The History of Oak Woodlands in California, Part I: The Paleoecologic Record

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Abstract
Oak woodlands are a fixture of California geography, yet as recently as 10,000 years ago, oaks were only a minor element in the landscape. In this paper, I review the long-term history of California oaks, beginning with the Tertiary fossil record from the Early Miocene (~20 million years ago), when oaks were present across the west, intermixed with deciduous trees typical of Eastern North America. As climate became drier, many species went locally extinct and oaks retreated west of the Sierra Nevada. During the ice ages (~ the last 2 million years), oaks nearly disappeared as cool and wet climate favored expansion of coniferous forests and oak woodlands persisted in refugia. After the last glacial maximum, oaks expanded rapidly to become the dominant trees in the Coast Ranges, Sierra Nevada foothills, and Peninsular Ranges. Within the last 10,000 years, climate change has continued to alter oak woodland distribution patterns. During this period, human impacts on oak woodlands have also caused significant changes. The human impacts on oaks, associated with Native Californians, and the Spanish, Mexican, and American populations that displaced them, will be reviewed in Part II.

Key Words: Oak woodlands, Quercus, California, paleoecology, vegetation history

Oak woodlands scattered across grass-covered hills represent the characteristic landscape of California. Yet this familiar scene is of relatively recent origin, and the oak woodlands that symbolize California today represent only the most recent pattern in a long history of change, influenced by both changing climates and changing land use practices. Fossil evidence shows that all of California’s oaks were present in western North America by about ten million years ago (Millar 1996), but their modern geographic ranges have been established within only the last 10,000 years. As the summer-dry Mediterranean climate developed and strengthened over time, the range and distribution of California oaks has changed. During
the last 100,000 years, oaks were a minor element of the landscape, most likely persisting as isolated refugia.

With the end of the last ice age, about 10,000 years ago, oaks rapidly expanded, creating the woodlands we recognize today. Even during this time period, climate change has influenced the range and distribution patterns of oak woodlands, such that in some locations, woodlands have been in place for only the last few thousand years. Evidence of the first appearance of humans in California also dates to about 10,000 years ago, so that the expansion of oak woodlands after the last glacial maximum coincides with a period of environmental modification through human use. Native Californians lived throughout the oak woodlands, and evidence suggests that their practice of frequently burning the landscape influenced the development of the open oak savannas commonly described in the earliest European accounts. Within just the last two centuries, intensive resource use has completely altered the distribution and abundance of oak woodlands throughout most of their range in California.

In this paper, I review the paleoecologic and historical literature to reconstruct the history of change in California’s oak woodlands. The paper has two parts. Part I focuses on the long-term geologic record reconstructed from fossil evidence. I begin with a brief overview of the ecology and geographic ranges of the nine tree oaks in California. Review of the geologic record starts in the Early Miocene (~ 20 million years ago) with the first oak fossils conformable to modern species, and continues through the Holocene. Since the formation and development of California’s Mediterranean climate is crucial to reconstructing the history of oak woodlands, the paleoecology discussion includes relevant aspects of climate change.

Part II encompasses the history of human interactions with oak woodlands, beginning with Native Californians and continuing through the Spanish, Mexican, and American periods. The section on the influence of native Californians on oak woodlands relies primarily on ethnographies and descriptions of early explorers, supported by fossil pollen evidence and studies of land use changes. To a certain extent, we can understand what the landscape must have been like during the aboriginal period by documenting the changes that happened after the removal of the native population from the landscape. European impacts are documented in diaries and written records from the early periods of settlement. Unfortunately, most of these accounts are descriptive and non-quantitative, and provide...
only a sketch of how oak woodlands were transformed over time. But the broad picture of large-scale landscape conversion can be easily read on the landscape as well as in the literature. People have always lived with oaks in California, and as land use has intensified, it has directly impacted the abundance and distribution of oak woodlands. In many ways, the history of California’s oak woodlands is the history of California.

**California’s Oaks**


Valley oak (deciduous) is the tallest of all California oaks and typically grows in riparian habitats or on rich, deep, valley soils below 600 m. It is endemic to California and is widespread in the Central Valley (including the Sacramento Valley in the north and the San Joaquin Valley in the south), as well as smaller valleys throughout the Coast and Transverse Ranges (Figure 1a) (Griffin and Critchfield 1976). Blue oak (deciduous), also endemic, commonly grows adjacent to valley oak and forms savanna woodlands in the low foothills surrounding the Central Valley, as well as extending into the foothills of the Coast Ranges (Figure 1b). This species tolerates the driest climate of all California tree oaks and can grow in areas where temperatures exceed 38°C for weeks at a time and annual precipitation is less than 250 mm, although it can also grow in areas with up to 1,000 mm annual precipitation (Pavlik et al. 1991). Nearly half of oak woodlands in California are dominated by blue oak.

Interior live oak (evergreen) a California endemic, commonly grows in association with blue oak and valley oak at lower elevations in the Sierra Nevada foothills and northern Coast Ranges (Figure 1c). In the south Coast Ranges and Transverse Ranges of southern California, the species is shrubby and grows at elevations above coast live oak (Griffin and Critchfield 1976). It is interesting to note that in the dry interior valleys of California, blue oak, a deciduous species, occupies the driest habitats with the most severe summer drought, while the evergreen interior live oak is absent from these sites. Evergreen sclerophyllous taxa are often considered to be classically

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adapted to the Mediterranean climate type; however, in California, deciduous oaks occupy this niche as well (Blumler 1991).

Coast live oak (evergreen) is the species that the early Spanish explorers were most familiar with, because it occupies the valleys and hills of the

Figures 1a–g. Distribution maps of the fossil localities and modern ranges of (a) valley oak (Quercus lobata), (b) blue oak (Q. douglasii), (c) interior live oak (Q. wislizeni), (d), coast live oak (Q. agrifolia), (e) Engelmann oak (Q. engelmannii), (f) black oak (Q. kelloggii), and (g) canyon live oak (Q. chrysolepis). Filled symbols represent sites where there is greatest confidence in the fossil identification, and open symbols are sites with the least confidence, following Table 1.
Coast Range (Figure 1d) where the Franciscans established their chain of missions (Griffin and Critchfield 1976). The species occupies the cooler coastal habitat and becomes restricted to streams at the southern extent of its range in Baja California (Minnich and Franco-Vizcaíno 1998). Another southern oak, Engelmann oak (semi-deciduous) is restricted to southern California and Baja California (Figure 1e), and populations are concentrated at elevations between 700 m and 1,250 m, where frosts are rare and precipitation typically exceeds 450 mm annually (Scott 1991). This species is most closely related to oaks in Arizona and the Sierra Madre Occidental of northern Mexico, and is considered the northern outpost of sub-
tropical oaks in the western United States (Pavlik et al. 1991; Minnich and Franco-Vizcaíno 1998).

Black oak commonly grows in mixed conifer forests of the Sierra Nevada, southern Cascades, and northern Coast Ranges at elevations between 600 m and 1,980 m (Figure 1f). The species prefers precipitation greater than 625 mm annually, and snow and frost are common within its range. Frequent fires favor the growth of black oak in place of conifers (Pavlik et. al 1991). The most widely distributed oak is canyon live oak, growing from near sea level to 2,700 m from Oregon to Baja California in nearly every major mountain range.
range in the state (Figure 1g) (Griffin and Critchfield 1976; Pavlik et al. 1991). This species is common in moist canyons and on steep slopes but does not occur in areas with frequent fires and is not common in the savanna habitat.

Two oaks—Oregon white oak and island oak—live primarily outside the typical range of Mediterranean oak woodlands. Oregon white oak ranges from the northern Coast Range and Klamath Mountains of northwest California north into Canada, and is associated with Douglas-fir (*Pseudotsuga menziesii*) and mixed evergreen forests. Island oak was distributed throughout southern California in the
Pliocene (ca 3 million years ago—Ma) (Axelrod 1973) but today is confined to the Channel Islands off the southern California coast and Guadalupe Island off of Baja California (Griffin and Critchfield 1976). While these two species are important in California and may have interesting histories that are worth examining, this review does not discuss them.
Figure 1f
Figure 1g
Paleoecology of California Oaks—The Paleoflora Record

Interpreting the Fossil Record

This review is not a taxonomic revision of oaks but a historical biogeography based on the existing fossil record. Oak taxonomy is complicated, and unraveling the potential evolution of lineages is a study in itself (Nixon 2002). I use the fossil record to map changes in distribution patterns of the ancestors of our modern oaks to document the history of California oaks and provide some insight into the climatic and geographic changes that may have been associated with the development of oak woodlands.

Since identification of the fossil flora is critical to interpreting historical distribution patterns, in addition to referring to photographs of type-specimens published in the literature, I examined the original fossil material of each oak type-specimen discussed in the literature, with the assistance of Howard Schorn and Diane Erwin of the California Museum of Paleontology. Most of the original fossils of the floras reviewed in this paper are held in the museum collection. In a few cases, the material was held elsewhere or unavailable, but we were able to check more than ninety percent of the original fossils, to make our own determination as to the relative confidence of the identity. I have not revised any original species identifications and present the species as published by the authors. However, where the literature is ambivalent, or preservation is poor, I have indicated those identifications that appear to be less certain and may require more careful analysis before being used to confidently reconstruct oak biogeography (Table 1).

Oak leaf morphology is notoriously variable, particularly among the live oaks, which have similarly shaped leaves. Differentiation between live oaks relies largely upon vein patterns (venation), which requires fossils with well-preserved secondary and tertiary veins. Even using the fossil material, we were unable to confidently identify some live oak specimens. Leaves of the deciduous oaks are more morphologically distinct and the fossil record seems clearer for these types. However, even in these cases, there is variation that may represent hybridization or lineages that went extinct. Within the three sections of oaks (Table 1), all species are known to hybridize (Nixon 2002), and hybrid swarms can produce a nearly continuous range of leaf morphologies between species (Benson et al. 1967).
Table 1. List of floras mentioned in the text in chronological order with the best known age in millions of years. Chronology follows Woodburne and Swisher (1995), and Schorn (unpublished data). # refers to site identification numbers in Figure 1. Taxa are arranged by section following Nixon (2002). Species are as follows: agri = Q. agrifolia, kell = Q. kellogii, wisl = Q. wislizenii, chry = Q. chrysolepis, engl = Q. Engelmanii, loba = Q. lobata, doug = Q. douglasii. X = fossil present that conforms to the modern species. x = fossil present that has been identified to the modern species but the identification was determined ambiguous after examination of the type fossil. 1Unpublished floras examined at the University of California Museum of Paleontology paleobotany collection.

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The fossil literature includes many species names that are overlapping or equivalent. To simplify this discussion, I refer to the most commonly used fossil name and its modern equivalent, and then simply use the common name thereafter. This does not imply that the species filled the exact ecological niche throughout its evolution. In fact, one of the important stories of California oaks is that they appear to have been able to adapt to an increasingly drier climate. Since the fossil record contains only leaves and occasionally acorns, we know nothing about the actual growth habits of the trees, which we assume were similar but have certainly changed over time.

Finally, an accurate chronology is key to interpreting the fossil record. Many of the studies cited in this review were done before the development of radiometric dating techniques. I used the chronology developed by Schorn (unpublished data), utilizing Ar/Ar, K/Ar, mammalian faunas, stratigraphic position, and floral evidence (Woodburne and Swisher 1995). Thus, the chronology will follow not the ages suggested in the original literature but the revised ages for each flora.

**Early Miocene (20–16 Ma)**

California oak history begins in the Pacific Northwest in the Early Miocene, with the first fossils that can be compared with ancestors of modern oaks (Wolfe 1980). The ancestor for black oak (*Q. pseudoloyrata*–*Q. kellogii*) and valley oak (*Q. prelobata*–*Q. lobata*) are found in Oregon (Figure 1) between 20 and 16 Ma (million years ago) in the Eagle Creek and Callawash floras (Chaney 1920; Peck et al. 1964). The Oil City flora in southern Oregon contains black oak. These oaks grew with an exotic mix of species within genera now commonly found in either East Asia ginko (*Ginko*) and zelkova (*Zelkova*), or the Eastern United States hickory (*Carya*), tulip tree (*Liriodendron*), sweet gum (*Liquidambar*), elm (*Ulmus*), and magnolia (*Magnolia*).

The earliest oaks were commonly associated with broadleaf deciduous trees that are now confined to mesic environments in the Eastern United States or to riparian habitats in the west, including maple (*Acer*), hornbeam (*Carpinus*), persimmon (*Diospyros*), beech (*Fagus*), witch hazel (*Hamamelis*), holly (*Ilex*), walnut (*Juglans*), tupelo (*Nyssa*), hornbeam (*Ostrya*), avocado (*Persea*), cherry (*Prunus*), and sassafrass (*Sassafras*) (Axelrod 1983). As summer rainfall disappeared through the late Cenozoic, most deciduous broadleaf species went locally extinct. California’s oaks did not evolve under the summer dry Mediterranean climate where they thrive today, but rather are
survivors of a rich and diverse flora dominated by year-round precipitation (Axelrod 1973). Today’s native species must have been pre-adapted to summer drought and were able to persist in the region as the climate became more Mediterranean (Blumler 1991).

Fossil oaks are always found as part of rich assemblages of sclerophyllous and deciduous woodlands, whereas today we typically find large expanses of woodlands comprised of pure stands of one species of oak. Wolfe (1980) suggests that such monoclimax communities represent a recent development. This is difficult to confirm, however, because preservation favors wet locations that are more likely to contain a mix of riparian and upland species. Even today, species diversity is greatest along riparian corridors, suggesting that even though single species stands are widespread throughout the state, depositional environments suitable for preserving macrofossils are uncommon within these stands.

**Middle Miocene (16–10 Ma)**

By the beginning of the Middle Miocene (~16 Ma), two additional oaks comparable to modern species are found in the fossil record: canyon live oak (Q. hannibali–Q. chrysolepis) and interior live oak (Q. wislizenoides–Q. wislizeni). The vast majority of oak woodlands were outside the present area of California, in Nevada, Idaho, Oregon, and Washington (Axelrod and Schorn 1994; Axelrod 1956, 1964, 1973, 1995).

Only two species were confidently present in California during the Middle Miocene: black oak, found in the Temblor flora of the southern Coast Range and the Gold Lake flora north of Lake Tahoe; and canyon live oak, found in the Temblor flora (Renny 1972) and Tehachapi flora (Axelrod 1939) of southern California (Table 1, Figure 1). In the Tehachapi, oaks grew alongside laurels (Persea), suggesting a wetter climate than now. These two species had the widest distribution pattern of all the oaks, also being found in Nevada, Oregon, Idaho, and in the case of black oak, southern Washington (Smiley 1963). Today these two species continue to have the widest geographic range of California oaks.

At the Blue Mountain and Mascall sites in Oregon, black oak, valley oak, and canyon live oak grew together in a mixed evergreen forest (Oliver 1936; Chaney and Axelrod 1959). This flora also included deciduous forest types such as tree of heaven (Ailanthus), maples (Acer), hawthorn (Crataegus), beech (Fagus), Eastern-type oaks (Quer-

cus prinus, imbricaria), walnut (Juglans), sweet gum (Liquidambar),
and sassafras (Sassafras). Conifers included fir (Abies), spruce (Picea),
Douglas-fir (Pseudotsuga), redwood (Sequoia), hemlock (Tsuga), and
western red cedar (Thuja) (Axelrod 1973). The association of both
Eastern deciduous species, as well as redwoods, with oaks indicates
mild temperatures with wet summers. At the Succor and Trout Creek
localities (Graham 1965) in southeastern Oregon, canyon live oak
grew in association with Zelkova, now restricted to Eastern Asia,
and Oreopanax, a genus that is not frost hardy and occurs primarily
in tropical America. The Mollalla and Faraday localities included
black oak and valley oak (Chaney 1944, 1959). Idaho floras included
genera now restricted to coastal sites, such as Sequoia at Hog Creek
and Highway (Dorf 1936; Smith 1939) and an ironwood type (Ly-
onothamnus) in the Pickett Creek flora (Buechler et al. 1998).

Lobed oaks similar to valley oak have been found only in Oregon,
Washington, and Idaho during the Middle Miocene. Leaf morphol-
ogy of these fossils resembles both valley oak and Oregon white oak.
These two species may have had similar progenitors in the Pacific
Northwest that diverged sometime after the Middle Miocene, with
valley oak becoming restricted to California.

Interior live oak fossils are restricted to Nevada during the Middle
Miocene (Figure 1c), where they co-occur with canyon live oak and
black oak. Sites with interior live oak included Middlegate, Eastgate,
Chloropagus (Axelrod 1956); Buffalo Canyon (Axelrod 1985); and
Fingerrock (Wolfe 1964). These sites had a mix of deciduous species
indicative of a summer wet climate, including ancestors of madrone
(Arbutus), walnut (Juglans), Eugenia (extinct), birche (Betula), maple
(Acer), buckeye (Aesculus), persimmon (Diospyros) hickory (Carya),
elm, (Ulmus), and zelkova (Zelkova) (Axelrod 1973).

The distribution pattern of interior live oak in central Nevada and
valley oak in the Pacific Northwest recalls the concept of separate
Arcto-Tertiary and Madro-Tertiary floras described by Axelrod
(1983). The genus Quercus first appears in the fossil record in the
late Cretaceous. Oaks today are widespread in Asia, Europe, and
North America, where the center of diversity is in montane forests
of Mexico (Nixon 2002). Axelrod (1983) suggests that live oaks
such as interior live oak are most closely allied to peninsular oaks
of Mexico and would be considered part of the Madro-Tertiary flora
characterized by shrubby taxa and semiarid climate with summer
rain. He suggested that many of the California oaks had their origins
in Mexico-Central America and the southwestern United States, spreading northward as aridity increased. Morphological data comparing modern interior live oak and coast live oak (red oaks in the section Lobatae) with Mexican red oaks find no obvious connections between Californian and Mexican species (Nixon 2002). California black oak, which looks more like oaks of Eastern North America, also has no particularly close morphological characteristics with Eastern species. In general, lobed-leaf species, or species thought to be derived from lobed-leaf ancestors (valley oak, black oak, blue oak, coast live oak), are characteristic of temperate or cold climates, and canyon live oak (Section Protobalanus), a true evergreen, probably originated in a more tropical region (Nixon 2002).

Late Miocene (11–5 Ma)
By the late Miocene, California oaks became restricted within the present political boundaries, with the only exception being just across the state line in Verdi, Nevada (Figures 1a–1g). Reliable fossil evidence for each species can be found within or near some portion of the species’ present boundaries, indicating that the mild and humid climate of the Early Miocene had begun to give way to a more seasonal Mediterranean climate.

The Remington flora (Condit 1944) and adjacent Burlington flora in the west central Sierra Nevada held five species of oak, including canyon live oak, black oak, interior live oak, valley oak, and the first appearance of blue oak (Q. douglasoides–Q. douglasii) (Table 1). Chaparral species from several genera are present, including manzanita (Arctostaphylos) and buckbrush (Ceanothus). These floras contain the first evidence of a diverse oak woodland within California associated with chaparral shrubs. Summer rainfall types present include maple (Acer), buckeye (Aesculus), sweetgum (Liquidambar), avocado (Persea), and elm (Ulmus), indicating that although oaks and chaparral are present, the landscape was still not comparable to modern oak woodlands. The Mediterranean climate typical of California today appears to have strengthened during the late Pliocene but did not fully develop until the Pleistocene (Axelrod 1980).

The first fossils that can be confidently attributed to coast live oak (Q. lakevillensis–Q. agrifolia) appear in the Mount Eden flora (Dorf 1930; Axelrod 1937, 1950a) about 5–6 Ma, on the northwest slopes of the San Jacinto Mountains in southern California. Coast live oak is found only at its southern limit, although this particular species is uncommon in the fossil record, indicating that it is either rare or...
difficult to differentiate. This locality also has blue oak, which places this species well south of its modern range limits.

Perhaps the most intriguing locality for the Late Miocene is the presence of Engelmann oak (Q. orindensis–Q. engelmannii) in the Verdi flora (Axelrod 1958) in western Nevada. This locality is in the rainshadow of the Sierra Nevada at ~1,700 m elevation, with average winter temperatures of -7°C and ~20–25 mm annual precipitation. Engelmann is frost intolerant and is restricted today to southern California. Presence of this species in Verdi suggests that the high desert climate of today did not yet exist. This is the only reliable oak species identified from this locality, and unfortunately there are no other late Miocene-age floras in Nevada to confirm whether other not oaks may have been more widespread across this region at this time. Today, small, isolated populations of canyon live oak are found in the Tahoe Basin and in the Carson Range of Nevada, but in general the vegetation on the eastern slope of this range is distinctly arid, dominated by sagebrush (Artemisia tridentata) below 1,650 m elevation.

**Pliocene (5–2 Ma)**

Evidence from the Pliocene is limited. The major sites are located near Santa Rosa, well within the modern distribution of the species today. The Central Valley was a large inland sea in the early Pliocene (Johnson et al. 1993) that would have modified temperature and precipitation patterns but prevented colonization of the Central Valley and created a barrier to dispersal. Fossil sites are missing from most of the potential ranges.

Mixed oak woodland appears to be well developed at the Sonoma and Napa localities (Axelrod 1944a, 1950b), with blue oak being associated with interior live oak, coast live oak, canyon live oak, and valley oak. Most of the fossils suggest a modern forest typical of the Coast Range with redwood (Sequoia), Douglas-fir (Pseudotsuga), alder (Alnus), tan oak (Lithocarpus), sycamore (Platanus), and shrubs such as mountain mahogany (Cercocarpus), buckbrush (Ceanothus), and manzanita (Arctostaphylos). Several fossils stand out as exotic, though, suggesting persistence of a wetter climate than today, including elm (Ulmus) and avocado (Persea).

One apparent outlier is the presence of valley oak at Long Valley, located on the eastern crest of the Sierra Nevada north of Reno and east of Quincy. Populations of black oak cross the Sierra Nevada
here today, nearly to the Nevada border where low passes provide dispersal routes, such as along the South Fork of the Feather River (Griffin and Critchfield 1976). This pattern appears to have possibly persisted here for at least 4 million years.

**Pollen Evidence for Oak Woodlands**

Macrofossil evidence from floras provides detailed lists of species presence or absence but cannot inform us about the abundance of individuals in the landscape. Alternatively, pollen microfossils provide a measure of abundance, although for oaks this is limited to the generic level. The relationship between species abundance on the landscape and abundance in the fossil pollen record is calibrated through surface samples that compare modern vegetation with the associated pollen rain. Studies from northwest California and southern Oregon (Heusser 1983), and along transects from the Central Valley, over the Sierra Nevada into the Great Basin (Adam 1967; Anderson and Davis 1988) found a positive correlation between oak abundance on the landscape and oak pollen in surface samples. When oak pollen is absent, oaks are typically not present in the region. Trace amounts of pollen up to about 5 percent indicate that oaks are either present locally in small numbers, or present in the region, however not as an important part of the plant community. Pollen sums of 30–40 percent represent oak-dominated landscapes, and sums between 5 and 30 percent suggest that oaks are locally abundant, roughly in proportion to their pollen sum (Anderson and Davis 1988).

Evidence for oak woodlands in the early Pliocene comes from pollen in sediment cores collected in the Pacific Ocean off the coast of California between Monterey and San Francisco (Heusser 2000a). Oak pollen typically cannot be identified below the genus level; however, as records move toward the present, species can sometimes be inferred from the modern ecology. Between 6 and 5 Ma, Heusser (2000a) found that *Quercus* pollen averaged 20–30 percent of the total pollen sum. Pollen of summer rainfall taxa now extinct in California was also identified, including sweetgum, hickory, linden, and wingnut (*Pterocarya*). This assemblage suggests a warm, moist climate along the coast, with a rich mixed woodland dominated by oaks. After 5 Ma, these summer rainfall taxa disappear from the pollen record, suggesting an increase in summer aridity. However, percent oak pollen also declines, typically averaging 10–15 percent, but sometimes dropping below 5 percent. Based on macrofossil
evidence from western North America, Axelrod (1973) suggests that oak woodland-savanna expanded in California in the early to mid-Pliocene, but declined in the late Pliocene as the climate cooled and precipitation increased. Recent evidence from marine $^{18}$O records supports the interpretation of a progressively cooler climate from 3.1 to 2.6 Ma, probably associated with growth of ice in Antarctica and the northern Hemisphere (Bradley 1999, p. 213). About 2.7 Ma, there was a dramatic increase in ice-rafted debris in the North Atlantic as the global climate continued to cool, leading to the ice ages of the Pleistocene. This climate shift brought a dramatic change to California oak woodlands.

**The Pleistocene (2 Ma–10,000 yr BP)**

The Pleistocene has been marked by a period of glacial and interglacial oscillations (Figure 2) that appear in the marine $^{18}$O record in the late Pliocene and become more pronounced toward the present (Raymo 1992). Although there is much debate concerning the exact periodicity of glacial cycles, estimated ages and terminations of the last six glacial cycles suggest a duration of approximately 100,000 years, with warm, largely “ice-free” interglacials lasting about 10,000 years, and cool, “ice-dominated” glacials lasting about 90,000 years (Bradley 1999). Oscillations within these cycles, termed **interstadials** (warmer periods) and **stadials** (cooler periods), provide evidence that glacials are not simply long cold periods. They are, however, largely dominated by cool climates, with maximum cooling occurring just prior to interglacials. The record of climatic oscillations has been subdivided into stages based on the marine oxygen isotope record, with odd numbers (1, 3, 5, etc.) representing warmer phases, and even numbers (2, 4, 6, etc.) representing cooler phases (Bradley 1999).

Northern hemisphere continental ice sheets were much larger over the last 1 million years as compared to the early Pleistocene, and the contrast between cold periods (glacials) and warm periods (interglacials) has become more pronounced in the last 600,000 years (Figure 2) (Raymo 1992). Axelrod (1973) has argued that the modern pattern of Mediterranean climate—nearly or completely rainless summers—originated during the Pleistocene in association with interglacial periods. The pollen record supports this conclusion and provides evidence that during the Pleistocene, oak woodlands have been a major part of the California landscape only during the short, warm, dry interglacial periods (Adam 1988; Heusser 1995; Davis 1999). Considered another way, during as
much as 80 percent the last two million years, oaks were rare in California. The last glacial maximum occurred about 18,000 $^{14}$C yr BP (radiocarbon years before present) and the current interglacial, termed the Holocene, began about 10,000 $^{14}$C yr BP. Widespread oak woodlands so characteristic of California today originated only within the last 10,000 years.

The majority of fossil evidence from the Pleistocene comes from pollen studies of sediment cores recovered from either unglaciated lakes or the Pacific Ocean (Figure 3). Macrofossil evidence of can-

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**Figure 2.** Benthic $^{18}$O curve from marine sediments illustrating the onset of glacial cycles in the Pleistocene (adapted from Raymo, 1992).
yon live oak and interior live oak comes from the Soboba flora in southern California (Axelrod 1966). Axelrod argues that this flora is early Pleistocene in age, based largely on the fossil composition. The flora is dominated by native California species except for the fossils of two extralocal types, magnolia (*Magnolia grandiflora*), now confined to the southeastern United States, and canyon maple (*Acer brachypterum*) with a modern distribution confined to the southwestern United States. Throughout the Miocene and Pliocene, species requiring summer rainfall were gradually extirpated from California, such that by the beginning of the Pleistocene, California’s flora was essentially modern in composition. The presence of only two exotic taxa suggests a fairly recent deposit; however, the continued existence of two species that survive today in regions dominated by summer rainfall suggests that even at the beginning of the Pleistocene, California’s Mediterranean climate was not as severe as today (Axelrod 1966, 1973).

Heusser et al. (2000) published a pollen record from a core taken off the northern California coast that goes back 350,000 years spanning the last four interglacials, including the Holocene. The pollen record for the last 140,000 years is presented here (Figure 4). Oak pollen ranges from 10 to 25 percent of the pollen sum for both the Holocene and the last interglacial (ca 125 Ka) (thousand years ago) while earlier interglacials averaged only 5–8 percent oak pollen. During glacial maximums, oak pollen is less than 5 percent. Within the last glacial cycle, percent oak pollen generally increases during interstadial (warmer periods) and decreases during stadials (cooler periods) (Figure 4). Although glacial cycles include a great deal of climate variability, the duration of cooler/wetter phases is longer than warm/dry phases. Interglacials persist for 10,000–15,000
years while glacials last 90,000–100,000 years. Pleistocene-age pollen records show that oak woodlands are regionally important during interglacials, but they nearly disappear from the landscape for very long periods of time during periods of glacial advance.

Adam’s (1988) findings at Clear Lake (404 m elev) in the northern Coast Ranges reinforce this interpretation. Oak woodland surrounds the lake today, composed predominantly of blue oak with gray pine (*Pinus sabiniana*) at lower elevations and interior live oak and black oak at higher elevations. Also present in smaller populations are canyon live oak, valley oak, and Oregon white oak. Oak pollen represents 40 percent of the total sum in modern surface pollen samples and averages 45 percent during the last 10,000 years since the last glacial maximum (Figure 4). Percentages of oak pollen dur-

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**Figure 4. Pleistocene age pollen diagrams for sites in California recording oak.** Filled circles represent packrat midden samples with oak pollen and open circles represent samples with no oak pollen. Note that each of the time series is based on independent age models. The marine oxygen isotope stages (1–6) are after Bradley (1999). Gray bands identify cold periods (stadials and glacial maxima) when percent oak pollen was generally very low.
ing the last interglacial centered about 125 Ka were even higher, ranging between 50 and 70 percent. In contrast, during periods of glacial maxima, (e.g., 70–10 Ka) oak pollen was reduced to 0–5 percent. Under these colder conditions, pines, sagebrush, and juniper dominated the landscape. Shifts from oak dominance to oak absence were abrupt (Adam and West 1983), suggesting that when the climate became wet and cold, oak woodlands were quickly replaced by pine forest, but when climate became warm and dry, oaks rapidly reestablished.

If oak woodlands were largely absent from their present range during glacial epochs, it is natural to ask where they were. One possibility would be that with cooler temperatures, oaks migrated downslope. Clear Lake drains into the Sacramento Valley via Cache Creek, providing a corridor for plant migrations to lower elevations. However, pollen evidence from Tulare Lake in the southern San Joaquin Valley does not show high percentages of oaks during glacial periods.

Tulare Lake was a large freshwater lake created by an outwash fan from the Sierra Nevada that blocked river drainage within the valley. Today the lake has been drained for agriculture, but it was originally a large body of water with extensive settlements of native Californians along the shore (Aikens 1978). Evidence of occupation has been dated to as early as 11 \(^{14}\text{C}\) yr BP Early accounts of the region note that although the western side of the lake was devoid of trees, the eastern side had open oak savanna on the flat valley floor where the water table was high (Preston 1981). On the nearby Kaweah River delta, oaks were so thick that settlers had trouble traversing the forest by wagon. Griffin (1988) relates that the eminent California botanist Jepson (1910) noted that “…four hundred square miles of Valley Oaks…” grew on alluvial soils of the Kaweah River. And yet during the last glacial maximum (~18 \(^{14}\text{C}\) yr BP), San Joaquin Valley vegetation was more similar to the Great Basin than to Mediterranean oak woodland (Davis 1999).

During the last glacial maximum, the Tulare Lake pollen record is dominated by pine (20–40 percent), juniper (20–40 percent), sagebrush (10–20 percent), and greasewood (5–10 percent) (Davis 1999), indicating a Pinyon-Juniper woodland with an understory of sagebrush similar to Nevada. The presence of greasewood suggests extensive salt flats surrounding a lowered lake. Oak pollen is less than 4 percent of the pollen sum, indicating that the Central Valley was not a refugium for oaks during the ice ages.
During glacial maxima, pluvial lakes and extensive wetlands covered much of the Central Valley, reducing available habitat for oaks. Temperature inversions associated with cold-air drainage off Sierra Nevada glaciers may have also affected oaks. During glacial periods, oaks were probably locally rare in California, persisting in small populations on favorable sites. It seems likely that they remained within their modern latitudinal and longitudinal range throughout each glacial cycle, but many populations were locally extirpated. With the return of favorable conditions, local populations increased rapidly, forming the woodlands we see today (Davis 1999).

Macrofossil evidence from a series of seven *Neotoma* (packrat) middens found in Kings Canyon in the Sierra Nevada foothills (920–1,270 m elev.) provide some clues as to the location of oak woodlands around the Central Valley during late glacial time (Cole 1983). These small rodents collect all types of vegetation to construct nests within the shelter of rock caves. The rats use the outer nest area as a latrine and the urine hardens over time, preserving the plant remains indefinitely if they are protected from moisture. Since *Neotoma* collect intensively, but only within 100 m of their nest, fossil middens provide an accurate account of local vegetation (Bettancourt et al. 1990). Today, the foothills of Kings Canyon lie within the oak-chaparral zone and include canyon live oak, but a midden sample dated to 17,500 $^{14}$C yr BP, immediately following the full glacial, contained no oak macrofossils and no oak pollen. Instead, Cole found red fir (*Abies magnifica*), western juniper (*Juniperus occidentalis*), incense cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*), and ponderosa pine (*P. ponderosa*). During periods of warmer climate, including the interstadial at marine oxygen isotope stage 3 and following the glacial maximum, oak is present (Figure 4). Pollen analysis of the midden found 20 percent oak pollen for the earliest midden (less than 45,000 yr BP), and 20 percent oak pollen during the late glacial (14,000 $^{14}$C yr BP) (Cole 1983).

Absence of oak pollen during the glacial maximum suggests that, under the coldest conditions, oaks were locally rare or absent. The Tulare Lake evidence indicates that the refugium was not on the valley floor (Davis 1999). It seems likely that oaks contracted into isolated populations, most likely within a narrow elevation band in the Sierra Nevada foothills. The presence of oak pollen at ~45,000 and 14,000 yr BP suggests that oaks must have been common in the canyon except during the coldest climates, and as the climate warmed after the full glacial, oaks rapidly expanded back upslope.
An alternative explanation is that as the climate warmed, montane conifers thinned, allowing an increase in the local pollen rain of low-elevation taxa (Edlund 1996). Both explanations, however, suggest a change in forest cover from montane conifers to chaparral-oak woodland.

Coastal oak woodlands appear to have followed the same pattern as that found at Clear Lake. Pollen analysis of marine sediments taken offshore of California record high percentages of oak pollen only during interglacials, with very low values during glacial maxima (Figure 4) (Heusser 1995; Poore et al. 2000). In coastal northern California, oaks are generally a minor component of woodlands; however, pollen evidence from two marine cores (Ocean Drilling Project (ODP) sites 1020 and 1080) provides a record similar to those from inland sites (Poore et al. 2000). During the interglacial marine oxygen isotope stage 5E (ca. 127–120 Ka), oak pollen reached its maximum values (15 and 25 percent respectively). During glacial periods, oak pollen typically averages less than 5 percent.

In the Santa Barbara Channel off the coast of southern California, pollen evidence (Figure 4) records 30 percent oak pollen at 124 Ka, with high values throughout the interglacial period (128–116 Ka), declining to 10 percent by 115 Ka (Heusser 1995). Values for oak pollen fluctuate during interstadials (brief warm episodes within longer glacial cycles), with increases between 106 and 108 Ka to 30 percent, and again to ca 10–15 percent at 94 Ka, 84 Ka, and 52 Ka (Heusser 1995; Heusser 2000b). The general trend following the end of the last interglacial is of a decline in percent oak, with values between 0 and 5 percent from 70–14 Ka. Between 70–14 Ka, TCT pollen (Taxodiaceae, Cupressaceae, Taxaceae), probably representing juniper, dominated the coastal region around Santa Barbara (Heusser 1995). Oak abruptly increased to 20 percent of the pollen sum at 14,000 \(^{14}\text{C}\) yr BP and averaged 20–40 percent throughout the Holocene.

Higher resolution analysis of the late Pleistocene and Holocene record from the Santa Barbara Basin shows that oak pollen reached about 15 percent by 12,135 \(^{14}\text{C}\) yr BP and increased to 25 percent by 7,750 \(^{14}\text{C}\) yr BP (Heusser 1978). Oak pollen increased to 30 percent after 7,750 \(^{14}\text{C}\) yr BP, averaging about 30 percent throughout the rest of the Holocene. Along the Santa Barbara coast, oak woodlands are dominated by coast live oak. Low percentages of oak pollen during the glacial maximum indicate that these oak woodlands did
not retreat to the coastal shelf during glacial climates. It also seems unlikely that Mediterranean climate and California oak woodlands migrated south en masse into southern California or Mexico. Given how rapidly oak pollen increased with the end of the ice age (from less than 5 percent to more than 50 percent at Clear Lake, from less than 1 percent to more than 20 percent at Tulare Basin, and from less than 5 percent to more than 30 percent in Santa Barbara), it seems more probable that oaks maintained their general distribution pattern, but were largely extirpated, with small populations persisting as isolated refugia where suitable habitat existed, such as rocky south facing slopes.

The pattern of nearly continuous expanses of oak woodlands in the Coast Ranges and around the Central Valley is a very recent phenomenon. During ice ages, low-elevation California would have been characterized by coniferous forest. The characteristic Mediterranean climate of California with its oak-covered rolling hills has existed only for brief periods during interglacial cycles like the one we enjoy today.

The Holocene (~10,000 yr BP to Historic)
The earliest evidence of human occupation in California based on lithic artifacts found at Borax Lake, north of San Francisco, and Tulare Lake, in the San Joaquin Valley, suggest an arrival date of 11,500–11,000 14C yr BP (Aikens 1978). However, evidence for direct Native Californian influence on oak woodlands is largely restricted to the last thousand years. Part II of this paper will review the impacts Native Californians have had on oak woodlands. This review will focus largely on climate-related explanations of Holocene oak woodland history, with the caveat that human impacts may have contributed to these changes.

Holocene California oak woodland history in the Coast Ranges and Central Valley is different from that reconstructed from sites in the Sierra Nevada. In the Sierra Nevada, pollen data indicate that oak populations increased soon after deglaciation and reached a maximum between 8,000–6,000 cal yr BP (calibrated radiocarbon years before present), declining after that date. In contrast, most coastal and low-elevation sites show a steady increase in importance following the end of the ice age, reaching maximum levels about 8,000–7,000 cal yr BP, but then remaining high throughout the Holocene (Byrne et al. 1991). While low-elevation oak woodlands (dominated by blue oak, valley oak, coast live oak and interior live
oak) became well established in the mid-Holocene, higher-elevation oak populations (primarily black oak and canyon live oak) decreased to become a minor component of the lower montane forests.

**The North Coast Range Record**

Unfortunately, the Holocene record of California oak woodlands is sparse, due to the lack of suitable fossil sites (lakes, meadows, fens) at low elevations (Mensing 1993). Two published pollen studies document changes in oak woodlands in the northern Coast Ranges. At Tule Lake (Figure 5), percent oak pollen began to increase at 7,000 cal yr BP, from ~5 percent up to 10 percent, and continued to increase, reaching 30 percent about 5,000 cal yr BP (West 1982). In the last 1,000 years, oak pollen decreased to about 15 percent at this site. Pine, which was abundant at 8,000 yr BP (more than 80 percent), decreased to 50 percent by 7,000 cal yr BP and remained at that level for the rest of the record. The increase in percent oak (primarily blue oak) at Clear Lake occurred earlier (Adam et al. 1981). Oak pollen represented 20 percent of the pollen sum at about 12,000 cal yr BP and increased to 40 percent by 9,500 cal yr BP. Maximum values (~50 percent) occurred between 6,000 and 3,500 cal yr BP, with a gradual decrease in abundance to 40 percent at the present.

**The Central Valley Record**

The only Holocene pollen record from the San Joaquin Valley is the Tulare Lake record (Davis 1999). The pollen assemblage between 10,100–8,500 cal yr BP is similar to that of the Pleistocene, suggesting that the climate did not support a shift to oak woodland. Beginning at 8,500 cal yr BP, oak woodland replaced pinyon-juniper woodland and sagebrush. Oak pollen increased from less than 5 percent to 25 percent (Figure 5), and the other types decreased. Throughout the Holocene at this site, the abundance of oak was associated with a high water table. Other than along riparian corridors, oaks are generally not present on the floor of the Central Valley (Griffin and Critchfield 1976). The extension of oak savanna onto the flat valley floor of the Central Valley is unique to the Tulare Lake Basin and most likely persists because of high ground-water levels under the alluvial fans of the Sierra Nevada (Preston 1981). Average annual precipitation for the period 1878–1978 recorded in the nearby town of Visalia is 255 mm, well below the average required for valley oak, supporting the assertion that oak woodlands in the region are largely supported by high groundwater levels.
Oaks remained abundant at this site until 7,000 cal yr BP when lake levels dropped, lowering the water table, and oaks abruptly declined. Increased concentrations of charcoal in the sediments indicate an increase of fire after 7,000 cal yr BP (Davis 1999). These fires are likely associated with the drier climate; however, this area was occupied from an early date and may be associated with human

Figure 5. Holocene age pollen diagrams for sites in California recording oak. Records vary in length. Note that each of the time series is based on independent age models. Pollen data from Smith and Anderson (1992) and Davis and Moratto (1988) obtained from the North American Pollen Database. All other data were digitized from published pollen diagrams.

Oaks remained abundant at this site until 7,000 cal yr BP when lake levels dropped, lowering the water table, and oaks abruptly declined. Increased concentrations of charcoal in the sediments indicate an increase of fire after 7,000 cal yr BP (Davis 1999). These fires are likely associated with the drier climate; however, this area was occupied from an early date and may be associated with human
activity. Lake levels remained low between 7,000–4,000 cal yr BP; however, by 5,500 cal yr BP, oak pollen increased to ~15 percent and remained high until ca 3,500 cal yr BP, when lake levels were once again high. In the last 3,000 years, the climate of the San Joaquin Valley has remained dry, and oaks have declined in importance as saltbush species have increased (Davis 1999). The evidence suggests that recent climate changes have influenced oak woodland distribution patterns, such that oaks were probably more widespread in the San Joaquin Valley 3,000 years ago.

A peculiar hybrid, Q. munzii, a cross between valley oak and desert scrub oak (Q. turbinella ssp. Californica) identified in Joshua Tree National Park, 200 km east of the modern range of valley oak, suggests that this species may have extended its range at some point in the last 150–175 years. Human transport is also possible, although the local Indians were not known for utilizing acorns (Tucker 1968). The migration most likely would have occurred after the warm, dry, mid-Holocene, during a time when cooler climates allowed dispersal along a corridor following the San Gabriel and San Bernardino mountains. However, no evidence supports the existence of former valley oak woodland connecting this disjunct hybrid with extant populations, and the origin of this unusual tree remains a conundrum.

**The South Coast Range record**

Along the coast of southern California, oaks were largely absent from the Santa Barbara region at 15,000 ¹⁴C yr BP (0–3 percent pollen) (Heusser 1995) but increased rapidly after that date to about 25 percent of the total pollen sum. Following the initial rapid expansion, oak populations increased slowly, reaching 30 percent of the pollen sum by about 8,000 cal yr BP (Heusser 1978). Pine pollen was also high between 15,000–8,000 cal yr BP (20–30 percent), suggesting that a mixed pine oak woodland grew along the coast. However, after 8,000 cal yr BP, pine decreased and oaks increased, marking a shift from a mixed forest to a coast live oak woodland. Coast live oak has persisted throughout the Holocene as the dominant oak woodland species in coastal California.

Pollen evidence from Zaca Lake (730 m), 50 km northwest of Santa Barbara, located at the transition zone between oak woodland (dominated by coast live oak) and pine forest (dominated by ponderosa pine, coulter pine (P. coulteri), and gray pine (P. sabiniana), confirms
that oak woodland has dominated the low-elevation coastal mountains in the region since at least 2,500 cal yr BP (Mensing 1998).

**The Sierra Nevada Record**

The majority of higher elevation Holocene paleoecologic studies come from lakes on the western slopes of the central and southern Sierra Nevada between 1,500 and 2,000 m elevation (Figure 5). These sites have been characterized as lower montane forest (Rundel et al. 1988), including black oak, white fir, ponderosa pine, jeffrey pine, and incense cedar. Black oak rarely forms oak woodlands and most commonly occurs today as a minor component of coniferous forests below 2,000 m elevation, but it has played a major role as a food plant for native Californians and is important to review for that reason.

Studies conducted near the modern-day upper-elevation limit of black oak provide a consistent story of vegetation change (Edlund 1996; Smith and Anderson 1992; Davis and Moratto 1988; Mackey and Sullivan 1986). Late Pleistocene records from these sites are dominated by juniper and/or incense cedar, sagebrush, and pine pollen, with oak pollen consistently less than 5 percent, suggesting an open landscape with a cooler, drier climate than today. Beginning about 10,000 cal yr BP, oak pollen began to increase, reaching maximum values of 20–30 percent between 7,000–6,000 cal yr BP. After 6,000 cal yr BP, oak declined and was generally replaced by fir, with oak pollen percentages averaging only 3–10 percent (Edlund 1996; Smith and Anderson 1992).

These authors interpret these data to represent a dry early Holocene, with oaks migrating upslope and becoming more abundant within the montane forest. The forest also became more open, probably having the appearance of a pine-oak parkland with abundant black oak scattered among ponderosa pine. Charcoal accumulations indicate that fires were increasingly important during this period, with more frequent and possibly larger fires (Edlund 1996). Both warmer climate and increased fire activity would maintain forest openings that favor black oak. In the presence of frequent burning, black oak increase in importance relative to pines (Reynolds 1959).

The increase in fires was probably a result of the change in climate, with hotter, drier summers providing conditions suitable for burning. Although humans reached California by ~11,000 years ago and are known to have actively burned the landscape to manipulate
vegetation (Lewis 1973; Blackburn and Anderson 1993), it is unlikely that they were responsible for the vegetation changes seen between 10,000 and 6,000 cal yr BP. Native populations probably were still quite low, and there is no clear evidence that they were relying on acorns as a major food crop at this early date. In addition, after 6,000 cal yr BP, conifers—including firs, pines, and incense cedar—again increased, suggesting a return to a cooler, wetter climate (Edlund 1996; Smith and Anderson 1992). Oaks remained a minor component in the montane forests of the Sierra Nevada until the late Holocene, when evidence suggests that burning by native Californians once again favored an increase in oak woodlands at the expense of conifers (Anderson and Carpenter 1991).

**Conclusion**

The oak species that now dominate California’s landscape evolved under a radically different climate than the Mediterranean climate of today. Oaks grew alongside a mix of deciduous broadleaf trees now restricted in distribution to eastern North America and Asia characterized by summer rainfall. As global climate cooled and became increasingly arid, eastern deciduous varieties became locally extinct. Oaks became restricted to California about 5 million years ago as the rainshadow of the Sierra Nevada and Cascade Range intensified. Over the last 2 million years, oak woodlands in California have come and gone regularly with glacial cycles. During periods of glacial maxima, cool, wet climate has favored coniferous forest and oaks have nearly disappeared, isolated as small populations hanging on as refugia in pockets with suitable microclimates. During brief interglacials, oak populations have exploded, forming near monoclimax stands that dominate the Coast Ranges and Sierra Nevada foothills. Within the last 10,000 years, oak woodland populations have changed in response to climatic shifts. However, these changes are modest in comparison with the changes following the last glacial maximum. Human impacts on oak woodlands probably have been significant only within the last few thousand years, after Native Californians began utilizing acorns as a major food source. Part II of this article will review the history of California oak woodlands as they were influenced first by Native Californians, and then by the Spanish, Mexican, and American populations.

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