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A 30 000 year record of vegetation dynamics at a semi-arid locale in the Great Basin

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Abstract. Plant macrofossils extracted from fossil woodrat (*Neotoma* spp.) middens at a single locale in the northwestern Great Basin were used to examine vegetation dynamics during the last 30 000 yr. Although the modern assemblage of xeric species at the study site is a recent occurrence, a large proportion of the modern plant taxa near the study locale were also found 12 000 - 30 000 yr BP. The persistence of extant species through time was likely facilitated by within-species genetic diversity and the formation of coenospecies. The diverse topographic and microhabitat features in the northwestern Great Basin also allowed different species to coexist during glacial periods. Changes in species composition occurred during two time intervals: 20 000 - 30 000 and 10 000 - 12 000 yr BP. Vegetation changes during 20 000 - 30 000 yr BP were cyclic; community composition oscillated between two groups of taxa. Vegetation changes between 10 000 - 12 000 yr BP occurred during the Pleistocene-Holocene transition and were largely directional from the Pleistocene assemblages through two transition assemblages to a Holocene assemblage. These changes in species composition generally reflect changes in climate. The presence of relatively mesic species during 10 000-30 000 yr BP is consistent with the regional late-Pleistocene climate, and the gradual loss of relatively mesic species during the Holocene parallels the change to a more xeric climate. Contrasted with other areas of North America and Europe, the magnitude of vegetation changes at our study area were relatively small. Furthermore, the persistence of many species through time at this site in the northwestern Great Basin also differs from results at other study sites in North America and Europe. These differences are probably related to land form characteristics and genetic diversity within species.

Keywords: Climate change; Migration; *Neotoma*; Paleoecology; Plant macrofossil; Quaternary; Woodrat midden.

Nomenclature: Hitchcock & Cronquist (1973).

Introduction

Most ecologists study organisms on a scale of less than 100 years, but many patterns or processes in the natural world are better understood on a scale of hundreds,

thousands or tens of thousands of years (Barnosky 1987; Schoonmaker & Foster 1991). The Quaternary ecological record provides insight into the nature of plant community variations. For example, the individualistic response of taxa to their environment is clearly evident from late-Pleistocene and Holocene data (Davis 1976; Huntley 1991; Nowak et al. 1994). Furthermore, modern plant communities are loose and relatively ephemeral assemblages of species whose occurrence in a particular area at a particular time results from range expansions or contractions induced by climatic variations (Schoonmaker & Foster 1991). Thus, the stability, resilience and persistence of plant communities are time-dependent characteristics that can be measured quantitatively using the paleoecological record (Delcourt & Delcourt 1991).

The Great Basin floristic province in western North America was initiated in the Miocene, about 26 million yr ago (Cronquist 1978). Formation of this floristic province coincides with the most significant uplifted and tilted position of the Sierra Nevada mountain range (Fiero 1986), which created the rainshadow on the west side of the Great Basin. Over geologic time, the climate was cool and moist during the late-Pliocene, about 7 million yr ago, which was followed by a period of alternating glacial and interglacial stages. Actual glaciers in the Great Basin were largely restricted to upper elevations in the mountains (Cronquist 1978; Morrison 1991), with the west side of the continental ice sheet (the Cordilleran) reaching into the Pacific Northwest of the North American continent (Booth 1987).

The vegetation of the semi-arid Great Basin in western North America generally spans wide environmental gradients because of the alternating basin and mountain range topography. Therefore, it is an excellent model system to study plant responses to climate variations. Although recent advances in the fields of climatology, paleobotany, and plant ecology have enhanced our understanding of vegetation responses to climatic variations in the Great Basin (e.g. Cronquist 1978; Axelrod 1981;

Wells 1983; Thompson 1988, 1990), much of this research has focused on high-elevation conifers in the eastern and southern portions of the Great Basin. The geographic limits of these conifers changed markedly during the last glacial period (Thompson 1988). Wells (1983) suggested that selected conifers formed continuous stands in the Great Basin during the late-Pleistocene and that island biogeographic processes largely accounted for the modern distribution of these species. For the Great Basin as a whole, Cronquist (1978) envisioned 'inverse' migrations of northern, mesic species and southern, xeric species during the climatic reversals of the Pleistocene; mesic species would displace xeric species during cool, wet periods only to have xeric species displace mesic species during warm, dry periods. Elevational migration of species is also evident (Thompson 1990), and macrofossil records from the southern Great Basin (Spaulding 1985) show extensive changes in plant assemblages during the late-Pleistocene and Holocene as plants migrated in response to climatic variations.

Little is known about the vegetation history of the northwestern Great Basin during the late-Pleistocene and Holocene. The only previously published report of woodrat macrofossil records near our study area in the northwestern Great Basin comes from the Winnemucca Lake basin area, which is approximately 40 km northeast of our study site. These data were assembled to complement a revised chronology for a regional pluvial lake called Lake Lahontan, and the authors only report radiocarbon dates between 11 000 - 12 500 yr Before Present (BP) for a subsample of midden strata and only discuss selected plant taxa (Thompson et al. 1986). The primary objectives of this study were: (1) to examine how vegetation in the northwestern Great Basin responded to climatic variations, rather than to infer climate from vegetation; and (2) to investigate perspectives of plant community dynamics over a considerable time scale. We used plant macrofossil data from fossil woodrat (*Neotoma* spp.) middens collected at a single locale to determine temporal vegetation dynamics. Patterns of regional climatic variations were obtained from reconstructions of the hydrologic balance of pluvial Lake Lahontan (Thompson et al. 1986; Benson & Thompson 1987; Benson 1991), which came within 0.5 km of our midden locale, and from regional climate simulation models (Anon. 1988; Hostetler et al. 1994). By collecting midden samples within a single 2 km² site or area, the confounding effects of site-to-site differences are held to a minimum. In addition, we utilize an extensive list of plant taxa that includes tree, shrub, herbaceous, and graminoid growth forms. Finally, the high frequency of our vegetation data across a broad temporal span (tens of thousands of years) at one site sets our data apart from many other plant macrofossil

studies, which contain a number of sites over a broad spatial domain with individual sites having low sampling frequency across the large temporal span (e.g. Wells 1983; Spaulding 1990; Thompson 1990). Our study provides a rare perspective because it allows us to address the vegetation dynamics at a local scale with more specificity and precision than many other paleoecological studies have done. Also, we have several midden strata samples clustered closely together in time, which allows us to examine regional vegetation dynamics and species richness over a relatively fine time resolution.

We obtained 20 different midden strata that spanned the time period from 30 000 yr BP to 1000 yr BP. Plant macrofossils from the midden strata allowed us to track the development of modern plant communities in the northwestern Great Basin and to correlate vegetation dynamics with paleoclimate variation for this region. Our results differ from many other plant history studies in North America and Europe in that a large proportion of taxa have continuously occupied the site for 12 000-30 000 yr.

Study site

The Painted Hills midden site (Fig. 1) is in the Virginia Mountains of northwestern Nevada, 7.7 km from Pyramid Lake (a remnant of pluvial Lake Lahontan). The name 'Painted Hills' refers to horizontal bands of multi-colored tuff that characterize the area. The modern climate of the area is characterized as a cold desert with an average of 180-200 mm of annual precipitation, which mostly occurs during the winter months. Active perennial streams are absent from the Painted Hills study area. Modern vegetation is comprised primarily of *Juniperus osteosperma*, shrubs such as *Artemisia tridentata* and *Atriplex confertifolia*, and bunchgrasses such as *Sitanion hystrix* and *Poa sandbergii*.

A large midden system located at 1380 m was subdivided into 18 sample strata. Two additional middens located at 1530 m and about 2 km northeast of the first one were also sampled. All middens are located in Tertiary-age volcanic rocks (moderately welded tuff).

Midden 1 (119° 38' 27" W, 39° 53' 09" N, 1380 m elevation) was a large (ca. 2.4 m × 1.4 m) midden system positioned in a vertical fracture within a welded tuff outcrop. This midden was rare in that macrofossils spanning 26 000 yr were preserved; this lengthy radiocarbon timeline was developed from 18 sampled strata. Radiocarbon dates for the strata are listed in Table 1.

Midden 2 (119° 39' 41" W, 39° 52' 51" N, 1530 m elevation) was located in a sheltered, vertical crack on the west side of a welded tuff outcrop. Midden 3 was on a small ledge on the west face of a large welded tuff

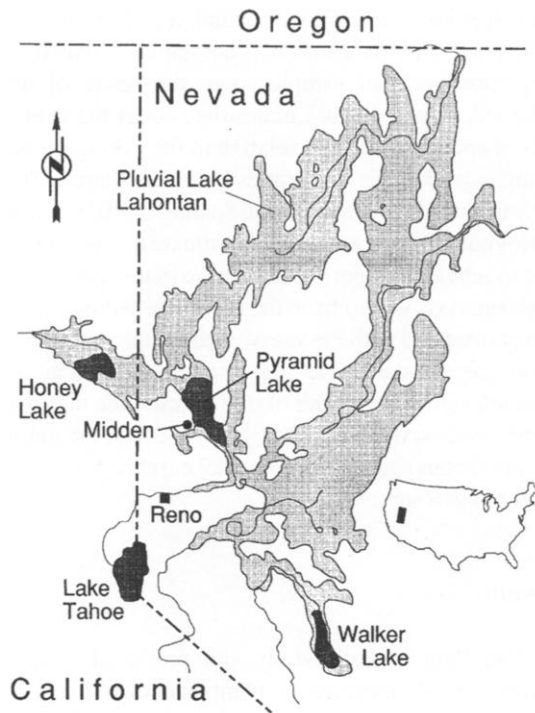


Fig. 1. Location of fossil midden study site (darkened circle). Present day lakes Pyramid Lake and Walker Lake are represented by a darker pattern.

outcrop about 10 m from midden 2 and was only slightly protected from weather by a rock overhang. Radiocarbon dates for these middens are also listed in Table 1.

Methods

Field samples from these ancient solidified middens were taken using a hammer, chisel, and crowbar. Aluminum tags with midden identification numbers were left at the site to mark the remaining portions of the middens. Modern flora within a 100m radius of the middens was compiled; 100m was used because it represents a typical maximum foraging distance of the woodrat (Betancourt et al. 1986; Wells 1976). The locality was visited throughout the year and in more than one year to obtain a more complete list of modern plants to compare with the retrieved fossil taxa list. Additionally, a survey of modern plants was obtained after receiving a record precipitation year that followed drought conditions that lasted for over six years.

Midden samples were processed in the laboratory using methods of Spaulding (1985), as modified by Mehringer & Wigand (1990). The extensive midden (#1) was subdivided along bedding planes of deposition into clearly-defined constituent strata. Approximately

Table 1. Sample identification; elevation from which the sample was taken; the material from each strata that was radiocarbon dated; radiocarbon age; and radiocarbon laboratory number for each sample in this fossil midden study.

Sample ID	Elevation m	Material dated	Radiocarbon age (yr BP)	Lab. Number
PH140889PEW1(1)	1530	Dung	1 180 ± 80	β-32940
PH140889PEW2(1,1)	1380	Dung	3 050 ± 90	β-32941
PH211089PEW1(1,1)	1380	Dung	4 070 ± 90	β-47201
PH140889PEW2(1,2)	1380	Dung	8 560 ± 120	β-32942
PH150990PEW1(1,8)	1380	Dung	8 760 ± 170	β-41917
PH120491PEW2(1,B)	1380	Juniper	9 640 ± 110	β-46256
PH150990PEW1(1,5)	1380	Juniper	10 450 ± 100	β-47202
PH140889PEW2(1,2)B	1380	Juniper	11 120 ± 100	β-35805
PH140889PEW2(1,4)	1380	Dung	11 530 ± 160	β-32944
PH140889PEW2(1,3)	1380	Dung	11 910 ± 110	β-32943
PH140889PEW2(1,4)	1380	Juniper	11 980 ± 180	β-35809
PH180589PEW3(2,1)	1380	Dung	16 280 ± 160	β-32401
PH150990PEW1(1,6)tp	1380	Juniper	20 070 ± 380	β-41915
PH150990PEW1(1,6)bt	1380	Juniper	21 290 ± 320	β-41916
PH180589PEW2(1)	1530	Dung	21 460 ± 420	β-32400
PH211089PEW1(1,5)	1380	Juniper	23 110 ± 410	β-34726
PH140889PEW2(1,5)	1380	Dung	24 580 ± 470	β-32945
PH211089PEW1(1,3)	1380	Juniper	28 560 ± 390	β-34724
PH211089PEW1(1,6)	1380	Juniper	29 410 ± 770	β-34727
PH211089PEW1(1,2)	1380	Juniper	29 630 ± 590	β-34723

500 grams from each subdivided stratum and from the other two middens were prepared for macrofossil analysis. The preparation techniques are detailed in Nowak (1991) and involve: (1) soak the sample to dissolve the crystallized urine and release botanical contents; (2) sieve the residue to separate macrofossils into size classes, which aids in sorting; and (3) sort and identify the macrofossil material with the aid of a stereoscopic microscope. Juniper twigs or woodrat dung were removed from each sample when present, and a subsample was submitted for radiocarbon dating from each stratum. Macrofossils were identified using modern seed, twig and leaf collections at the Quaternary Sciences Center of the Desert Research Institute in Reno, Nevada. Identification was also aided by regional flora guides and plant keys, notably Cronquist et al. (1972-1984) and Vasek (1966).

Analysis of plant macrofossils from woodrat middens

Woodrats are small herbivores that build large nesting systems of sticks and other plant debris, which are referred to as middens. As woodrats make many relatively short trips from the nest to forage for food and nest materials, they accumulate samples of the local flora in the form of fruits, seeds, leaves, twigs, flowers, etc. in the nest. A collecting bias by any one woodrat at any point in time should minimally affect the composition of the midden because one nest contains several woodrat generations and each generation has a 2 - 3 yr life span. Thus, woodrat middens contain a fair repre-

sensation of plants growing near the nest (Dial & Czaplewski 1990). Plant material that is deposited in woodrat middens becomes covered with excreta, which leads to long-term preservation (Wells & Berger 1967). Woodrat middens with contents cemented by crystallized urine are preserved in dry caves or rockshelters in arid portions of the western United States for thousands to tens of thousands of years (Wells 1976). Plant assemblages that are retrieved from individual strata of a woodrat midden accurately reflect the composition of the local vegetation over a discrete time span up to a few decades (Thompson 1985, 1990).

Radiocarbon dates for each stratum insure chronological order. The assumption for our midden studies is that components of a single stratum have a contemporaneous age, which is similar to that for other stratigraphic-dependent sciences such as geology, archaeology, and paleobiology as well as previous fossil woodrat midden studies (Betancourt et al. 1990). Although different macrofossils from the same midden and/or stratum occasionally have different radiocarbon ages (Van Devender et al. 1985), cost constraints clearly made it impractical to date each plant fragment extracted from each stratum. Our previous research of several middens across several locales (Nowak et al. 1994) revealed that the average difference in age between different biological components from a single stratum of randomly selected middens was relatively small and provided a sufficiently accurate time resolution.

Analysis of plant remains from woodrat middens has been used since the 1960s to reconstruct late-Pleistocene and Holocene paleovegetation in semi-arid to arid western United States (Wells & Jorgensen 1964; Wells & Berger 1967; Mehringer & Ferguson 1969). Because of the various biological activities within the woodrat's home (Vaughan 1990), certain statistical analyses of plant macrofossil data, namely reconstructing percent composition for individual species in paleovegetation, are precluded (Dial & Czaplewski 1990; Spaulding et al. 1990). Although some researchers report midden macrofossil data in the form of relative abundance for individual taxa, a more conservative but ecologically useful approach to analyze the retrieved plant assemblages is based on the presence/absence of taxa from each midden stratum coupled with a list of modern species for the study site. For the purpose of this paper, we report our data in this manner.

We used three multivariate methods to assess the effects of temporal environmental variation on vegetation. The first method was a cluster analysis that used a standard unweighted pair group average method (UPGMA; Ludwig & Reynolds 1988; Sørensen's similarity index) to group species assemblages from individual midden strata according to their similarity in

plant species composition. Second, a β -diversity index (Wilson & Shmida 1984) was computed between each contiguous pair of samples over the range of dates obtained. This index calculates the sum of the gain and loss of species over time relative to the average species richness of the pair of samples being compared. Third, Non-metric Multi-Dimensional Scaling (NMDS; Ludwig & Reynolds 1988) was used to ordinate the midden data and to reveal gradients based on the plant species composition. Axis values from the first three ordination axes were correlated with the age of each sample and selected plant species data. The plant species data that were selected were the number of tree species, the number of shrub species, the number of grass species, the number of herbaceous species, and the total number of species in each midden sample.

Results

The Painted Hills study site produced a unique chronological sequence of plant macrofossil material that is unlike any other previously reported in the northwestern Great Basin. The three middens represent 20 radiocarbon dates between 1000 and 30 000 yr BP. For the purpose of this paper, the dates and their plant constituents were grouped into five time intervals that reflect typical climatic periods in the late-Quaternary: Pre-Full-Glacial, Full-Glacial, Late-Glacial, Early-Holocene, and Mid-to-Late-Holocene. These chronological divisions are similar to those used by Thompson (1990) in his Great Basin paleoecology research.

Frequently, plant macrofossils recovered from the midden strata were identifiable to the genus and species level. However, the taxonomic resolution of some macrofossils was restricted either because the macrofossil was too fragmented for further identification or because the particular plant part did not have sufficient detail for further identification. To facilitate the discussion of results, the fossil and modern taxa were grouped into the major growth forms of trees, shrubs and subshrubs, graminoids, and herbs. Subshrubs are shrubby, perennial plants that are primarily herbaceous but have woody root crowns (Mozingo 1987; Seymour 1990).

Trees

Tree taxa were divided into two basic categories (Fig. 2): (a) the taxon that appears in the fossil record as well as the modern flora (i.e. within a 100 m radius of the middens); and (b) those taxa that appear only in the fossil record. Tree taxa are represented by three different species at the Painted Hills study site. Group (a), *Juniperus osteosperma*, is the most persistent, occurring

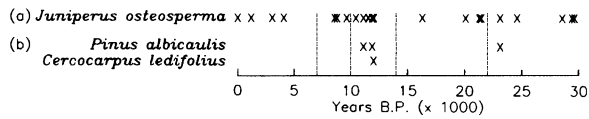


Fig. 2. Presence of tree taxa in midden strata or in modern flora, designated by an 'X'. (a) Taxon that appears in the fossil record as well as the modern flora. (b) Taxa that appear only in the fossil record. Vertical dotted lines designate the approximate boundary between climate periods for the Great Basin as used by Thompson (1990).

in all of the fossil midden strata as well as presently growing near the middens. Group (b) of the tree taxa consists of two species. *Pinus albicaulis* appears 3 times in the fossil record; once at ca. 23 000 yr BP and twice between 11 000 - 12 000 yr BP. The presence of *P. albicaulis* at 1380m represents approximately a 1100m drop in elevation from its present position 50 km to the west in the Sierra Nevada. *Cercocarpus ledifolius* appears only once in the fossil record at about 12 000 yr BP. Its current elevational range is approximately 1000 m higher in the same mountain range as the Painted Hills study site.

Shrubs and subshrubs

Shrub and subshrub taxa were divided into three categories (Fig. 3): (a) those taxa that appear in the fossil record as well as the modern flora; (b) those taxa either that appear only in the fossil record or that appear in the fossil record and exclusively in the modern flora at the higher elevation middens (1530m); and (c) those taxa that appear only in the modern flora. Although some macrofossils were only identifiable to the genus level because of their fragmented nature, some of these taxa were combined with taxa identified to the species level to facilitate the discussion of the presence/absence data. For example, many of the fossils listed as *Artemisia* spp. very likely belong in the *Artemisia tridentata* taxon because *A. tridentata* is the dominant species for our locale and was the only species identified in the fossil record. Similarly, the *Brickellia* spp. taxon very likely belongs with the *Brickellia microphylla* taxon. For these and other groups of taxa, a completely certain identification cannot be made without additional diagnostic techniques.

The shrubs and subshrubs that occur in both the fossil and modern floras, group (a), have many taxa with a lengthy record of occurrence from fossil to modern (Fig. 3). *Artemisia/Artemisia tridentata*, *Atriplex confertifolia*, *Brickellia/Brickellia microphylla*, and *Symphoricarpos/Symphoricarpos oreophilus* have representation in almost all the midden strata and the defined climatic



Fig. 3. Presence of shrub and subshrub taxa in midden strata or in modern flora, designated by an 'X'. An 'H' designates a taxon found only at the higher elevation (1530m) midden locale and an 'L' designates a taxon found only at the lower elevation. (a) Taxa that appear in the fossil record as well as the modern flora. (b) Taxa either that appear only in the fossil record or that appear in the fossil record and exclusively in the modern flora at the higher elevation midden locale. (c) Taxa that appear only in the modern floral surveys. Vertical dotted lines designate the approximate boundary between climatic periods for the Great Basin as used by Thompson (1990).

periods, including the modern flora. The most common taxa for group (a), *Artemisia* spp. and *A. confertifolia*, are also widely distributed within the shrub and grassland habitats in the Great Basin today. *Tetradymia glabrata* is only present in a few midden strata, but in three climatic periods over a broad time span of about 30 000 yr BP to modern times. *Atriplex canescens*, *Chrysothamnus/Chrysothamnus nauseosus/Chrysothamnus viscidiflorus*, and *Ericameria/Ericameria nanus* appear during the last three climatic periods from about 12 000 yr BP to modern. *Grayia spinosa* appears twice in the fossil record, at about 30 000 and 9000 yr BP, as well as in modern vegetation. *Kochia americana* and *Tetradymia canescens* appear once in the fossil record at about 12 000 yr BP and in the modern record.

Group (b) of the shrubs and subshrubs has a few taxa with lengthy occurrences and taxa with occurrences within one or two climatic periods (Fig. 3). *Salvia dorrii* is represented in most of the midden strata and all of the climatic periods, but appears today only at the higher elevation (1530m) midden site and above. *Forsellesia nevadensis* appears in the fossil record first at about 11 000 yr BP and is present through the three most recent climatic periods. Modern representation also oc-

curs only at the higher elevation site and above. *Ephedra* spp. appeared in most of the midden strata at both elevations between 30 000 yr BP and 8000 yr BP, which includes four of the five climatic periods. *Ribes/Ribes cereum/Ribes velutinum* and *Purshia tridentata* appear during the two climatic periods between 12 000 yr BP and 8000 yr BP. *Kochia americana*, *Rosa woodsii* and *Prunus andersonii* appear only once in the fossil record.

Group (c) of the shrubs and subshrubs (Fig. 3) contains taxa that only have modern representatives. *Artemisia spinescens* is only present at the lower elevation midden whereas *Eriogonum heermannii* is only present at the higher elevation midden site.

Graminoids

Graminoid taxa were also divided into three categories (Fig. 4): (a) those taxa that appear in the fossil record as well as the modern flora near the middens; (b) those taxa that appear only in the fossil record; and (c) those taxa that appear only in the modern flora.

Group (a) of the graminoids shows a lengthy, but somewhat intermittent record for the *Poa* taxa, *Stipa* taxa, and *Sitanion hystrix* (Fig. 4). *Poa* spp. appear in the fossil record around 23 000 yr BP and again in the modern record. *Stipa* spp. are more common in the fossil record, with representation in the earliest climatic period and the three most recent climatic periods, spanning about 30 000 yr of time. *Sitanion hystrix* first occurs about 12 000 yr BP in the fossil record and is represented through the three most recent climatic periods including the modern. *Poaceae* is a generalized identification grouping for the fragments of grass stems and other plant parts that can not be readily assigned a genus or species level, but occur in the fossil record. Many of these are probably the same taxa as the contemporary constituents.

The second group of graminoids, group (b), occurred only in the fossil record (Fig. 4). Two taxa had long and almost continuous fossil records: *Oryzopsis hymenoides* and *Agropyron* spp. These two taxa do not appear in the modern flora within the 100 m range of the middens, but are near the study site. *Eleocharis quinqueflora* and *Deschampsia* spp. are both relatively mesic plants and occur in the earlier climatic periods, but not later on.

The last group of graminoids, group (c), consists of two *Bromus* species, *B. tectorum* and *B. carinatus*, which are present only in the modern flora (Fig. 4). *Bromus tectorum* has been introduced from Eurasia within the last 100 yr and is present at the study site as well as the general vicinity. *Bromus carinatus* is a native brome grass and was found only at the higher elevation site.

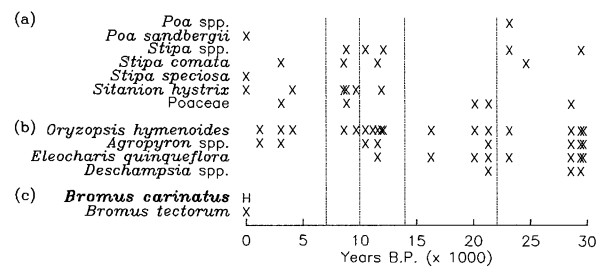


Fig. 4. Presence of graminoid taxa in midden strata or in modern flora, designated by an 'X'. A 'H' designates a taxon found only at the higher elevation (1530 m) midden locale. Bolded letters of taxon name indicate appearance in modern survey after extremely wet winter that followed over 6 yr of drought conditions. (a) Taxa that appear in the fossil record as well as the modern flora. (b) Taxa that appear only in the fossil record. (c) Taxa that appear only in the modern flora. Vertical dotted lines designate the approximate boundary between climatic periods for the Great Basin as used by Thompson (1990).

Herbs

Because of the large number of herb taxa and because some fragmented plant parts could only be identified to genus or family levels, we have listed the herbaceous taxa so that similar family and/or genus taxa are listed nearest each other (Fig. 5). Herb taxa were then divided into three categories similar to the above plant life forms: (a) those taxa that have fossil and modern representatives within their genera groups; (b) those taxa either that appear only in the fossil record or that appear in the fossil record and exclusively in the modern flora at the higher elevation middens (1530 m); and (c) those taxa with only modern occurrences. In some cases, the assignment of an individual taxon to group (a), (b), or (c) may be somewhat artificial. For example, all six of the *Cryptantha* taxa were placed in group (a) because three common taxa, *Cryptantha circumscissa*, *C. gracilis*, and *C. pterocarya* were present in the modern flora. Nonetheless, the groups are generally reasonable because: (1) the distribution of different species within Great Basin herbaceous genera often overlap; and (2) the lack of detailed information about these genera precludes the use of hierarchical grouping techniques.

Of the herb taxa within group (a), the genera *Amsinckia*, *Cryptantha*, *Galium*, *Phacelia*, *Descurainia*, and *Mentzelia* have representatives in all five of the climatic phases, most of the midden strata, and the modern flora (Fig. 5). The genera *Astragalus* and *Eriogonum* are represented in only some of the midden strata, but show a lengthy record of occurrence at this site, similar to other plant life forms already discussed.

The herb taxa in group (b) are those that have repre-

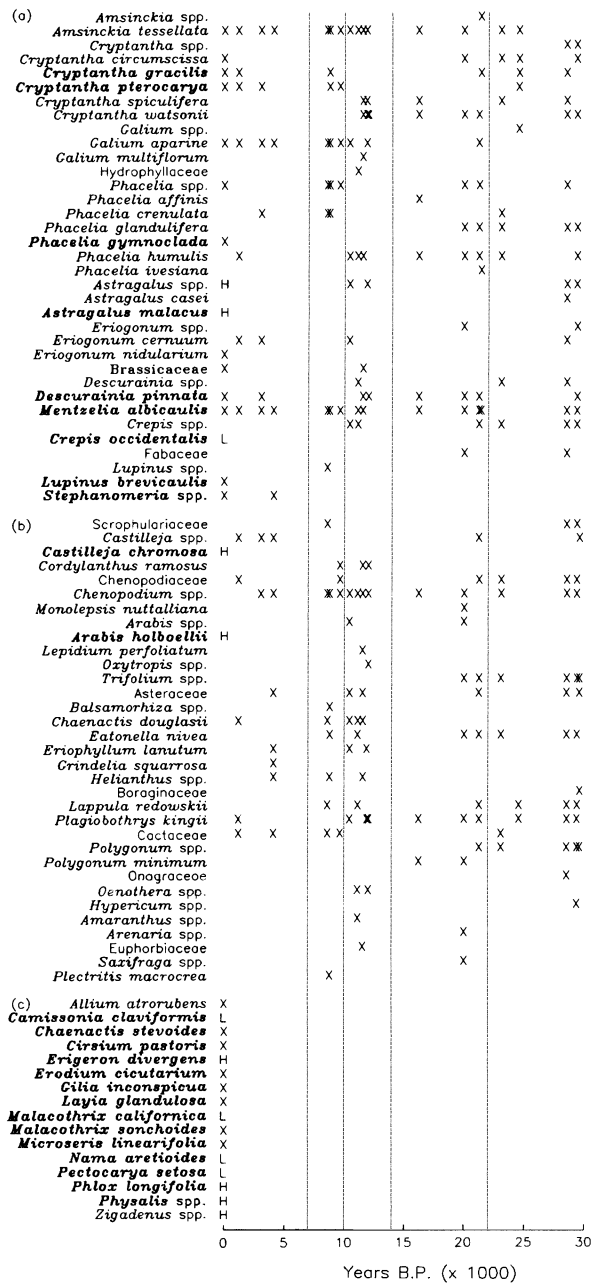


Fig. 5. Presence of herb taxa in midden strata or in modern flora, designated by an 'X'. An 'H' designates a taxon found only at the higher elevation (1530 m) midden locale. An 'L' designates a taxon found only at the lower elevation (1380 m) midden locale. Bolded letters of a taxon name indicate appearance in modern survey after extremely wet winter that followed over 6 yr of drought conditions. (a) Taxa that have fossil and modern representatives amongst their genera groups. (b) Taxa either that appear only in the fossil record or that appear in the modern flora exclusively at the higher elevation locale and match genera groups from the fossil record. (c) Taxa with only modern occurrences. Vertical dotted lines designate the approximate boundary between climatic periods for the Great Basin as used by Thompson (1990).

representatives mainly in the fossil record. Taxa from the families *Scrophulariaceae*, *Chenopodiaceae*, *Brassicaceae*, *Fabaceae*, *Asteraceae*, and *Boraginaceae* occur in almost all the climatic periods and several midden strata. Some taxa such as the members of the genus *Polygonum* and the family *Cactaceae* have a few occurrences in two or three climatic periods, with *Cactaceae* being widely distributed in time. Taxa such as *Oenothera* spp., *Hypericum* spp., and *Amaranthus* spp. have only one or two occurrences in the fossil record (Fig. 5).

Group (c) of the herbs (Fig. 5) consists of taxa that are in the modern flora but are not represented in the fossil record. Quite a few of these taxa were found in our modern survey only after an extremely wet winter that followed over 6 yr of drought conditions. Thus, species richness of herbaceous taxa is sensitive to relatively short-term climatic variations. The herbaceous plants often have short life spans, and their abundance is sensitive to short-term droughts. Therefore, local abundance of herbs is much more variable than trees and shrubs by nature.

Vegetation assemblages through time

Cluster analysis grouped the vegetation assemblages from individual midden strata into six groups (Fig. 6A). Two periods of major changes in vegetation assemblages were evident: during the Pleistocene and during the transition between the Pleistocene to the Holocene. During the Pleistocene time interval of 20 000 - 30 000 yr BP, changes in vegetation assemblages oscillated between two cluster groups. During the Pleistocene-Holocene transition of 10 000 - 12 000 yr BP, changes in vegetation assemblages were rapid and largely directional. In about 2000 yr, vegetation changed from one of the two Pleistocene cluster groups through 2 transition cluster groups to a fifth cluster group. This last cluster group characterized most of the Holocene, except for the modern vegetation, which is its own cluster group.

Patterns of species turnover during the 30 000 yr of record were similar to the cluster analyses (Fig. 6B). This plot of β -diversity provides an index of species turnover; the higher the line between two samples, the higher the level of species turnover between them. Periods of high species turnover occurred between 20 000 and 30 000 yr BP and during the Pleistocene-Holocene transition. The glacial maximum of the Wisconsinan as well as the Holocene are time intervals with low levels of species turnover. An extensive search of the modern vegetation for species presence resulted in a high species richness compared to the youngest midden contents (Fig. 6B).

The first three axes of the NMDS ordination separated vegetation assemblages into the Holocene, the

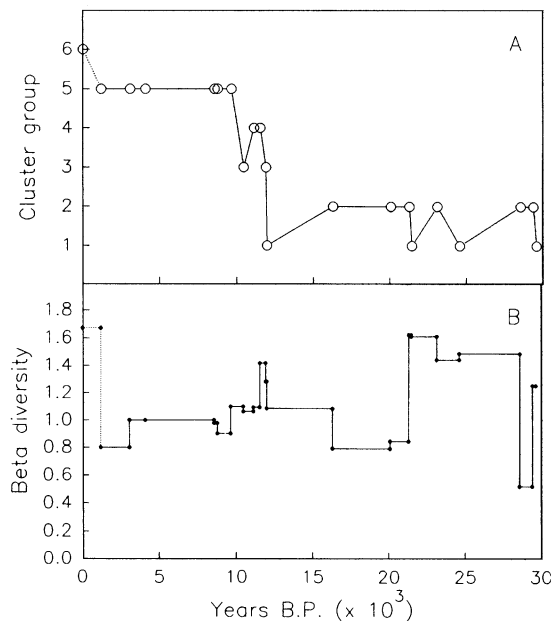


Fig. 6. A. Cluster analysis of species assemblages for individual midden strata based upon a similarity index. B. β -diversity between contiguous pairs of vegetation assemblages for individual midden strata. For both A and B, dashed lines are used to connect modern vegetation surveys with the youngest midden strata because the two vegetation samples are not equivalent.

Pleistocene, and the Pleistocene-Holocene transition. Axis 1 from the analysis was significantly and positively correlated with the number of grass species, herb species, and total species as well as with the age of the sample (Table 2). The number of shrub species were significantly and positively correlated with Axis 2. Axis 3 was significantly but negatively correlated with the number of shrub species. Finally, the number of shrub species was negatively correlated with the age of the sample. Thus, a general trend from a higher proportion of herbaceous to a higher proportion of shrubby species has occurred with the warming and drying of the climate from the Pleistocene to the Holocene.

Discussion

Our study site is notable in that it has yielded high-frequency plant macrofossil data across a broad temporal gradient that spans major climatic variations. Because of the proximity of our midden locale to pluvial Lake Lahontan (the midden at 1380 m was within 0.5 km of the lake's highstand), the documented climatic variations that are provided by the history of lake levels (Fig. 7; Thompson et al. 1986; Benson & Thompson

Table 2. Correlation coefficients between ordination values for Axis 1 through Axis 3 and the number of tree, shrub, grass, herb, and all species in each sample as well as age of sample.

	Ordination values for:			Age of sample
	Axis 1	Axis 2	Axis 3	
Total species	0.46 *	0.40 #	-0.31	0.09
Tree species	-0.13	-0.02	-0.39 #	-0.04
Shrub species	-0.31	0.63 **	-0.53 *	-0.45 *
Grass species	0.66 **	0.37	-0.01	0.28
Herb species	0.59 **	0.11	-0.09	0.26
Age of sample	0.57 **	-0.29	0.13	1.00

$p \leq 0.10$; * $p \leq 0.05$; ** $p \leq 0.01$.

1987; Benson et al. 1990; Benson 1991; Morrison 1991) is directly applicable to our study of vegetation responses to climatic variations. In addition, pluvial Lake Lahontan has an exceptional stratigraphic-climatic record because its sedimentary sequences are deeply exposed and relatively complete (Morrison 1991). Further evidence for substantial climatic variation over the last 30 000 yr is provided by paleohydrological modeling for the region (Anon. 1988; Hostetler et al. 1994), vertebrate paleontology research (Grayson 1993), tephrochronologic studies (Davis 1978), and other proxy data (Thompson 1990; Morrison 1991; Grayson 1993). An important aspect from our fossil midden record is the large number of modern plant taxa that frequently occurred throughout the fossil record even though large changes in local and regional climate occurred. For example, the (a) groups, i.e. taxa that occurred in both modern and fossil records, have a large number of taxa. The (b) groups also have a large number of taxa, and although most of these taxa were not within 100 m of the middens, many of these taxa are present locally. In contrast, the (c) groups have a relatively low species richness. This pattern is observed in all four of the life forms: trees, shrubs and subshrubs, graminoids, and herbs. Additionally, our results from a spatial scale that involves many midden sites across the northern Great Basin (Nowak et al. 1994) showed a similar pattern of continuous occurrence of tree and shrub species.

Although many taxa occurred almost continuously for long periods of time at our midden site, vegetation assemblages changed through time. A general trend from a higher proportion of herbaceous to a higher proportion of shrubby species over the 30 000 yr record was observed at the study site. The plant dynamics at our study site generally parallel the documented climatic variations. To facilitate the discussion of how the plants near our study area responded to climate variations, we have summarized the relative climatic requirements of the major tree and shrub/subshrub taxa. *Pinus*

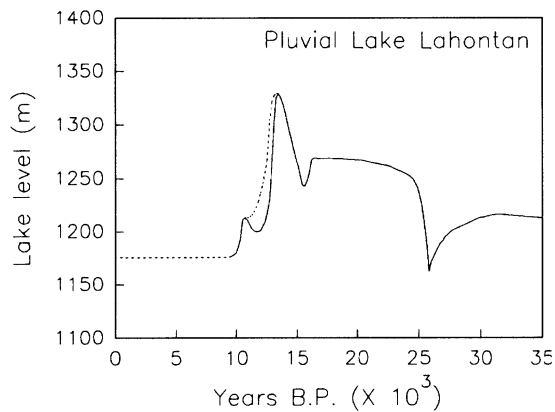


Fig. 7. Reconstructed lake levels for pluvial Lake Lahontan during the past 35 000 yr. Dashed line between 10 000 and 15 000 yr BP represent an alternative chronology. Redrawn from Benson et al. (1990).

albicaulis is the most mesic of the three fossil tree species, *Cercocarpus ledifolius* is intermediate, and *Juniperus osteosperma* is the most xeric of the trees that occurred during the entire record at our study site. Among the shrub and subshrub species, *Forsellesia nevadensis*, *Ribes cereum*, *R. velutinum*, *Rosa woodsii*, *Salvia dorrii*, and *Symphoricarpos oreophilus* form a group of relatively mesic shrubs. *Artemisia* spp., *Atriplex canescens*, *A. confertifolia*, *Chrysothamnus* spp., *Ephedra* spp., *Haplopappus* spp., *Prunus andersonii*, and *Purshia tridentata* are a group of taxa with wide ecological distribution. The taxa *Brickellia microphylla*, *Ceratoides lanata*, *Kochia americana*, *Tetradymia canescens*, *T. glabrata*, and *Grayia spinosa* are associated with a relatively more xeric habitat.

The mixture of mesic and xeric plants at the Painted Hills study site during the two oldest climatic periods, the Pre-Full-Glacial and Full-Glacial, is accounted for by the presence of cooler and moister conditions than today as well as by the presence of variable microhabitat conditions. The occurrence of mesic species such as *Pinus albicaulis*, *Deschampsia* spp., and *Eleocharis quinqueflora* are consistent with the more mesic regional climate suggested by pluvial lake levels (Fig. 7). The more xeric species, such as *Brickellia* taxa, *Tetradymia glabrata*, and *Stipa* taxa, probably occupied xeric microhabitats. The late-Pleistocene vegetation was also generally characterized by herbaceous species. The sparse record of shrub and graminoid species is noticeable for these two time intervals, and overall, species richness is lower during the latter part of the Full-Glacial period than during the climatic period before or after. Temperature and seasonal water availability are important influences on the vegetation composition in the Great Basin shrub steppe (Smith & Nowak 1990).

Harsh climatic conditions of the full-glacial (such as low annual temperature, seasonal timing of precipitation, and frequent cloud cover) that are associated with proximity of ice masses were probably very important limitations on plant growth.

The vegetation assemblages during the Late-Glacial and Early-Holocene periods had the greatest richness of trees and shrubs. Mesic, xeric, and widespread species occur in midden strata from these time periods. Some of the mesic species, such as *Pinus albicaulis*, *Cercocarpus ledifolius*, *Forsellesia nevadensis* and *Salvia dorrii*, occur today only at higher elevations within the same mountain range or in nearby ranges to the west. Recent studies suggest the timing of the last high stand of pluvial Lake Lahontan occurred between 14 500 and 15 000 yr BP and was followed by a rapid drop in lake level (Fig. 7; Benson 1991). The large and rapid change in climate that caused these changes in lake level are also contemporaneous with a large turnover of species (Fig. 6) as well as a transition from the Pleistocene cluster groups through two transitional cluster groups to a Holocene cluster group.

Mid-to-Late Holocene floras are most similar to the modern flora, suggesting a trend towards the modern floral components that occurred during this time. None of the most mesic tree and graminoid taxa are found in these more recent midden strata, and only two of the more mesic shrub taxa are present. Many of the ecologically widespread and more xeric taxa that are currently present near the midden site also occur within the last 7000 yr. The results from cluster and β diversity analyses suggest that vegetation assemblages during the Holocene have been relatively stable. Although these same analyses suggest that a change in vegetation occurred between 1000 yr BP and modern, this change may be an artifact of the data. The vegetation sample that is derived from the modern species list is not equivalent to that derived from the midden samples for at least two reasons: (1) modern plants were identifiable to species level, whereas some macrofossils could only be identified to the genus or family level; and (2) vegetation sampling by humans is more complete than that by woodrats.

Vegetation composition during the last 30 000 yr in the northwestern Great Basin experienced a relatively smaller magnitude of change than those for other areas of North America and of Europe. For example, available data from the eastern and southern portion of the Great Basin differ from our results: the full-glacial floras in those areas were impoverished and many of the modern species were absent (Thompson 1990). The relatively large degree of vegetation continuity in the northwestern Great Basin during the last 30 000 yr also contrasts with the large-scale migrations and range expansions of

plants in eastern North America (Davis 1976, 1983) and the continuous patterns of vegetation changes that occurred in Europe (Huntley 1990a,b). These differences in vegetation responses to climate changes may be partially due to differences in land form characteristics. The northwestern Great Basin has a steep precipitation gradient because of the rainshadow effect from the north-south trending Sierra Nevada, and this rainshadow has been present for about the last 20 million years (Fiero 1986). Furthermore, the diversity of landforms that make up the basin and range pattern of the Great Basin produces a variety of localized microhabitats, which in turn may have allowed species with mesic and xeric habitat requirements to coexist at our study site. Eastern North America received more stabilized atmospheric circulation patterns during the late-Pleistocene and Holocene due to a low diversity of landforms (Huntley 1990b), which allowed species to migrate considerable distances in an individualistic manner in response to large magnitude changes in Quaternary climates (Davis 1976, 1983). The European vegetation history had greater magnitudes of vegetation change than the northwestern Great Basin because the predominately east-west trending mountains of Europe do not block or stabilize the atmospheric circulation patterns along the North Atlantic. Changes in circulation patterns resulted in a European vegetation history within the Quaternary that is characterized by unstable and continuously changing vegetation assemblages (Huntley 1990b).

The differences in vegetation responses may also be related to differences in genetic diversity. Because species that have stayed in place for great periods of time may survive climatic variation by possessing large genetic plasticity (Bradshaw & McNeilly 1991), we hypothesize that the low magnitude of change in species composition in the northwestern Great Basin is partially due to high genetic diversity within species. Plants of the sagebrush steppe of the northern Great Basin appear to possess a high degree of genetic variability within a species, which allows these species to tolerate a high degree of climatic variation. Evidence for a high degree of genetic diversity within a variety of modern Great Basin shrub species comes from modern plant ecology studies conducted by the USFS Shrub Laboratory and by other scientists. For example, studies on *Artemisia* spp. (Shultz 1986; McArthur et al. 1988; Welch & McArthur 1990), *Chrysothamnus* spp. (Anderson 1986a,b), and *Atriplex* spp. (Stutz 1978, 1984; Sanderson et al. 1990) suggest that these and other Great Basin plants may belong to coenospecies, which are groups of populations that form a common gene pool (Ogden 1989). In contrast, we speculate that the higher magnitude of changes in vegetation composition for eastern North

America and Europe may be associated with a much lower degree of genetic diversity within species. Genetic fingerprinting across the modern distributional range of species coupled with that of retrieved macrofossils from temporal middens such as our midden is needed to substantiate this hypothesis.

An alternative mechanism to explain the difference between our results and those in other geographic areas is that the magnitude of *temporal* change in paleoclimate at our study site is similar to the magnitude of *spatial* variation in modern climate at the site. In other words, if temporal climatic variations are similar to spatial variations, then vegetation of the area would not be expected to change. However, as discussed above, all the paleoclimate evidence indicate that major changes in climate have occurred both locally and regionally. In contrast, the spatial variation in modern environment within 100 m of the midden is very small. Thus, this alternative hypothesis cannot account for the relatively small magnitude of vegetation change that we document for our site in the northwestern Great Basin.

Our results may have many applications involving landscape management as well as plant responses to future climatic changes. An understanding of why species remained in place during past climatic variations will improve our ability to evaluate the scale of vegetation changes likely to occur with future ecological or environmental changes. However, particular abiotic and biotic factors may confound these predictions. One major confounding factor that may affect future plant growth is the differential sensitivity of plants to rising CO₂ concentrations (e.g. Polley et al. 1993; Sage & Sharkey 1987). Another major confounding factor is the large number of introduced exotic species and their interactions with native plant species in regions such as western North America. The interactions between exotic and native species impact the dynamics of the plant communities and confound the ability of models to predict vegetation change with future climate change. More plant ecology studies such as those by Melgoza et al. (1990) that investigate these interactions are needed to assess vegetational trends and predictions. Nonetheless, the Quaternary ecological record such as that from Painted Hills helps identify the sensitivity of individual species to past climatic changes, which in turn gives insights into future vegetation changes as well as provides key information for land managers of our ecosystems.

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