Late Pleistocene and Holocene.

Most late Quaternary vegetation evidence in California comes after the last glacial maximum (25 ka). Climatic and vegetation changes are unavoidably discussed together at this point because the Quaternary has been defined by climatic events. Emphasis here is given to California studies as summarized from pollen and packrat midden studies by Woolfenden (1996), Spaulding (1990), and Van Devender (1990).

Late Pleistocene. GCMs for the late glacial maximum (LGM) (21-16 ka, Bartlein et al. 1998) show the equatorward displacement of the jet stream and moist surface westerlies to lat. 35°N along the Pacific Coast by the Laurentide ice sheet. Sea surface temperature variations in the western and eastern Pacific, using magnesium/calcium ratios in foraminifera suggest that a persistent El Niño-like pattern existed in the tropical Pacific during full glacial climates (super ENSO) (Stott et al 2002; Koutavas et al. 2002). A super ENSO may have contributed to the southward displacement of the jet stream and precipitation along the Pacific coast. High surface albedos of the Laurentide ice sheet maintained a strong jet stream in summer over the western US.

Evidences for cooler wetter climates in California include glaciation along the crest of Sierra Nevada and pluvial lakes in the Great Basin. Oxygen isotope and total inorganic carbon values of cored sediments from Owens Lake indicate there may be as many as 19 glacial advances in the Sierra Nevada from 52.5 to 12.5 ka (Benson et al 1996). Glacier equilibrium line altitudes (ELAs) at the LGM are estimated to be ca. 800 m below the ELAs of modern cirque glaciers in the Sierra Nevada (Broecker and Denton 1990; Burbank 1991; Dawson 1992, p. 68). The lowest glacial cirques on windward mesic mountain escarpments range from 2000 m in the Siskiyou-Cascades to 2400 m in the northern Sierra, 2700 m at Yosemite, and 3000 m at Sequoia and San Bernardino Mountains of southern California. Cosmogenic dating of terminal moraines indicate that mountain glaciers in the San Bernardino Mountains reached maximum extent at ca. 20.0 and 16.0 ka with recessional moraines correlating with the Dryas at 12.0 ka (Owen et al, 2003), in phase with glacial advances in Yellowstone National Park (Locciardi et al 2001) and the Sierra Nevada (Benson et al 1998). Carbonate-free clay-size fraction of Owens Lake sediments indicate that the crest of the Sierra Nevada was continuously glaciated since at least 52.0 ka with the greatest extent of valley glaciers occurring during the Tioga advance from 24.5 to 13.6 ka (Benson et al. 1998). Pluvial lakes in the Great Basin were supported by reduced evaporation rates due to cool summers associated with a strong summer jet stream (Spaulding 1990; Bartlein et al 1998). Lake stand data indicate that the pluvial lakes increased after 32.0 ka and reached highstands between 15.0 and 13.5 ka (Benson et al 1990). Lakes had dried or decreased to modern levels by 10 ka (Street and Grove 1979). The California deserts were still semiarid to arid in the LGM due to rain shadows from the California ranges. Drill cores at five sites along the floor of Death Valley show only periodic lacustrine deposits indicating that Lake Manley, fed
largely by the Armagosa River, was a small shallow lake over most of Pleistocene (Anderson 1998).

Pollen and Packrat midden studies in the Sierra Nevada reveal profound vegetation shifts during the LGM (summary in Woolfenden 1996; Anderson 1990, 1996). Late glacial pollen sites at 1500-2200 m in the Sierra Nevada (Nichols Meadow, Nelder giant sequoia grove, Balsam Meadow, Exchequer Meadow) record mostly Artemisia and Poaceae, which is interpreted to reflect a sagebrush steppe vegetation. Whether modern alpine herbs contributed to this assemblage or whether the landscape was barren with exotic Artemisia/Poaceae pollen passing through is unknown. Other genera recorded include limited amounts of Pinus and Cupressaceae. These sites, which lie only 500 m below full-glacial ELAs of the Sierra Nevada ice sheet, were apparently near or above the treeline. Packrat (Neotoma) middens dating from 40.0 to 12.7 ka in Kings Canyon (alt. 920-1270 m; Cole 1983) record a mesic mixed conifer forest consisting of Pinus cf. ponderosa, P. lambertiana, Abies grandis, Calocedrus decurrens, Juniperus occidentalis and Pinus monophylla, with understory of Ceanothus integerrimus, Garrya flavescens, and a single record of Torreya californica. Pollen of Sequoiadendron giganteum suggest a stand close to the site. Beginning at ca. 13.7 ka, pollen sites record increasing conifer pollen and macrofossils (Abies concolor, Pinus lambertiana, Pinus ponderosa, Calocedrus decurrens, Sequoiadendron) suggest that mixed conifer and subalpine forest ascended the west slope at least to the altitudes of these pollen sites. The transition from steppe to forest took place in 10.0 ka in the Stanislaus River drainage of the northern Sierra Nevada.

Late glacial maximum macrofossil assemblages along coastal California (40.0-14.0 ka) at Tomales Bay, Carpinteria, Santa Cruz Island, and Rancho La Brea Tarpits (summarized in Johnson 1977) record floras that are comparable to the vegetation seen today, with the southward extension of some mesic species. These sites record chaparral species in Adenostoma, Arctostaphylos, Ceanothus, Garrya, Heteromeles, Quercus, and Rhamnus and closed-cone conifer forests of Pinus radiata and P. muricata. Closed-cone conifer forests were also recorded at Point Sal Ridge, and San Miguel Island. The Tomales Bay flora records riparian forests (Acer macrophyllum, Alnus rubra), mixed evergreen forest (Arbutus menziessii, Pseudotsuga menziesii, Umbellularia californica, Quercus agrifolia, Torrya californica) as well as Picea sitchensis, now found as far south as Cape Mendocino. Chaparral at Carpenteria (Arctostaphylos, Ceanothus) contained trees now common in the area including Quercus agrifolia, Umbellularia californica, and Pseudotsuga macrocarpa. The Carpenteria flora also contains mesic and xeric trees now exotic to this region including P. muricata, P. radiata, Cupressus forbesii, C. goveniana, C. macrocarpa, Juniperus californica, Pinus sabiniana and Sequoia sempervirens. Nearby Santa Cruz Island has late glacial records in Arctostaphylos, Ceanothus, and Garrya and Pinus remorata (=P. muricata), as well as the exotic Pseudotsuga menziesii and Cupressus goveniana. The Rancho La Brea site in Los Angeles has a rich assemblage of chaparral species now common in the area (e.g., Adenostoma fasciculatum, Arctostaphylos glauca) or found on the channel islands and central California coast (Arctostaphylos viscata, A. morroensis). Modern tree elements include Alnus rhombifolia, Juglans californica, Platanus racemosa, Quercus agrifolia, Q. lobata, as well as exotic species Pinus muricata, P. radiata, P. sabiniana, Cupressus forbesii, C. goveniana, C. macrocarpa, Juniperus californica, and the mixed evergreen forest component Sequoia sempervirens. The McKittrick flora in the southern San Joaquin valley contains pinyon-juniper woodland of Pinus monophylla and Juniperus californica with Arctostaphylos glauca.
and *A. pungens*. Pinyon-juniper now occurs 50 km from this site at the south end of Cuyama Valley.

Packrat middens in the Mojave and Sonoran Deserts (Spaulding 1990; Van Devender 1990; McAuliffe and Van Devender 1998) record a rich late Pleistocene-Holocene fossil flora. Because fossil middens are selectively preserved in rock shelters, midden vegetation records tend to be biased to mountainous slopes rather than alluvial bajadas and plains. In the late Pleistocene (25 ka to 12 ka), Mojave Desert middens show that pinyon-juniper woodlands formed extensive cover from 1000-1800 m, with juniper woodlands occurring < 1000 m elevation. Only the lowest basins such as Death Valley were free of tree cover (Wells and Woodcock 1985; Woodcock 1986). Associated species in pinyon-juniper woodlands include arboreal leaf succulents *Yucca schidigera, Y. brevifolia, Y. baccata,* and *Y. whipplei* and subshrub understory consisting of species in *Artemisia, Chrysanthemum, Lycium, Ephedra,* and *Atriplex*. The highest peaks such as the Clark Mountains had subalpine forests of *Pinus longaeva* and *P. flexilis*. In the Owens Valley, middens at Owens Lake and the Alabama Hills record Utah Juniper-pinyon woodland with *Yucca brevifolia* and understory of Great Basin sagebrush and Mojave Desert scrub including *Artemisia tridentata, Purshia tridentata, Atriplex confertifolia, Ericameria cuneata, Ephedra viridis,* and *Glossopetalon spinescens* (Koehler and Anderson 1994, 1995). A pollen record from Owens Lake (Mensing 2001) reveals that juniper woodland dominated Owens Valley from 16.2-15.5 BP. Woodlands were replaced by shrubland, mostly sagebrush from 15.5 to 13.1 (cal) BP. Chenopodiaceae soon replaced *Artemisia*. Pinyon-juniper woodland (*Pinus monophylla, Juniperus californica*) with desert chaparral (*Quercus turbinella, Ceanothus greggii*) and Mojave Desert scrub was recorded in the Scobie Mountains on the eastern escarpment of the Sierra Nevada (McCarten and Van Devender 1988). Middens in the White Mountains and nearby Volcanic Tablelands at ca 1300 m record Utah juniper with understory of desert scrub of *Purshia tridentata, Tetradymia axillaris, T. canascens,* and *Ericameria cuneata* (Jennings and Elliott-Fisk 1993).

In the Sonoran Desert (Van Devender 1990), middens record pinyon-juniper woodlands with scrub live oak (*Quercus turbinella, Q. dunnii*) to as low as 500 m elevation. There were few modern Sonoran Desert plants at this time. The lowest basins from 600-300 m had juniper woodland-shrub live oak assemblages with *Juniperus californica, Yucca brevifolia, Y. whipplei* and *Nolina bigelovii*. Most of these species grew 400 to 1200 m below present elevations. Members of Creosote bush scrub, including the modern dominants *Larrea tridentata, Ambrosia dumosa* and *Encelia farinosa* were present in full-glacial climate in the Tinajas Atlas of the upper Gulf of California at 18 ka. Middens show that wildflowers in the same genera were present in the Mojave Desert since at least the late Pleistocene (Table 2-3). It appears that there has been little change in the distribution and composition of desert annuals, even though there were large changes in woody cover. Because annual forb species persist on seed banks, selection may have been lacking for long range seed dispersal, even with climate change as large as that in the Pleistocene-Holocene transition. Conifer woodlands and chaparral extended as far south as central Baja California. *Juniperus californica* and chaparral species were recorded in the Sierra San Francisco at 10.2 ka (Rhode 2002). *J. californica* and *Pinus quadrifolia* and chaparral (*Adenostoma fasciculatum, Quercus turbinella*) were recorded in a full glacial midden (17.5 ka) in the northern Vizcaino Desert. *J. californica, Pinus quadrifolia* and chaparral dominated by *Adenostoma fasciculatum* and *Quercus turbinella* persisted on the site until at least 10.0 ka (Wells 2000).
Early and Middle Holocene. The Pleistocene-Holocene transition at ca. 10 ka was a period of profound global climate change with deglaciation. The Laurentide ice sheet collapse by ca. 8000 bp (Dawson 1992), and Milankovitch solar maximum appears to have contributed to warmer and drier climates than at present. GCM simulations by Bartlein et al (1998) suggest that the modern global circulation was fully established in the western US. However, the combination of remnant ice sheets over northeastern Canada (Dyke and Prest 1987; Broecker et al. 1989), colder continental winters (the Earth's orbit was at perihelion), and higher Pacific Ocean SSTs may have encouraged the poleward displacement of moist surface westerlies to British Columbia (Bartlein et al. 1998). Direct thermal evidence for warmer temperature comes from bristlecone pines (*Pinus longaeva*) that were analyzed for stable hydrogen isotopic composition (Feng and Epstein 1994). Based on ring chronologies matching living trees with dead trees in a continuous time-series from 8000 to present, they found that temperatures reached maximum levels at 6800 BP. Submerged pine stumps dated 6.3 to 4.8 ka (cal) reveal that Lake Tahoe was below sill heights (Lindstrom 1990). Nearby Walker Lake, which drains the eastern Sierra Nevada south of Lake Tahoe, was shallow and desiccated from 5300-4800 (Benson et al. 1991). Clark and Gillespie (1997) provide evidence that glaciers in the Sierra Nevada may have been entirely absent during much of the Holocene. Konrad and Clark (1998) obtained three cores from a meadow directly below the Powell Rock Glacier and found only non-glacial grus deposition from the early Holocene. Evidence of early Holocene aridity is also seen in the West Berkeley shell mounds (Ingram 1998). Radiocarbon ages of marine shells and charcoal suggest changes in the 14C content of San Francisco Bay surface waters relative to the atmosphere (the oceanic reservoir age) was high at the beginning of the record at 4970 bp. This period is coincident with relatively high salinity in San Francisco Bay (low freshwater inflow) and dry climate in California. Changes in the radiocarbon reservoir age may be due to changes in the strength of seasonal wind-driven upwelling off coastal California, where upwelling brings 14C-depleted waters to the surface. Ingram (1998) proposes that the region was influenced by an abnormally strong Pacific anticyclone, northward displacement of the jet stream, and low rainfall. Enhanced upwelling is physically consistent with the poleward displacement of moist westerlies along the Pacific coast (Bartlein et al. 1998).

Pollen evidence in the Oregon Cascade Range shows open conifer forests of *Pseudotsuga* and *Quercus* with a *Pteridium* understory in areas now covered with mesic taxa in *Thuja*, *Tsuga*, and *Picea* (Thompson et al. 1993; Sea and Whitlock 1995; Long et al 1998). At Diamond Pond in the Great Basin, shadescale expanded at the expense of sagebrush during 7000-4000 bp (Wigand 1987; Thompson 1990). In the central Sierra Nevada, pollen and macrofossils at localities such as Giant Forest and Starkweather Pond suggest that forests had ascended to current limits by 10.5-9.0 ka. Some conifers were still colonizing new habitat as late as 6.3 ka (Anderson 1990). Pollen records also show a decrease in *Pinus* and *Abies*, and an increase in Cupressaceae and *Quercus* (Woolfenden 1996). Increasing charcoal suggests increasing fuel build-up and densification of stands (Woolfenden 1996). However, Anderson (1990) indicates that forests were more open and contained abundant shrubs, such as *Chrysolepis sempervirens*, compared to forests at present. *Pinus contorta* experienced successive disappearance from lower elevation sites (Anderson 1996). At Nichols meadow, pollen evidence documents the development of a lower montane forest and giant sequoia (*Sequoiadendron giganteum*) community around a small meadow between 12.5-8.8 ka (Koehler 1994). Poor pollen preservation at 8.8 to 6.0 bp was attributed to early Holocene
aridity. Barrett Lake at 2900 m was colonized by forest by 10.0 ka, with shrub pollen increasing from 10.0 to 6.0 ka (Anderson 1990). Scuderi (1987a) found that the Sierra Nevada tree line at Cirque Peak was 70 m higher than at present, with the maximum levels occurring between 7150 to 3800 cal. BP. The tree line was 125 m higher in the White Mountains (La Marche 1973). These displacements reflect a global trend, as higher tree lines were reported in Scandinavia, Carpathian Mountains, European Alps and the Rocky Mountains (Bradley 1999).

Packrat middens show that pinyon-juniper woodlands in the Mojave Desert in full-glacial climates were quickly replaced by modern desert scrub assemblages in the early Holocene (Van Devender 1990; Spaulding 1990). In the Sonoran Desert, Pinus monophylla dropped out at ca. 11.0 ka, leaving xeric juniper scrub--live oak woodlands or chaparral, with Juniperus californica and Lycium spp. continuing to ca. 9.0 ka. Pinyon-juniper retreated upslope to higher ranges exceeding 1200 m. Creosote bush scrub (CBS) was recorded as far north as Picacho Peak near Yuma Arizona by 12.7 ka. and the Whipple Mountains near the Colorado River at 10 ka. By 10 ka much of the Mojave Desert was covered with desert scrub but the flora still lacked Larrea tridentata and other members of CBS. However, Cole (1986) indicates that CBS in the lower Colorado River Valley had a modern aspect beginning at 12 ka. In the Mojave Desert middens record L. tridentata, Encelia farinosa, and Ambrosia dumosa at the Marble Mountains by 7.9 ka (Spaulding 1990). At Lucerne Valley a high desert flora recorded between 11.0 and 7.8 ka contained A. dumosa. Modern CBS was recorded in middens dating to 5.9-3.6 ka (King 1976). L. tridentata reached the Skeleton Hills northwest of Las Vegas by 8.2 ka and Ambrosia dumosa was recorded at Death Valley by 10 ka. In the northwestern Mojave Desert, fossil charcoal fragments from a seismic trench extending to 7.0 ka were identified as members of Zygophyllaceae, Asteraceae, Ephedraceae, and Rosaceae, consistent with the modern species composition on the site (Minnich et al, in review). Owens Lake pollen records indicate a decrease in Juniperus pollen. Packrat middens in the Alabama Hills record the arrival of Chrysothamnus teretifolius, Grayia spinosa, Lycium andersonii and Krascheninnikovia lanata (Koehler and Anderson 1995). Middens dated to 8.7 and 7.8 ka in the White Mountains at 1830 m record pinyon-juniper-sagebrush woodland with a similar species composition to that at present (Jennings and Elliott-Fisk 1993). This record appears to capture the northward expansion of Pinus monophylla because a 9.8 ka midden in the nearby Volcanic Tablelands did not record the species. The full glacial northern limit was at the southern Inyo Mountains (Koehler and Anderson 1994). Consistent with higher tree lines in the White Mountains and Sierra Nevada, a midden at 5.6 ka at 3038 m in Silver Canyon of the White Mountains records P. monophylla and Juniperus osteosperma at higher elevations than at present, in areas now covered with subalpine forest of Pinus longaeva and P. flexilis. Packrat middens in northwestern Nevada reveal only small changes in pinyon-juniper and shrubland elements, even after the Pleistocene-Holocene transition (Nowak et al 1994).

The early Holocene may have been wetter than present in far southeastern California. Wells and McFadden (1987) found several deep lakes in the Lake Mojave basin between 9.5 and 8 ka, and attributed it to enhanced summer monsoon of the Milankovich solar maximum. This is supported by late Holocene lake stands that persisted until 7450 years BP at Laguna Chapala in central Baja California (Davis 2003). An intensified summer monsoon, rather than winter rains, is the most likely explanation because the jet stream had already retreated to modern latitudes by this time, far north of Laguna Chapala. Tropical cyclones reaching the
southwestern United States may have produced heavy rains more frequently compared to the present. The persistence of *Juniperus californica* and chaparral species in the California and Baja California deserts into the early Holocene (Wells and McFadden 1987; Wells 2000; Rhode 2002) may reflect phenological plasticity from winter to summer rains (Barbour and Minnich 1985), until the decline of summer rains resulted in extirpations by ca. 7000 BP.

Mid-Holocene. The mid-Holocene in California (5.0-3.5 ka) is a period of greater rainfall, enlargement of Sierra Nevada alpine glaciers and small interior lakes. The most important trend in GCM simulations is the increasing presence of moist westerlies on the Pacific Coast (Bartlein et al. 1998). West Berkeley shell mounds (Ingram 1998) show that the 14C content of San Francisco Bay surface waters has low radiocarbon reservoir age from 4970 to 2000 bp and especially from 3800 to 2800 cal yr bp. This trend was attributed to a reduced strength of seasonal wind-driven upwelling off coastal California. This period is also coincident with relatively low salinity in San Francisco Bay (indicating high freshwater inflow) and wet climate in California. Benson et al (1991) found that Walker Lake was relatively high between 5100-3170 cal bp. High stands occurred between 4000 and 3600 bp (uncalibrated) at Mono Lake, Silver Lake, and Searles Lake (Stine 1990; Enzel et al. 1992). Peat deposits developed in this period at Ash Meadows in the Armagosa Desert. Analysis of marine and nonmarine groups in a pollen core at Newport Bay, southern California, show periodic intrusions of fresh habitat from 4190 to 2500 cal BP (Davis 1992).

In the Sierra Nevada, glaciers established in areas where they were apparently absent in the early Holocene. The Recess Peak advance in alpine cirque glaciers in the central Sierra Nevada is based on morainal deposits aged at ca. 3000 bp on the basis of lichemistry (Burke and Birkeland 1983). A lake core from below Conness glacier reveals alternating gyttja and silt after about 3900 cal yr bp (Konrad and Clark 1998). The transition from higher-organic sediments to lower organic sediments, at ca. 3400 cal yr bp indicate formation and growth of the glacier in the cirque at that time. Cosmogenic records of moraines left by small headwall glaciers on Mt. San Gorgonio give Holocene dates, but the resolution of the method does not permit correlation with the mid-Holocene advance in the Sierra Nevada (Owen et al. 2003).

Several localities reveal a shift toward mesic vegetation. In the Cascade Mountains there was a decrease in *Quercus* and *Pseudotsuga*, and an increase in *Thuja, Tsuga heterophylla, Picea*, and *Alnus rubra* (6850-2750 bp; Long et al 1998; Thompson et al 1993). At Diamond Pond in the Great Basin, sagebrush gradually replaced shadeseed between 5400 and 4000 bp, with juniper and grasses reaching greatest abundance at 4000-2000 bp. Pollen profiles show short-term maxima in juniper abundance at 3500 and 2500 bp and a grass/sage maximum at 3600 and 3100 bp (Wigand 1987; Miller and Wigand 1994). There were few changes in the floristic composition of Great Basin woodlands during the late Holocene, although pollen evidence suggest that sagebrush expanded and shadeseed steppe contracted (Thompson 1988; 1990). Fossil middens show little vegetation change in the Mojave Desert, although middens in the Sheep Range of Nevada record a shift from pinyon dominance at 3520 bp to juniper dominance at 1990 bp (Spaulding 1985, 1990). Middens in northwestern Nevada show that *Pinus monophylla* entered this region only by 3000 bp (Nowak et al., 1994). This trend is attributed to a post-glacial migrational lag rather than climate change due to frost and soil heaving, as evidenced by the absence of *P. monophylla* from cold basin floors. *P. monophylla* recruitment appears to be dependent on nurse plants until canopy closure (Wangler and Minnich 1996; Chambers 2001). Hence, *P. monophylla* migration may have been limited to
contagious diffusion of mature stands rather than more efficient long-distance disjunct expansions (see Clark 1998). Fossil charcoal from the El Paso Peaks seismic trench in the northwestern Mojave Desert show a period of high fire activity in creosote bush scrub from 5000-4000 bp.

Pollen abundances on the midslopes of the Sierra Nevada show an increase in Abies and Cupressaceae (Calocedrus decurrens) relative to Pinus and a decrease in Quercus (Davis and Moratto 1988; Anderson 1990). Pollen profiles along the crest of the Sierra Nevada record an increase in upper mixed-conifer and subalpine forest species, especially Tsuga mertensiana and Abies magnifica by 6000 bp (Anderson 1990). Pollen and macrofossil data suggest that Pinus contorta experienced a return to lower elevation sites by 1700 bp. Early Holocene tree lines in the southern Sierra Nevada persisted until 3500 bp, then declined in response to cooler, wetter conditions (Scuderi 1987a; Lloyd and Graumlich 1997). Scuderi (1987a) argued that tree lines declined about 70 m at 3400 and 2400 bp, similar to trends in the White Mountains (La Marche 1973). He attributes the decline to Feng and Epstein's (1994) decreasing temperature profile recorded in White Mountain bristlecone pines. Graumlich (1993) proposes that tree line stands experienced no recruitment and that old trees slowly perished during marginal episodes.

Middens in the Sonoran Desert show that desert microphyll woodland species such as Cercidium floridum and Olneya tesota did not arrive into the region from Mexico until ca. 6000-4000 (Van Devender 1990; McAuliffe and Van Devender 1998). These studies suggest that desert microphyll species are frost-sensitive and were kept out of the region by colder winters caused by a Milankovitch winter insolation minimum of the early Holocene.

Late Holocene Drought. An extended period of reduced precipitation occurred from ca. 2000 to 600 bp that culminated in profound drought beginning ca. 1000 bp. Ingram (1998) found the highest C14 content of marine shells over the past 5000 years at 1900 to 1200 cal yr bp. She points out that the age of the top of West Berkeley mound and several other mounds in the San Francisco Bay region (1100 to 1300 cal yr bp) coincides with a prolonged dry period in California, stronger northerly winds and coastal upwelling and low river inflow to San Francisco Bay. Evidence for regional drought is seen in low lake stands at Walker Lake and Mono Lake (Benson 1991; Stine 1990). Tree stumps rooted in present-day lakes, marshes and streams of Sierra Nevada was attributed to severe drought from 1000-700 bp (Stine 1994). Scuderi (1987b) give evidence that tree-ring widths in Pinus balfouriana were inversely related to glacial expansions, and he found a period of pronounced warmth (growth) from 1200-1000 bp.

Packrat midden data are too sparse to indicate broad scale effects of the Medieval Drought on desert vegetation. Spaulding (1990) noted small movements of vegetation zones upslope by as much as 100-200 m between 1500 and 500 bp, and Van Devender (1990) found little evidence of vegetation change. At Greenwater Valley in the eastern Mojave Desert, Cole and Webb (1985) described a decrease in Larrea tridentata since 2235 bp, but most other shrubs remained unchanged during the period. Sparse fossil charcoal at El Paso Peaks seismic trench suggests limited fire activity between 2800 and 700 cal bp.

Little Ice Age. The "Little Ice Age" (700-200 bp) was a global event as mountain glaciers expanded in Europe, North America and elsewhere (Lamb 1995). In the Sierra Nevada, fresh moraines (virtually lacking lichen) of the little ice age Matthes advance are found below
hundreds of modern and extinct cirque glaciers (Burke and Birkeland 1983; Clark and Gillespie 1997). Hydrogen stable isotope data for bristlecone pine in the White Mountains indicate a period of rapid cooling at 1600 AD, with temperatures during the remainder of the Little Ice Age being as cold as any period in the Holocene (Feng and Epstein 1994). The Little Ice Age is associated with high stands between 600 and 300 bp at Mono Lake, Silver Lake and Cronise Lakes at the mouth of the Mojave River, as well as episodes of marsh growth in Panamint Valley, and peat growth in Ash Meadows (summarized in Enzel et al. 1992). Pulses of sediment activity developed in the Kelso dunes, apparently derived from the Mojave River date to 690 and 450 bp (Clarke and Rendell 1998). There was another intrusion of fresh water habitat at Newport Bay at 560 BP (Davis 1992). Scuderi (1990) found a sharp decline in indexed ring width of timberline trees at Cirque Peak at 1600. Tree ring widths were inverse to glacial expansions in Pinus balfouriana, with minima in widths in 810, 1470, 1610, 1700, and 1810. Graumlich (1993) found a period of cold temperatures from ca. 1450 to 1850. Lloyd and Graumlich (1997) describe a decline in treeline and treeline forest abundance from 450 to 50 bp. Tree ring data for Pseudotsuga macrocarpa indicate more frequent wet winters in late 1500s and 1600s than in recent centuries (Michaelson and Haston 1988).

There is limited evidence of vegetation change during the Little Ice Age. Wigand (1987) found that juniper abundance increased at Diamond Pond at 300-150 bp. At Greenwater Valley in the eastern Mojave Desert, there was a small downward shift in Coleogyne ramosissima of 100 m between 205 and 565 bp (Cole and Webb 1985). Examination of vegetation descriptions in late 18th century Spanish diaries in northern Baja California show the broad scale distribution, species composition, and local patterning of communities are consistent with those today (Minnich and Franco 1998).

Climate and vegetation change in California

A comprehensive synthesis on the role of climate and the paleobiogeography of the California flora is not possible in this review. Moreover, the spatial and temporal data of past climate and pale terrains are still poorly constrained and the legacy of fossil floras is fragmentary. What remains elusive is the history of selection and adaptation of lineages contributing to the modern floras. It is best here to assess the broad trends, and to entertain important paradigms one should consider in the interpretation of vegetation-climate relationships.

Late Quaternary

California ecosystems doubtless experienced large shifts in the latitudinal and altitudinal zonation of vegetation since the last glacial maximum. Perhaps the clearest example is that Sierra Nevada subalpine forests now occupy extensive areas that were covered with mountain ice sheets in the late glacial maximum. The available paleobotanical data permit only broadscale reconstruction of vegetation assemblages. The strongest case has been made from packrat midden records on the replacement of late glacial pinyon-juniper woodlands by creosote bush scrub in the Mojave and Sonoran Deserts (Spaulding 1990; Van Devender 1990).

There is limited consensus on the character of full-glacial climates in California. To resolve differences in California studies, an important goal is that interpretations be consistent with the emerging global database of marine oxygen isotope records, as well as global climate model simulations (summarized in Bradley 1999). Adam (1981) and Adam and West (1983),
working at Clear Lake, hypothesize LGM-present temperature departures of 7-8°C, which exceeds Pacific Ocean SSTs (CLIMAP 1976; Moore et al. 1980; Lowe and Walker 1998). Since winter temperatures at Clear Lake now average 5°C, LGM temperatures would be -2 to -3°C. Atmospheric lapse rates require freezing Pacific Ocean SSTs, but this is unsupported by marine isotope records (Bradley 1999). However, the lapse rate method used in the study overestimates full-glacial precipitation and temperature changes because it assumes that vertical lapse rates account for latitudinal displacement of temperature and precipitation fields. A 7-8°C decrease in mean annual temperature is physically inconsistent with estimates of 1-3°C decreases in Pacific Ocean SSTs (CLIMAP 1976; Moore et al. 1980; Lowe and Walker 1998). Modern mean winter temperature of 5°C at Clear Lake suggests that full-glacial temperatures averaged -2 to -3°C. Hence, average atmospheric lapse rates would require the Pacific Ocean SSTs to be near freezing, but this is unsupported by oxygen isotope records from deep sea cores (Bradley 1999). Precipitation was estimated to be an astonishing 200 cm greater than the present AAP of 120 cm. However, the lapse rate method in the study overestimates precipitation departures because it assumes vertical lapse rates account for latitudinal displacement of temperature and precipitation fields. Estimates from glacial cirque equilibrium line altitudes (ELA) methods, give LGM-present temperature departures of 10-13°C, based on the assumption that summer ELA temperatures are 0°C (Owen et al. 2003). The ELA approach does not account for lateral snow transport (LST) and avalanching in cirque headwalls during winter storms that result in local snow accumulations 2 to 3 times greater than AAP. Present-day Sierra Nevada glaciers and perennial snow on Mt. San Gorgonio (Owen et al. 2003), which depend on LST, exist with mean summer temperatures of 6-8°C. Assuming no change in AAP, an 800 m down slope displacement of mountain ELAs in California—the global average (Denton and Broecker 1990)—implies a decrease in mean temperatures of 5°C at moist adiabatic lapse rates. An estimated 0.6°C of this departure results from lowering of mean sea level and the atmosphere, i.e., increased relative elevation of California mountains of 100 m, increasing them to greater exposure of jet stream wind, making LST more efficient. The southward displacement of the jet stream, predicted by all GCMs, results in exponential increase in LST due to longer periods of precipitation, atmospheric vapor flux, and total precipitation. Hence, temperature departures required to produce mountain glaciation was likely < 5°C. GCMs of Bartlein et al. (1998) suggest that mean annual precipitation was ca. 150-200% of modern levels. A moist Sierra Nevada climate appears to be reflected in full-glacial middens in Kings Canyon which records a rich mixed-conifer forest in an area now cover by oak-pine-chaparral woodland (Cole 1983). Pleistocene middens along the California give records of mixed evergreen forest, closed-cone conifer forest and chaparral, with the southward displacement of *Picea sitchensis*, *Sequoia sempervirens*, and *Pseudotsuga menziesii*.

Using pollen records in the Sierra Nevada, Koehler (1994) concluded that high *Artemisia* and Poaceae pollen percentages for 18.5-12.5 ka was evidence for a cold-dry steppe-woodland environment with low snow melt rates. However, wind-pollinated dominants such as *Artemisia tridentata* presently grow at altitudes ranging from 600 to 3800 m, thus limiting the climatic indicator value of the species. A dry climate is inconsistent with the year-round presence of a strong jet stream (high atmospheric vapor flux compared to present), and orographic lift of moist Pacific air masses over the Sierra Nevada (Pacific air masses moving over the Sierra Nevada cannot be dry). Climates far colder than present are unlikely because ocean temperatures were only 2-4°C below those at present, and the influence of cold air
masses forming over the Laurentide ice sheet in California was limited by strong westerlies (Shackelton 1987; Bartlein et al. 1998). Solar radiant energy, the dominant energy source in snowmelt (Miller 1981), was as high in the late glacial as at present (Bradley 1999). Hence, Sierra Nevada ice sheets are evidence for heavier snowfall, not reduced snowmelt.

In summer, LGM-present temperature departures in California were below global average due to coastal upwelling of deep water with small departures (Bradley 1999). Hence, the lowest temperature departures in California were those areas most influenced by the marine layer. GCMs predict the largest departures in the interior during summer when the Laurentide ice sheet maintained a strong jet stream over the west. Pacific air intrusions prevented the build up of hot summer air masses seen today over the western US, with lower temperatures and ET being instrumental in the development of Great Basin pluvial lakes (Spaulding 1990). A modern analogue exists in mediterranean climates of central Chile, where a strong summer jet stream due to the Antarctic ice sheet, and small continental area compared to North America, produce summer temperatures 5-8° C colder than at comparable latitudes of California. West of the California mountains, the coastal marine layer reinforced summer drought, as simulated by GCMs (Bartlein et al. 1998) and supported by late Pleistocene records of a modern chaparral flora (Johnson 1977). California fire regimes were comparable to those at present, only the distribution of burning was cued to full-glacial vegetation distributions. The deserts were arid in the LGM due to rain shadows from the coastal ranges, and the Sierra Nevada, as evidence by sagebrush and Mojave Desert scrub assemblages in most midden sites. Sierra Nevada montane forests species did not reach the base of the eastern escarpment (McCarten and Van Devender 1988). Summer precipitation may have been lower than present in the Mojave and Sonoran Deserts because the stronger westerlies displaced the North American monsoon into Mexico.

Rapid vegetation change occurred in response to climatic change of the Pleistocene-Holocene transition. Members of creosote bush scrub advanced rapidly across the Sonoran and Mojave Deserts, reaching their modern limits by ca. 8 ka (Spaulding 1990; Van Devender 1990). Plant migrations appeared to have lagged behind climatic fluctuations, even at scales of millennia. In long-lived communities, a span of centuries is brief for even short-term population changes. Selection processes that result in changes in recruitment or disturbance patterns require several generations to reach mature phases of vegetation (Sauer 1988; Thompson 1988, 1990). Some species were undergoing range adjustments in the late Holocene. Pinus monophylla may have reached the Reno area only in the past 2.0 ka (Nowak et al. 1994). In the central Sierra Nevada, Anderson (1990) concluded that open forests at 10 ka, reflected drier conditions than at present. However, the openness of stands may also reflect poor soil development after deglaciation. Van Devender (1990) concluded that desert scrub changed little since the early Holocene suggesting that modern floras have equilibrated to modern climate.

In the mid- and late Holocene, changes in precipitation, as evidence by small high stands and glacier advances, were apparently insufficient to cause broadscale changes in vegetation. This is understood by the different scales by which water fluxes affect land surfaces. Holocene precipitation variability had lasting geomorphic impact where water was stored with long residence time, i.e., lakes and glaciers. The effects of precipitation variability on soil water and vegetation are fleeting because there is little interannual water storage, especially in shrublands and forests whose growth represents the integration of climate over long time scales.
Holocene geomorphic evidences may more reflect short-term climatic singularities than broad structural changes in global circulation. Enzel et al. (1992) proposed that the concurrent snow accumulation in Sierra Nevada, high precipitation, stream flows in southern California, and high lake stands in Mojave River at 1600 all can be explained from singular flood-producing events during a single season. For example, high snow accumulations in a few wet years in the high Sierra Nevada will ultimately produce more uniform runoff into Mono and Walker Lakes. A striking example is a large flood in 1605 based on the thickness of sea floor varves in the Santa Barbara Channel (Schimmelmann et al. 1998) that is rivaled only by two other events in the past 1000 years, floods in 1414 and 1969. The 1605 flood is apparently reflected in other proxy data. Graumlich (1993) concluded from tree-rings that 1602 was the end of a drought that began in 1566. Scuderi (1990) shows evidence of a sharp decline in ring-width at this time. Using tree-ring width data for *Pseudotsuga macrocarpa* in coastal central California, Hasten and Michaelsen (1994) found that 1611 was the 3rd wettest 11-yr period since 1366. But tree rings describe changes in growth rates, not changes in vegetation.

**AREAS FOR FUTURE RESEARCH**

The future of paleobotany and paleoecology bodes well with the emergence of stable isotope geochemistry which has made possible the independence of data on fossil floras and proxy data on climate. The marine stable isotope record now provides well constrained timeline over the period of evolution of modern assemblages from greenhouse climates in late Cretaceous-early Tertiary to modern ice house climates. The research agenda should continue in similar directions. Studies of new and existing macrofossil and microfossil assemblages can be assessed on their own terms with respect to plant evolution and migration (Sauer 1988), and can be correlated with emerging climatic proxy evidences from geochemistry, seen in a variety of such sediments as lake beds, marine shell deposits, varved sediments, wood of ancient trees, as well as physical evidences in lake stands, glaciation, stabilized sand dunes, and fossil charcoal left by fires. Perhaps most frustrating is the dearth of macrofossil data from packrat middens in the mediterranean climates of California, due possibly to poor preservation in mesic climates compared to the rich record in deserts, as well as the scarcity of rock shelters. Global climate models (GCMs) have elegant physics which provide scenarios of past global atmospheric and oceanic circulations, but models are always incomplete. In that vein, GCMs provide scenarios of “fiction” as in a mystery novel. In the novel, the author gives a web of facts and unravels key new findings that permit the deduction of multiple solutions, and ultimately a “smoking gun” piece of the puzzle that resolves to a single explanation. The difference is that the novelist defines the entire web of information; Smoking guns seldom exist in the unfathomable complexities of nature. Hence, the relevance of GCMs will be bolstered by empirical guidance. While global climate models help constrain climatic inference from proxy data, conflicting proxy data will always encourage the investigation of model assumptions. Answers concerning the effects of recent global warming are unlikely to come from deductive global climate models, but rather from the oceans which are the primary heat reservoirs of the planet. Nature is the best teacher. Increasing the empirical domain from the kinds of evidences given above will slowly but surely lead to important advances in the paleobotany and paleoecology in California, as well as our understanding of the modern flora and vegetation.