen from Snowbird Bog (Madsen and Currey, 1979) also indicates an early Holocene warming prior to ca. 8 Ka (Figure 23). These records are consistent with general circulation models, suggesting increased solar insolation and warming of continental interiors during the early Holocene (COHMAP Members, 1988).

It is notable that early Holocene records indicating relatively cooler, moister conditions than today are typically (1) derived from packrat middens, (2) montane in distribution, and (3) more southerly in distribution; whereas those records emphasizing the early Holocene warming trend tend to be (1) pollen based, (2) from lowland or valley bottom settings, and (3) more northerly in distribution. The differing interpretations might have resulted from the different kinds of data sets being interpreted, or geographical climate gradients, or the differential response of plants to early Holocene climate in lowland versus montane habitats. Enhanced seasonality resulting from orbital forcing during the early Holocene (Thompson et al., 1993) may have affected montane woodlands in a different way than lowland shrub communities. Vegetational inertia (Cole, 1985; Davis, 1986) may also play a role here. It seems likely that, because of a warmer and drier early Holocene climatic regime, mesophilic plants had already been eliminated from valley floors; and although they had not yet disappeared from uplands they may have been growing there under stress. New techniques for assessing plant physiological stress from macrofossil remains may address this issue.

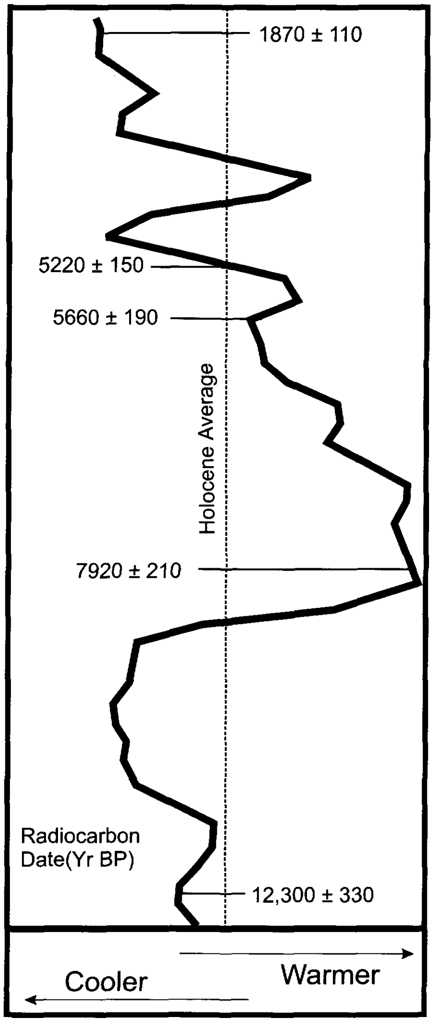

FIGURE 23.—Estimate of Holocene temperature change in the Wasatch Range, illustrated by curve showing changes in the relative abundance ratio of conifer pollen (*Abies* + *Picea* + *Pinus* + *Pseudotsuga*) to all other pollen in Snowbird Bog, Little Cottonwood Canyon (Madsen and Currey, 1979), with the average ratio (dashed line) and selected temporal controls indicated. Cooler temperatures are indicated by relatively greater abundances of conifer pollen. The curve is smoothed by a weighted three-level moving average. (Modified from Madsen, 2000, fig. 5.)

Beginning in the latest Wisconsin period and continuing through the early Holocene and into the middle Holocene, a variety of plant taxa underwent substantial range shifts, apart from simple changes in local abundance or upslope retreat. These range shifts are best attested by the evidence from packrat middens. One example is Rocky Mountain juniper, a temperate mesophilic conifer. First known in the region during the terminal Wisconsin, Rocky Mountain juniper became common in upland settings in the early Holocene and through the middle Holocene as well.

Singleleaf piñon pine also began to expand northward during the early Holocene. Its distribution apparently remained south of Meadow Valley Wash (37°30′N) until at least 8.5 Ka (Madsen, 1973), but by 7 Ka, piñon pine had reached the vicinity of Danger Cave (41°N). Expansion of piñon pine woodlands is typically facilitated by corvid birds, which can carry the heavy pine nuts for distances of up to 22 km (Lanner, 1983). The rapid initial northward expansion is faster, however, than current estimates allow for piñon pine migration via corvid birds (Lanner, 1983; Wells, 1983). The initial spread of piñon pine northward may also have been aided by people who brought pine nuts with them on their journeys (Mehringer, 1986; Madsen and Rhode, 1990; Rhode and Madsen, 1998). The chronology of piñon pine migration is complicated by the Danger Cave remains, which are older than all other piñon pine records north of ~37°N in the central or eastern Great Basin. How it happened to arrive in the vicinity of Danger Cave by 7 Ka is difficult to trace in the absence of any intervening records of earlier age.

Utah juniper was common in the southern Bonneville Basin by the beginning of the Holocene, and it reached the Onaqui and Stansbury Mountains by about 6.6 Ka (Rhode and Madsen, 1995), but it was apparently a rather late arrival elsewhere in the northern Bonneville Basin. Because Utah juniper and piñon pine are rather closely associated today, why do they have distinctly different Holocene migration histories? West et al. (1978) noted that the two taxa have somewhat different climatic requirements and tolerances, and perhaps these climatic factors account for the differences in timing and range.

MIDDLE HOLOCENE (7 TO 4 KA)

Vegetation records dating from the middle Holocene are relatively sparse but come from a variety of sources, including woodrat middens, archaeological sites, and pollen cores. These provide limited, but nevertheless useful, information on the timing of migration of certain taxa into the region, on the nature of vegetation community composition, and on climatic conditions during this interval. The general size and level of Great Salt Lake during the period is not known, but it is likely to have been low (Currey, 1980).

As the middle Holocene began in the southern Bonneville Basin, conifers such as limber pine, bristlecone pine, and Rocky Mountain juniper, as well as mesophilic shrubs, had declined substantially in abundance or were restricted to higher elevations (Thompson, 1984). Piñon pine, Utah juniper, ponderosa pine (*Pinus ponderosa* P. Lawson & C. Lawson) and white fir became increasingly abundant. Thompson (1984, 1990) suggested that increased abundance of some of these taxa may reflect increased amounts of summer precipitation from subtropical sources, as well as warmer growing-season temperatures.

Further west, at Gatecliff Shelter, singleleaf piñon pine appears in the region by about 5.3 Ka (Rhode and Thomas, 1983) in a conifer woodland containing both Rocky Mountain juniper and Utah juniper (Thompson and Hattori, 1983). Using sedimentary evidence from Gatecliff Shelter and nearby Triple T Shelter, and closely following the arguments of Van Devender and Spaulding (1979), Davis (1983) proposed that the interval prior to 6300 years B.P. was relatively cool and winter-wet with relatively abundant snowfall but deficient in summer moisture. Davis thought that after this time until about 5000 years B.P., annual temperatures were somewhat warmer and summer precipitation increased with often intense storms, leading him to support the "moist Altithermal" of Martin (1963). It is not certain how far northward from central Nevada the enhanced stormy summer precipitation regime may have occurred. It is notable that pollen samples from Gatecliff and Triple T Shelters show a marked increase in representation of juniper and pine between 6 and 5 Ka (Thompson and Kautz, 1983). After 5000 years ago, according to Davis (1983), temperatures apparently cooled slightly and summer rainfall decreased in amount.

Several middens dating to the middle Holocene are known from the northern Bonneville Basin and vicinity (Rhode, 2000b; see Figure 22). Upland areas in this region appear to have contained woodlands dominated by Rocky Mountain juniper, with a secondary component of piñon pine. Rocky Mountain juniper grew with piñon pine in the Toano Range, in the northern Pequop Range, and in the Cherry Creek Range; it is the only conifer known from the Silver Island Range. Sagebrush and rabbitbrush were the most common understory shrubs. In a few protected settings, such as the north-facing Icicle Cave in the Pequop Range, limber pine and common juniper were also minor components of the vegetation, growing at relatively low elevations compared with today. Utah juniper was quite scarce in the northern Bonneville Basin. One record from the Toano Range contains Utah juniper remains dating from the middle Holocene, and it is also known from a midden in the Onaqui Range, east of the Bonneville Basin, dating to 6.6 Ka. The dominance of Rocky Mountain juniper, rather than the more thermophilic Utah juniper, may indicate that middle-Holocene climate in the uplands was not so warm and dry as is sometimes thought. Alternatively, it may suggest that growing-season precipitation derived from summer convective storms was more common in the Bonneville Basin than elsewhere in the Great Basin.

Lowland vegetation patterns are better shown in pollen records. At Great Salt Lake, high ratios of shadscale and other chenopod shrubs relative to sagebrush and conifers prevailed from 7 Ka until about 5.5 Ka, suggesting that the early part of the middle Holocene was warmer and drier than today (Mehringer, 1977, 1985). Between 5.5 and 4 Ka, relative pollen ratios approached modern values, suggesting that climatic conditions were generally cooler and/or wetter in the latter part of the middle Holocene than in the first part. At Snowbird Bog in the Wasatch Range, Madsen and Currey (1979) found pollen evidence indicating that the period from 8 to 6 Ka was relatively warm and dry, whereas the following period until 5.2 Ka was warm but wetter (Figure 23). The Ruby Marsh sediment record documents lower-than-modern water levels and an expansion of shadscale at the expense of sagebrush steppe vegetation from ca. 7.4 to 5 Ka. Mission Cross Bog, in the Jarbidge Mountains, shows evidence of an increase in juniper woodland and shadscale steppe and a decline in subalpine woodlands from about 8 to 5 Ka (Thompson, 1984).

LATE HOLOCENE (<4 KA)

Great Salt Lake rose in elevation and expanded substantially in area at least twice during the late Holocene (Currey et al., 1984). The lake rose to an elevation of 1284 m, then receded, then advanced again to an elevation of 1287 m, flooding most of the Great Salt Lake Desert and forming a broad shallow lake that extended to the Utah–Nevada border.

The midden record representing the late Holocene is more abundant than that representing the previous several thousand years (Figure 22), possibly because of better preservation of the younger middens, but also perhaps because woodrats may have been more abundant during the late Holocene than earlier. Midden records indicate that the flora of the region was largely modern by this time and that plant taxa were for the most part close to their modern distribution. Many of the midden samples have contents that are quite similar to the vegetation that grows around them today.

Thompson (1984) found only rather modest vegetation changes in the Snake Range and southern Bonneville region, suggesting that late-Holocene climates were relatively stable, at least on the scale recorded in midden plant records (Thompson, 1984). The midden record from the northern Bonneville Basin (Rhode, 2000b) indicates that although modern vegetation associations were largely in place by the late Holocene, the abundance of certain plant taxa within those vegetation associations varied substantially through time (Figure 22). Some taxa only achieved their present importance in plant communities within the last 2000 years. The distribution of some taxa shifted in elevation in response to climatic variation.

A prominent late-Holocene vegetation shift concerns the distribution of Utah juniper and Rocky Mountain juniper. Utah juniper apparently arrived in northeastern Nevada, as noted previously, during the middle to late Holocene. In some areas Utah juniper was a minor component in woodlands dominated by Rocky Mountain juniper (e.g., Cherry Creeks, Silver Island Range); but in other nearby areas, midden contents show it was the dominant woodland conifer (e.g., Goshute Range). These differences are probably related to differences in elevation or topographic position of the midden sites, as well as to other factors. Utah juniper is the most common juniper today in all of these areas, and Rocky Mountain juniper has become much less common in the last 2000 years. A similar pattern is shown in middens from Gatecliff Shelter, central Nevada, where Rocky Mountain juniper disappears from the midden record between 2.3 and 1.7 Ka (Thompson and Hattori, 1983).

Several midden records from Antelope Island and the Promontory Mountains, near Great Salt Lake, indicate that Utah juniper grew 50–100 m lower during the Neoglacial interval between ca. 3.5 and 2.9 Ka than it occurs today (Rhode, 2000b). Lower-than-modern elevations of Utah juniper are also recorded in middens dating to 2.3 and 1.0 Ka from the Cricket Mountains in the southernmost Bonneville Basin (Madsen, 1984). It is likely that Utah juniper retreated upslope from these relatively low elevations toward elevations where we see it today as the late-Holocene climate warmed and dried after the Neoglacial. Presumably the lower tree line of Utah juniper has migrated up- and downslope several times in response to climatic variation during the past few thousand years.

Another example of late-Holocene range changes may be green mormon tea (*Ephedra viridis* Cov.). Green mormon tea is a common shrub in uplands throughout the region, including the vegetation surrounding midden localities on the western slope of the Goshute Range today, and it is found in modern midden samples in the region; but midden samples dating to 3.8–3.1 Ka lack green mormon tea. Other paleoecological records also indicate that green mormon tea was a late entry into the vegetation of the northern and central Great Basin, within the past 3000 years (e.g., Thompson and Kautz, 1983). It should be noted, however, that mormon tea is generally uncommon in late-Holocene midden samples, suggesting that the lack of mormon tea in middens may be partly related to collection habits of woodrats rather than abundance in the landscape.

Additional late-Holocene vegetation changes of importance are shown in pollen records from the region. A pollen record from Crescent Spring (Mehringer, 1977, 1985) shows that sagebrush and conifer pollen became increasingly important after 4 Ka, suggesting overall greater effective moisture than during the middle Holocene, albeit with several warmer and/or drier intervals during the period since then. These warmer/drier excursions occurred approximately 3.2, 2.5, and 1.8 Ka; substantial cool/wet episodes centered on 3.6, 2.7, 2.2, and 1.5 Ka (Mehringer, 1985). As noted in previous sections, these periods correspond to drier and wetter periods indicated in the pollen record of the northern Great Basin (Wigand, 1987) and the northern Mojave Desert (Wigand, 1997b).

The pollen record at Ruby Marsh indicates that, after ca. 4.5 Ka, "shadscale declined in importance in the valley bottom and marsh waters deepened, in turn reflecting cooler temperatures and/or greater precipitation" (Thompson, 1992:13). In addition, an increase in sagebrush pollen and higher water levels at

Ruby Marsh during the last 500 years indicate that "the coolest and/or moistest conditions since the early Holocene" presumably correlated with the Little Ice Age (Thompson, 1992:13). The late-Holocene record from Mission Cross Bog in the Jarbidge Mountains shows an increase in pollen from spruce, fir, and pine after 5.0–4.3 Ka, with a peak around 3.6 Ka, suggesting this was the most mesic episode in the last 8000 years (Thompson, 1984). At Swan Lake (Bright, 1966), warm, dry middle-Holocene conditions became cooler by 3.1 Ka, with a lowering of the forest tree line and a decrease in sagebrush steppe. Warmer conditions apparently returned by 1.7 Ka, with increased sagebrush and less limber pine. Cooler late-Holocene climate from ca. 5.0 Ka onward is also reflected in the pollen from Snowbird Bog in the Wasatch Range (Figure 23; Madsen and Currey, 1979).

At Gatecliff Shelter, central Nevada, packrat midden and sedimentary evidence (Davis, 1983; Thompson and Hattori, 1983) indicate that a cool, winter-wet interval began rather suddenly about 3400 years ago, during which time mormon tea became established in the region. The period between 3400 and 2800 years B.P. may have been cooler and moister than any time in the last 6000 years. These records also suggest that summer-dominant rainfall may have appeared between 1500 and 800 years ago.

Pollen and plant macrofossil evidence from archaeological sites (Aikens, 1970; Harper and Alder, 1970, 1972; Kelso, 1970; Dalley, 1976) also document late-Holocene vegetation changes (see Currey and James, 1982). At Swallow Shelter and Hogup Cave, grass pollen began to increase ca. 1.5 Ka, again suggesting an increase in effective growing-season moisture. This increase in summer precipitation may have helped to support the spread and success of the Fremont peoples' maize-based horticultural systems in the Bonneville Basin from ca. 1.5 to 0.9 Ka. Harper and Alder (1970, 1972) used the record of plant remains from Hogup Cave and Danger Cave to suggest that the last 1000–600 years have been among the driest and warmest of the entire Holocene.

DISCUSSION: VEGETATION AND AQUATIC HISTORY IN THE BONNEVILLE BASIN

In general outline, vegetation history, as represented by widespread pollen and macrofossil records, and aquatic history, as represented by the lake chronology and other records, appear to be mostly but not entirely concordant. Shallow saline lakes during the middle Wisconsin are matched with cold but dry limber pine woodlands. As Lake Bonneville began to rise from 28 to 20 Ka, evidence for more mesophilic montane plants became increasingly common. By the time of the Bonneville highstand ca. 16–15 Ka, very cold conditions are reflected in now subalpine conifers in the southern Bonneville Basin and in cold sagebrush steppe tundra in the north. The recession of Lake Bonneville from the Provo shoreline coincides with considerable evidence of expansion of plants requiring warmer and drier conditions than prevailed during the full glacial. However, as noted above (see discussion of late Bonneville cycle in "Bonneville Basin and Eastern Great Basin"), the terrestrial vegetation record from the northern Bonneville Basin is not consistent with the timing and magnitude of certain models of Lake Bonneville recession (e.g., Oviatt et al., 1992). The postulated Younger Dryas rise of Lake Gilbert is also not strongly reflected in the vegetation records, although available vegetation records are quite rare. Holocene fluctuations in vegetation appear to coincide with lacustrine history of Great Salt Lake, although comparison is limited by the state of knowledge of Holocene lake history and by lags in response of vegetation to climate change.

A number of reasons may account for discordance between lake history and vegetation history:

1. Differential sensitivity or rapidity of response of different systems to the same climatic factors (e.g., inertia of vegetation to climate change).
2. Responses of different systems to different parameters within "climate space" (e.g., temperature versus precipitation; growing-season precipitation versus winter precipitation).
3. The presence of local or regional factors that affect one system but not the other (e.g., downcutting that lowered Lake Bonneville in the absence of climatic change; tectonics or isostatic rebound that altered the configuration of the lake basin; or altered growth tolerances of certain plants in relation to atmospheric chemistry or competitive relationships with other plants).
4. Data gaps in one or both proxy records causing difficulties of correlation.
5. Uncertainties in how one or both proxy records are related to underlying climatic factors.

Causes for some of the discordance between vegetation and aquatic history in the Bonneville Basin (e.g., vegetation change during the post-Provo recession and Gilbert Lake interval) remain to be worked out in detail.

The packrat midden record suggests a substantial north-to-south gradient in both floristic and vegetation representation existed through the most of the record. For one example, bristlecone pine was abundant in the south and nearly absent in the north, replaced by limber pine; for another, during the full glacial the southern area bore conifer forests while a cold sagebrush steppe prevailed in the north. How and why this gradient might have varied through time, and the location of substantial biotic discontinuities, are subjects for future biogeographic research.

Summary

The foregoing regional discussions highlight the wealth of empirical evidence now available to reconstruct the history of vegetation in the Great Basin. The combined and complementary evidence found in pollen profiles, packrat middens, archaeological sites, and other localities present a detailed record of broad regional trends and local variability of vegetation through time.

The existing paleoenvironmental record for the last 35 Ka reveals periods when vegetation changes occurred simultaneously and in the same relative direction throughout the Great Basin. At other times, each of the subregions seems to have responded quite differently. These differences directly reflect the relative influence of monsoonal versus Pacific storm systems during the Holocene and earlier interglacials, and the relative strength of polar air masses during glacials.

Although the vegetation history of the Great Basin is marked by numerous high-frequency changes in climate, there are easily recognizable crosscutting events that can be tracked in each subregion by tracing the response of indicator species. These species are characterized by wide spatial distribution and relatively rapid response to changes in climatic input. In addition, these species are easily identified and can be tracked in one or more of the most commonly used paleoenvironmental data sets mentioned above.

To summarize some of the trends from a basinwide perspective and to get a broader view of Great Basin vegetation history during the last 40,000 years, we compare what was happening in the three regions considered above during a dozen separate snapshot "moments" in the past.

40 KA

The limited empirical record available from this time suggests that vegetation in much of the Great Basin and on the Snake River Plain was dominated by sagebrush or saltbush steppe, with a mosaic of sagebrush, montane brush, and patches of conifers in upland areas. Pollen records from the northeastern Great Basin suggest that conifers were not very abundant in the region (Beiswenger, 1991; Thompson, 1992), although they may have been more common further south (Thompson, 1984). The conifers consisted of limber pine and bristlecone pine at relatively low elevations in the eastern basin, with mesophilic shrubs as understory or shrub layer associates. A cold and somewhat mesic interval is indicated. In the southern Great Basin, woodlands dominated by Utah juniper and mountain mahogany were present in upland areas, where present vegetation appears broadly similar, as well as in lower elevation areas now dominated by desert scrub species (Spaulding, 1985). According to Spaulding, the presence of certain desert plant species in these middens indicate that "winter minimum temperatures were within 2° to 3°C of today's values" (Spaulding, 1985:30). The pollen record from the Bed and Breakfast locality in the Summer Lake basin indicates that sagebrush steppe was widespread. Juniper woodland was present as well but not as abundant as it was to be during the succeeding period. Lower grass pollen values than before 40 Ka and after 34 Ka indicate that conditions were drier during this period than either before or after. Sedge-dominated marshes together with abundant eutrophic algae (*Botryococcus* sp.) indicate that pluvial Summer Lake was low. The same may have been true of pluvial Lake Lahontan during this period.

32 KA

In the northwestern Great Basin the onset of a series of cool, moist cycles from ~34 to 30 Ka resulted in the extension of patches of mixed-conifer woodland—comprising pines (probably whitebark pine, western white pine (*Pinus monticola* Douglas ex D. Don), and lodgepole pine), fir, and occasional spruce—into relatively low elevations in mountainous terrain. More-continuous woodlands dominated by Utah juniper with an understory of sagebrush grew over much of the area, with a lower elevational range greater than at present. This expansion appears to have climaxed around 32–30 Ka and was followed by a dramatic return to drier conditions. In the southern Great Basin and northern Mojave Desert, subalpine conifers also grew at relatively low elevations in the mountains. Whereas white fir had been a substantial part of this woodland between 34 and 32 Ka, it declined in abundance after 32 Ka, leaving limber pine alone at these lower elevations, which suggests that climate was cool but becoming increasingly arid. Utah juniper was abundant or common from as low as ~750 m in elevation, growing in association with shadscale and rabbitbrush, to elevations as high as 1860 m (Spaulding, 1985). In the northeastern Great Basin, limber pine dominated the patchy mountain woodlands, accompanied by montane shrubs that indicate drier conditions than had occurred at 40 Ka. Sagebrush steppe continued to prevail in valley floors and on the Snake River Plain. In the southern Bonneville Basin, bristlecone pine woodlands dominated the mountains, while sagebrush and shadscale occupied valley bottoms.

28 KA

In the northwestern Great Basin, this time marks the beginning of a major drought stretching from ~28 to 26 Ka. It is immediately preceded and followed by regionally correlatable grass expansions in the woodrat midden pollen record at Pyramid Lake as well as in the sediments of Summer Lake. The drought is characterized by saltbush expansion and is reflected in lowered lake levels throughout the northwestern Great Basin. In the southern Great Basin, Utah juniper continued to grow fairly abundantly at lower elevations, below about 1300 m; piñon pine is virtually unreported the region (Spaulding, 1985). Limber pine and white fir disappeared from the record of the area but may have retreated to widely scattered settings above about 2000 m in elevation. In the eastern Great Basin, sagebrush and shadscale steppe continued to dominate valley settings, but Lake Bonneville was beginning to rise, flooding portions of the valley habitat in that large basin. In montane settings, limber pine was declining in abundance and spruce increased; montane mesophilic shrubs also increased in abundance. The climate appears to have become wetter and colder than previously.

22 KA

Increasingly moister conditions beginning ~24 Ka were reaching a pre–glacial maximum climax by 22 Ka. A transition toward much colder temperatures, however, was continuing and affecting vegetation in all parts of the Great Basin and the northern Mojave Desert. In the northwest Great Basin, the expansion of patchy woodlands, including subalpine whitebark pine, to elevations below 1380 m reflected moister conditions with a reliable wet season. Lake Lahontan was apparently rising rapidly and was probably at the level of the Astor Pass sill (1222 m), but it had not yet reached the Darwin Pass sill (1265 m) to spill into the Carson Basin (Benson et al., 1995). According to Benson et al. (1995), this rapid rise probably coincided with passage of the jet stream over the Lahontan Basin. In the southern Great Basin and northern Mojave Desert, cooler, wetter conditions are also indicated for this period, as subalpine conifer woodlands dominated by limber pine with some bristlecone pine, and also containing white fir, descended to elevations below 1600 m (Spaulding, 1985; Forester et al., 1996). In the eastern Great Basin, Lake Bonneville had also risen rapidly, and patchy, subalpine conifer woodlands dominated by spruce (in the north) and bristlecone pine (in the south) were present in upland environments. Cold but moister conditions are indicated in the Bonneville Basin and also in the Snake River Plain during that time (Beiswenger, 1991).

18 KA

At the height of the full glacial, vegetation throughout the Great Basin records cold and fairly dry climatic conditions. In the northwest Great Basin, these cold, dry glacial conditions fostered a mixed-shrub steppe comprising primarily sagebrush, saltbushes, and rabbitbrush with rare clumps of juniper in scattered sheltered areas. Whitebark pine, which had appeared between 24 and 22 Ka, disappeared. To the south, cold and fairly dry conditions are also indicated by the widespread presence of limber pine and bristlecone pine, without white fir, in the region's mountains, to elevations as low as 1600 m. Juniper woodlands retreated upward almost 450 m to elevations around 1200 m. Piñon pine was rare to absent in most of these woodlands. In the northeastern Great Basin, a sagebrush steppe–tundra apparently existed in montane settings, with very limited patches of conifers including spruce and occasional limber pine. Southward, bristlecone woodlands prevailed in uplands. Sagebrush steppe dominated in lowland settings, while deepening lakes existed in many of the valley basins. The vegetation is consistent with expectations drawn from global circulation models (COHMAP Members, 1988; Thompson et al., 1993) that suggest atmospheric circulation in the region at the time was dominated by cold, dry air moving southwestward from the continental glacial sheet.

12.5 KA

This period marks the transition from the Pleistocene to the Holocene in the northwestern Great Basin. Whitebark pine reappeared briefly at elevations around 1380 m on the west shore of pluvial Lake Lahontan around 12.5 Ka but disappeared shortly thereafter. Although Utah juniper woodland reexpanded after the glacial maximum, it was sagebrush that experienced its most dramatic expansion of the last 35 Ky during this period. By 11.5 Ka, however, severe drought had not only driven whitebark pine from the area but also had brought an end to the sagebrush expansion and encouraged the regional expansion of saltbushes as well. Pluvial Lake Lahontan dropped dramatically from its late-Pleistocene high at this time. The so-called "Younger Dryas," centered around 10.6 Ka, is evidenced by a renewed abundance of juniper woodland and by an apparent still-stand of pluvial Lake Lahontan. The same pattern of change was occurring in the southern Great Basin and northern Mojave Desert. Limber pine retreated up the mountainsides while juniper retreated from the valley floors. By 10 Ka, limber pine no longer grew below about 2300 m in elevation (Spaulding, 1985), and juniper was approaching its modern elevational distribution. In the northeastern Great Basin, limber pine had expanded widely into lower montane settings. It also occurred at fairly low elevations around the northwest side of the Bonneville Basin in a mosaic with sagebrush, prostrate juniper, and mesophilic shrubs. To the south, woodlands were dominated by bristlecone pine. Thermophilous shrubs such as *Atriplex* spp. were just beginning to appear in the region, and these would expand after ca. 11 Ka as climate grew warmer and drier. It is at this time that plant communities were undergoing major restructuring as they moved into new areas on the landscape. What probably had been a mosaic of highly variable plant community patches occupying discrete microhabitats regulated by slope, aspect, and soils, as well as effective moisture, began the transformation into the more familiar vegetation zones of the Holocene.

9 KA

In the northwestern Great Basin, the early Holocene thermal maximum was characterized by major expansion of desert scrub vegetation around the margins of still-drying pluvial lake basins. In the Carson Sink, a subbasin of pluvial Lake Lahontan, extensive marshes were exploited by Native Americans for food and raw materials to make basketry, matting, and other items. Expansion and density of sagebrush steppe in the uplands reached its Holocene climax at this time. Low-elevation outliers of Utah juniper woodland that had survived early Holocene droughts or had reexpanded during the Younger Dryas finally disappeared. Evidence of monsoonal penetration, which is weak in the northern Great Basin, is strong in the southern Great Basin and northern Mojave Desert during this period. The expansion of grasses without a corresponding expansion of winter-rainfall-dependent plants suggests that summer rainfall had increased. The appearance of hackberry in locations indicating a proliferation of seeps along cliff-faces suggests the presence then of year-round water where it is not found today. Summer monsoons provided the additional rainfall nurturing these springs. Black mat formation, whether it was related to increased spring discharge or soil formation (or perhaps to the increase in grasses), certainly reflects greater organic production, which may have been stimulated by increased summer precipitation in combination with warm temperatures. In the eastern Great Basin, the early Holocene was marked by warmer and drier conditions than the terminal Wisconsin, but the degree of warming is not certain. Some records indicate substantial warming by ca. 9 Ka to levels as warm or warmer than today, whereas other records indicate that early Holocene climate was cooler and wetter than today, though warmer than the terminal Wisconsin. The limited vegetation record indicates that shadscale and xerophytic shrub associations were well established in valley bottoms and around the margins of the Bonneville Basin, alongside sagebrush steppe. In montane settings, limber pine (in the north) and bristlecone pine (in the south) declined in abundance, and more-temperate conifers, such as Rocky Mountain juniper, began to dominate. Mesophilic mountain shrubs were declining in abundance and were being replaced by more thermophilous plants.

7 KA

Although the thermal maximum had passed, climatic conditions were still harsh, and severe regional drought characterized the northwestern Great Basin. Desert scrub communities dominated the slopes surrounding dry playas. Eolian activity generated extensive, and very active, dune fields downwind of valley bottom playas (Mehringer and Wigand, 1986). Absence of vegetation cover prevented stabilization of these dunes for the next 3 Ka. In the southern Great Basin, little information exists from this period. However, the few woodrat middens and pollen records that do exist indicate periodic, severe drought. True Mojave Desert plant species, such as creosote bush and white burrobush, became dominant during this period. Their appearance reflects not only warmer temperatures but also establishment of the current pattern of convective summer storms. On the western fringe of the Great Basin, piñon–juniper woodland was forced to retreat into areas occupied by limber pine and bristlecone pine near the top of the White Mountains. In the eastern Great Basin, warm and relatively dry conditions also prevailed, but a possible increase in growing-season precipitation from summer monsoons may have enhanced the northward migration of piñon pine, ponderosa pine, douglas fir, and other temperate conifers. Rocky Mountain juniper was a major element of woodland forests in the northeastern Great Basin, while limber pine still persisted in protected localities at relatively low elevations. Utah juniper was common in the southern Bonneville Basin.

5.5 KA

This marks the termination of the long middle-Holocene drought in the northern Great Basin as a result of a dramatic increase in winter rainfall. Areas that had been dominated by greasewood just decades earlier were replaced by sagebrush steppe. Ephemeral ponds began to retain water year-round. Periodic droughts still punctuated the next 1.5 Ka, but there was never a return to the conditions that had characterized the middle Holocene. In the southern Great Basin and northern Mojave Desert, renewed growth of peat in the White River Valley, at Ash Meadows, and at Little Lake indicates a rejuvenation of springs in response to the sudden increase in rainfall. Juniper woodland seems also to have begun moving downslope again. Pollen records indicate that the eastern Great Basin at about this time underwent a similar change to relatively cooler and perhaps more winter-wet conditions, as sagebrush and conifers increased slightly at the expense of shadscale and saltbush. A number of middens dating to this moment suggest that montane woodlands in the northeastern Great Basin were dominated by Rocky Mountain juniper and piñon pine, with a small amount of newly immigrant Utah juniper present as well. A similar situation apparently prevailed in the southern Bonneville Basin and into central Nevada, although Utah juniper was more common in these latter areas.

3.5 KA

The climax of the so-called "Neoglacial" or "Neopluvial" in the northwestern Great Basin occurred at this time. Juniper woodland expansion in south-central Oregon, which began dramatically 500 years earlier, reached the first of its three greatest late-Holocene limits. Fostered by major increases in winter precipitation, regional water tables probably reached their late-Holocene maximum ~3.7 Ka. (Two additional expansions of woodland ~2.7 and 2.1 Ka occurred during what remained of the Neoglacial.) In the west-central Great Basin on the east slope of the Sierra Nevada, fir lowered its elevational distribution and previously grassy meadows became sedge-dominated bogs that were soon invaded by birch (*Betula* sp.), and willow. The increase in winter precipitation was not as marked in the southern Great Basin or the northern Mojave Desert. Although each of the three major wet episodes of the Neoglacial are evidenced in the south, they are much less pronounced there than in the north. This period is marked by the increased abundance of piñon pine on the landscape. It clearly becomes a codominant in the semiarid woodland of the southern Great Basin and northern Mojave Desert. In the eastern Great Basin, the Neopluvial episode resulted in increased lake levels; greater abundance of sagebrush, grass, and conifers relative to chenopod shrubs; and Utah juniper occurring at elevations more than 100 m below its current distribution. Climatic conditions substantially cooler and more winter-wet than today are suggested. Rocky Mountain juniper still persisted in some montane settings, but Utah juniper and piñon pine were increasingly the dominant lower-montane conifers represented.

1.5 KA

This period marks the climax of late-Holocene warm, wet conditions. Beginning about 1.8 Ka, annual rainfall decreased substantially. At the same time, however, the peak of its annual distribution slipped later into the year, into summer. Grass abundance in sagebrush steppe increased greatly in the northern Great Basin at the same time that juniper woodland contracted. Ponds indicate very shallow eutrophic conditions, though they do not seem to dry seasonally. Although the climatic variability of this period was great, there was an overall increase in precipitation that peaked around 1.5 Ka. Bison followed the expansion of grasses into the sagebrush steppe. Further south in the west-central Great Basin, piñon pine expanded dramatically northward and downward in elevation, finally becoming a major component of the semiarid woodland. In southern Nevada, piñon pine increased in abundance in the woodland as well. Summer-shifted rainfall enabled shallow lakes to survive year-round despite a general decline in annual rainfall. In the eastern Great Basin, an increase in growing-season precipitation at this moment is suggested by increases in grass pollen in some records. Modern plant communities are fairly well established by now, including the presence of mormon tea through most of the region. The increase in summer precipitation may have also facilitated the success and spread of agricultural societies, known as the Fremont cultures, through much of the eastern Great Basin.

0.5 KA

Drought beginning around 1 Ka continued with brief interruptions until about 0.35 Ka. Retrenchment of juniper woodland in the northern Great Basin and of piñon–juniper woodland in the west-central Great Basin characterized this period. Increased fire activity marked the retreat of the forests. Ponds that had been wet for almost 5000 years occasionally dried during this period. This drought ended about 0.35 Ka with the Little Ice Age. Renewed expansion of juniper woodland in the northern and western Great Basin marked this period. It was only after the end of the Little Ice Age that piñon pine began its reexpansion in the northern and western Great Basin. Drought also characterized this period in the southern Great Basin and northern Mojave Desert. Saltbush expansion characterized many areas. Lakes became marshes until the wetter conditions of the Little Ice Age led to groundwater recharge and the return of shallow lakes. Expansion of woodland also characterized the Little Ice Age in southern Nevada with piñon pine expansion first occurring at the end of the period. In the eastern Great Basin, the record from 500 years ago is somewhat mixed, possibly reflecting natural variability and the finer resolution that comes with recency. In some areas such as Ruby Marsh, this moment marked the beginning of the coolest and moistest period since the early Holocene, with increases in marsh level and expansion of sagebrush steppe at the expense of saltbush and shadscale. On the other hand, some researchers (e.g. Harper and Alder, 1972) find the last 1000 years to have been among the warmest and driest of the Holocene. Clearly, the climatic variability inherent in the late Holocene should not be underestimated.

Retrospective and Future Directions

One of the landmark findings in plant ecology of the last 50 years is the widespread documentation that plants respond in highly individualistic fashion to both long- and short-term changes in climate and other ecological forcing mechanisms. This has led to the understanding that vegetation associations are rather loosely knit assemblages of plant taxa brought together by historical contingency and individual response to environmental factors, instead of strongly coevolved communities held together in a dynamic equilibrium. In the first part of the twentieth century, such a position had been favored by plant ecologists such as Shreve and Hinckley (1937) and Gleason (1939), but it was countered by the prevailing climax community viewpoint of Clements (1916, 1936) and others (e.g., Weaver and Clements, 1938). However, improved understanding of the Late Quaternary paleovegetation record within the last 50 years has provided strong evidence supporting the individualistic, nonequilibrium model (Davis, 1986; Huntley, 1991). In response to climatic amelioration since the last glacial period, plant taxa did not respond as communities or vegetation formations, but singly and uniquely, with different tempos of migration. The rapid rates and directions of the shifts taken by various species may be explained in part by the concepts of thresholds, steady states, and multiple successional pathways described by Tausch et al. (1993). Some taxa responded by large-scale range shifts, others by more spatially restricted shifts in elevation (Thompson, 1988). Such migrations and range expansions did not commence with the Holocene. In the northern Bonneville Basin, for example, substantial expansion of shadscale began about 12 Ka, limber pine began at 13 Ka, and expansion of montane shrubs such as currant occurred before that. Nor did substantial range shifts end in the early or middle Holocene, as the examples of western juniper, Utah juniper, and mormon tea demonstrate. In fact, some major range changes were not completed until the last few hundred years: e.g., singleleaf piñon pine in northwestern Nevada. An additional finding is that plants that now do not occur together very frequently were often associated in the past, when climatic conditions were quite different than anything found today. In western North America, the evidence of this was revealed by numerous packrat midden studies conducted in the 1970s and 1980s (e.g., Van Devender and Spaulding, 1979; Spaulding, 1981, 1985; Thompson, 1984; Cole, 1985; Betancourt, 1990; Van Devender, 1990a, 1990b).

These insights set the modern baseline of understanding for a variety of approaches that seek to explain why changing plant distributions took the form that they did. As the above summary indicates, changing climate has played the major role during the Late Quaternary (Whitlock and Bartlein, 1997) but not the only role. Paleoecologists quickly realized that it was not simply different tolerances to climate that affected how rapidly plant taxa changed their distributions through time. Available mechanisms for dispersal of disseminules and how well the plant is able to compete with existing vegetation are also important components that figure into the concept of vegetation "inertia," or the occasional apparent lag of biogeographic range response after a climatic change (Cole, 1985; Markgraf, 1986; Thompson, 1990:232–233). In addition, some plants are relatively tolerant to climatic variation and, therefore, did not exhibit substantial range changes through widely variable conditions, whereas other taxa showed extensive range alterations (Barnosky, 1987; Thompson, 1988). Furthermore, the biogeographic patterns of different taxa are also related to the high topographic variability in parts of western North America, especially in the Great Basin, which can create a mosaic of microhabitats that may serve as suitable refugia for dispersed relict populations throughout a region (Whitlock and Bartlein, 1993). Chance may play an important role here too, for not all small, relict populations may survive in all the same microhabitats, simply through stochastic processes. Nonclimatic factors such as atmospheric CO_2 concentration and fire frequency (though these may correlate with climatic parameters) also play major roles in the fitness of plant taxa and their ability to survive and spread.

The population genetics of certain taxa in these settings may be critical to understanding biogeographic patterns (Hamrick et al., 1994). Nowak et al. (1994b) asserted that in the northwestern Great Basin, Utah juniper was present through much of the late Wisconsin and that it probably remained in the region because its interbreeding populations were sufficiently variable genetically to enable the species to adapt via genetic heterogeneity. Following example of Barnosky (1987), these researchers called species with this conservative mode of geographic range movement "orthoselective," and they contrasted Utah juniper with piñon pine, which they considered to be a migratory species, one that expanded its range when climatic conditions are right. It should be noted, however, that the interpretation of Nowak et al. (1994b) regarding the sensitivity of juniper to climate change was based upon a single 35,000-year-long woodrat midden record of juniper from northwestern Nevada. It is clear even from that record that juniper may have been absent from the locality during periods of the most extreme climate conditions, including the glacial maximum and the middle-Holocene drought (Wigand and Nowak, 1992; see discussion of middle Holocene above in "Northern and Western Great Basin"). The pollen record from this midden also suggests substantial variation in the abundance of juniper during the last 35,000 years. For these reasons we disagree with the interpretation of Nowak et al. (1994b) that Utah juniper was as complacent or unchanging as they suggest. We find the distinction drawn by Barnosky (1987), however, to be potentially useful in accounting for differential responses of taxa to climate change (see also Thompson, 1988).

Recall, however, that Utah juniper had a very different history in the northeastern Great Basin, where it was absent since before 50,000 years B.P. until approximately 6600 years B.P. In this region, Utah juniper must be considered migratory rather than orthoselective. Why should this be? Does it relate to the severe continentality of climate in the eastern Great Basin during the late Wisconsin? Is it a function of a possible lack of genetic variability in the eastern Great Basin compared with the western Great Basin (perhaps a lack of introgression with western juniper)? Determining why different plant taxa respond differently to climatic changes is an important challenge for ecology in the twenty-first century, particularly as the global climate and atmospheric composition are undergoing rapid human-induced change, with dramatic ecophysiological response. Fortunately, new genetic techniques are rapidly being developed to allow studies of these issues on fossil materials, providing a longer-term perspective of similar changes in the past.

The view that Great Basin plant communities are, in large measure, products of historical circumstance (a corollary to the recognition that plant taxa have individualistic histories) is partly supported by the fossil record but is also tempered by it. Certain combinations of plants often appear to recur and persist in dynamic equilibria through long periods of time, as appropriate environmental conditions allow. The composition of sagebrush steppe, for example, appears largely unchanged since the terminal Wisconsin and possibly since the middle Wisconsin. Indeed, some researchers see marked long-term stability in many steppe and woodland communities in the eastern Great Basin (Thompson, 1988, 1992; Thompson et al., 1994; Moutoux and Davis, 1995; Davis, 2002). Again, this is not to say that the sagebrush steppe formation did not respond to past climate change; it clearly has, primarily through major shifts in its geographical distribution. In any event, the interplay of individual histories and tolerances that led to long-term associations or recurrence of associated taxa remains to be explored more fully.

Certain plants may have altered their climatic tolerances during the last 30,000 years, affecting their utility as proxy records for climatic change. Limber pine may have substantially increased its water use efficiency after the late Wisconsin in response to rising concentrations of atmospheric CO_2 (Van de Water et al., 1994). If so, it suggests that late-Pleistocene populations were more susceptible to water stress from warm, dry (or cold, dry) growing seasons than are modern populations. If not taken into account, this factor could result in substantial underestimation of the true rainfall and temperature values for the southern Great Basin and the northern Mojave Desert during the late Pleistocene, as projected by Forester et al. (1996). Various species of saltbush also may have altered their tolerances, as the genus apparently went through substantial genetic reassortment during the latest Pleistocene and Holocene when it recolonized valley bottoms vacated by Lakes Bonneville and Lahontan (Stutz, 1978). The effects of genetic variability upon the climatic tolerances of *Atriplex* species are currently unknown.

In the last few years, some studies of past environments and climates have begun to move beyond documentation of the historical sequence of change in vegetation and climate toward the relationships among climatic input, vegetation response, landscape change, and feedbacks into vegetation change. Indeed, the requirements of current paleoenvironmental studies are leading the field in establishing the climatic limits of many plant species (e.g., Bartlein et al., 1998; Thompson et al., 2000). One recent model that relates climate and plant distributions (Thompson et al., 2000; cf. also Bartlein et al., 1998) uses a geographic grid of current climatic parameters and overlays it onto the current distribution of some of the more common plant species. The model then derives the climatic tolerances of individual plant species through the correspondence of plant species with the modern analogue climate. Once these parameters have been derived they are used to estimate past climates from dated assemblages of plant macrofossils at specific points on the landscape. Contemporaneous, spatially distributed assemblages of macrofossils (e.g., dated woodrat midden strata) can then be used to generate isobars of past rainfall and temperature or other climatic parameters as modeled.

Care should be taken in interpreting the results of such models, however. Bartlein et al. (1998) point out several possible discrepancies between model predictions and actual plant distributions. One potential problem is that plant distributions may be constrained not by climatic forces but by competition with associated or neighboring taxa. For example, Thompson (1990) suggested that the lower limit of limber pine in the mountains of the eastern Great Basin often may be constrained more by competition from piñon pine than by climatic factors. This would not have been the case before the arrival of piñon pine toward the end of the early Holocene. Consequently the forces constraining a plant species' distribution may vary through time—and, indeed, through the range of the plant—in ways that may not be related directly to climate.

Another potential problem is the use of modern plant distributions to establish climatic limits: climatic limits of what? Seedling establishment? Survival of mature individuals? Regenerating plant associations? A modern plant community is not unlike a medieval manuscript that has been reused numerous times; each successive use of the palimpsest manuscript is visible. Likewise, modern species distributions combine currently reproducing populations, relict stands established during previous climatic regimes, and effects of disturbance factors (e.g., insect infestations, fire, pollutants). For example, the old-growth forests of the Sierra Nevada contain large white fir and red fir that were established during cooler, wetter conditions 200–300 years ago. Beneath this canopy lie ponderosa pine and/or Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) established during warmer, drier conditions 100 years ago. Finally, there are saplings of red fir and white fir that were established during the wetter conditions of the late 1970s and early 1980s. A similar pattern can be seen in the semiarid woodlands of the northern Great Basin where stands of Utah juniper, established as far back as 700–800 years ago, now stand side by side with piñon pines less than 150 years old (Tausch et al., 1981). Testing of the model by predicting the geographic distribution of a particular species based upon current climates would not reveal the problem. Because the data used to generate the model include modern plant distributions affected by both modern and past climates, the model will predict the current distribution of both regenerating and relict plant populations on the current landscape. Therefore the model does not predict the distribution of currently active, regenerating forests.

As noted above, a third problem that may affect use of such models for reconstruction of Pleistocene and early Holocene climates is the uniformitarian assumption that plant taxa have the same response to present-day climate as they did in the past. Anatomical evidence has shown that plants may not have had a stable response to climatic factors—e.g., the change in stomatal density of limber pine from the Pleistocene to Holocene and its relationship to atmospheric CO_2 and water use efficiency (Van de Water et al., 1994). Decreased water use efficiency during the late Wisconsin could have resulted in substantially greater plant sensitivity to climatic conditions of that time. Therefore, estimates of Pleistocene climates obtained by using modern analogue climates that were derived from modern limber pine distribution might be in error (cf. Rhode and Madsen, 1995). In the future, the use of other corroborating proxy data sets and refinement of our understanding of the physiology of the more important indicator plant species will allow us to resolve some of these problems.

Discussion of Late Quaternary vegetation history would not be complete without reference to the effects of human populations upon the distributions of individual plant species and the composition and structure of modern and past plant communities. Two areas of potential effect are especially germane: (1) the role of human land management practices in fire histories, and (2) humans as agents of substantial range expansion of certain taxa. During the last 50 years, Federal land managers have continually discussed the influences of grazings by sheep and cattle and of fire suppression in forming today's rangeland and woodland plant communities (Miller and Wigand, 1994). Indeed, some recognition has even been made of the role of Native Americans' use of fire in shaping the environment as well (Barrett and Arno, 1982). The roles played by Native American populations (if any) in shaping Great Basin vegetation history, however, remain to be much more fully explored.

With respect to fire history, the paleoenvironmental record indicates that climate is still a prime mover (perhaps *the* prime mover) in effecting the frequency and magnitude of fire (e.g., Wigand, 1987; Swetnam, 1990; Swetnam and Betancourt, 1990). A strong deterministic link is clear between climate, fuel build-up, cycles of drought, and the resulting occurrence of fire. That human land use practices are important in this dynamic is also obvious, as amply demonstrated by the historic record, but the importance of fire in prehistoric Native American "range management" in the Great Basin is, as yet, rather poorly understood (Stewart, 1954, 1955a, 1955b, 1956, 1963, 1982; Downs, 1966; Mellars, 1976; Lewis, 1977, 1982, 1985; Barrett and Arno, 1982; Hemphill, 1983; Fowler, 1996). Prehistoric peoples may have substantially affected fire histories on a local scale. Effects by humans may have been important under certain threshold conditions of population, fuel buildup, and drought, but at present we do not know what thresholds (if any) may have existed or whether the effects were substantial. Interregional correlation among the histories of climate, vegetation, and fire may serve to show that climate is the driving force in regional fire histories in the prehistoric and possibly historic periods and that prehistoric human activities were a relatively minor element in regional fire histories (e.g., Swetnam and Baisan, 1996). A great deal of additional research is needed to determine how the dramatic changes in land use practices (including fire suppression) that occurred during the last 1000 years may have affected plant community distribution and structure in the context of changing climates.

The role of people as disseminators of plant species during the historic period is also clear with regard to cheatgrass (*Bromus tectorum* L.) and other range weeds as well as exotic tree and shrub species. The role of Native Americans in the spread of native plants is less clear. The ethnographic record shows that economically valuable plants were often managed and pruned, collecting areas were cleared or burned or irrigated, and in some cases plants may have been artificially transplanted or sown to increase their range (Steward, 1930, 1938; Downs, 1966; Fowler, 1986, 1996). The magnitude and antiquity of these practices is not known, however (Winter, 1976; Winter and Hogan, 1986). As noted above, people may have had a role in the rapid early Holocene expansion of piñon pine (Mehringer, 1986; Madsen and Rhode, 1990; Rhode and Madsen, 1998). This speculation is based in part upon the rapid rate of piñon pine expansion as indicated by the paleobotanical record compared with the presumed speed of its expansion based on an avian dispersal model, which seems too slow to account for the rate of postglacial reexpansion into the Great Basin. The available archaeological record indicates that early Holocene people consumed and transported piñon pine nuts (Rhode and Madsen, 1998), and mobile human groups could be a much faster agent of seed dispersal than corvids. But it is not certain whether the avian dispersal model is accurate, nor is the early Holocene piñon pine distribution or its rate of expansion known with enough certainty to completely rule out the avian model. In addition, for any attempt at dissemination of such species to be successful, climatic conditions would have to be favorable. The paleoenvironmental record indicates that piñon pine expansion can be quite rapid, and it is not necessary for human intervention to be involved (Tausch et al., 1981; and see above). The rapid spread of piñon pine during the last 150 years presumably did not have, nor did it need, the benefit of human intervention. It is likewise probable that piñon pine's expansion in the northwestern Great Basin 1.6 Ka was a response to natural processes (i.e., climate) because many other plant species including grasses, juniper, saltbush, and sagebrush responded as well (Wigand, 1997b). The evidence presented in the discussion above suggests that piñon pine has responded as rapidly to stressful climates as it apparently did to favorable climates. Retreat of piñon pine woodland after 0.9 Ka was as rapid as its expansion around 1.6 Ka in the northern Great Basin. The historic expansion of western juniper in the northern Great Basin via animal vectors of seed dispersal has been as dramatic as any prehistoric expansion of plant species. These cases confirm the premise that if conditions are favorable, and appropriate agents of dispersal are available, the plant species will spread. Native Americans may have been appropriate agents of dispersal for some plant species, substantially affecting their ranges, but the role of native peoples in the distribution of piñon pine or other plants in the Great Basin remains uncertain and, indeed, may have been quite limited.

In any case, and as Whitlock and Bartlein (1997) and Prentice et al. (1991) have previously observed in other areas, most of the dramatic changes in plant distributions and community structure observable in the Great Basin during the Late Quaternary were ultimately constrained by climatic causes—although mediated by a host of more local, proximate factors. As our understanding of plant responses to past climates, landscape change, and the role of disturbance phenomena (including fire, plant diseases, insect infestations, and human manipulation) is refined, the lines between paleoecology, modern plant ecology, plant physiology, and genetics will become ever more blurred. These are directions for the next half century of study.

Literature Cited

Adam, D.P., J.P. Bradbury, W.E. Dean, J.V. Gardner, and A.M. Sarna-Wojcicki
1995. Report of 1994 Workshop on the Correlation of Marine and Terrestrial Records of Climate Changes in the Western United States. *United States Geological Survey Open-File Report,* 95-34: 92 pages. United States Department of the Interior, United States Geological Survey.

Aikens, C.M.
1970. Hogup Cave. *University of Utah Anthropological Papers,* 93: 286 pages.
1984. *Archaeology of Oregon.* 134 pages. Portland, Oregon: United States Department of the Interior, Bureau of Land Management.

Albee, B.J., L.M. Shultz, and S. Goodrich
1988. Atlas of the Vascular Plants of Utah. *Occasional Publication of the Utah Museum of Natural History,* 7: 670 pages.

Allen, B.D., and R.Y. Anderson
1993. Evidence from Western North America for Rapid Shifts in Climate

during the Last Glacial Maximum. *Science,* 260:1920–1923.

Antevs, E.

1938. Rainfall and Tree Growth in the Great Basin. *Special Publication of the Carnegie Institution of Washington,* 469: 97 pages.

1948. Climatic Changes and Pre-White Man. *In* The Great Basin, with Emphasis on Postglacial Times. *Bulletin of the University of Utah,* 38(20):167–191.

Axelrod, D.I.

1939. A Miocene Flora from the Western Border of the Mohave Desert. *Publications of the Carnegie Institution of Washington,* 516:1–129.

1944. The Alvord Creek Flora (Oregon). *Publications of the Carnegie Institution of Washington,* 553:263–284.

1948. Climate and Evolution in Western North America during Middle Pliocene Time. *Evolution,* 2:127–144.

1990. Age and Origin of Subalpine Forest Zone. *Paleobiology,* 16: 360–369.

Axelrod, D.I., and P.H. Raven

1985. Origins of the Cordilleran Flora. *Journal of Biogeography,* 12: 21–47.

Barnosky, C.W.

1987. Response of Vegetation to Climate Changes of Different Duration in the Late Neogene. *Trends in Ecology and Evolution,* 2:247–250.

Barrett, S.W., and S.F. Arno

1982. Indian Fires as an Ecological Influence in the Northern Rockies. *Journal of Forestry,* 80:647–651.

Bartlein, P.J., K.H. Anderson, P.M. Anderson, M.E. Edwards, C.J. Mock, R.S. Thompson, R.S. Webb, T. Webb III, and C. Whitlock

1998. Paleoclimate Simulations for North America over the Past 21,000 Years: Features of the Simulated Climate and Comparisons with Paleoenvironmental Data. *Quaternary Science Reviews,* 17:549–585.

Beiswenger, J.M.

1991. Late Quaternary Vegetational History of Grays Lake, Idaho. *Ecological Monographs,* 61:165–182.

Benson, L., and R.A. Darrow

1981. *Trees and Shrubs of the Southwestern Deserts.* 416 pages. Tucson: University of Arizona Press.

Benson, L.V., D.R. Currey, R.I. Dorn, K.R. Lajoie, C.G. Oviatt, S.W. Robinson, G.I. Smith, and S. Stine

1990. Chronology of Expansion and Contraction of Four Great Basin Lake Systems during the Past 35,000 Years. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 78:241–286.

Benson, L.V., D. Currey, Y. Lao, and S. Hostetler

1992. Lake-size Variations in the Lahontan and Bonneville Basins between 13,000 and 9000 ^{14}C yr B.P. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 95:19–32.

Benson, L.V., M. Kashgarian, and M. Rubin

1995. Carbonate Deposition, Pyramid Lake Subbasin, Nevada, 2: Lake Levels and Polar Jet Stream Positions Reconstructed from Radiocarbon Ages and Elevations of Carbonates (Tufas) Deposited in the Lahontan Basin. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 117:1–30.

Benson, L.V., J.P. Smoot, M. Kashgarian, A. Sarna-Wojcicki, and J.W. Burdett

1997. Radiocarbon Ages and Environments of Deposition of the Wono and Trego Hot Springs Tephra Layers in the Pyramid Lake Subbasin, Nevada. *Quaternary Research,* 47:251–260.

Benson, L.V., and R.S. Thompson

1987. The Physical Record of Lakes in the Great Basin. *In* W.F. Ruddiman and H.E. Wright, Jr, editors, North America and Adjacent Oceans during the Last Deglaciation. *The Geology of North America, K-3:* 241–260. Boulder, Colorado: Geological Society of America.

Benson, L.V., L.D. White, and R.O. Rye

1996. Carbonate Deposition, Pyramid Lake Subbasin, Nevada, 4: Comparison of the Stable Isotope Values of Carbonate Deposits (Tufas) and the Lahontan Lake-Level Record. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 122:45–76.

Betancourt, J.L.

1990. Late Quaternary Biogeography of the Colorado Plateau. *In* J.L. Betancourt, T.R. Van Devender, and P.S. Martin, edittors, *Packrat Middens: The Last 40,000 Years of Biotic Change,* pages 259–292. Tucson: University of Arizona Press.

Betancourt, J.L., T.R. Van Devender, and P.S. Martin, editors

1990. *Packrat Middens: The Last 40,000 Years of Biotic Change.* 467 pages. Tucson: University of Arizona Press.

Billings, W.G.

1951. Vegetational Zonation in the Great Basin of Western North America. *In* Les Bases écologiques de la regénération de la végétation des zones arides. *International Union de la Société Biologique, Series B,* 9:101–122.

Bond, G., and R. Lotti

1995. Iceberg Discharges into the North Atlantic on Millennial Time Scales during the Last Glaciation. *Science,* 267:1005–1010.

Born, S.M.

1972. *Late Quaternary History, Deltaic Sedimentation, and Mudlump Formation at Pyramid Lake, Nevada,* 97 + xi pages. Reno, Nevada: Center for Water Resources Research, Desert Research Institute.

Bradbury, J.P., R.M. Forester, and R.S. Thompson

1989. Late Quaternary Paleolimnology of Walker Lake, Nevada. *Journal of Paleolimnology,* 1:249–267.

Bright, R.C.

1966. Pollen and Seed Stratigraphy of Swan Lake, Southeastern Idaho: Its Relation to Regional Vegetational History and to Lake Bonneville History. *Tebiwa,* 9(2):1–47.

Bright, R.C., and O.K. Davis

1982. Quaternary Paleoecology of the Idaho National Engineering Laboratory, Snake River Plain, Idaho. *American Midland Naturalist,* 108(1):21–33.

Brown, R.W.

1949. Pliocene Plants from Cache Valley, Utah. *Journal of the Washington Academy of Science,* 39:224–229.

Brown, W.J., S.G. Wells, Y. Enzel, R.Y. Anderson, and L.D. McFadden

1990. The Late Quaternary History of Pluvial Lake Mojave–Silver Lake and Soda Lake Basins, California. In *At the End of the Mojave: Quaternary Studies in the Eastern Mojave Desert,* pages 55–72. 1990 Mojave Desert Quaternary Research Center Symposium, May 18–21, 1990. Special Publication of the San Bernardino County Museum Association.

Byrne, R., C. Busby, and R.F. Heizer

1979. The Altithermal Revisited: Pollen Evidence from the Leonard Rockshelter. *Journal of California and Great Basin Anthropology,* 1(2): 280–294.

Clark, P.U., and P.J. Bartlein

1995. Correlation of Late Pleistocene Glaciation in the Western United States with North Atlantic Heinrich Events. *Geology,* 23(6):483–486.

Clements, F.E.

1916. Plant Succession: Analysis of the Development of Vegetation. *Publications of the Carnegie Institute of Washington,* 242:1–512.

1936. Nature and Structure of the Climax. *Journal of Ecology,* 24:252–284.

Cohen, A.S., M. Palacios, R.M. Negrini, P.E. Wigand, and D.B. Erbes

2000. A Paleoclimate Record for the Past 250,000 Years from Summer Lake, Oregon, U.S.A., II: Sedimentology, Paleontology, and Geochemistry. *Journal of Paleolimnology,* 24(2):151–182.

COHMAP Members

1988. Climatic Changes of the Last 18,000 Years: Observations and Model Simulations. *Science,* 241:1043–1052.

Cole, K.L.

1985. Past Rates of Change, Species Richness, and a Model of Vegetational Inertia in the Grand Canyon, Arizona. *Quaternary Research,* 25:392–400.

Currey, D.R.

1980. Coastal Geomorphology of Great Salt Lake and Vicinity. *In* J.W. Gwynn, editor, The Great Salt Lake: A Scientific, Historical and Economic Overview. *Bulletin of the Utah Geological and Mineralogical Survey,* 116:69–82. Salt Lake City.

1990. Quaternary Paleolakes in the Evolution of Semidesert Basins, with Special Emphasis on Lake Bonneville and the Great Basin, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 76:189–214.

Currey, D.R., G. Atwood, and D.R. Mabey

1984. Major Levels of Great Salt Lake and Lake Bonneville. *Utah Geological and Mineralogical Survey Map,* 73. Salt Lake City.

Currey, D.R., and S.R. James

1982. Paleoenvironments of the Northeastern Great Basin and Northeastern Basin Rim Region: A Review of Geological and Biological Evidence. *In* D.B. Madsen and J.F. O'Connell, editors, Man and Environment in the Great Basin. *Papers of the Society for American Archaeology,* 2:27–52. Washington, D.C.

Currey, D.R., and D.B. Madsen

1974. Holocene Fluctuations of Great Salt Lake. *American Quaternary Association Programs with Abstracts,* 3:74.

Currey, D.R., and C.G. Oviatt

1985. Durations, Average Rates, and Probable Causes of Lake Bonneville Expansions, Still-Stands, and Contractions during the Last Deep-Lake Cycle, 32,000 to 10,000 Years Ago. *In* P.A. Kay and H.F. Diaz, editors, *Problems of and Prospects for Predicting Great Salt Lake Levels: Papers from a Conference Held in Salt Lake City, March 26–28, 1985*, pages 9–24. Salt Lake City: University of Utah Center for Public Affairs and Administration.

Dalley, G.F.

1976. Appendix II: Palynology of the Swallow Shelter Deposits. *In* G.F. Dalley, Swallow Shelter and Associated Sites. *University of Utah Anthropological Papers,* 96:171–174. Salt Lake City.

Davies, K.G., A.M. Johnson, and D.O. Johansen, editors

1961. *Peter Skene Ogden's Snake Country Journal 1826-27.* 255 pages. London: The Hudson's Bay Record Society.

Davis, J.O.

1978. Quaternary Tephrochronology of the Lake Lahontan Area, Nevada and California. *Research Paper of the Nevada Archaeological Survey,* 7: 137 pages.

1982. Bits and Pieces: The Last 35,000 Years in the Lahontan Area. *In* D.B. Madsen and J.F. O'Connell, editors, Man and Environment in the Great Basin. *Papers of the Society for American Archaeology,* 2:53–75. Washington, D.C.

1983. Geology of Gatecliff Shelter: Sedimentary Facies and Holocene Climate. *In* D.H. Thomas, The Archaeology of Monitor Valley, 2: Gatecliff Shelter. *Anthropological Papers of the American Museum of Natural History,* 59(1):64–87. New York.

1985. Sediments and Geological Setting of Hidden Cave. *In* D.H. Thomas, The Archaeology of Hidden Cave, Nevada. *Anthropological Papers of the American Museum of Natural History,* 61(1):80–103. New York.

Davis, M.B.

1986. Climatic Instability, Time Lags, and Community Disequilibrium. *In* J. Diamond and T.J. Case, editors, *Community Ecology,* pages 269–284. New York: Harper and Row.

Davis, O.K.

1981. Vegetation Migration in Southern Idaho during the Late-Quaternary and Holocene. 252 pages. Doctoral dissertation, University of Minnesota, St. Paul.

2002. Late Neogene Environmental History of the Northern Bonneville Basin: A Review of Palynological Studies. *In* R. Hershler, D.B. Madsen, and D.R. Currey, editors, Great Basin Aquatic Systems History. *Smithsonian Contributions to the Earth Sciences,* 33:295–307.

Davis, O.K., J.C. Sheppard, and S. Robertson

1986. Contrasting Climate Histories for the Snake River Plain, Idaho, Resulting from Multiple Thermal Maxima. *Quaternary Research,* 26: 321–339.

DeBolt, A.M., and B. McCune

1995. Ecology of *Celtis reticulata* in Idaho. *Great Basin Naturalist,* 55: 237–248.

Deevey, E.S., Jr.

1949. Biogeography of the Pleistocene, Part I: Europe and North America. *Bulletin of the Geological Society of America,* 60:1315–1416.

Downs, J.F.

1966. The Significance of Environmental Manipulation in Great Basin Cultural Development. *In* W.L. d'Azevedo, W.A. Davis, D.D. Fowler, and W. Suttles, editors, The Current Status of Anthropological Research in the Great Basin: 1964. *Desert Research Institute Technical Report, Series S-H, Social Sciences and Humanities Publications,* 1:39–56. Reno, Nevada.

Dugas, D.P.

1998. Late Quaternary Variations in the Level of Paleo-Lake Malheur, Eastern Oregon. *Quaternary Research,* 50(3):276–282.

Eardley, A.J., and V. Gvosdetsky

1960. Analysis of Pleistocene Core from Great Salt Lake, Utah. *Geological Society of America Bulletin,* 71:1323–1344.

Eardley, A.J., R.T. Shuey, V. Gvosdetsky, W.P. Nash, M. Dane Picard, D.C. Grey, and G.J. Kukla

1973. Lake Cycles in the Bonneville Basin, Utah. *Geological Society of America Bulletin,* 84(1):211–216.

Eiselt, B.S.

1997. Fish Remains from the Spirit Cave Paleofecal Material: 9,400 Year Old Evidence for Great Basin Utilization of Small Fishes. *Quarterly of the Nevada Historical Society,* 40(1):117–139.

Ely, L.L., Y. Enzel, V.R. Baker, and D.R. Cayan

1993. A 5000-Year Record of Extreme Floods and Climate Change in the Southwestern United States. *Science,* 262:410–412.

Enzel, Y., W.J. Brown, R.Y. Anderson, L.D. McFadden, and S.G. Wells

1992. Short-Duration Holocene Lakes in the Mojave River Drainage Basin, Southern California. *Quaternary Research,* 38(1):60–73.

Enzel, Y., D.R. Cayan, R.Y. Anderson, and S.G. Wells

1989. Atmospheric Circulation during Holocene Lake Stands in the Mojave Desert: Evidence of Regional Climate Change. *Nature,* 341:44–48.

Feng, X., and S. Epstein

1994. Climatic Implications of an 8000-Year Hydrogen Isotope Time Series from Bristlecone Pine Trees. *Science,* 265:1079–1081.

Forester, R.G., J.P. Bradbury, C. Carter, A.B. Elvidge, M.L. Hemphill, S.C. Lundstrom, S.A. Mahan, B.D. Marshall, L.A. Neymark, J.B. Paces, S.E. Sharpe, J.F. Whelan, and P.E. Wigand

1996. Synthesis of Quaternary Response of the Yucca Mountain Unsaturated and Saturated Zone Hydrology to Climate Change. *1996 Milestone Report,* 3GCA102M: 110 pages. United States Geological Survey, Yucca Mountain Project Branch.

Fowler, C.S.

1986. Subsistence. *In* W.L. d'Azevedo, volume editor, *Great Basin. Handbook of North American Indians*, vol. 11:64–97. W.C. Sturtevant, general editor.Washington, D.C.: Smithsonian Institution.

1996. Historical Perspectives on Timbisha Shoshone Land Management Practices, Death Valley, California. *In* E.J. Reitz, L.A. Newsom, and S.J. Scudder, editors, *Case Studies in Environmental Archaeology,* pages 87–101. New York: Plenum Press.

Frémont, J.C.

1845. *Report of the Exploring Expedition to the Rocky Mountains in the Year 1842, and to Oregon and California in the Years 1843–1844.* 427 pages. Washington, D.C.: Goles and Seaton.

Fritts, H.C. and W. Xiangdig

1986. A Comparison between Response-Function Analysis and Other Regression Techniques. *Tree-ring Bulletin,* 46:31–46.

Gehr, K.D.

1980. Late Pleistocene and Recent Archaeology and Geomorphology of the South Shore of Harney Lake, Oregon. Master's thesis, Portland State University, Portland, Oregon. [Unpublished.]

Gleason, H.A.

1939. The Individualistic Concept of the Plant Association. *American Midland Naturalist,* 21:92–110.

Graumlich, L.J.

1993. A 1000-Year Record of Temperature and Precipitation in the Sierra Nevada. *Quaternary Research,* 39:249–255.

Graybill, D.A., M.R. Rose, and F.L. Nials

1994. Tree-Rings and Climate: Implications for Great Basin Paleoenvironmental Studies. *High-Level Radioactive Waste Management Conference: Proceedings of the Fifth Annual International, Sponsored by the American Society of Civil Engineers and the American Nuclear Society; Co-sponsored by the American Chemical Society ... [et al.] in Cooperation with U.S. Department of Energy ... [et al.],* volume 4:2569–2573. La Grange Park, Illinois: American Nuclear Society; New York: American Society of Civil Engineers.

Grayson, D.K.

1993. *The Desert's Past: A Natural Prehistory of the Great Basin.* 356 pages. Washington, D.C.: Smithsonian Institution Press.

1998. Moisture History and Small Mammal Community Richness during the Latest Pleistocene and Holocene, Northern Bonneville Basin, Utah. *Quaternary Research,* 49:330–334.

Hamrick, J.L., A.F. Schnabel, and P.V. Wells

1994. Distribution of Genetic Diversity within and among Populations of Great Basin Conifers. *In* K.T. Harper, L.L. St. Clair, K.H. Thorne, and W.M. Hess, editors, *Natural History of the Colorado Plateau and Great Basin,* pages 147–162. Niwot, Colorado: University Press of Colorado.

Hansen, H.P.

1947. Postglacial Vegetation of the Northern Great Basin. *American Journal of Botany,* 34(3):164–171.

Hardman, G., and O.E. Reil

1936. The Relationship between Tree-Growth and Stream Runoff in the Truckee River Basin, California–Nevada. *University of Nevada Agricultural Experiment Station Bulletin,* 141: 38 pages.

Harper, K.T., and G.M. Alder

1970. Appendix I: The Macroscopic Plant Remains of the Deposits of Hogup Cave, Utah, and Their Paleoclimatic Implications. *In* C.M. Aikens, Hogup Cave. *University of Utah Anthropological Papers,* 93:215–240. Salt Lake City.

1972. Paleoclimatic Inferences concerning the Last 10,000 Years from a Resampling of Danger Cave, Utah. *In* D.D. Fowler, editor. Great Basin Cultural Ecology. *Desert Research Institute Publications in the Social Sciences,* 8:13–23. Reno.

Hastings, J.R., and R.M. Turner

1965. *The Changing Mile: An Ecological Study of Vegetation Change with Time in the Lower Mile of an Arid and Semiarid Region.* 317 pages. Tucson: University of Arizona Press.

Harvey, A.M., P.E. Wigand, and S.G. Wells.

1999. Response of Alluvial Fan Systems to the Lake Pleistocene to Holocene Climatic Transition: Contrasts between the Margins of Pluvial Lakes Lahontan and Mojave, Nevada and California, U.S.A. *Catena,* 36:255–281.

Heinrich, H.

1988. Origin and Consequences of Cyclic Ice Rafting in the Northeast Atlantic Ocean during the Past 130,000 Years. *Quaternary Research,* 29:189–199.

Hemphill, M.L.

1983. Fire, Vegetation, and People—Charcoal and Pollen Analysis of Sheep Mountain Bog, Montana: The Last 2800 Years. 70 pages. Master's thesis, Department of Anthropology, Washington State University. [70 pages.]

Holmes, R.L., R.K. Adams, and H.C. Fritts

1986. Tree-Ring Chronologies of Western North America: California, Eastern Oregon and Northern Great Basin with Procedures Used in the Chronology Development Work Including Users Manuals for Computer Programs COFECHA and ARSTAN. *Chronology Series VI*: 182 pages. Tucson, Arizona.

Houghton, J.G.

1969. *Characteristics of Rainfall in the Great Basin.* 205 pages. Reno: Desert Research Institute, University of Nevada.

Houghton, J.G., C.M. Sakamoto, and R.O. Gifford

1975. Nevada's Weather and Climate. *Special Publication of the Nevada Bureau of Mines and Geology,* 2: 78 pages. Reno: Mackay School of Mines, University of Nevada.

Hubbs, C.L., and R.R. Miller

1948. II: The Zoological Evidence. *In* The Great Basin, with Emphasis on Glacial and Post-glacial Times. *Bulletin of the University of Utah, Biological Series,* 10(7):18–166.

Hunt, J., D. Rhode, and D.B. Madsen

2000. Homestead Cave Flora and non-Vertebrate Fauna. *In* D.B. Madsen, Late Quaternary Paleoecology in the Bonneville Basin. *Utah Geological Survey Bulletin,* 130:47–58.

Huntley, B.

1991. How Plants Respond to Climate Change: Migration Rates, Individualism and the Consequences for Plant Communities. *Annals of Botany,* 67:15–22.

Iversen, J.

1973. The Development of Denmark's Nature since the Last Glacial; Translation from Danmarks Natur, vol. 1, pp. 345–445, 1967, by Michael Robson. *Danmarks Geologiske Undersøgelse,* series 5, Raekke, number 7-c. Copenhagen: C.A. Reitzels Forlag.

Jahren, A.H.

1996. The Stable Isotope Composition of the Hackberry (*Celtis*) and Its Use as a Paleoclimate Indicator. 136 pages. Doctoral dissertation, University of California, Berkeley. [Unpublished.]

Jahren, A.H., R. Amundson, C. Kendall, and P.E. Wigand

2001. Paleoclimatic Reconstruction Using the Correlation in Delta ^{18}O of Hackberry Carbonate and Environmental Water, North America. *Quaternary Research,* 56(2):252–263.

Jennings, S.A., and D.L. Elliot-Fisk

1993. Packrat Midden Evidence of Late Quaternary Vegetation Change in the White Mountains, California–Nevada. *Quaternary Research,* 39:214–221.

Kaufman, D.S., S.L. Forman, and J. Bright

2001. Age of the Cutler Dam Alloformation (Late Pleistocene), Bonneville Basin, Utah. *Quaternary Research,* 56:322–334.

Kelso, G.

1970. Hogup Cave, Utah: Comparative Pollen Analysis of Human Coprolites and Cave Fill. *In* C.M. Aikens, Hogup Cave. *Anthropological Papers of the University of Utah,* 93:251–262.

Koehler, P.A., and R.S. Anderson

1994. Full-Glacial Shoreline Vegetation during the Maximum Highstand at Owens Lake, California. *Great Basin Naturalist,* 54(2):142–149.

1995. Thirty Thousand Years of Vegetation Changes in the Alabama Hills, Owens Valley, California. *Quaternary Research,* 43:238–248.

Krajicek, J.E., and R.D. Williams

1990. *Celtis occidentalis* L. Hackberry. *In* R.M. Burns and B.H. Honkala, coordinators, Silvics of North America. *United States Department of Agriculture, Agriculture Handbook,* 654:262–265.

Ku, T.L., T.K. Lowenstein, J. Li, and R.J. Spencer

1998. U-Series Chronology of Lacustrine Deposits in Death Valley, California. *Quaternary Research,* 50(3):261–275.

Kutzbach, J.E., and P.J. Guetter

1986. The Influence of Changing Orbital Parameters and Surface Boundary Conditions on Climate Simulations for the Past 18,000 Years. *Journal of the Atmospheric Sciences,* 43(16):1726–1759.

Kutzbach, J.E., P.J. Guetter, P.J. Behling, and R. Selin

1993. Simulated Climatic Changes: Results of the COHMAP Climate-

Model Experiments. *In* H.E. Wright, Jr., J.E. Kutzbach, T. Webb III, W.F. Ruddiman, F.A. Street-Perrott, and P.J. Bartlein, editors, *Global Climates since the Last Glacial Maximum*, pages 24–93. Minneapolis: University of Minnesota Press.

LaMarche, V.C., Jr.

1974. Paleoclimatic Inferences from Long Tree-Ring Records. *Science*, 183(4129):1043–1048.

La Motte, R.S.

1936. The Upper Cedarville Flora of Northwestern California and Adjacent California. *Publications of the Carnegie Institution of Washington*, 455:57–142.

Lanner, R.M.

1983. The Expansion of Singleleaf Piñon in the Great Basin. *In* D.H. Thomas, The Archaeology of Monitor Valley, 2: Gatecliff Shelter. *Anthropological Papers of the American Museum of Natural History*, 59(1):169–171.

Laudermilk, J.D., and P.A. Munz

1934. Plants in the Dung of *Nothrotherium* from Gypsum Cave, Nevada. *Publications of the Carnegie Institution of Washington*,453:29–37.

1938. Plants in the Dung of Nothrotherium from Rampart and Muav Caves, Arizona. *Publications of the Carnegie Institution of Washington*, 487:271–281.

Leonard, S., R. Miles, and H. Summerfield

1987. Soils of the Piñon–Juniper Woodlands. *In* R. Everett, editor, Proceedings—Piñon–Juniper Conference, Reno, Nevada, January 13–16, 1986. *United States Forest Service, General Technical Report*, INT-215:227–230.

Lewis, H.T.

1977. Maskut: The Ecology of Indian Fires in Northern Alberta. *Western Canadian Journal of Anthropology*, 7(1):15–52.

1982. Fire Technology and Resource Management in Aboriginal North America and Australia. *In* N.M. Williams and E.S. Hunn, editors, Resource Managers: North American and Australian Hunter-Gatherers. *American Association for the Advancement of Science, Selected Symposium*, 67:45–67. Washington, D.C.

1985. Why Indians Burned: Specific Versus General Reasons. *In* J.E. Lotan, B.M. Kilgore, W.C. Gischer and R.W. Mutch, coordinators, Proceedings, Symposium and Workshop on Wilderness Fire, Missoula, Montana, November 15–18, 1983. *United States Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report*, INT-182:75–80. Ogden, Utah.

Li, J., T.K. Lowenstein, C.B. Brown, T. Ku, and S. Luo

1996. A 100 ka Record of Water Tables and Paleoclimates from Salt Cores, Death Valley, California. *Palaeogeography, Palaeoclimatology, Paleoecology*, 123:161–178.

Light, A.

1996. Amino Acid Paleotemperature Reconstruction and Radiocarbon Shoreline Chronology of the Lake Bonneville Basin, USA. 142 pages. Master's thesis, Department of Geography, University of Colorado, Boulder, Colorado.

Lindström, S.

1990. Submerged Tree Stumps as Indicators of Mid-Holocene Aridity in the Lake Tahoe Basin. *Journal of California and Great Basin Anthropology*, 12(2):146–157.

Madsen, D.B.

1973. Late Quaternary Paleoecology in the Southeastern Great Basin. 117 pages. Doctoral dissertation, Department of Anthropology, University of Missouri, Columbia.

1984. Pollen, Packrats, and Pine along the I.P.P. *In* S. Simms and M.C. Isgreen, editors, Archaeological Excavations in the Sevier and Escalante Deserts, Western Utah: The Intermountain Power Project Transmission Line, Utah Section IPP Generating Plant to Deadhorse Junction. *University of Utah, Department of Anthropology, Reports of Investigations*, 83-12:353–363. Salt Lake City.

1985. Two Holocene Pollen Records for the Central Great Basin. *In* B.F. Jacobs, P.L. Fall, and O.K. Davis, editors, Late Quaternary Vegetation and Climates of the American Southwest. *American Association of Stratigraphic Palynologists Contributions*, 16:113–126.

2000. Late Quaternary Paleoecology in the Bonneville Basin. *Utah Geological Survey Bulletin*, 130: 190 pages. Salt Lake City, Utah.

Madsen, D.B., and D.R. Currey

1979. Late Quaternary Glacial and Vegetation Changes, Little Cottonwood Canyon Area, Wasatch Mountains, Utah. *Quaternary Research*, 12: 254–270.

Madsen, D.B., and P.A. Kay

1982. Late Quaternary Pollen Analysis in the Bonneville Basin. *American Quaternary Association Conference Abstracts*, page 128. Seattle, Washington.

Madsen, D.B., and D. Rhode

1990. Early Holocene Pinyon (*Pinus monophylla*) in the Northeastern Great Basin. *Quaternary Research*, 33:94–101.

Madsen, D.B., D. Rhode, D.K. Grayson, J.M. Broughton, S.D. Livingston, J. Hunt, J. Quade, D.N. Schmitt, and M.W. Shaver III

2001. Late Quaternary Environmental Change in the Bonneville Basin, Western USA. *Palaeoecology, Palaeogeography, Palaeoclimatology*, 167(3/4):243–271.

Markgraf, V.

1986. Plant Inertia Reassessed. *American Naturalist*, 127:725–726.

Martin, P.S.

1963. *The Last 10,000 Years: A Fossil Pollen Record of the American Southwest*. 87 pages. Tucson: University of Arizona Press.

Martin, P.S., and P.J. Mehringer, Jr.

1965. Pleistocene Pollen Analysis and Biogeography of the Southwest. *In* H.E. Wright, Jr., and D.G. Frey, editors, *The Quaternary of the United States*, pages 433–451. Princeton, New Jersey: Princeton University Press.

Martinson, D.G., N.G. Pisias, J.D. Hays, J. Imbrie, T.C. Moore, Jr., and N.J. Shackleton

1987. Age Dating and the Orbital Theory of the Ice Ages: Development of a High-Resolution 0 to 300,000-year Chronostratigraphy. *Quaternary Research*, 27(1):1–29.

Marwitt, J.P.

1973. Median Village and Fremont Culture Regional Variation. *Anthropological Papers of the University of Utah*, 95: 193 pages.

McCoy, W.D.

1981. Quaternary Aminostratigraphy of the Bonneville and Lahontan Basins, Western U.S., with Paleoclimatic Implications. 603 pages. Doctoral dissertation, University of Colorado, Boulder.

Mead, J.I., R.S. Thompson, and A. Long

1978. Arizona Radiocarbon Dates IX: Carbon Isotope Dating of Packrat Middens. *Radiocarbon*, 20:171–191.

Mehringer, P.J., Jr.

1967. Pollen Analysis of the Tule Springs Area, Nevada. *In* H.M. Wormington and D. Ellis, editors, Pleistocene Studies in Southern Nevada. *Anthropological Papers of the Nevada State Museum*, 13:129–200.

1977. Great Basin Late Quaternary Environments and Chronology. *In* D.D. Fowler, editor, Models and Great Basin Prehistory: A Symposium. *Desert Research Institute Publications in the Social Sciences*, 12:113–167.

1985. Late-Quaternary Pollen Records from the Interior Pacific Northwest and Northern Great Basin of the United States. *In* V.M. Bryant, Jr., and R.G. Holloway, editors, *Pollen Records of Late-Quaternary North American Sediments*, pages 167–189. Dallas, Texas: American Association of Stratigraphic Palynologists.

1986. Prehistoric Environments. *In* W.L. d'Azevedo, editor, Great Basin. *Handbook of North American Indians*, vol. 11:31–50. Washington, D.C.: Smithsonian Institution.

1987. *Late Holocene Environments on the Northern Periphery of the Great Basin, Final Report*. 71 pages. Portland, Oregon: United

States Bureau of Land Management.

Mehringer, P.J., and W.J. Cannon

1994. Volcaniclastic Dunes of the Fort Rock Valley, Oregon: Stratigraphy, Chronology, and Archaeology. *In* C.M. Aikens and D.L. Jenkins, editors, Archaeological Research in the Northern Great Basin: Fort Rock Archaeology since Cressman. *Anthropological Papers of the University of Oregon,* 50:283–327.

Mehringer, P.J., Jr., and C.W. Ferguson

1969. Pluvial Occurrence of Bristlecone Pine (*Pinus aristata*) in a Mojave Desert Mountain Range. *Journal of the Arizona Academy of Science,* 5(4):284–292.

Mehringer, P.J., Jr., and J.C. Sheppard

1978. Holocene History of Little Lake, Mojave Desert, California. *In* E.L. Davis, editor, The Ancient Californians: Rancholabrean Hunters of the Mojave Lakes Country. *Science Series,* 29:153–185.

Mehringer, P.J., Jr., and C.N. Warren

1976. Marsh, Dune and Archaeological Chronologies, Ash Meadows, Amargosa Desert, Nevada. *Research Report of the Nevada Archaeological Survey,* 6:120–150.

Mehringer, P.J., and P.E. Wigand

1986. Holocene History of Skull Creek Dunes, Catlow Valley, Oregon, U.S.A. *Journal of Arid Environments,* 11:117–138.

1987. Western Juniper in the Holocene. *In* R.L. Everett, editor, Proceedings of the Piñon–Juniper Conference. *United States Forest Service, General Technical Report,* INT-215:13–16.

1990. Comparison of Late Holocene Environments from Woodrat Middens and Pollen. *In* J.L. Betancourt, T.R. Van Devender, and P.S. Martin, editors, *Packrat Middens: The Last 40,000 Years of Biotic Change,* pages 294–325. Tucson: University of Arizona Press.

Mellars, P.

1976. Fire Ecology, Animal Populations and Man: A Study of Some Ecological Relationships in Prehistory. *Proceedings of the Prehistoric Society,* 42:15–45.

Mifflin, M.D., and M.M. Wheat

1979. Pluvial Lakes and Estimated Pluvial Climates of Nevada. *Bulletin of the Nevada Bureau of Mines and Geology,* 94: 57 pages.

Miller, R.F., and P.E. Wigand

1994. Holocene Changes in Semiarid Piñon–Juniper Woodlands: Response to Climate, Fire, and Human Activities in the US Great Basin. *BioScience,* 44(7):465–474.

Morrison, R.B.

1964. Lake Lahontan: Geology of Southern Carson Desert, Nevada. *United States Geological Survey Professional Paper,* 401: 156 pages.

1965. Quaternary Geology of the Great Basin. *In* H.E. Wright, Jr., and D.G. Frey, editors, *The Quaternary of the United States*, pages 265–285. Princeton, New Jersey: Princeton University Press.

1991. Quaternary Stratigraphic, Hydrologic, and Climatic History of the Great Basin, with Emphasis on Lakes Lahontan, Bonneville, and Tecopa. *In* R.B. Morrison, editor, Quaternary Nonglacial Geology: Conterminous U.S. *The Geology of North America,* K-2:283–320. Boulder, Colorado: Geological Society of America.

Morrison, R.B., and J.C. Frye

1965. Correlation of the Middle and Late Quaternary Successions of the Lake Lahontan, Lake Bonneville, Rocky Mountain (Wasatch Range), Southern Great Plains, and Eastern Midwest Areas. *Report of the Nevada Bureau of Mines,* 9: 45 pages.

Moutoux, T.E., and O.K. Davis

1995. Neogene through Pleistocene Paleoclimate of the Great Salt Lake Region, Northeastern Great Basin, USA. *In* C.M. Isaacs and V.L. Tharp, editors, Proceedings of the Eleventh Annual Pacific Climate (PACLIM) Workshop, April 19–22, 1994. *Interagency Ecological Program, Technical Report,* 40:127–135. Sacramento: California Department of Water Resources.

Mozingo, H.N.

1987. *Shrubs of the Great Basin: A Natural History.* 342 pages. Reno: University of Nevada Press.

Negrini, R.M.

2002. Pluvial Lake Sizes in the Northwestern Great Basin throughout the Quaternary Period. *In* R. Hershler, D.B. Madsen, and D.R. Currey, editors, Great Basin Aquatic Systems History. *Smithsonian Contributions to the Earth Sciences,* 33:11–52.

Negrini, R.M., and J.O. Davis

1992. Dating Late Pleistocene Pluvial Events and Tephras by Correlating Paleomagnetic Secular Variation Records from the Western Great Basin. *Quaternary Research,* 38:46–59.

Negrini, R.M., D.B. Erbes, K. Faber, A.M. Herrera, A.P. Roberts, A.S. Cohen, P.E. Wigand, and F.F. Foit, Jr.

2000. A Paleoclimate Record for the Past 250,000 Years from Summer Lake, Oregon, U.S.A., I: Chronology and Magnetic Proxies for Lake Level. *Journal of Paleolimnology,* 24(2):125–149.

Nowak, C.L., R.S. Nowak, R.J. Tausch, and P.E. Wigand

1994a. A 30,000 Year Record of Vegetation Dynamics at a Semi-Arid Locale in the Great Basin. *Journal of Vegetation Science,* 5:579–590.

1994b. Tree and Shrub Dynamics in Northwestern Great Basin Woodland and Shrub Steppe during the Late-Pleistocene and Holocene. *American Journal of Botany,* 81(3):265–277.

Oviatt, C.G.

1997. Lake Bonneville Fluctuations and Global Climate Change. *Geology,* 25:155–158.

Oviatt, C.G., D.R. Currey, and D.M. Miller

1990. Age and Paleoclimatic Significance of the Stansbury Shoreline of Lake Bonneville, Northeastern Great Basin. *Quaternary Research,* 33:291–305.

Oviatt, C.G., D.R. Currey, and D. Sack

1992. Radiocarbon Chronology of Lake Bonneville, Eastern Great Basin, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 99: 225–241.

Oviatt, C.G., and W.D. McCoy

1986. New Radiocarbon and Amino Acid Constraints on Holocene Expansions of Great Salt Lake, Utah. *American Quaternary Association, Programs with Abstracts, Ninth Biennial Meeting,* page 103.

Oviatt, C.G., W.D. McCoy, and R.G. Reider

1987. Evidence for a Shallow Early or Middle Wisconsin Lake in the Bonneville Basin, Utah. *Quaternary Research,* 27:248–262.

Oviatt, C.G., D.M. Miller, C. Zachary, and J.P. McGeehin

2001. Refining the Age of the Lake Transgression to the Gilbert Shoreline in the Bonneville Basin. *Eos, Transactions of the American Geophysical Union*, 82(47), fall meeting supplement, abstract PP22A–0496.

Phillips, F.M., A.R. Campbell, G.I. Smith, and J. Bischoff

1993. Interstadial Climate Cycles: A Link between Western North America and Greenland? *Geology,* 22:1115–1118.

Pisias, N.G., D.G. Martinson, T.C. Moore, Jr., N.J. Shackleton, W. Prell, J. Hays, and G. Boden

1984. High Resolution Stratigraphic Correlation of Benthic Oxygen Isotopic Records Spanning the Last 300,000 Years. *Marine Geology,* 46: 217–233.

Poinar, H.N., M. Hofreiter, W.G. Spaulding, P.S. Martin, B.A. Stankiewicz, H. Bland, R.P. Evershed, G. Possnert, and S. Pääbo

1998. Molecular Coproscopy: Dung and Diet of the Extinct Ground Sloth *Nothrotheriops shastensis. Science,* 281(5375):402–406.

Prentice, I.C., P.J. Bartlein, and T. Webb III

1991. Vegetation and Climate Change in Eastern North America since the Last Glacial Maximum. *Ecology,* 72:2038–2056.

Quade, J., R.M. Forester, W.L. Pratt, and C. Carter

1998. Black Mats, Spring-Fed Streams, and Late-Glacial-Age Recharge in the Southern Great Basin. *Quaternary Research,* 49(2):129–148.

Quade, J., M.D. Mifflin, W.L. Pratt, W. McCoy, and L. Burckle

1995. Fossil Spring Deposits in the Southern Great Basin and Their Implications for Changes in Water-Table Levels near Yucca Mountain, Nevada, during Quaternary Time. *Geological Society of America Bulletin,* 107(2):213–230.

Rhode, D.

1998. 50,000 Years of Vegetation Change in the Northeastern Great Basin: An Analysis of Packrat Middens Located on Federal Lands Administered by the Bureau of Land Management, Elko District. 57 pages. Report prepared for the United States Department of Interior, Bureau of Land Management, Elko, Nevada. [Unpublished.]

2000a. Middle and Late Wisconsin Vegetation History in the Bonneville Basin. *In* D.B. Madsen, Late Quaternary Paleoecology in the Bonneville Basin. *Utah Geological Survey Bulletin,* 130:137–148.

2000b. Holocene Vegetation History in the Bonneville Basin. *In* D.B. Madsen, Late Quaternary Paleoecology in the Bonneville Basin. *Utah Geological Survey Bulletin,* 130:149–164.

Rhode, D., and D.B. Madsen

1995. Early Holocene Vegetation in the Bonneville Basin. *Quaternary Research,* 44(2):246–256.

1998. Pine Nut Use in the Early Holocene and Beyond: The Danger Cave Archaeobotanical Record. *Journal of Archaeological Science,* 25: 1199–1210.

Rhode, D., and D.H. Thomas

1983. Flotation Analysis of Selected Hearths. *In* D.H. Thomas, The Archaeology of Monitor Valley, 2: Gatecliff Shelter. *American Museum of Natural History Anthropological Papers,* 59(1):151–156.

Richmond, G.M.

1964. Glaciation of Little Cottonwood and Bells Canyon, Wasatch Mountains, Utah. *United States Geological Survey Professional Paper,* 454-D: 41 pages.

1986. Stratigraphy and Correlation of Glacial Deposits of the Rocky Mountains, Colorado Plateau, and the Ranges of the Great Basin. *Quaternary Science Reviews,* 5:99–127.

Russell , I.C.

1885. *Geological History of Lake Lahontan, A Quaternary Lake of Northwestern Nevada.* United States Department of the Interior, Geological Survey, Monograph, 11. Washington, D.C.: Government Printing Office.

Schroedl, G.F.

1973. The Archaeological Occurrence of Bison in the Southern Plateau. *Reports of Investigations,* 51: 77 pages. Pullman, Washington: Laboratory of Anthropology, Washington State University.

Schulman, E.

1956. *Dendroclimatic Changes in Semiarid America.* 142 pages. Tucson: University of Arizona Press.

Scott, W.E.

1988. Temporal Relations of Lacustrine and Glacial Events at Little Cottonwood and Bells Canyons, Utah. *In* M.N. Machette, editor, In the Footsteps of G.K. Gilbert—Lake Bonneville and Neotectonics of the Eastern Basin and Range Province. *Miscellaneous Publication of the Utah Geological and Mineralogical Survey,* 88-1:78–81.

Scott, W.E., W.D. McCoy, R.R. Shroba, and M. Rubin

1983. Reinterpretation of the Exposed Record of the Last Two Cycles of Lake Bonneville, Western United States. *Quaternary Research,* 20: 261–285.

Sears, P.B.

1937. Pollen Analysis as an Aid in Cultural Deposits in the United States. *In* G.G. MacCurdy, editor, *Early Man,* pages 61–66 . London: Lippincott & Company.

Shackleton, N.J., and N.D. Opdyke

1973. Oxygen Isotope and Paleomagnetic Stratigraphy of Equatorial Pacific Core V28-238: Oxygen Isotope Temperature and Ice Volumes on a 10,000 and 100,000 Year Time Scale. *Quaternary Research,* 32:39–55.

Shreve, F., and A.L. Hinckley

1937. Thirty Years of Change in Desert Vegetation. *Ecology,* 18:463–478.

Siegal, R.D.

1983. Paleoclimatic Significance of D/H and ^{13}C/^{12}C Ratios in Pleistocene and Holocene Wood. 105 pages. Master's thesis, University of Arizona, Tucson.

Smiley, T.L., and P.J. Mehringer, Jr.

n.d. Post-Pluvial History of the Spring-Fed Salt Marshes of the Amargosa Drainage. Report to National Science Foundation for Research Supported by NSF Grant GB-8646, 35 pages.

Smith, G.I., and J.L. Bischoff, editors

1997. An 800,000-Year Geologic and Climatic Record from Owens Lake, California: Core OL-92. *Special Paper of the Geological Society of America,* 317: 165 pages.

Spaulding, W.G.

1977. Late Quaternary Vegetation Change in the Sheep Range, Southern Nevada. *Journal of the Arizona Academy of Sciences,* 22(2): 183–188.

1980. Presettlement Vegetation of the California Desert. 97 pages. Unpublished report submitted to the Desert Planning Staff, California Bureau of Land Management, Riverside.

1981. The Late Quaternary Vegetation of a Southern Nevada Mountain Range. 271 pages. Doctoral dissertation, University of Arizona, Tucson. [Unpublished.]

1985. Vegetation and Climates of the Last 45,000 Years in the Vicinity of the Nevada Test Site, South-Central Nevada. *United States Geological Survey Professional Paper,* 1329: 83 pages.

1990. Vegetational and Climatic Development of the Mojave Desert: The Last Glacial Maximum to Present. *In* J.L. Betancourt, T.R. Van Devender, and P.S. Martin, editors, *Packrat Middens—The Last 40,000 Years of Biotic Change,* pages 166–199. Tucson: University of Arizona Press.

1991. A Middle Holocene Vegetation Record from the Mojave Desert of North America and Its Paleoclimatic Significance. *Quaternary Research,* 35:427–437.

1994. *Paleohydrologic Investigations in the Vicinity of Yucca Mountain: Late Quaternary Paleobotanical and Paleontological Records.* 80 pages. Las Vegas, Nevada: Mifflin & Associates, Inc.

Spaulding, W.G., and L. Graumlich

1986. The Last Pluvial Climatic Episodes in the Deserts of Southwestern North America. *Nature,* 320:441–444.

Spencer, R.J., M. Baedecker, H.P. Eugster, R.M. Forester, M.B. Goldhaber, B.F. Jones, K. Kelts, J. McKenzie, D.B. Madsen, S.L. Rettig, M. Rubin, and C.J. Bowser

1984. Great Salt Lake and Precursors, Utah: The Last 30,000 Years. *Contributions to Mineralogy and Petrology,* 86:321–334.

Steward, J.H.

1930. Irrigation Without Agriculture. *Papers of the Michigan Academy of Science, Arts, and Letters,* 12:149–156.

1938. Basin–Plateau Aboriginal Sociopolitical Groups. *Bulletin of the Bureau of American Ethnology,* 120: xii + 346 pages.

Stewart, O.C.

1954. Forest Fires with a Purpose. *Southwestern Lore,* 20(3):42–47.

1955a. Why Were the Prairies Treeless? *Southwestern Lore,* 20(4):59–64.

1955b. Forest and Grass Burning in the Mountain West. *Southwestern Lore,* 21(1):5–9.

1956. Fire as the First Great Force Employed by Man. *In* W.L. Thomas. editor, *Man's Role in Changing the Face of the Earth,* pages 115–133. Chicago: The University of Chicago Press.

1963. Barriers to Understanding the Influence of Use of Fire by Aborigines on Vegetation. *Proceedings, Second Annual Tall Timbers Fire Ecology Conference, March 14–15, Tallahassee, Florida,* pages 117–126.

1982. Origin of Control of Fire. *Southwestern Lore,* 48(4):14–21.

Stine, S.

1990. Late Holocene Fluctuations of Mono Lake, Eastern California. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 78:333–381.

Stutz, H.C.

1978. Explosive Evolution of Perennial *Atriplex* in Western America. *Memoirs of the Great Basin Naturalist,* 2:161–168.

Swetnam, T.W.

1990. Fire History and Climate in the Southwestern United States. *In* J.S. Krammes, editor, Effects of Fire Management of Southwestern Natural Resources: Proceedings of the Symposium. *United States Forest Service, General Technical Report,* RM-191:6–17.

Swetnam, T.W., and C.H. Baisan

1996. Historical Fire Regime Patterns in the Southwestern United States since AD 1700. *In* C. Allen, editor, Fire Effects in Southwestern Forests: Proceedings of the Second La Mesa Fire Symposium. *United States Forest Service, General Technical Report,* RM-286: 11–32.

Swetnam, T.W., and J.L. Betancourt

1990. Fire–Southern Oscillation Relations in the Southwestern United States. *Science,* 249:1017–1020.

Szabo, B.J., P.T. Kolesar, A.C. Riggs, I.J. Winograd, and K.R. Ludwig

1994. Paleoclimatic Inferences from a 120,000-Yr Calcite Record of Water-Table Fluctuations in Browns Room of Devils Hole, Nevada. *Quaternary Research,* 41:59–69.

Tausch, R.J., N.E. West, and A.A. Nabi

1981. Tree Age and Dominance Patterns in Great Basin Piñon–Juniper Woodlands. *Journal of Range Management,* 34:259–264.

Tausch, R.J., P.E. Wigand, and J.W. Burkhardt

1993. Viewpoint: Plant Community Thresholds, Multiple Steady States, and Multiple Successional Pathways: Legacy of the Quaternary? *Journal of Range Management,* 46:439–447.

Thompson, R.S.

1984. Late Pleistocene and Holocene Environments in the Great Basin. 256 pages. Doctoral dissertation, Department of Geosciences, University of Arizona, Tucson.

1988. Western North America. *In* B. Huntley and T. Webb III, editors, Vegetation History. *Handbook of Vegetation Science,* 7:415–459. Dordrecht, The Netherlands: Kluwer Academic Publishers.

1990. Late Quaternary Vegetation and Climate in the Great Basin. *In* J.L. Betancourt, T.R. Van Devender, and P.S. Martin, editors, *Packrat Middens: The Last 40,000 Years of Biotic Change,* pages 200–239. Tucson: University of Arizona Press.

1991. Pliocene Environments and Climates in the Western United States. *Quaternary Science Reviews,* 10:115–132.

1992. Late Quaternary Environments in Ruby Valley, Nevada. *Quaternary Research,* 37:1–15.

Thompson, R.S., K.H. Anderson, and P.J. Bartlein

2000. Atlas of Relations between Climatic Parameters and the Distributions of Important Trees and Shrubs in North America. *United States Geological Survey Professional Paper,* 1650A-B: 423 pages. Denver, Colorado.

Thompson, R.S., L.V. Benson, and E.M. Hattori

1986. A Revised Chronology for the Last Pleistocene Lake Cycle in the Central Lahontan Basin. *Quaternary Research,* 25:1–10.

Thompson, R.S., and E. Hattori

1983. Paleobotany of Gatecliff Shelter: Packrat (*Neotoma*) Middens and from Gatecliff Shelter and Holocene Migrations of Woodland Plants. *In* D.H. Thomas, The Archaeology of Monitor Valley, 2: Gatecliff Shelter. *Anthropological Papers of the American Museum of Natural History,* 59(1):157–167.

Thompson, R.S., and R.R. Kautz

1983. Paleobotany of Gatecliff Shelter: Pollen Analysis. *In* D.H. Thomas, The Archaeology of Monitor Valley, 2: Gatecliff Shelter. *Anthropological Papers of the American Museum of Natural History,* 59(1): 136–151.

Thompson, R.S., and J.I. Mead

1982. Late Quaternary Environments and Biogeography in the Great Basin. *Quaternary Research,* 17:39–55.

Thompson, R.S., C.G. Oviatt, A.P. Roberts, J. Buchner, R. Kelsey, C. Bracht, R.M. Forester, and J.P. Bradbury

1994. Stratigraphy, Sedimentology, Paleontology, and Paleomagnetism of Pliocene–Early Pleistocene Lacustrine Deposits from Western Utah. *United States Geological Survey Open-file Report,* 95-1: 91 pages.

Thompson, R.S., L.J. Toolin, R.M. Forester, and R.J. Spencer

1990. Accelerator-Mass Spectrometer (AMS) Radiocarbon Dating of Pleistocene Lake Sediments in the Great Basin. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 78:301–313.

Thompson, R.S., C. Whitlock, P.J. Bartlein, S.P. Harrison, and W.G. Spaulding

1993. Climate Changes in the Western United States since 18,000 yr B.P. *In* H.E. Wright, Jr., J.E. Kutzbach, T. Webb III, W.F. Ruddiman, F.A. Street-Perrott, and P.J. Bartlein, editors, *Global Climates since the Last Glacial Maximum,* pages 468–513. Minneapolis: University of Minnesota Press.

Tidwell, W.D., S.R. Rushforth, and D. Simper

1972. Evolution of Floras in the Intermountain Region. *In* A. Cronquist, A.H. Holmgren, N.H. Holmgren, and J.L. Reveal, *Intermountain Flora: Vascular Plants of the Intermountain West, U.S.A.,* volume 1, pages 19–39. New York: Hafner Publishing Co.

Van Devender, T.R.

1990a. Late Quaternary Vegetation and Climate of the Sonoran Desert, United States and Mexico. *In* J.L. Betancourt, T.R. Van Devender and P.S. Martin, editors, *Packrat Middens: The Last 40,000 Years of Biotic Change,* pages 134–163. Tucson: University of Arizona Press.

1990b. Late Quaternary Vegetation and Climate of the Chihuahuan Desert, United States and Mexico. *In* J.L. Betancourt, T.R. Van Devender, and P.S. Martin, editors, *Packrat Middens: The Last 40,000 Years of Biotic Change,* pages 104–133. Tucson: University of Arizona Press.

Van Devender, T.R., and W.G. Spaulding

1979. Development of Vegetation and Climate in the Southwestern United States. *Science,* 204:701–710.

Van Devender, T.R., R.S. Thompson, and J.L. Betancourt

1987. Vegetation History of the Deserts of Southwestern North America: The Nature and Timing of the Late Wisconsin–Holocene Transition. *In* W.F. Ruddiman and H.E. Wright, Jr., editors, North America and Adjacent Oceans during the Last Deglaciation. *The Geology of North America,* K-3:323–352. Boulder, Colorado: Geological Society of America.

Van de Water, P.K., S.W. Leavitt, and J.L. Betancourt

1994. Trends in Stomatal Density and ^{13}C/^{12}C Ratios of *Pinus flexilis* Needles during Last Glacial–Interglacial Cycle. *Science,* 264:239–243.

Walter, H.

1954. Le facteur eau dans les regions arides et sa signification pour l'organisation de la vegetation dans les contrees sub-tropicales. In *Les Divisions Ecologiques du Monde,* pages 27–39. Paris: Centre Nationale de la Recherche Scientifique.

Weaver, J.E., and F.E. Clements

1938. *Plant Ecology.* Second edition, 601 pages. New York: McGraw-Hill Book Co.

Wells, P.V.

1983. Paleobiogeography of Montane Islands in the Great Basin since the Last Glaciopluvial. *Ecological Monographs,* 53:341–382.

Wells, P.V., and R. Berger

1967. Late Pleistocene History of Coniferous Woodland in the Mohave Desert. *Science,* 155(3770):1640–1647.

Wells, P.V., and C.D. Jorgensen

1964. Pleistocene Wood Rat Middens and Climatic Change in the Mohave Desert: A Record of Juniper Woodland. *Science,* 143(3611):1171–

1174.

Wells, P.V., and D. Woodcock

1985. Full-Glacial Vegetation of Death Valley, California: Juniper Woodland Opening to Yucca Semidesert. *Madroño,* 32:11–32.

West, N.E., R.J. Tausch, K.H. Rea, and P.T. Tueller

1978. Phytogeographical Variation within Juniper–Piñon Woodlands of the Great Basin. *In* K.T. Harper and J.L. Reveal, editors, Intermountain Biogeography: A Symposium. *Great Basin Naturalist Memoirs,* 2:119–136.

Whitlock, C., and P.J. Bartlein

1993. Spatial Variations of Holocene Climatic Change in the Yellowstone Region. *Quaternary Research,* 39:231–238.

1997. Vegetation and Climate Change in Northwest America during the Past 125 kyr. *Nature,* 388(6637):57–61.

Wigand, P.E.

1987. Diamond Pond, Harney County, Oregon: Vegetation History and Water Table in the Eastern Oregon Desert. *Great Basin Naturalist,* 47:427–458.

1989. Vegetation, Vegetation History, and Stratigraphy. *In* K.C. Reid, J.A. Draper, and P.E. Wigand, editors, Prehistory and Paleoenvironments of the Silvies Plateau, Harney Basin, Southeastern Oregon. *Project Report,* 8:37–85. Pullman, Washington: Center for Northwest Anthropology, Washington State University.

1995. Stable Isotopic Analyses in Paleoclimatic Reconstruction. *In* W.J. Waugh, editor, *Proceedings of the Workshop—Climate Change in the Four Corners and Adjacent Regions: Implications for Environmental Restoration and Land-Use Planning,* CONF-9409325, pages 27–38. Grand Junction, Colorado: United States Department of Energy.

1997a. Native American Diet and Environmental Contexts of the Holocene Revealed in the Pollen of Human Fecal Material. *Nevada Historical Society Quarterly,* 40(1):105–116.

1997b. A Late-Holocene Pollen Record from Lower Pahranagat Lake, Southern Nevada, USA: High Resolution Paleoclimatic Records and Analysis of Environmental Responses to Climate Change. *In* C.M. Isaacs and V.L. Tharp, editors, Proceedings of the Thirteenth Annual Pacific Climate (PACLIM) Workshop, April 15–18, 1996. *Interagency Ecological Program, Technical Report* 53:63–77. Sacramento: California Department of Water Resources.

Wigand, P.E., M.L. Hemphill, and S. (Manna) Patra

1994. Late Holocene Climate Derived from Vegetation History and Plant Cellulose Stable Isotope Records from the Great Basin of Western North America. *High-Level Radioactive Waste Management Conference: Proceedings of the Fifth Annual International, Sponsored by the American Society of Civil Engineers and the American Nuclear Society; Co-sponsored by the American Chemical Society ... [et al.] in Cooperation with U.S. Department of Energy ... [et al.],* volume 4:2574–2583. La Grange Park, Illinois: American Nuclear Society; New York: American Society of Civil Engineers.

Wigand, P.E., M.L. Hemphill, S.E. Sharpe, and S. Patra

1995. Great Basin Woodland Dynamics during the Holocene. *In* W.J. Waugh, editor, *Proceedings of the Workshop-Climate Change in the Four Corners and Adjacent Regions: Implications for Environmental Restoration and Land-Use Planning,* CONF-9409325, pages 51–69. Grand Junction, Colorado: United States Department of Energy.

Wigand, P.E., and P.J. Mehringer, Jr.

1985. Pollen and Seed Analyses. *In* D.H. Thomas, The Archaeology of Hidden Cave, Nevada. *Anthropological Papers of the American Museum of Natural History,* 61(1):108–124.

Wigand, P.E., and C.L. Nowak

1992. Dynamics of Northwest Nevada Plant Communities during the Last 30,000 Years. *In* C.A. Hall, V. Doyle-Jones, and B. Widawski, editors, The History of Water: Eastern Sierra Nevada, Owens Valley, White–Inyo Mountains. *White Mountain Research Station Symposium,* 4:40–62.

Wigand, P.E., and M.R. Rose

1990. Calibration of High Frequency Pollen Sequences and Tree-Ring Records. *High-Level Radioactive Waste Management: Proceedings of the International Conference Topical Meeting, Sponsored by the American Society of Civil Engineers and the American Nuclear Society; Co-sponsored by the American Chemical Society ... [et al.],* in Cooperation with the U.S. Department of Energy ... [et al.], volume 2:1240–1250. La Grange Park, Illinois: American Nuclear Society; New York: American Society of Civil Engineers.

Winograd, I.J., T.B. Coplen, J.M. Landwehr, A.C. Riggs, K.R. Ludwig, B.J. Szabo, P.T. Kolesar, and K.M. Revesz

1992. Continuous 500,000-Year Climate Record from Vein Calcite in Devils Hole, Nevada. *Science,* 258:255–260.

Winograd, I.J., J.M. Landwehr, K.R. Ludwig, T.B. Coplen, and A.C. Riggs

1997. Duration and Structure of the Past Four Interglacials. *Quaternary Research,* 48:141–154.

Winograd, I.J., B.J. Szabo, T.B. Coplen, and A.C. Riggs

1988. A 250,000-Year Climatic Record from Great Basin Vein Calcite: Implications for Milankovitch Theory. *Science,* 242(4883):1275–1280.

Winter, J.C.

1976. The Processes of Farming Diffusion in the Southwest and Great Basin. *American Antiquity,* 41(4):421–429.

Winter, J.C., and P.F. Hogan

1986. Plant Husbandry in the Great Basin and Adjacent Northern Colorado Plateau. *In* C.J. Condie and D.D. Fowler, editors, *Anthropology of the Desert West: Essays in Honor of Jesse D. Jennings,* pages 117–144. Salt Lake City: University of Utah Press.

Woolfenden, W.B.

1993. Pollen Present in Cores OL-92-1, -2, and -3. *In* Core OL-92 from Owens Lake, Southeast California. G.I. Smith and J.L. Bischoff, editors, *United States Geological Survey Open File Report,* 93-683: 314–332.

1997. Late-Quaternary Vegetation History of the Southern Owens Valley Region, Inyo County, California. 347 pages, 22 figures, 5 tables. Doctoral dissertation, Department of Geosciences, University of Arizona, Tucson. [Unpublished.]