

Natural Range of Variation in Hardwood Vegetation In the Sierra Nevada, California Over the Holocene Epoch

By Kyle Merriam, Sierra Cascade Province Ecologist,
USDA Forest Service, Region 5
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PHYSICAL SETTING AND GEOGRAPHIC DISTRIBUTION

Hardwood vegetation in the assessment area occurs across a range of habitats and environments, including blue oak (*Quercus douglasii*) woodlands and savannahs in the lower elevations foothills, canyon live oak (*Quercus chrysolepis*) and interior live oak (*Quercus wislizeni*) growing on steep canyon slopes between foothill and higher elevation montane habitats, California black oak (*Quercus kelloggii*) and Oregon white oak (*Quercus garryana* var. *garryana*) growing in association with conifers such as ponderosa pine (*Pinus ponderosa*) at higher elevations in lower montane forests, and tanoak (*Notholithocarpus densiflorus*) mixed evergreen forests growing in association with Douglas fir (*Pseudotsuga menziesii*) in moister habitats of the northern Sierra Nevada. Hardwood vegetation is distributed along elevational and water availability gradients in the assessment area (Fites-Kaufman et al. 2007). Most species occur at higher elevations in the southern portion of the assessment area, where water availability is higher than in the northern portion of the assessment area. Similarly, most hardwood species are found on north facing slopes in areas where water availability is low, and on south facing slopes in areas where water availability is higher. The common hardwood species addressed here are more drought tolerant than other, less common hardwoods in the assessment area, such as big leaf maple (*Acer macrophyllum*), California bay (*Umbellularia californica*), and Pacific madrone (*Arbutus menziesii*), many of which are associated with riparian areas or restricted to northern, mesic forests. The common, widespread hardwoods can tolerate warmer conditions, but are less drought tolerant than, co-occurring conifers (Stephenson 1990, McDonald and Tappeiner 1996a).

A number of hardwood species found in the assessment area are addressed in other chapters of this Natural Range of Variation (NRV) assessment. Hardwoods associated with riparian corridors are described in the Riparian Chapter, aspen (*Populus tremuloides*) is discussed in the Aspen Chapter, and the shrubby forms of canyon live, interior live and Oregon white oak are addressed in the Chaparral Chapter. The Mixed Conifer and Yellow Pine Chapters describe conifer dominated vegetation types that include a California black oak and/or Oregon white oak component; however, these chapters focus primarily on conifer species. Geographic, physical, and ecological differences between the major hardwood species addressed in this chapter are summarized in **Table 1**, and described below.

Blue Oak (*Quercus douglasii*)

Geographic Distribution

Blue oak dominated woodlands and savannahs grow on low-elevation slopes and foothills of the assessment area, forming a nearly continuous band along the Sierra Nevada-Cascade foothills of the Sacramento-San Joaquin Valley. Blue oak also occupies a transition zone between annual grassland and valley oak (*Quercus lobata*) savannahs on the Central Valley floor and chaparral and mixed-conifer forests found at higher elevations. Blue oak woodlands are found between 165 and 5,900 feet, occurring at the lower end of this elevation range in the northern portion of the assessment area. Blue oak distribution also varies with aspect. In Sequoia National Park, blue oak occurs from 2,000 to 3,000 feet (600-800 m) on south-facing slopes and below 1,600 feet (500 m) on north-facing slopes (Baker et al. 1981). At lower elevations on gentle slopes, blue oak woodlands typically occur as monospecific stands. On steeper slopes and at higher elevations, blue oak

typically grows in association with grey pine (*Pinus sabiniana*), interior live oak, and California buckeye (*Aesculus californica*). In grey pine-blue oak woodlands, blue oak is usually the most abundant species, although foothill pine is taller and can eventually dominate the overstory. In higher elevation mixed oak woodlands on poor sites, blue oak may be a minor component.

Physical Setting

In general blue oak is found in mesic soils at lower elevations where the climate is very hot and dry; however, blue oak will occupy more xeric sites at higher elevations where more moderate climatic conditions can promote competition (Fryer 2007a). Blue oak-foothill pine woodlands are found on steeper, drier slopes with shallower soils than blue oak woodlands. Blue oak woodlands are generally found in areas that receive from 1000 to 300 mm mean annual precipitation (McClaran and Bartolome 1989, McDonald 1990). Most blue oak woodlands occur where mean maximum July temperatures are 90 °F (32 °C), although midday temperatures in this vegetation type can exceed 100 °F (38 °C) for extended periods (Pavlik 1991). Mean minimum January temperatures are generally around 30 °F (-1 °C) (McDonald 1990).

Canyon Live Oak (*Quercus chrysolepis*)

Geographic Distribution:

Canyon live oak occurs from Oregon to Baja California (Griffin and Critchfield 1972). Canyon live oak is common throughout lower montane conifer and mixed evergreen forests, foothill woodlands, and mixed-chaparral communities in the assessment area. It is most common at middle elevations (), but can occur between 300 and 9,000 feet (90-2,700 m). Canyon live oak grows in association with California black oak, blue oak, Oregon white oak and interior live oak over portions of its range (Tollefson 2008). In lower montane forests, canyon live oak co-occurs with ponderosa pine on harsher sites and with Douglas fir and/or sugar pine on more mesic sites (Fites 1993).

Physical Setting:

Canyon live oak is associated with steep slopes and shallow, often rocky soils where it often forms almost pure stands throughout the assessment area. However, this species can grow on a wide variety of sites including canyon bottoms, ridgetops, rock crevices, riparian areas, sheltered coves, and deep, moist, shady ravines. Canyon live oak grows in a wide variety of soils; from deep, rich soils to rocky, shallow, infertile soils where it often assumes a small, shrubby growth form with multiple trunks. On deeper soils in moister areas, canyon live oak may grow to between 60 and 70 feet tall (Standiford et al. 1996b). This species can occur in locations that receive as little as 6 inches (150 mm) and as much as 110 inches (2,790 mm) of annual precipitation. Mean temperatures in the northern portion of canyon live oak's range are 68 to 74 °F (20-23 °C) in the summer and 37 to 41 °F (3-5 °C) in the winter. In the southern portion of its range, average temperatures are 70 to 77 °F (21-25 °C) in the summer and 41 to 45 °F (5-7 °C) in the winter (Thornburgh 1990).

Interior Live Oak (*Quercus wislizeni*)

Geographic Setting:

Interior live oak tends to occur at lower elevations in northern part of the assessment area than in the south, forming mixed-oak woodlands with blue oak and valley oak in the western foot-

hills of the Sierra Nevada and with Oregon white oak in the northern portion of the assessment area. Gray pine and California buckeye are also commonly associated with interior live oak in mixed oak woodlands, which extend from about 1,000 to 2,500 feet (300-800 m) elevation in the assessment area. Interior live oak occurs with canyon live oak or alone on rocky, steep canyon slopes throughout the assessment area. At higher elevations, interior live oak can be found in mixed woodlands with ponderosa pine in the southern and central portions of the assessment area, and with Douglas-fir in the more mesic northern forests. This species also occurs in riparian communities. Its growth form varies much like canyon live oak, including both shrub and tree forms; about 25 percent of interior live oak populations occur in shrub form where it is a major component of chaparral ecosystems.

Physical Setting:

Interior live oak mostly grows on harsh, dry sites that many other hardwood species cannot tolerate. Alternately, interior live oak can also grow on deep, moist soils in riparian and other wetland areas. Interior live oak tends to occur on shallow soils in chaparral and on deeper soils in oak woodlands. Mean annual precipitation across interior live oak's distribution in the assessment area ranges from 15 to 50 inches (380-1,300 mm), with maximum summer temperatures sometimes reaching 105° F (41° C).

California Black Oak (*Quercus kelloggii*)

Geographic Distribution:

California black oak is most often found between 1500 and 1650 m in elevation, occurring at higher elevations than other hardwood species addressed in this assessment (McDonald and Tappeiner 1996b, Allen-Diaz et al. 2007). California black oak hardwood forests range in elevation from between 300 to 1800 m in the northern portion of the assessment area and from 1,200 to 2,100 m in the southern portion (Fites-Kaufman et al. 2007). The upper elevational limit of California black oak varies with evaporative demand, remaining below 1500 m on north facing aspects, and above 1500 m on south facing aspects where evaporative demand is higher (Fites-Kaufman et al. 2007). Associates of California black oak on higher elevation, good quality sites include ponderosa pine, Douglas-fir, Pacific madrone, Jeffrey pine, sugar pine, incense-cedar, and white fir. At lower elevations and on poor soils with steep slopes, associates include foothill pine, knobcone pine, tanoak, and Pacific madrone.

Physical Setting:

California black oak is most common where precipitation exceeds 625 mm annually, but can be found in areas receiving as little as 12 to 15 inches (300-400 mm) of annual precipitation in northeastern California. California black oak can grow on a wide range of slopes and soils, but is often associated with upper slope positions, gentle topography, and productive soils where it generally grows in tree form and may reach heights of 70 to 80 feet at maturity (Fites-Kaufman et al. 2007). North and east facing aspects favor California black oak in the central and southern portions of California black oak's range, while it is most often found on south and west facing slopes in the northern portion of the assessment area (McDonald and Tappeiner 1996b, Allen-Diaz et al. 2007). California black oak forests are generally found on where average summer temperatures are moderate and where average winter temperatures range from near freezing to above

40° F (Standiford et al. 1996a, Allen-Diaz et al. 2007). California black oak dominated hardwood forests may experience snow in the winter at higher elevations, but snow is not as persistent as on adjacent conifer-dominated habitats (Standiford et al. 1996a).

Oregon White Oak (*Quercus garryana* var. *garryana*)

Geographic Distribution

Varieties of Oregon white oak occur from Vancouver Island, British Columbia to southern California. In this assessment we focus on the tree form of Oregon white oak, (*Quercus garryana* var. *garryana*), which is limited in distribution to the northern portion of the assessment area. Other varieties which most often occur in shrub form are more appropriately included in the chaparral chapter of this assessment. Oregon white oak occurs in scattered populations at elevations from 1,000 to 5,000 feet, where it can dominate lower montane hardwood forests in the northern Sierra Nevada and Cascades. Oregon white oak grows to a height of 50 to 80 feet at maturity.

Physical Setting

Across its range, Oregon white oak occupies dry prairies, wooded slopes, rocky bluffs, and montane coniferous forests. Oregon white oak occurs on a variety of soils, from gravelly to heavy clay substrates, ranging from dry to very moist and poorly to rapidly draining. Annual precipitation between 20 and 50 inches (510-1,300 mm) are reported in Oregon white oak habitats in the assessment area. Throughout Oregon white oak's range, low January temperatures typically range from 13 to 50 °F (-11 to 10 °C), and high July temperatures are often 60 to 84 °F (16-29 °C). Similar to California black oak, Oregon white oak is somewhat resistant to freezing, snow and ice damage.

Tanoak (*Notholithocarpus densiflorus*)

Geographic Distribution:

Tanoak is native and endemic to southern Oregon and California. Mixed evergreen forests with a significant tanoak component occupy mid-elevation slopes averaging 1,900-4,000 feet (580-1,220 m) in the northern portion of the assessment area, where it is most common in Yuba and Butte counties (Tappeiner et al. 1990). Tanoak is often associated with Douglas fir, Pacific madrone (*Arbutus menziesii*) and other montane hardwoods.

Physical Setting:

Tanoak is most common where average annual precipitation is greater than 1,500 mm, although mean annual precipitation across tanoak's distribution ranges from 40 to 100 inches (1,020-2,540 mm) (Fryer 2008). Tanoak is absent in the southern portion of the Sierra Nevada, which is relatively drier. Tanoak requires relatively high moisture levels and mild temperatures, restricting it from xeric or cold sites. Besides growing well on deep soils, tanoak also thrives on stony and shallow soils that are less suitable for conifers. Yet tanoak requires more moisture than many other hardwoods. It will grow well on the shallow and stony soils of north slopes, for example, but will be replaced by Pacific madrone (*Arbutus menziesii*), Oregon white oak, or California black oak on warmer, drier south slopes. On unproductive sites and in the southern portion of its range, tanoak is restricted to riparian zones, shady, sheltered habitats, and north slopes.

ECOLOGICAL SETTING

Hardwood species can tolerate warmer conditions than conifers because of morphological features such as special structures and coatings on leaves and stems to inhibit moisture loss, smooth upper-stem bark to facilitate the transport of water to the base of the tree via stem flow, and an extensive root system (McDonald and Tappeiner 1996a). Many hardwoods are either winter or drought deciduous, allowing them to tolerate cold winters and/or drought through dormancy. Hardwoods are well adapted to a variety of substrates, and can enhance soil fertility through decomposition of their nutrient rich leaves (Dahlgren et al. 1997b). Although genetic variation will cause some hardwoods to grow only in shrub form, some hardwood species can assume different growth habits in response to site condition as well. For example, oaks growing on thin, rocky soils or in areas of low precipitation will often grow as shrubs, while on more productive sites these same species will grow as trees. Hardwood growth rates and time to maturity also depends largely on site conditions. California oaks on poor sites are generally slow growing, taking 30 years to produce acorns and up to 175 years to reach full maturity. Slow growth allows California oak species to occupy sites that other species cannot tolerate, and to be relatively resistant to short-term changes in climate and other environmental conditions. Most hardwood species are also able to produce large seed crops when conditions are favorable, although acorn production is highly variable and may not occur at all in some years.

Hardwood species in the assessment area have a number of adaptations that allow them to tolerate disturbances, most importantly the ability to sprout from cut stumps following fire, grazing, or other disturbances that kill above ground stems (McDonald and Tappeiner 1996a). Sprouting can be vigorous, with up to 100 sprouts observed emerging from a single stump. Growth rates of sprouts can also be high, allowing them quickly reoccupy original sites after disturbance. For example, McClaren (1986) reported that growth rates of blue oaks establishing within one year of fire were significantly greater than growth rates of blue oaks establishing at other times. Even first year seedlings and saplings can resprout after being top-killed by fire or other disturbances (Standiford et al. 1996b).

Differences among key hardwood species in the Sierra Nevada

Although hardwoods in the assessment area share many adaptations to ecological disturbances such as fire, there are important differences between species. Primarily as a result of differences in bark characteristics, many hardwood species differ in their response to fire. Mature California black oak, Oregon white oak, and blue oak can survive low to moderate intensity fire, while canyon live oak and interior live oak have relatively thin bark that makes them more susceptible to top-kill even by low intensity fire (Plumb 1979). Even relatively fire resistant species such as California black oak have bark that is thinner than that of ponderosa and sugar pines of similar size, making it more sensitive to moderate-severity fire than associated conifers in lower montane forests (Skinner et al. 2006). Seedlings and saplings of all hardwood species are more susceptible to mortality from fire than mature trees (Holmes et al. 2008).

Hardwood species in the assessment area vary in their tolerance to drought. With the exception of tanoak, which grows in mesic areas with average annual precipitation greater than 203 cm (80 in), the common, widespread species addressed here are more drought tolerant than most Califor-

nia hardwoods, many of which are restricted to riparian habitats. Evergreen sclerophyllous taxa are often considered to be best adapted to the Mediterranean climate; however, in California, deciduous oaks are very well adapted to the Mediterranean climate as well (Blumler 1991, Mensing 2005). For example, the deciduous blue oak tolerates the driest climate of all California tree oaks, including the live oaks, and can grow in areas where temperatures exceed 38°C and annual precipitation is less than 250 mm (Pavlik 1991, Mensing 2005). Knops and Koenig (1994) found that among five associated oak species, blue oak was the most drought tolerant based on xylem water potentials. California black oak is among the most drought tolerant of hardwood species in the lower montane forests (Fites-Kaufman et al. 2007). On the other hand, most hardwood species in the assessment area are not well adapted to snowy or cold sites, with the exception of California black oak and Oregon white oak, which generally replace interior live oak and canyon live oak at higher elevations.

Wildlife Use and Biodiversity

Hardwoods provide important habitat for diverse communities of plants and animals. Oak species, with their large, nutrient rich acorns, may be the single most important genus used by wildlife for food and cover in California forests and rangelands (Fryer 2007b). California oak woodlands provide habitat for over 300 vertebrate wildlife species; more than 2000 plant species; and an estimated 5000 species of insects (Allen-Diaz et al. 2007). A three year study in the central Sierra Nevada foothills showed that 92 species of birds utilized blue oak woodlands, with 60 species nesting there (Block and Morrison 1990). Hardwood forests also provide downed woody debris and snags critical for many other species of wildlife, including reptiles, amphibians, and insects. Oak species are susceptible to stem rot, which creates large cavities in the tree bole that are used for nesting by many bird and mammal species (Motroni et al. 1991). Hardwood tree cavities filled with rainwater or detritus provide habitat unique invertebrate communities, some of which are entirely restricted to these cavities during a portion of their life cycle.

Rare and threatened species

A number of rare and threatened wildlife species depend on hardwoods in the assessment area. California spotted owls use blue oak, California black oak, tanoak, canyon live oak, and interior live oak for nesting, foraging, and cover (McKelvey et al. 1992, Steger et al. 1997). Mixed-evergreen forests with tanoak provide habitat for fishers (Zielinski et al. 2004), and the presence of California black oak and other hardwoods have been found to increase habitat quality for fishers in mixed-conifer forests (Zielinski et al. 2004). Rare and threatened species found in blue oak woodlands include bald and golden eagles, peregrine falcons, western spadefoot toads and the state-endangered foothill yellow-legged frog (Fryer 2007a), (Verner and Boss 1980).

CULTURAL SOCIOECONOMIC SETTING

Hardwood species were used extensively as food and raw material for basketry, tools, and clothing by Native Americans in the assessment area (Wolf 1945, Baumhoff 1963). During early European settlement beginning with the Gold Rush in 1849, lower elevation oak woodlands were logged for mining related construction and infrastructure and for fuel wood. Since the early 20th century, these oak woodlands have also been managed for livestock production (Holzman and Allen-Diaz 1991). Until the early 1970s, a number of studies showed that forage production increased with oak removal (see review by (Fryer 2007a) leading to statewide rangeland improvement projects resulting in the loss of more than 1 million acres (0.4 million ha) of blue oak woodland from cutting, burning, and herbicides (Fryer 2007a). More recently, lower elevation hardwood woodlands have also been extensively lost and fragmented for housing and commercial developments in the foothills of the assessment area.

Other cultural values of hardwoods include wildlife use described above, watershed protection, aesthetics and wood products (McDonald and Huber 1995). Utilization of Sierra Nevada hardwoods for lumber and wood products began with the Gold Rush of 1849. Although lower elevation woodlands are rarely utilized for lumber today, primarily as a result of their strongly curved and branched growth forms that reduce lumber quality, lower montane hardwoods such as California black oaks can be valuable timber trees for making cabinets, furniture, flooring, high-grade lumber, pallets, and industrial timbers (McDonald and Huber 1994). Widespread hardwood logging in lower montane forests has been avoided because is more difficult and expensive than softwood logging as a result of widely dispersed trees and stands, lack of concentrated stocking, and logistical challenges of skidding and loading heavy, curved and branched hardwood logs. Most hardwood species are used as fuel wood as well as habitat restoration where they can help reduce erosion and protect watersheds (McDonald 1969). For example, canyon live oak's deep root system and its ability to grow on rocky, unstable sites make it useful for soil stabilization on steep slopes (Thornburgh 1990).

NRV COMPOSITION

Indicators and Variables

Indicators of composition in hardwood vegetation types over the NRV period include species composition, geographic distribution, and species diversity. Indicators associated with succession, including variables such as the proportion of late and early seral, shade tolerant and intolerant, and hardwood and conifers are also briefly described here, as well as changes in the proportion of perennial and annual species since European settlement.

Changes in hardwood composition over the NRV period are primarily evaluated using pollen records, as described in the Methods Chapter of this assessment. These records provide detailed information about changes in the presence and abundance of oak (*Quercus*) pollen at a number of sites. However, pollen data for other hardwood species are generally lacking, and species level identification of oak pollen grains is difficult (Mensing 2005). Although inferences to species can be made based on the elevation of the pollen record site, patterns addressed here generally focus on oaks, but not specific hardwood types or species.

Species composition

Anderson and Davis (1988) demonstrated that pollen samples can indicate not only the presence or absence of taxa, but their abundance as well, roughly in proportion to their pollen sum. Their evaluation of oak pollen found that 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 as a minor component of the plant community in the region, sums between 5 and 30 percent suggest that oaks are locally abundant, and pollen sums of 30 to 40 percent represent oak-dominated landscapes (Anderson and Davis 1988). We can therefore use pollen diagrams to infer both diversity and composition.

Mensing (2005) reviewed studies by (Mackey and Sullivan 1986, Davis and Moratto 1988, Edlund and Byrne 1991, Smith and Anderson 1992) conducted near the modern upper-elevation limit of California black oak (between 1,500 and 2,000 m) to illustrate similarities in patterns of vegetation change in lower montane forests from 15,000 ybp to present. Edlund and Byrne's (1991) diagram (**Figure 1**) shows percent pollen of different species over time in sediment taken from Lake Moran (elevation 2107 m). This record that demonstrates a strong, but representative pattern of change in oak and other species pollen abundance over the past approximately 15,000 years at mid-elevations in the Sierra Nevada (Millar and Woolfenden 1999). Mensing (2005) describes that late Pleistocene (i.e. 15,000 to 10,000 ybp) records from these sites reveal a plant community dominated by juniper, incense cedar, sagebrush, and pine pollen. Approximately 15,000 ybp, oak species were relatively rare and the site was dominated a dense, closed canopy forest including species whose distributions no longer overlap in the Sierra Nevada. Summers were sufficiently warm to support sugar pine (limited to <2100 meters elevation in the central Sierra today), while moisture was adequate for the survival of mountain hemlock, today restricted to high elevation sites (generally > 2500 meters) with abundant snowpack.

At the start of the Holocene, approximately 10,000 ybp, oaks became a significant component of the Sierra Nevada montane forest, with oak pollen comprising between 20 and 30 percent of the total pollen rain around 7,000 to 6,000 ybp (Byrne et al. 1991, Smith and Anderson 1992, Mensing 2005). These were mostly California black oak and shrubs such as huckleberry oak (*Quercus vaccinifolia*) (Standiford et al. 1996b). During this period, the pollen record also indicates that oaks were associated with understory species characteristic of open, seasonally dry regions, such as perennial grasses (Bartolome 1989, Holmes 1990, Standiford et al. 1996b, Allen-Diaz et al. 2007).

Work by (Mackey and Sullivan 1986, Davis and Moratto 1988) Davis and Moratto 1988 indicates that some lower elevation taxa increased in importance at higher elevations in the early and middle Holocene, approximately 10,000-5,000 ybp (Mensing 2005). Even species of oaks that are now found only at low elevations in the Central Valley and foothill regions, such as blue and valley oak, were present at higher elevations between 10,000 and 5,000 ybp (Byrne et al. 1991). Mensing (2005) concluded that low-elevation oak woodlands became well established in their current ranges during the mid-Holocene, while higher-elevation oak populations, including California black oak and canyon live oak, decreased to become a minor component of lower montane forests after 6,000 ybp, being generally replaced by fir species (Byrne et al. 1991, Edlund and Byrne 1991, Smith and Anderson 1992).

Compositional changes associated with succession

Changes in the proportion of late and early seral, shade tolerant and intolerant, hardwood and conifer, and woody and herbaceous species are briefly described here as they relate to the composition of hardwood forests over the NRV period. Successional processes in hardwood forests are also described in the Function section below. The pollen record suggests that hardwood vegetation types have experienced repeated episodes of succession following changes in climate and disturbances such as fire (**Figure 2**). At the beginning of the Holocene, drier climates and increased fire activity shifted most hardwood vegetation types to an early seral state, resulting in greater abundances of hardwoods and other shade intolerant species. Open conditions associated with these early seral habitats also supported an increase in herbaceous understory species. As climates cooled approximately 4,500 ybp, these communities gradually shifted back to one dominated by conifers, with a greater proportion of late seral, shade tolerant species, and a decrease in herbaceous understory species. The pollen record at several sites indicates this process has occurred at least several times during the NRV period.

Diversity

Although the distribution of hardwood species has changed significantly over the NRV period, at the landscape scale plant diversity appears to have changed little (Millar and Woolfenden 1999). Species associated with hardwood forests and other vegetation types have remained within approximately the same geographic area and distinct from species characteristic of other regions, throughout the Quarternary (dates) (Millar and Woolfenden 1999).

Current Conditions and Comparison with NRV

Current conditions and comparison with NRV for species composition, successional indicators, and diversity are described in combination here. As described in the Invasives section, the greatest change in species composition in hardwood vegetation types since European settlement has been the displacement of native understory species by alien annuals from Europe, Asia, Africa and South America. Exotic species were first introduced to California during the Spanish mission days, and since that time the understory vegetation of hardwood woodlands, and to a lesser extent lower montane forests, has changed dramatically (Standiford et al. 1996b, Allen-Diaz et al. 2007). As a result of nonnative invasive species, Holzman and Allen-Diaz (1991) found that species diversity in blue oak woodlands had increased by two new species per plot between 1932 and 1990. The invasion of nonnative species has likely reduced the abundance of both native perennials and annuals, shifting species composition to one that is comprised almost totally of annuals, particularly of lower elevation blue oak forests and woodlands (Heady 1977, Bartolome et al. 1986, Holmes 1990, Allen-Diaz et al. 2007).

Geographic Distribution

Fossil evidence shows that all of California's oaks were present in western North America by about ten million ybp and began to occupy their current ranges by about five million ybp (Millar 1996, Mensing 2005). The restriction of oaks to their modern ranges coincided with the transition of the mild and humid climate of the Early Miocene to the drier, warmer, and more seasonal Mediterranean climate typical of California today (Mensing 2005). Prior to 10,000 ybp, persistent snowpacks and the relative absence of fire may have maintained the dominance of dense coniferous forest types (Standiford et al. 1996b). Since the beginning of the Holocene (10,000 ybp) variation in the geographic distribution of hardwood forests has largely occurred along elevational gradients (**Figure 3**), (Anderson and Smith 1994, Standiford et al. 1996b, Millar and Woolfenden 1999). Increased charcoal accumulations indicate that fires became more frequent and possibly larger between 8,000–6,000 ybp; at this time oaks were also becoming more abundant and expanding their ranges to higher elevations (**Figure 4**) (Byrne et al. 1991, Edlund and Byrne 1991). It is likely that increasing drought stress and fire activity caused this relatively quick compositional change from a fir dominated forest to one dominated by oaks (Byrne et al. 1991). Pollen evidence from higher elevation sites between 1,500 and 2,000 m, including Gabbott Meadow (Mackey and Sullivan 1986) in the central Sierra Nevada, Swamp Lake and Lake Moran sites in the Stanislaus drainage (Byrne et al. 1991), and further south at Exchequer Meadow (Davis and Moratto 1988) show an increase in oak pollen at higher elevations than their current distributions, with maximum pollen abundances occurring between approximately 8,000-6,000 ybp (Byrne et al. 1991, Mensing 2005) (**see Figure 4**). Lower elevation sites, dominated by blue oak and interior live oak, exhibit a similar pattern, with oak pollen increasing after deglaciation 10,000 ybp and reaching maximum levels approximately 8,000 to 7,000 ybp (Byrne et al. 1991).

When the climate began cooling approximately 6,000 ybp, oaks became much less common in lower montane forests, with oak pollen percentages averaging only 3 to 10 percent (Edlund 1996; Smith and Anderson 1992). At lower elevation sites, on the other hand, oak pollen remained high throughout the Holocene (Byrne et al. 1991). Higher elevation oaks remained a minor compo-

ment of montane forests in the assessment area until the late Holocene, when evidence suggests that burning by Native Californians (described in the Fire section below), and later widespread logging, once again favored an increase in hardwoods at the expense of conifers (Anderson and Carpenter 1991).

Current Conditions and Comparison with NRV

The most significant change in the distribution of hardwoods in the assessment area has been the loss of lower elevation blue oak woodlands as a result of conversion to agriculture and low density rural residential development (Spero 2001). Many of the remaining low elevation woodlands have been degraded by intensive livestock grazing, climate change, and fire suppression. Thorne et al. (2008) examined vegetation changes between 1936 and 1996 in the northern Sierra Nevada and found that loss of blue oak woodlands and increase of grasslands were the dominant trends at low elevation, with the distribution of low elevation oak woodlands decreasing by 50 percent. Species occurring at higher elevations and more frequently on public land, such as California black oak, appear to have increased in distribution since the NRV period. In a review of forest vegetation changes between the 1930's and the present, Thorne et al. (2008) found that California black oak, interior live oak and canyon live oak had increased by almost 300 percent between 1936 and 1996. Conversely, the extent of ponderosa pine was reduced by 64 percent. Thorne et al. (2008) suggested this pattern was either due to a loss of conifer overstory where California black oak was a sub-dominant and able to persist, or a result of succession, where California black oaks was able to become dominant following fire or logging. This pattern of lower ponderosa pine forests being replaced by oaks was also observed in 1934, when Weeks *et al.* (1934) estimated that the conifers had been present at elevations as low as 305 m in 1850, but had been limited to much higher elevations since that time.

Projected Future Trends

The Oaks 2040 survey estimated that 750,000 acres (3,000 km²) of lower elevation oak woodlands are seriously threatened as a result of population growth and urbanization (Gaman and Firman 2006). Grazing and climate change were also identified as major threats to these systems.

NRV STAND STRUCTURE

Indicators

Indicators of structure in hardwood forests and woodlands include attributes such as canopy cover, density, basal area, age and size class distributions, coarse woody debris volume, snag density, litter and duff depth, and patchiness. Only a few of these measures have been estimated for hardwoods during the NRV period; values for other indicators are inferred from modern sources where disturbance processes have not been significantly altered since the NRV period.

Canopy cover, density and basal area

Pollen and macrofossil data indicate that for at least a thousand years prior to the beginning of the Holocene (10,000 ybp) much of the assessment area was characterized by dense, closed canopy forests (see reviews by (Millar and Woolfenden 1999, Mensing 2005). An abundant snowpack probably limited the presence and abundance of hardwood species, and oak pollen is relatively absent from sediment cores at this time. A shift to a warmer, drier climate at the beginning of the Holocene, accompanied by increased fire activity during that time, caused a shift in species composition from dense conifer forests to one dominated by oaks (see Species Composition discussion above). Between about 10,000 and 5,000 ybp, frequent fires caused a general thinning of oak forests, creating more open stands with lower tree densities, basal areas, and canopy cover (Bartolome 1989, Byrne et al. 1991, Holzman and Allen-Diaz 1991). Frequent, low severity fire between 10,000 and 5,000 ybp would have maintained open stand conditions by thinning young fire-sensitive conifers and shrubs and by selectively retaining larger, fire resistant trees (Van Wagtenonk and Fites-Kaufman 2006). As the climate began to cool during the late Holocene, beginning around 5,000 ybp, increases in stand density, canopy cover, and basal areas were accompanied by shifts back to more dense, conifer dominated forests.

Modern references to sites where fire has been reintroduced may provide some insight into the cover, density and basal areas of hardwoods during the NRV period. Roy and Vankat (1999) conducted a survey to evaluate the effect of a prescribed burning program conducted in Sequoia National Park beginning in the 1960s. They found that overall forest density was lower in burned compared to unburned plots (**Table 2**). An earlier study in the same area (Vankat and Major 1978) found that prescribed burning had reduced tree density in the blue oak woodlands by 19 percent, and by 15 percent in the live oak woodlands, indicating that lower tree densities are associated with more active fire regimes typical of the NRV period.

Gruell (2001) provides a series of repeat photographs, starting in 1849, that document extensive, open ponderosa pine-California black oak woodlands in the Sierra Nevada in the mid-1800s. Pioneer naturalists (Muir 1901) and (Jepson 1921) also described open, park-like forests in low elevations of the Sierra Nevada. Hardwood species were a large component of these open forests; General Land Office survey data collected in the late 1800s showed that California black oak represented between 23 and 28 percent of total stems per acre at that time (Fites-Kaufman et al. 2007).

Current Conditions and Comparison with NRV

Using extensive historical and modern forest inventories, Dolanc et al (In review) compared montane forest structure in the early 1930s with modern (2001-21 2010) conditions across the northern two-thirds of the Sierra Nevada (~45,000 km²), along an elevational gradient from near sea level to ~4000 m. They examined species-specific changes in density of all the most common tree species. Their findings highlight changes in hardwood density and cover in the modern period. The authors found that densities of small trees (10.2 to 30 cm dbh) increased significantly from historical to modern periods. The greatest proportional changes occurred between 500 and 2000 m in elevation, where most hardwood vegetation is found. Overall, stand densities had increased by an average of 33.5 stems per ha between the 1930s and 2000s. Percent changes in density observed for individual hardwood species include: 1) 145 percent increase for interior live oak; 2) 156 percent increase for canyon live oak; 3) 168 percent increase for tanoak, and 4) 10 percent increase for interior live oak (Table 3). Blue oak showed no significant increase. Dolanc et al. (in review) found that the density of large trees (>61.0 cm dbh) had decreased, so that forests in the assessment area are generally denser and contain more small trees than in the 1930s. The authors concluded that these demographic trends appear to favor hardwood species in mixed evergreen and mixed conifer forests, and that the increase in small tree density is primarily a result of fire suppression, although historic logging practices may have also increased the density of hardwoods in lower montane forests due to prolific sprouting after widespread logging (Bolsinger 1988). Other authors have also observed increased density, canopy cover, and basal area among hardwood species over the past century, including tan oak (Holzman and Allen-Diaz 1991, Atzet 1996), interior live oak (Vankat and Major 1978), canyon live oak (Holzman and Allen-Diaz 1991), and mixed oak forests (Stephens 1997). Most authors also attribute these changes to fire suppression and forest management practices such as logging.

Dolanc et al. (in review) found no change in blue oak densities between 1930 and 2000. However, a number of other authors have documented increases in density, cover and basal areas at the stand scale in low elevation blue oak woodlands. Repeat photography studies near Sequoia-Kings Canyon National Park showed a large increase in blue oak cover and density beginning in the late 1800s (Vankat and Major 1978). A number of authors have shown increased blue oak recruitment between 1850 and 1890, leading to increased stand densities in some modern stands of blue oaks (Vankat and Major 1978, Bartolome 1989, Holzman and Allen-Diaz 1991, Mensing 1992). Vankat and Major (1978) hypothesized that livestock grazing in the nineteenth century initiated the density increase by removing herbaceous competition for blue oak seedlings and decreasing fuel levels, so that fires were less intense. Swiecki et al. (1993, 1997b, 1997c) suggests this increase was related to the release of existing seedlings after removal of the mature blue oak overstory through widespread cutting and clearing during early European settlement. However, at the landscape scale, widespread clearing, grazing, and lack of recruitment has led to widespread losses of blue oak woodlands throughout the assessment area.

Projected Future Trends

Low rates of regeneration currently observed in blue oak woodlands suggest that stand densities will decrease in the future (Muick and Bartolome 1986, Bolsinger 1988, Swiecki et al. 1997c)

Age and size class distribution

Although we do not have direct evidence for age and size class distribution of hardwood woodlands and forests over the past 10,000 years, data collected in more recent times provides some insight into factors that likely influenced these indicators over the NRV period. As a result of post-fire sprouting, the distribution of hardwood size class is usually related to the fire history of the site (Mensing 1992). For example, McClaran and Bartolome (1989) compared blue oak stand structure with fire history and showed that recruitment was associated with fire events; with most recruitment occurring during periods of high fire frequency in the 1880s to 1940s. Stand structure in hardwood woodlands and forests likely included more size classes during periods of more active fire regimes, when heterogeneity in fire size and severity resulted in a variety of size classes across the landscape (Stephens 1997). Low grazing utilization by native grazers would have allowed more hardwood seedlings to establish and grow into larger size classes, and the presence of native predators would have reduced populations of small mammals that can significantly reduce hardwood recruitment (Swiecki et al. 1997b), resulting in higher numbers of seedlings and saplings in most hardwood stands during the NRV period.

Current Conditions and Comparison with NRV

Although there have been large increases in the numbers of small trees (described in the canopy cover and density section above), hardwood seedlings and saplings in modern hardwood forests and woodlands are often rare or absent (Griffin 1977, Bolsinger 1988). Examinations of black oak woodlands have found that most trees are 75 years or older, and although acorn production and germination appear to be occurring, sapling survival is low (Standiford et al. 1997, Kuhn and Johnson 2008, Ripple and Beschta 2008). In Yosemite National Park, the younger size classes of California black oak are almost entirely absent (Kuhn and Johnson 2008, Ripple and Beschta 2008). In stands where fire has been excluded, there is a trend towards mostly mature (>50 years) California black oaks, few seedlings and sprouts, and almost no saplings.

Although blue oak seedlings are plentiful on some sites, saplings and pole-sized trees are generally rare, and several researchers have suggested that current sapling recruitment is not sufficient to offset losses of mature blue oaks (Muick and Bartolome 1986, Bolsinger 1988, Swiecki et al. 1993, Swiecki et al. 1997b, Swiecki et al. 1997c, Swiecki and Bernhardt 1998). Mature blue oaks in many stands can range up to over 400 years in nominal age (Bartolome et al. 1986), and blue oak seedlings may require up to 30 years to transition to the sapling stage, a process that can be repeatedly set back by top killing events such as grazing or fire (McClaran and Bartolome 1989, Bernhardt and Arnold 1991, Swiecki et al. 1997b, Swiecki et al. 1997c, Swiecki and Bernhardt 2001).

On the other hand, seedling and sapling density data suggest that canyon live oak does not have a regeneration problem. Seedlings were found on 94 percent of the canyon live oak vegetation type sampled throughout California, and saplings were found on 81 percent of this type (Bolsinger 1988). In the southern Sierra Nevada, canyon live oak seedlings were present in 75 percent of oak woodland plots sampled, and saplings were present in 48 percent of plots (Standiford et al. 1997).

Altered fire regimes, grazing, climate change and invasive species have all been implicated in the lack of recruitment observed among hardwood species in the assessment area (Standiford et al. 1996b, Tyler et al. 2006). Since young, vigorous blue oaks can stump sprout readily, while older, decadent trees cannot, younger stands are more likely to regrow after fires and very frequent fires can exhaust the sprouting capability of even young trees (Swiecki and Bernhardt 2001). Browsing by cattle, deer, and rodents can significantly reduce seedling and sapling recruitment (Swiecki et al. 1997b, Swiecki et al. 1997c, Davis et al. 2011). Bartolome (1989) suggested that seedling survival and regeneration may be tied to climatic shifts, as indicated by regional differences in the regeneration of blue oak, which appear to be regenerating better in areas with higher rainfall (Muick and Bartolome 1986). Blue oak savannas occurring in areas that currently receive less than 750 mm annual rainfall could have established during the wetter periods, such as the little ice age between 1500 and 1850, with infrequent new establishment since. Standiford et al. (1991) found blue oak saplings in Madera and Kern counties were more common on relatively high-elevation sites than on low-elevation sites that received less rain, and suggested that moisture may limit blue oak sapling recruitment. Introduced annual grasses can out-compete blue oak seedlings for soil moisture and provide habitat for small mammals that browse seedlings (Gordon et al. 1989, Gordon and Rice 1993, Swiecki et al. 1997b). Increased overstory canopy cover can also negatively affect seedling establishment, which is often associated with canopy gaps (Swiecki et al. 1997b).

Patch Size

There is little direct evidence for patch sizes in hardwood forests and woodlands throughout the NRV period. Patch sizes in modern hardwood types are generally related to fire regimes, and it is likely that patch sizes throughout the NRV period fluctuated with changes in fire size and severity (Skinner and Chang 1996). The size and frequency of high severity fire is probably the strongest indicator of patch size, as stand replacing events often delineate the area of hardwood dominated vegetation occurring post-fire, because hardwoods are well adapted to quickly colonize sites after stand replacing disturbances, provided there were at least some mature adults present on the site prior to disturbance (see Ecological Condition section above). In lower montane hardwood forests containing California black oak and Oregon white oak, high severity, stand replacing fires were probably rare, but not altogether absent during the NRV period (see Fire discussion below). Long-term data from giant sequoia stands in lower montane forests containing black oak suggests that although large surface fires were predominant, high severity fire did occur historically in small patches (Parsons 1981, Stephenson et al. 1991, Caprio and Swetnam 1995). Patchy stand-replacement fire is important in maintaining California black oak stands because it can reduce the density of competing conifer species (McDonald 1969), and pioneer accounts (Leiberg 1902) of persistent California black oak stands within ponderosa pine and mixed-conifer forests suggest that stand-replacement fire did occur occasionally at small scales. Mixed evergreen and tanoak forests are more likely to contain larger patches created by high severity fire than other hardwood types. The moister conditions typical of tanoak dominated forests, and higher foliar water content of tanoaks, reduces fire severity in most years but allows fuels to accumulate leading to large high severity fires at longer fire return intervals. Lower elevation forests, such as blue oak woodlands, probably did not experience much high severity fire during the NRV period, but fine scale heterogeneity was likely promoted by canopy gap recruitment events (Swiecki et

al. 1997b). Canyon live and interior live oak woodlands and forests may have occurred in patch sizes concurrent with fire regimes in these types during the NRV period, including mostly homogenous stands where fire was historically of low severity, and more heterogeneous conditions characterized by smaller patches on steeper slopes, north facing aspects, and other areas where fire regimes were more often characterized by mixed severity fires, including small areas of high severity.

Current Conditions and Comparison with NRV

It is likely that Sierra Nevada hardwood forests and woodlands are more homogenous, with very little fine scale patch structure, than during the NRV period as a result of fire suppression, clearing, grazing and other management practices (Van Wagtendonk and Fites-Kaufman 2006). Recent increases in both the size and severity of fires as a result of fuels accumulation and climate change also may have increased patch sizes in some hardwood vegetation types since the NRV period.

Coarse woody debris, snag density, duff and litter depth

There is no direct evidence for the amount of coarse woody debris (CWD), snags, duff and litter in hardwood forests and woodlands in the assessment area during the NRV period. Many of the factors that determine the production and character of these variables, including inherent tree characteristics, insects, diseases, windstorm, drought, and old age, generally have not changed since the NRV period. Therefore, modern information about the potential for hardwoods to produce CWD, snags, and duff and litter is presented here. However, the actual amount of CWD, snags, and duff and litter in hardwood forests and woodlands is strongly controlled by fire, and are described in the Current Conditions section below.

As described in more detail in the Insects and Disease section below, most California oaks are susceptible to heart and root rot fungi that decay the inner heartwood of living trees and promote the production of CWD by killing branches and ultimately entire trees (McDonald 1990, Bull et al. 1997). Fire and drought can also kill and weaken trees, creating snags and eventually CWD (Tietje et al. 1993). It is likely that during the NRV period, active fire regimes both promoted the production of CWD and snags, and reduced the amount of CWD through consumption.

Tietje et al. (2002) found the highest volume of CWD in California black oak forests, and (McDonald 1969) also suggested that this species adds substantially to large woody debris fuel loads. An inventory of dead crown fuels in ponderosa pine and California black oak stands in the northern portion of the assessment area showed that California black oak had significantly more dead branches per tree than ponderosa pine (Garrison et al. 2002), particularly large California black oaks infected with Pacific mistletoe (*Phoradendron villosum*).

Snags

Hardwood snags tend to be rare. For example, an inventory on the Modoc and Lassen National Forests showed a total of four California black oak snags in 24 five-ha plots (Laudenslayer 1999). Hardwoods generally sprout after top-killing events, limiting snag formation to tree mortality. Relatively young stands have limited mortality, often occurring only in small diameter suppressed trees that do not persist as snags for very long. Decay from various rot promoting fungi

(see also Insect and Disease section) is the most common causes of mortality of trees in the largest size classes, and generally results in bole failure causing the tree to fall and instead of remaining standing as a snag. However, a declining, highly decayed standing hardwood tree provides most of the habitat features found in snags.

Duff and Litter

Although evergreen species such as interior and canyon live oak contribute less leaf litter to the soil than deciduous species such as blue, California black, and Oregon white oak, faster rates of decomposition of deciduous leaves may result in similar contributions of litter and duff to the forest floor among these species. Average annual litter accumulation under a 75-year-old California black oak stand in the Sierra National Forest was 0.6 ton/acre, and total litter accumulation was 6.2 tons/acre. Plumb and Gomez (1983) report that the litter layer of interior live oak is typically thick (7 inches deep or more), but the amount of litter and duff at a site primarily depends on the time since the last fire.

Current conditions and comparison with NRV period

Changes in the amount and composition of CWD, snags, and duff and litter in hardwood forests and woodlands since the NRV period are likely the result of fire suppression, grazing, and non-native annual grass invasion. Fire exclusion has resulted in a major increase in understory fuels in lower montane forests containing California black oak (Taylor and Skinner 2003, Riegel et al. 2006, Van Wagendonk and Fites-Kaufman 2006). Conversely, Tietje et al. (2002) conducted an extensive forest inventory to estimate the amount and distribution of CWD on 5.6 million acres of lower elevation woodlands in California and found that almost three million acres (61 percent of the sampled area) were estimated to have no CWD. The authors concluded that CWD is not common across much of California's lower elevation woodlands today (**Table 4**). In blue oak ecosystems, changes in fuel loads caused by annual grass invasion has created a more continuous and earlier drying litter layer, resulting in increased rates of fire spread and altered fire seasonality. Livestock grazing may reduce annual grass fuels, depending upon livestock utilization, however, fuel loads may be heavy where livestock are excluded or utilization is low to absent (Standiford 1996). In an interior live oak-valley oak community dried annual grasses comprised a far larger proportion of the ground layer (26.3%) than did evergreen leaves (0.6%) (Tietje et al. 2002).

NRV FUNCTION

Indicators and variables

In this section we assess indicators of ecological function in hardwood forests and woodlands over the NRV period, including climatic variables such as patterns of glaciation and extreme climatic events such as drought. We also address the role of fire as an important indicator of function in hardwood vegetation types, including fire return interval, fire severity, and fire season. Other important functional indicators in hardwood forests and woodlands addressed here include grazing, insects and disease, successional patterns, soil properties, and other, less common disturbance process. We also examine modern functional indicators such as the presence of invasive species and management practices such as logging that influence hardwood woodlands and forests today.

Climate/Drought

Hardwood species have been resilient to climatic fluctuations and extreme climatic events since they first evolved between 12 and 26 million years ago (Standiford et al. 1996b, Millar and Woolfenden 1999). The oak species that are now common in the assessment area evolved under a radically different climate than the Mediterranean climate of today. Initially, oaks grew alongside a mix of deciduous broadleaf trees now restricted to eastern North America and Asia in climates characterized by summer rainfall (Axelrod 1983, Mensing 2005). As the global climate cooled and became increasingly arid, and the rain shadow effect of the Sierra Nevada and Cascade Range intensified about between 11 and 5 million years ago eastern deciduous hardwoods became extinct and common hardwoods in the assessment area became mostly restricted to California (Mensing 2005). Over the last two million years, the distribution and abundance of oak woodlands in the assessment area have fluctuated in response to glacial cycles (**Figure 5**). (Mensing 2005). During periods of glacial maxima, the cool, wet climate favored coniferous forests, and oaks nearly disappeared, remaining only as small, isolated populations in refugia with suitable microclimates. During brief interglacial periods, oak populations expanded, often forming near monoclimate stands.

Within the last 10,000 years, hardwood populations have continued to change in response to more moderate climatic shifts. These patterns suggest that hardwood species have been positively associated with warm, dry periods in the assessment area over the NRV period. Pollen records indicate that oak species were most abundant during warmer, drier periods of the NRV period, and were reduced in abundance and extent during cooler, wetter periods over the past 10,000 years. The most dramatic increase in oak pollen coincided with a significant warming trend beginning about 10,000 and 8,000 ybp, and lasting until approximately 5,000 ybp. This early Holocene period moved the region's climate from one that was much colder than today, to one that was much hotter and drier than today (Bartolome 1989). Pollen records from across the assessment area demonstrate that oak pollen increased during this time (Mensing 2005). The regional climate of the assessment area then became wetter and cooler approximately 5,000 ybp (Davis et al. 1985), accompanied by a decrease in oak pollen in lower montane forests. On the other hand, at lower elevation sites oak pollen remained high throughout the Holocene (Byrne et al. 1991).

Projected Future Conditions

Predicting future climates is extremely complex, most models agree that temperatures in the assessment area will warm between 2.6 to 3.9°C by 2100 (Gonzalez et al. 2010). Projected changes in precipitation are more equivocal; of the 18 general circulation models that include California, about half predict decreases and half predict increases in precipitation for the assessment area. These changes could have a number of consequences for hardwood vegetation types. For example, longer dry seasons may compromise oak recruitment, as seedling survival is dependent on sufficient rainfall (Pavlik 1991, Tyler et al. 2006, Davis et al. 2011). Lower elevation hardwoods, such as blue oak, are predicted to experience high climate stress at the lower limits of their range (Cayan et al. 2008), which may lead to loss of oak habitat, especially on drier south facing slopes. Blue oak expansion upslope beyond the current range is predicted if dispersal is sufficient and soils are suitable (Cayan et al. 2008). Projected future climate change also may affect hardwoods by altering fire regimes. Different climate change scenarios produce divergent projections of future fire probability for the lower elevations of oak woodlands, but agree on generally higher fire probabilities for upper elevations hardwood and mixed conifer forests. Higher fire probability could be beneficial or detrimental for oak woodlands and research on the subject is mixed. Some studies suggests that increased fire activity may favor hardwood species, particularly in lower montane forests where conifers have encroached hardwood stands (Thorne et al. 2008). On the other hand, very frequent fire or high severity fire can significantly suppress hardwood recruitment (Swiecki and Bernhardt 2001, Holmes et al. 2008).

Fire

Fire has been an ecological process in the assessment area since glacial retreat more than 10,000 years ago (Van Wagtenonk and Fites-Kaufman 2006). The presence of charcoal throughout the paleoecological record indicates that fire activity has varied according to changes in climate during the NRV period (Davis et al. 1985, Anderson and Smith 1997). Variation in the abundance of charcoal also coincides with rapid changes in the abundance of hardwood vegetation, suggesting that fire and climate have been the primary drivers for changes in the abundance and distribution of hardwoods over the NRV period (Edlund and Byrne 1991, Millar and Woolfenden 1999, Mensing 2005). The first charcoal peak in the Holocene epoch occurred between 9,500 and 8,700 ybp (Anderson and Smith 1997) (**Figure 3**). At this time oak pollen significantly increased at a number of sites in the Sierra Nevada (Mensing 2005).

Very low charcoal abundances between 8,700 to 4,500 ybp indicate warm, dry conditions that created open, sparse forests with low biomass and flammability (Anderson and Smith 1997, Millar and Woolfenden 1999). Frequent, low severity fires were likely common during this time, and oak pollen remained high throughout most of this period. A second charcoal peak around 4,500 ybp is associated with a second increase in oak pollen. From 4,500 ybp ago until the early 20th century, charcoal has been continuously abundant through the records. This pattern suggest that during the mid to late Holocene, moister conditions led to higher accumulations of fuels and higher fire severities during the last 4,500 years (Anderson and Smith 1997). In lower montane forests, this shift in charcoal was accompanied by a gradual decrease in oak pollen, while in lower elevation sites oak pollen remained relatively abundant throughout the late Holocene (Smith and Anderson 1992, Mensing 2005).

Within the last 1,000 years, more detailed reconstructions of fire occurrence have been made possible using tree ring analysis. Although pollen records generally cannot differentiate between species of oak, these more recent dendrochronology reconstructions allow us to differentiate between the fire regimes of major hardwood dominated vegetation types present in the assessment area today. Fire-scar evidence is difficult to obtain from most hardwood species due to the prevalence of heart rot in old trees, so fire-scarred conifers growing in association with hardwoods are usually used to obtain fire histories.

Most dendrochronology records have shown that fire return intervals in hardwood forests and woodlands were among the shortest of all vegetation types found in the assessment area, and may have been as frequent as every few years prior to European settlement (Allen-Diaz et al. 2007, Fites-Kaufman et al. 2007). The exception to this pattern is mixed evergreen forests including tanoak, which are characterized by longer fire return intervals. A review of fire return intervals and other fire regime characteristics of hardwood forests and woodlands is provided in **Table 5**. Additional fire regime information for the common hardwood species addressed in this chapter is described below.

Blue Oak Woodland

Blue oak woodlands historically had a fire regime of frequent summer and fall surface fires, fueled primarily by light herbaceous fuels of perennial bunchgrasses and forbs, and occasional downed woody debris (Fryer 2007a). Leiberg (1902) noted that wildfires were “extensive” in blue oak-gray pine communities in the foothills of the Sierra Nevada. McClaran and Bartolome (1989) calculated mean fire return intervals of 25.2 years from 1681 to 1848 in blue oak woodlands. (Van de Water and Safford 2011) reported median fire return intervals of 12 years in blue oak/gray pine forests prior to European settlement based on their review of nine fire history studies.

Canyon and Interior Live Oak

Both canyon live oak and interior live oak grow in a wide variety of vegetation types, including mixed evergreen forests in association with tanoak, lower montane forests in association with California black oak and Oregon white oak, foothill woodlands with blue oak, and in chaparral. Fire regimes in each of these vegetation types differ, ranging from median fire return intervals of between seven and 35 years prior to European settlement (Van de Water and Safford 2011). In general, historic fire regimes in canyon live oak and interior live oak forests and woodlands were characterized by low to moderate severity fires with short to medium fire-return intervals of less than 35 years (White and Sawyer Jr 1994, Skinner and Chang 1996, Arno 2000, Paysen et al. 2000, Skinner et al. 2006). Fires occurred mainly in the summer and fall and were medium to large in size; fire severity would have been higher on steep slopes where both species often grow (Taylor and Skinner 2003).

California black oak

Forests and woodlands with a significant California black oak component historically experienced predominately frequent surface fire (Kauffman and Martin 1987, Dwire and Kauffman 2003, Taylor and Skinner 2003, Van de Water and Safford 2011). In their review of 61 fire history studies addressing dry mixed conifer and yellow pine forests with a California black oak

component, Van de Water and Safford (2011) reported median fire return intervals of 11 years, with mean fire return intervals ranging from seven to 50 years. Although both widespread and localized surface fires were common in these lower montane forests (Caprio and Swetnam 1995), long-term data from giant sequoia stands suggests that severe fires did occasionally occur in small patches (Parsons 1981, Stephenson et al. 1991). These small patches of stand-replacement fire were likely important in maintaining California black oak stands (McDonald 1969), particularly at higher elevations, where conifers can outcompete hardwood species without disturbance. Pioneer accounts of persistent California black oak and chaparral stands (Leiberg 1902) also suggest that patchy, stand-replacement fire occurred occasionally in low and mid-elevation forests (Vankat and Major 1978). Fire frequency and severity in lower montane forests are related to climatic patterns, latitude, elevation, and topography (Taylor and Skinner 2003, Stephens and Collins 2004). For example, historic fire return intervals in black oak and ponderosa pine forests increased with increasing elevation (Caprio and Swetnam 1995, Van Wagtenonk and Fites-Kaufman 2006). In the northern portion of the assessment area, mean fire return intervals were shorter, between five and 15 years, and more regular on drier south and west facing upper slopes, and longer, between 15 and 25 years, and less regular than on mesic, north and east facing lower slopes (Van Wagtenonk and Fites-Kaufman 2006). California black oak forests in drier areas with longer fire seasons, such as in the southern and central portion of the assessment area and throughout the range on south aspects, ridges, and lower elevations, experience the most frequent and regular fires (Van Wagtenonk and Fites-Kaufman 2006).

Oregon white oak

Fire return intervals of between five and 19 years have been reported for Oregon white oak forests (Taylor and Skinner 2003). Short fire return intervals restricted conifer encroachment and allowed Oregon white oak forests to persist prior to European settlement. Fuel loads in Oregon white oak forests were generally comprised of grasses and forbs, resulting in mostly low severity fires burning in the late summer and fall. These low severity fires did not normally scar trees, making fire regime reconstruction for Oregon white oak forests difficult.

Tanoak/mixed evergreen

Mixed evergreen forests with a major tanoak component historically experienced mostly mixed severity fires consisting of frequent fires of low to moderate severity, with occasional fires of locally high severity (Agee 1990). These fires generally occurred in mid-summer or early fall, although some occurred in spring, early summer, and even winter (Van Wagtenonk and Fites-Kaufman 2006). Patchy, stand-replacement fires were most common on north-facing slopes and during extended droughts. As a result of this mixed severity fire regime, fire return intervals of tanoak and mixed-evergreen forests are more variable than those of other hardwood vegetation types, with a median fire return intervals of 13 years, but ranging from 15 to 80 years (Agee 1990, Van de Water and Safford 2011).

Native American Use of Fire

The impact of Native American burning may be difficult to discern in many vegetation types in the assessment area. However, the critical role that hardwoods played in the survival and culture of California's Native American tribes, particularly in the late Holocene, make it difficult to sepa-

rate the natural role of fire from the human use of fire as a management tool in hardwood forests and woodlands (Standiford et al. 1996b, Allen-Diaz et al. 2007). Although the first humans in California probably arrived about 11,000 years ago, populations probably were small during the early Holocene, i.e. between 10,000 and 6,000 ybp (Mensing 2005), these early people probably did not rely on hardwood resources, such as acorns, as a major food crop (Wohlgemuth 1996). It wasn't until Native American populations increased, accompanied by a shift to a more agriculturally based food system during the late Holocene, that Native American burning began to significantly affect the abundance, distribution and stand conditions of hardwood forests and woodlands in the assessment area (Moratto et al. 1978, Anderson and Carpenter 1991, Mensing 2006, Nowacki et al. 2012).

Mensing (2006) provides a comprehensive review of the evidence of Native American use of fire to manage hardwood forests. For example, pollen cores collected in Yosemite Valley indicating that the site was between 60 and 70 percent pine and other conifers between 1,550 and 650 ybp; oak represented only about 6 percent of the pollen rain at that time (Anderson and Carpenter 1991). After 650 ybp, pine pollen decreased, oak pollen increased to 15 percent, and shrubs and fern spores became more abundant, indicating a shift from a closed canopy pine forest, to an open forest dominated by oaks. A peak in charcoal was also recorded at this time. Anderson and Carpenter (1991) attributed the decline in pine pollen and the increase in oak pollen, coupled with the increase in charcoal, to expanding populations of Native Americans and their increased use of fire as a management tool. Mensing (2006) describes that although Yosemite had been occupied by Native Americans for at least 3,000 years, between 750–650 ybp populations increased and shifted to a greater reliance on horticulture, including acorns as a major food source. At the time of European contact, the Sierra Miwok tribes inhabiting Yosemite Valley regularly used fire to keep the forest in an open state, and much of the Yosemite Valley was an open grassland dominated by oaks (Lewis 1993).

Mensing (2006) also reviews archeological evidence suggesting that Native Americans in the assessment area promoted hardwood forest vegetation through the use of fire. For example, Bennyhoff (1956) documented extensive mortar holes used for grinding acorns at sites near the upper elevational limit of California black oak's range today (2,100 m elevation). Although this was a pine-dominated forest at the time of discovery, the extensive grinding complex suggests that oaks must have been common in the area during habitation by Native Americans, likely maintained by frequent burning that allowed oak woodlands to persist at higher elevations than if their distribution was controlled by climate alone (Reynolds 1959).

By the late Holocene, virtually every tribe in California relied upon acorns as a major food source (Pavlik 1991). Acorns were second to salt among the most frequently traded foods among California's native peoples. Miwoks from the western Sierra traded California black oak acorns for pinyon pine nuts with the Mono Lake Paiute on the east side of the Sierra (Pavlik 1991). Extensive ethnographic evidence documents widespread use of fire by indigenous people to manipulate hardwood forests to promote acorn crops, facilitate acorn gathering, enhance habitat for game species, and improve access for hunting (Jepson 1910, Anderson and Moratto 1996, Anderson 2006, Mensing 2006). Fires set by Native Americans were likely frequent and of low intensity, promoting oak growth and reducing fuel loads and the probability of high severity fire that can damage large, mature oaks (Nowacki et al. 2012). Frequent fire also prevents oaks

woodlands from being dominated by conifer species (Lewis 1993). Native Americans in the assessment area managed hardwood forests using fire for a number of other purposes. California's native people did not develop pottery, and instead relied upon basketry made from plant materials for the storage, transport, and preparation of food and water (Anderson 1999, Mensing 2006). Sprouts of hardwood species were one of the most common materials used for basketry, tools and clothing. Indigenous burning was used to encourage sprouting and to influence the quality of sprouted material by hardwood species, including California black oak, blue oak, interior live oak, and riparian hardwoods (Anderson 1999, Mensing 2006). Epicormic branches from recently burned California black oak were harvested for spoons, winnowing baskets, and fishing baskets, and blue oak branches were used for cradleboards (Anderson 1993, 2005). Frequent burning by Native Americans likely influenced the development of the open oak savannas commonly described in the earliest European accounts of California (Mensing 2006).

Current Conditions and Comparison with NRV

Although fire suppression was widely implemented in lower montane forests containing black oak and Oregon white oak at the beginning of the 20th century, lower elevation hardwood forests and woodlands comprised of canyon live, interior live, and blue oak were not subject to wide-spread fire suppression efforts until almost 50 years later. McClaran and Bartolome (1989) identified three primary eras of fire history in blue oak woodlands, those observed prior to European settlement around 1850, those associated with early European settlement from 1850 to around 1950, and a post-settlement fire regime characterized by fire suppression after 1950. They documented a mean fire return interval of 25.2 years in blue oak woodlands from 1681 to 1848. From 1848 to 1948, mean fire return intervals shortened to 7.1 years. No fires were recorded at the study site from 1949 to the time of the study in 1989. Standiford et al. (2012) also found mean fire return intervals of 12.8 years in a southern Sierra blue oak woodland between 1850 and 1965, with no fires recorded since that time. Stephens (1997) calculated a mean fire return interval of 7.8 years between 1850 and 1947, followed by a complete absence of fires in a mixed oak-pine forest, including blue oak, gray pine, interior live and canyon live oak in the central Sierra, with Stuart (1987) also found differences in fire return intervals in tanoak forests associated with early European settlement. Past fire return intervals were estimated at 4.5 years prior to 1875, 7.5 years between 1875 and 1897, and 13.3 years for the post settlement era between 1898-1940 (Stuart 1987, Stuart and Stephens 2006).

Significant European settlement in the foothill woodlands started shortly after the discovery of gold in 1848, and large numbers of livestock were present by 1900 (Mensing 2006). Early investigators reported that burning was a common practice in the foothills of the Sierra Nevada from 1900 to 1940 (Leiberg 1902, Sampson 1944); many ranchers used frequent prescribed surface fire to increase forage production and to keep stands open for livestock. Mining towns and camps may have also been the source of unplanned ignitions during this time, so that fires during early European settlement may have been even more frequent than those set by Native Americans.

Fire suppression

Fire suppression has had dramatic effects on lower montane hardwood forests including Oregon white and California black oak. In Oregon white oak forests, an estimated pre-European fire rotation of 19 years increased to 238 years after 1905 (Taylor and Skinner 2003), and fires in mixed

evergreen/tanoak forests are now significantly larger than those during the pre-settlement and settlement periods (Franklin et al. 2006). As described above in the Stand Structure section, fire suppression has led to increased stand density and cover in lower montane hardwood forests, as well as a shift in species composition to more late seral, shade tolerant species such as conifers. Fire suppression has also changed fire behavior in lower montane hardwood forests. Although fires are now less frequent, they are generally larger and of higher severity when they occur (Skinner and Chang 1996). The large size and high severity of modern fires is in large part a result of increased fuels accumulations over a century of fire suppression. For example, increased surface and ladder fuels, and dense stand conditions in California black oak forests have led to a higher proportion of high severity fire (Agee 1993, Taylor and Skinner 2003) that can sometimes be fatal to California black oak (Kauffman and Martin 1987). Historically, surface fires and only occasional torching occurred in Oregon white oak communities; currently, however, torching is more common, and crown fires are possible with extreme fire weather conditions (Sugihara et al. 2006). On the other hand, fuel loading may now be lower in foothill oak woodlands as a result of grazing, leading to lower fire frequency and severity there.

Projected Future Trends

Projected future trends in fire regimes in hardwood woodlands and forests are generally linked to climate change. Different climate change scenarios produce divergent projections of future fire probability for the lower elevations of oak woodlands, but agree on generally higher fire probabilities for the higher elevation lower montane hardwood forests including California black and Oregon white oak. Some studies suggests that increased fire activity will generally favor hardwood species (Thorne et al. 2008), however many species are vulnerable to higher severity fire, particularly in the seedling and sapling stages (Holmes et al. 2008) (**Table 6**), suggesting that altered fire behavior could negatively affect hardwood recruitment in the future.

Grazing

NRV period grazing regimes and species

Paleoecological evidence, such as the abundance of dung fungus (*Sporormiella*) in meadow sediment cores, suggests that grazing animals were abundant in the assessment area until approximately 11,000 ybp (Davis and Moratto 1988, Davis and Shafer 2006) Davis and Shafer 2006. Wagner (1989) lists twenty species of grazing mammals that existed in California at this time, including two or more species of horse, tapir, llama, camel, pronghorn, and bison, as well as mammoth, mastodon, shrub ox, musk ox. Hardwood species currently found in the assessment area were present during the late Pleistocene, and likely experienced heavy grazing pressure at that time (Kinney 1996).

At the end of the Pleistocene, approximately 43 genera of California's animal species went extinct, including large grazing animals (Marshall 1988, Webb and Barnosky 1989). Subsequently all vegetation types in the Sierra Nevada, including hardwoods, experienced a significant reduction in herbivore pressure (Davis and Moratto 1988, Davis and Shafer 2006). After this megafaunal collapse, hardwood species in the assessment area were grazed at low to moderate intensity by a small suite of remaining native herbivores, including deer (*Odocoileus hemionus*), bighorn

sheep (*Ovis canadensis*), antelope (*Antilocapra americana*), and elk (*Cervus sp.*) (Ratliff 1985). All of these species still show preferences for hardwood species today, suggesting they have grazed hardwood habitats throughout the NRV period.

One of the most important native herbivores throughout the NRV period was the mule deer (Dull 1999), and this species still relies on hardwood vegetation today. New spring growth and sprouts arising after fire or other top-killing events are highly palatable to mule deer (Biswell and Gilman 1961). Blue oak acorns provide a critical fall and winter food source for mule deer after they migrate from dry, high-elevation summer ranges (McDonald 1990). Evergreen oaks provide a dependable food source for deer and other wildlife through the winter (Van Dersal 1940), and deer feed on canyon live oak foliage and twigs throughout the year (Leach 1956, Lawrence and Biswell 1972) Lawrence and Biswell 1972. California black oak woodlands and forests provide mule deer cover and habitat; California black oak acorns are especially important in early spring just before and during snowmelt when new green forage is still scarce (McDonald 1969, Klinger et al. 1989). Oregon white oak also provides important habitat and food for white tailed deer and mule deer, particularly in winter when other food sources are scarce (Coblentz 1980, McCorquodale 1999). Mule deer also consume tanoak leaves, shoots, and acorns (Tappeiner et al. 1990)

Grazing utilization during the NRV period

Prehistoric herbivores likely played a role in the disturbance ecology of hardwood species in the assessment area; however their contemporary foraging and habitat use patterns suggest that the intensity and frequency of this disturbance was much lower than that of domesticated livestock, which are the primary grazing animals in hardwood woodlands and forests today (Hobbs 1996). Studies comparing foraging behavior and habitat preferences in native and domestic ungulates have shown that native herbivores are less likely to congregate for long periods in specific areas and have more dispersed grazing behavior than domestic livestock (Loft et al. 1991, Kie and Boroski 1996).

Lower elevation oak woodlands and savannahs, which support productive grassland and herbaceous understory vegetation, may have been more heavily utilized by grazing species than other hardwood vegetation types in the assessment area over the past 10,000 years (Kinney 1996). These woodlands are commonly referred to as rangelands because they support productive forage for grazing animals. Historical accounts in the late 1800's indicate that highly productive rangeland communities existed throughout the foothills and higher elevation meadows of the Sierra Nevada when Europeans first arrived, often supporting large populations of native grazing animals. Jedediah Smith is believed to have been the first American explorer to cross the Sierra Nevada in 1827; he reported seeing oak savannas, wildflowers, and brushlands in the foothills, and a wide variety and abundance of wildlife, including elk, antelope, and wild horses (Smith and Brooks 1978). Large elk herds were present on the west side of the range, and populations of antelope and tule elk remained high until the early 1800s (McCullough 1969).

Current Conditions and Comparison with NRV

Although livestock were first introduced to California during the Spanish Mission days, they were not present in the assessment area until sometime in the early 1800s (Mensing 2006). By 1830, estimates for cattle in California ranged from 180,000 to 423,000 head (Burcham

1957), and by 1860 livestock were extensively utilizing hardwood woodlands and savannahs in the assessment area (Mensing 2005). Blue oak woodlands are the most heavily utilized cattle rangelands in California with 65 percent of California's total livestock forage provided by blue oak-gray pine woodlands (Borchert and Allen-Diaz 1991). The effects of livestock use are both direct, including herbivory and trampling, as well as indirect, by promoting the invasion of non-native annuals, suppressing recruitment, and through rangeland management practices such as hardwood clearing. Livestock grazing can reduce the growth of hardwood species, and may also limit recruitment (Borchert et al. 1989, Mensing 1992, Mensing 2006). The spread of nonnative annual species is generally associated with livestock introduction in California, and has led to widespread changes in species composition and fuel characteristics in low elevation hardwoods (see also discussion of Invasives below). However the most significant effect of annual species invasion is probably increased hardwood seedling mortality and lack of recruitment as a result of competition for soil moisture (Gordon and Rice 1993) and increased habitat quality for small mammals such as voles that can suppress oak regeneration ((Swiecki et al. 1993).

In the period from about 1940 until 1970, rangeland clearing was the major cause for removal of oak woodlands in California (Bolsinger 1988). It was assumed that removal of blue oak would improve forage production, so inexpensive methods were devised for killing and removing oaks, including herbicides, burning and bulldozing ((Rossi 1980, Mensing 2006). Between 1945 and 1973, about 356,000 ha of oak woodland were cleared for range improvements, averaging about 12,800 ha per year (Bolsinger 1988). In 1973, a study found that livestock forage was actually better under oaks than on the cleared land (Holland 1973), prompting a reassessment of the policy on woodland clearing.

Succession

NRV

General patterns of succession over the past 10,000 years can be observed in pollen records, where pine, juniper and incense cedar present in early Holocene pollen cores approximately 10,000 ybp were rapidly replaced by oak dominated forests between 9,000 and 5,000 ybp. After that time, a gradual increase in pine, and ultimately fir species, indicate a second successional transition to a moister, conifer dominated forest that still persists today (see **Figure 1**). Successional patterns that have likely been important among hardwoods throughout the Holocene are described below.

Successional pathways among major hardwood species addressed in this assessment differ. In general, higher elevation deciduous species such as California black oak and Oregon white oak are replaced by conifers without disturbance. On mesic sites where other species can outcompete them, other shade intolerant hardwoods such as interior live oak and to some degree blue oak also require disturbance to persist. On the other hand, species that are more shade tolerant, such as tanoak and canyon live oak, can persist in the absence of disturbance. Blue oak occupies habitats that are generally too warm for conifers, but may be replaced by invasive annual grassland or chaparral depending on disturbance regimes. Successional pathways for individual species are described in more detail below.

California black oak

California black oak is very well adapted to early seral conditions, requiring light for rapid growth in both the seedling and sapling stages (McDonald and Tappeiner 1996a). Surface fires thin the canopy and create small openings for California black oak seedling establishment by killing fire intolerant, late successional conifers (Plumb 1979). However, once California black oak matures, it can persist for decades beneath the canopy of other trees before successional replacement by understory conifers. However, these suppressed trees may have higher mortality rates after fires (Cocking et al. 2012). Eventually, continued absence of disturbance will eliminate California black oak, and it will be replaced by ponderosa pine and Douglas-fir at low elevations, or by ponderosa pine, sugar pine, incense-cedar, and white fir in mid-elevation mixed-conifer forests.

Oregon white oak

Mature Oregon white oaks are not considered shade tolerant, although seedlings may be better able to tolerate shade (Fuchs et al. 2000). Site conditions can affect the persistence and successional status of Oregon white oak (Gucker 2007). On very dry sites, or sites with very poor soils, Oregon white oak may dominate without disturbance (Stein 1980). However, on more productive sites Oregon white oak is eventually replaced by Douglas fir or ponderosa pine in the absence of fire.

Tanoak

Tanoak is shade tolerant when young and can persist in moderate shade as a mature tree (Fryer 2008). Tanoak also tolerates full sunlight, so it can be either a pioneer species after disturbances such as fire, or a sub-canopy component in old-growth forests, which comprise the largest portion of tanoak's current distribution which is a major component of its distribution (McDonald and Tappeiner 1987, Tappeiner et al. 1990, Fryer 2008). (McDonald and Tappeiner 1987). Fires severe enough to kill overstory conifers and eliminate conifer seed sources generally favor tanoak (Sessions et al. 2004), and successive, stand-replacement fires may create stands dominated by tanoak and other hardwoods for decades until Douglas-fir invades from off-site seed sources. (Agee 1990).

Canyon live oak is shade tolerant and long lived, and can occur as either a tree or a shrub depending on site conditions and genetic variant. These attributes enable canyon live oak to persist in a variety of late seral and climax communities including old-growth mixed-evergreen, mixed-conifer, and lower montane forests. Canyon live oak is also an important component of many early seral communities, primarily because of rapid, prolific sprouting that enables it to grow much faster after disturbance than conifers that reproduce only by seed (Thornburgh 1990). In some areas, vigorous, shade-tolerant sprouters such as canyon live oak slow the development of conifer forests by interfering with conifer regeneration (Tollefson 2008).

Interior live oak is more frequent in open or early-seral environments than in late-seral communities. It is moderately shade tolerant; young plants are more tolerant than mature individuals (Plumb and Gomez 1983). Conversely, Douglas-fir may replace interior live oak on favorable sites in mixed evergreen communities (Hunter and Barbour 2001).

Blue oak is poorly shade tolerant when mature and is unable to survive under dense overstory canopies. Seedlings and saplings can persist in shade but require canopy gaps to become pole-sized trees. Blue oak is typically the longest lived tree within the lower elevation oak woodlands, often being the dominant component of climax oak woodland communities (Holzman and Allen-Diaz 1991).

Current Conditions and Comparison with NRV

Modern land management practices such as grazing, logging and fire suppression have interfered with successional processes in hardwood forests and woodlands in the assessment area. Logging may have promoted the abundance of hardwood species such as California black oak in lower montane forests (Bolsinger and Forest 1980). California black oak responds to release when conifers are removed from the overstory; logging has favored California black oak on some sites by selective removal of ponderosa pine and sugar pine (McDonald 1979). Fire suppression also may benefit some hardwoods. Fire-free intervals of 50 to 100 years may be required for the development of tree-sized canyon live oaks (Minnich 1988), and tanoak can survive as a sub-canopy dominant in old growth forests in late succession (McDonald and Tappeiner 1987, Bingham and Sawyer Jr 1991, Franklin and Spies 1991, Agee 1993)

Fire suppression has negatively affected successional processes for lower montane hardwood species in the assessment area. On mesic sites, ponderosa pine and other conifers can replace interior live oak without fire [(Holland 1986). Oregon white oak experiences Douglas-fir invasion and California black oak is replaced by a number of conifer species in the absence of fire. On the other hand, in lower elevation foothill woodlands, grazing is the primary factor that has altered successional pathways by suppressing oak recruitment, ultimately converting hardwood woodlands to annual grassland (Swiecki and Bernhardt 1998).

Future

Current and projected increases in fire size and severity suggest that hardwood species will retain or increase dominance throughout the assessment area. Oak species have increased in range and abundance during periods of increased fire activity during the NRV period, and will likely do so in the future. As described in the Ecological Conditions section above, all hardwood species are well adapted to frequent fire. The exception to this may be the lower elevation blue oak woodlands and savannahs, where significant fragmentation from urban development has eliminated the potential for future fires, and shifts in climate may preclude reestablishment of this vegetation type even where historic disturbance processes can be restored (Thorne et al. 2008).

Soil properties and nutrient cycling

I could not find any information about soil properties or rates of nutrient cycling in hardwood forests over the NRV period. It is likely that the presence of hardwood species has contributed to soil development and fertility throughout the NRV period, particularly since soil development in the assessment area is generally weak due to the cold winter temperatures, steep slopes, dry summers, resistant parent materials, and the short time period since deglaciation, especially at higher elevations.

As described in the Stand Structure section above, hardwoods contribute large amounts of litter and coarse woody debris to the soil. A number of studies have found that oak trees create islands of enhanced fertility beneath their canopies through organic matter incorporation and enhanced nutrient cycling. Studies comparing soil physical and chemical properties in open grasslands to soils under blue oak, interior live oak, and foothill pine canopies have found greater amounts of organic carbon, nitrogen, total and available P, lower soil bulk densities, larger cation exchange capacity, higher pH, and greater amounts of most soil nutrients below hardwood tree canopies compared to adjacent open grasslands or shrublands (Frost and Edinger 1991, Dahlgren et al. 1997b, Camping et al. 2002, Dahlgren et al. 2003, Tate et al. 2004).

The effects of hardwoods on soil properties is generally attributed to organic matter contributions from leaf litter; there are considerably greater inputs of litterfall beneath oak canopies than beneath grassland, shrubland, or conifer vegetation, providing the additional organic matter necessary for soil development (Dahlgren and Singer 1991). In addition to the positive effect of organic matter on soil nutrient status, higher organic matter concentrations lead to lower soil bulk density and greater porosity, which increases water infiltration rates and reduces surface runoff, water erosion, and stream water sediment. Because oak roots are found at greater depths compared to the shallow rooted annual grasses, nutrient uptake by oak roots can also reduce leaching losses of nutrients from the soil. Dahlgren et al (1997b) also found that transpiration was greater in the oak understory compared to the open grasslands and that canopy interception reduced the amount of water reaching the soil surface; resulting in 30 percent less water available for leaching in the soils beneath the oak canopy.

Hardwood forests occur at lower elevations in the assessment area, which may also contribute to the productivity of soils in hardwood forests. Dahlgren et al. (1997a) investigated soil development along an elevational transect from 198 to 2865 m on the western slopes of the central Sierra Nevada to assess the effects of climate on soil properties and processes. They found that while some soil properties showed a continuous progression with elevation, other properties, including organic carbon pools, exhibited a pronounced change between the oak woodland and mixed-conifer sites. The authors suggested this pattern may be related to the fact that the transition between oak woodland and mixed conifer sites corresponds to approximate elevation of the average winter snow-line.

Current Conditions and Comparison with NRV

Changes in nutrient cycling have occurred as a result of grazing management practices, particularly in low elevation hardwood woodlands and savannahs. Grazing can reduce organic matter inputs to the soil by removing surface litter. Camping et al. (2002) compared soil quality between ungrazed and moderately grazed sites in oak woodland and found that soil surface bulk density was higher under grazed conditions. Tate et al. (2004) also found that soil bulk density was significantly higher on grazed than ungrazed sites under the canopy of blue oaks. Compaction can have negative effects on the health of oak roots and exacerbate the effects of various diseases, such as root rot fungi. Highly compacted soils can also reduce oak germination rates. The presence of blue oaks and other hardwood species is a major factor affecting soil properties in hardwood woodlands (Dahlgren et al. 2003); and the removal of oaks may result in large losses of nutrients and soil fertility from these ecosystems.

Insects/Disease

NRV

There is no direct evidence for the range of variation in insects and disease in hardwood forests in the assessment area over most of the past 10,000 years. It is likely that most of the native insects and diseases that infect hardwood species today have been present over the NRV period, and hardwood species have evolved mechanisms to persist despite them. Many of these species are influenced by climate, fire, and other disturbance processes, suggesting they have varied in abundance and effect over the NRV period. Significant insect and disease impacts were noted in some of the earliest description of oaks in California (Sudworth 1900, Jepson 1910)

Swiecki et al. (1997a) compiled information on agents that colonize or feed on oaks in California, including insects and mites, nematodes, microorganisms, viruses, and abiotic disease agents. They identified 853 insect species and 378 species of fungi that utilize oaks. Most of the arthropods are native species that appear to be in ecological equilibrium with their hosts, and the impact of the 350 species of insects that feed on or produce galls on oak leaves is generally considered to be minor. Insects that damage acorns, such as the filbertworm (*Cydia latiferreana*) and filbert weevils (*Curculio* spp.) may have more significant effects on oak populations by destroying a large percentage of acorn crops in a given year (Swiecki et al. 1991). However, the diseases that have the greatest potential to affect the reproduction and survival of California oaks are those caused by acorn pathogens and wood decaying fungi. Acorn pathogens most frequently access the tree bole through wounds caused by insects, and can destroy acorns even when insect damage is minor (Swiecki et al. 1991). Swiecki et al. (1997a) identified more than 40 species of fungi that cause branch or trunk cankers or decay the trunk, root crown, or roots of oaks growing under natural conditions, including *Inonotus* spp., *Armillaria mellea*, *Phytophthora* spp, and *Ganoderma*. Wood-decay fungi constitute the most significant oak pathogens in California. Oaks colonized by wood-decay fungi usually decline slowly and literally fall apart as large branches, and eventually the trunk, fail, affecting the amount of dead and downed wood and standing snags in oak woodlands ((Swiecki et al. 1991, Tietje et al. 1997). Wood-decay and root-rot fungi can kill mature oaks in undisturbed stands, but also play a direct role in improving wildlife habitat value by promoting the development of cavities in trees, which are utilized by a number of different vertebrate species (Swiecki et al. 1991, Swiecki et al. 1997a).

Current Conditions and Comparison with NRV

Some insects and diseases are recent introductions and have had significant effects on hardwood forests since European settlement. The most significant of these may be a fungus-like water mold known as sudden oak death, caused by the pathogen *Phytophthora ramorum*. First diagnosed in 2000, sudden oak death is responsible for killing tens of thousands of tanoaks along the central coast of California. It continues to spread and is now found in numerous coastal counties in California. It has an ever expanding range of hosts worldwide including hardwoods, conifers, shrubs, ferns and herbaceous plants. Tanoak is more susceptible to damage and death from sudden oak death disease than any other North American species. Sudden oak death infection is nearly always fatal to tanoaks (Rizzo and Garbelotto 2003), but may sudden oak death may also infect California black oak and canyon live oak, as well as a number of other species. Blue oak

is resistant to the pathogen. Sudden oak death thrives in cool, wet climates, and has not yet been detected in the assessment area, although known hosts are widespread.

Goldspotted oak borer (GSOB) (*Agrilus auroguttatus*) was first detected in San Diego County, California in 2004. It is a serious pest of coast live oak (*Quercus agrifolia*), canyon live oak and California black oak, and has killed thousands of trees. Although it has not yet been detected in the assessment area, oak species in the Sierra Nevada range could be susceptible to this invasive beetle.

Fire suppression and livestock grazing may have altered the susceptibility of hardwood species to insects and disease since the NRV period. For example, Native Americans burned California black oak populations to reduce the loss of acorns to insects such as filbert worms and filbert weevils (Anderson 2006), suggesting that the abundance of these insects may have been lower during periods of more active fire regimes during the NRV period. Livestock grazing also may have increased blue oak susceptibility to root-rot fungi as a result of soil compaction (Costello et al. 1991).

Invasive Species

Current Conditions and Comparison with NRV

Invasive species are a modern phenomenon in hardwood dominated vegetation types in the assessment area, and by definition did not exist during the NRV period. Although the first non-native species were likely introduced to California by the Spanish during the mission days in the 1500s, most species did not reach the assessment area until widespread settlement and ranching occurred after the California gold rush in 1850 (Burcham 1970, Mensing 2006). The abundance of nonnative species in hardwood woodlands and forests in the assessment area today is strongly primarily associated with elevation. The extent and effect of invasive species is greatest in the lower elevation foothills and woodlands dominated by blue oak. In higher elevation California black oak and Oregon white oak forests nonnative species are often relatively rare and have less impact on ecosystem function.

California grasslands probably historically supported a higher abundance of perennial bunchgrasses such as purple needlegrass (*Nassella pulchra*) and bottlebrush squirreltail (*Elymus elymoides*) than they do today (Heady 1977, Bartolome et al. 1986). Widespread conversion of native grasslands, containing a diverse assemblage of native annuals and perennials, to an understory dominated by exotic annuals in hardwood woodlands probably occurred in the late 1850s and early 1860s as a result of drought and extremely heavy grazing pressure during this interval (Burcham 1957, Byrne et al. 1991). The invasion of annual species in oak woodlands has not only led to the decline of many native grasses and forbs, but has also caused alterations in fire regimes. Annual species may promote an earlier burning season because they senesce and dry out earlier than perennials. The conversion from perennial bunchgrass to annual grassland is likely irreversible (Keeley et al. 2003).

Perhaps the greatest impact of nonnative annual plants on hardwoods is their ability to negatively affect oak seedling emergence and growth. Competition for soil water with introduced annual species contributes to increased rates of blue oak seedling mortality currently observed in Cali-

ifornia woodland systems (Gordon and Rice 2000). Blue oak seedlings do not compete well with annual grasses; annual grasses often outcompete blue oak seedlings for space, water, and light (Gordon and Rice 2000) (Borchert et al. 1989, Gordon et al. 1989, Adams Jr et al. 1991, Davis et al. 1991).

Other Disturbance Processes

Indicators

The fossil record reveals that montane hardwoods evolved as part of the Mascall flora during the Miocene epoch of 12-26 million years ago. Consequently, they have survived glaciation, volcanism, upthrusting and subsidence (McDonald and Tappeiner 1996a). Other disturbance processes such as wind and heavy snow loads likely played a minor role in hardwood vegetation types over the past 10,000 years. Most species are restricted to lower elevations and slope positions where snow and extreme wind events does are not common. The limited information about hardwood susceptibility to these processes is presented here.

NRV

Disturbance processes such as wind and heavy snow fall have likely varied with climatic changes over the past 10,000 years. Information related to the susceptibility of modern hardwood forests to these kinds of disturbances may provide some insight into the response of these species to such disturbance factors throughout the Holocene. Heavy, wet snow can break California black oak branches, and broken limb edges can then become portals for fungal infection (McDonald 1969). Oregon white oak trees, on the other hand, are somewhat resistant to snow and ice damage (Niemi et al. 1995). There is evidence that wind may topple fire-damaged tanoaks. Tanoak is intolerant of heavy snow loads and decayed or damaged trees susceptible to high winds, so tanoak breakage from heavy snow and/or high winds can create heavy loads of downed woody debris (Stuart and Stephens 2006). Interior live oak's evergreen leaves help protect it from desiccation, but it is not well adapted to snowy or cold sites because the branches break easily under snow loads and the evergreen leaves freeze easily (Fryer 2012).

Current Conditions and Comparison with NRV

Current climates are within the range of climatic conditions experienced by hardwood species over the past 10,000 years, and there is no evidence that snow and wind related disturbances have changed dramatically in modern times.

Projected Future Trends

Future climates, projected to be warmer than climates experienced by hardwood species today, may reduce snow load damage to many species of oak and allow them to persist at higher elevations than they inhabit today. See also discussion of Climate and Geographic Distribution for a discussion of climatic factors that influence the distribution of hardwood species in the assessment area.

SUMMARY OF NRV FINDINGS AND DEVIATIONS

The primary findings from this NRV assessment are presented in Table 20 and summarized briefly below.

- The current species composition in hardwood forests and woodlands in the assessment area is outside of the NRV as a result of nonnative species invasion. Most of these invasive species are annuals, and as a result, the proportion of annual species has also increased in hardwood woodlands and forests compared to the NRV period. This deviation is greater in lower elevation hardwood savannahs and woodlands than in lower montane hardwood forests. Species composition in lower montane forests has also been altered by fire suppression, resulting in higher proportions of shade tolerant species than found throughout the NRV period.
- Although many hardwood species occurred at higher elevations during the Xerithermic period, their current geographic distributions are within the NRV for the entire Holocene. The exception may be low elevation woodlands and savannahs, which have been extensively lost and fragmented as a result of agricultural conversion, urbanization, overgrazing, climate change, and altered fire regimes.
- Although the abundance of many species, particularly native understory plants, has probably changed in hardwood forests and woodlands since the NRV period as a result of grazing, invasive species, and fire suppression, species diversity in these systems has likely remained relatively constant.
- The seral stage distribution of most hardwood forests and woodlands is likely outside of the NRV. In lower montane forests, early seral stages are generally lacking as a result of fire suppression, with the possible exception of tanoak. In low elevation woodlands, lack of recruitment and absence of early seral stages is attributed to grazing, altered fire regimes, hardwood clearing, and fragmentation.
- Pollen records indicate that the abundance of shade tolerant species, such as fir, began increasing during the past 100 years and are currently above levels seen throughout the NRV period. As a result, the proportion of conifers in lower montane hardwood forests is currently higher than that observed during the NRV period.
- Canopy cover and density are now higher in most hardwood dominated vegetation types than during the NRV period. In lower montane hardwood forests, productivity indicators such as volume and basal area are also currently higher than during the NRV period as a result of fire suppression.
- The current age and size class distribution of hardwood forests and woodlands has significantly deviated from the NRV as a result of very low recruitment for many hardwood species. Lack of recruitment is likely the result of overgrazing, nonnative plant invasion, fire suppression in lower montane hardwood forests, and widespread clearing of low elevation woodlands.
- In lower montane hardwood forests, coarse woody debris, duff and litter depth have all increased since the NRV period as a result of fire suppression.

- Fire return intervals have increased in hardwood forests and woodlands across the assessment area. When fires do occur, they are likely burning with higher severity than typical during the NRV period, possibly resulting in larger patch sizes. Fire seasons also tend to be earlier as a result of increased anthropogenic ignitions and invasive annual grasses.
- The introduction of domestic livestock grazing, nonnative plant species, and introduced insects and pathogens beginning with European settlement have altered the function of hardwood forests and woodlands in the assessment area since the NRV period.

NRV Table

Ecosystem Attribute	Indicator	Within NRV	Confidence	Notes	Direction of change	Pages in text
Composition	Species composition	No	High	<i>Invasive species Fire suppression</i>	<i>Native species replaced by invasives, more shade tolerant conifers in fire suppressed lower montane forests</i>	6-7
Composition	Geographic distribution	Yes	High/Moderate			8
Composition	Species diversity	Yes	Moderate			6-7
Composition	Seral stage distribution	No	Moderate	<i>Fire suppression, grazing, clearing</i>	<i>Reduction of early seral stages</i>	6-7
Composition	Shade tolerance distribution	No	High	<i>Pollen records indicate current abundance of shade tolerant species are above levels seen throughout rest of Holocene</i>	<i>Higher proportion shade tolerant species</i>	6-7
Composition	Proportion perennial and annual	No	High	<i>Invasive species</i>	<i>Higher proportion annuals</i>	6-7
Composition	Proportion conifer and hardwood	No	High	<i>Fire suppression in lower montane forests</i>	<i>Increased dominance of conifers in lower montane forests</i>	6-7
Structure	Canopy cover	No	Moderate	<i>Fire suppression in lower montane forests</i>	<i>Higher</i>	9-10
Structure	Density	No	Moderate	<i>Fire suppression in lower montane forests</i>	<i>Higher</i>	9-10
Structure	Age/size class distribution	No	High	<i>Lack of hardwood recruitment for many species</i>	<i>Lower seedling and sapling occurrence</i>	10-11
Structure	Coarse woody debris, litter and duff	No	High	<i>Fire suppression in lower montane forests</i>	<i>Higher</i>	13
Structure	Volume/basal area	No	Moderate	<i>Fire suppression in lower montane forests</i>	<i>Higher</i>	9-10

Structure	Patch size	Yes	Low/Moderate	<i>Fire suppression in lower montane forests, grazing and clearing in foothill woodlands</i>	<i>Fewer fine scale patches</i>	12
Function	Extreme climatic events	Yes	High			13
Function	Fire return interval	No	High	<i>Fire suppression</i>	<i>Higher</i>	14-18
Function	Fire severity	No	High	<i>Fire suppression</i>	<i>Higher</i>	14-18
Function	Fire season	No	Moderate	<i>Anthropogenic ignitions, invasive species</i>	<i>Earlier</i>	14-18
Function	Grazing utilization	No	High	<i>Domestic livestock</i>	<i>Higher</i>	20
Function	Soil properties and nutrient cycling	No	Moderate	<i>Domestic livestock, invasive species</i>	<i>Lower rates of nutrient cycling</i>	23
Function	Invasive species	No	High	<i>Invasive species</i>	<i>Higher</i>	24-25
Function	Insects and pathogens	No	High	<i>Introduced diseases</i>	<i>Higher</i>	32-24
Function	Successional patterns	No	Moderate	<i>Fire suppression in lower montane forests, grazing, clearing in foothill woodlands</i>	<i>More late seral species and habitats</i>	20-22
Function	Wind, snow	Yes	Moderate			25

LITERATURE CITED

- Adams Jr, T. E., P. B. Sands, W. H. Weitkamp, and N. K. McDougald. 1991. Blue and valley oak seedling establishment on California's hardwood rangelands. USDA General Technical Report PSW-126:41-47.
- Agee, J. 1993. Fire ecology of Pacific Northwest forests. Island Press.
- Agee, J. K. 1990. The historical role of fire in Pacific Northwest forests. *Natural and prescribed fire in Pacific Northwest forests*:25-38.
- Allen-Diaz, B., R. Standiford, and R. D. Jackson. 2007. Oak woodlands and forests. Pages 313-338 in M. G. Barbour, T. Keeler-Wolf, and A. A. Schoenherr, editors. *Terrestrial vegetation of California*. University of California Press, Berkeley, California.
- Anderson, M. K. 1999. The fire, pruning, and coppice management of temperate ecosystems for basketry material by California Indian tribes. *Human Ecology* 27:79-113.
- Anderson, M. K. 2006. The use of fire by Native Americans in California. *Fire in California's ecosystems*. University of California Press, Berkeley, California, USA:417-430.
- Anderson, M. K. and M. J. Moratto. 1996. Native American land-use practices and ecological impacts. Pages 187-206 *Sierra Nevada Ecosystem Project: Final report to Congress, Vol. II, Assessments and scientific basis for management options*, University of California, Davis.
- Anderson, R. S. and S. L. Carpenter. 1991. Vegetation changes in Yosemite Valley, Yosemite National Park, California, during the protohistoric period. *Madrono* 38:1-13.
- Anderson, R. S. and O. K. Davis. 1988. Contemporary pollen rain across the central Sierra Nevada, California, USA: relationship to modern vegetation types. *Arctic and Alpine Research*:448-460.
- Anderson, R. S. and S. J. Smith. 1994. Paleoclimatic interpretations of meadow sediment and pollen stratigraphies from California. *Geology* 22:723-726.
- Anderson, R. S. and S. J. Smith. 1997. The sedimentary record of fire in montane meadows, Sierra Nevada, California, USA: A preliminary assessment. *Nato asi series i global environmental change* 51:313-328.
- Arno, S. F. 2000. Fire in western forest ecosystems.
- Atzet, T. 1996. Fire regimes and restoration needs in southwestern Oregon. United states department of agriculture forest service general technical report int:74-76.
- Axelrod, D. I. 1983. Biogeography of oaks in the Arcto-Tertiary province. *Annals of the Missouri Botanical Garden*:629-657.
- Baker, G. A., P. W. Rundel, and D. J. Parsons. 1981. Ecological relationships of *Quercus douglasii* (Fagaceae) in the foothill zone of Sequoia National Park, California. *Madrono* 28.
- Bartolome, J. W. 1989. Ecological history of the California Mediterranean-type landscape. Pages 2-15 in *Proceedings of Man and the Biosphere Symposium: Landscape Ecology: Study of Mediterranean Grazed Ecosystems*, Nice, France.
- Bartolome, J. W., S. E. Klukkert, and W. J. Barry. 1986. Opal phytoliths as evidence for displacement of native Californian grassland. *Madrono* 33:217-222.
- Baumhoff, M. A. 1963. Ecological determinants of aboriginal California populations. University of California Press, Berkeley, California.

- Bennyhoff, J. A. 1956. An appraisal of the archaeological resources of Yosemite National Park. University of California, Dept. of Anthropology.
- Bernhardt, T. J. S. E. A. and R. A. Arnold. 1991. Insect and Disease Impacts on Blue Oak Acorns and Seedlings. Pages 149-155 in Proceedings of the symposium on oak woodlands and hardwood rangeland management. U.S. Department of Agriculture, Forest Service, PacificSouthwest Research Station, Berkeley, CA., Davis, CA.
- Bingham, B. B. and J. O. Sawyer Jr. 1991. Distinctive features and definitions of young, mature, and old-growth Douglas-fir/hardwood forests. USDA Forest Service general technical report PNW-GTR-Pacific Northwest Research Station.
- Biswell, H. H. and J. H. Gilman. 1961. Brush management in relation to fire and other environmental factors on the Tehama deer winter range. California Fish and Game 47:357-389.
- Block, W. and M. Morrison. 1990. Wildlife diversity of the central Sierra foothills. California Agriculture 44:19-22.
- Blumler, M. A. 1991. Winter-deciduous versus evergreen habit in mediterranean regions: a model. Notes.
- Bolsinger, C. L. 1988. The hardwoods of California's timberlands, woodlands, and savannas. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon.
- Bolsinger, C. L. and P. N. Forest. 1980. California forests: trends, problems, and opportunities. US Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.
- Borchert, M. and B. Allen-Diaz. 1991. ENVIRONMENTAL RELATIONSHIPS OF HERBS IN BLUE OAK (QUERCUS DOUGLASII) WOODLANDS OF CENTRAL COASTAL CALIFORNIA. Madrono 38:249-266.
- Borchert, M. I., F. W. Davis, J. Michaelsen, and L. D. Oyler. 1989. Interactions of factors affecting seedling recruitment of blue oak (*Quercus douglasii*) in California. Ecology:389-404.
- Bull, E. L., C. G. Parks, and T. R. Torgersen. 1997. Trees and logs important to wildlife in the Interior Columbia River Basin.
- Burcham, L. T. 1957. California range land. Dept. of Natural Resources, Division of Forestry. Sacramento, CA.
- Burcham, L. T. 1970. Ecological significance of alien plants in California grasslands. Proceedings of the Association of American Geographers 2:36-39.
- Byrne, R., E. Edlund, and S. Mensing. 1991. Holocene changes in the distribution and abundance of oaks in California. Pacific Southwest Forest and Range Experiment Station, Berkeley, CA.
- Camping, T. J., R. A. Dahlgren, K. W. Tate, and W. R. Horwath. 2002. Changes in soil quality due to grazing and oak tree removal in California blue oak woodlands. Oaks in California's changing landscape. USDA, Gen. Tech. PSW-184. Berkeley, CA:75-85.
- Caprio, A. C. and T. W. Swetnam. 1995. Historic fire regimes along an elevational gradient on the west slope of the Sierra Nevada, California.
- Cayan, D. R., E. P. Maurer, M. D. Dettinger, M. Tyree, and K. Hayhoe. 2008. Climate change scenarios for the California region. Climatic Change 87:21-42.
- Coblentz, B. E. 1980. Production of Oregon white oak acorns in the Willamette Valley, Oregon. Wildlife Society Bulletin:348-350.
- Cocking, M. I., J. M. Varner, and R. L. Sherriff. 2012. California black oak responses to fire severity and native conifer encroachment in the Klamath Mountains. Forest Ecology and Management 270:25-34.
- Costello, L. R., J. D. MacDonald, and K. A. Jacobs. 1991. Soil aeration and tree health: correlating soil oxygen measurements with the decline of established oaks. Notes.

- Dahlgren, R., W. Horwath, K. Tate, and T. Camping. 2003. Blue oak enhance soil quality in California oak woodlands. *California Agriculture* 57:42-47.
- Dahlgren, R. and M. J. Singer. 1991. Nutrient cycling in managed and unmanaged oak woodland-grass ecosystems. Notes.
- Dahlgren, R. A., J. L. Boettinger, G. L. Huntington, and R. G. Amundson. 1997a. Soil development along an elevational transect in the western Sierra Nevada, California. *Geoderma* 78:207-236.
- Dahlgren, R. A., M. J. Singer, and X. Huang. 1997b. Oak tree and grazing impacts on soil properties and nutrients in a California oak woodland. *Biogeochemistry* 39:45-64.
- Davis, F. W., M. Borchert, L. E. Harvey, J. C. Michaelsen, and R. B. Standiford. 1991. Factors affecting seedling survivorship of blue oak (*Quercus douglasii* H. & A.) in central California. in Proceedings of the symposium on oak woodlands and hardwood rangeland management, Davis, CA, USFS, Pacific Southwest Research Station.
- Davis, F. W., C. M. Tyler, and B. E. Mahall. 2011. Consumer control of oak demography in a Mediterranean-climate savanna. *Ecosphere* 2.
- Davis, O. K. and M. J. Moratto. 1988. Evidence for a warm dry early Holocene in the western Sierra Nevada of California: pollen and plant macrofossil analysis of Dinkey and Exchequer Meadows. *Madroño* 35:132-149.
- Davis, O. K., R. Scott Anderson, P. L. Fall, M. K. O'Rourke, and R. S. Thompson. 1985. Palynological evidence for early Holocene aridity in the southern Sierra Nevada, California. *Quaternary Research* 24:322-332.
- Davis, O. K. and D. S. Shafer. 2006. *Sporormiella* fungal spores, a palynological means of detecting herbivore density. *Palaeogeography, Palaeoclimatology, Palaeoecology* 237:40-50.
- Dolanc, C. R., H. D. Safford, S. Z. Dobrowski, and J. H. Thorne. In review. Seven decades of forest change in the Sierra Nevada, California, USA. Manuscript in review in *Forest Ecology and Management*.
- Dull, R. A. 1999. Palynological evidence for 19th century grazing-induced vegetation change in the southern Sierra Nevada, California, USA. *Journal of Biogeography* 26:899-912.
- Dwire, K. and J. Kauffman. 2003. Fire and riparian ecosystems in landscapes of the western USA. *Forest Ecology and Management* 178:61-74.
- Edlund, E. G. and R. Byrne. 1991. Climate, fire, and late Quaternary vegetation change in the central Sierra Nevada. Pages 390-396 in *Fire and the environment: ecological and cultural perspectives*, proceedings of an international symposium. Asheville, NC: USDA Forest Service, Southeastern Forest Experiment Station, General Technical Report SE-69.
- Fites, J. A. 1993. Ecological guide to mixed conifer plant associations. USDA Forest Service Pacific Southwest Region R5-ECOL-TP-001.
- Fites-Kaufman, J. A., P. Rundel, N. Stephenson, and D. A. Weixelman. 2007. Montane and subalpine vegetation of the Sierra Nevada and Cascade ranges. *Terrestrial Vegetation of California*. University of California Press, Berkeley:456-501.
- Franklin, J., L. A. Spears-Lebrun, D. H. Deutschman, and K. Marsden. 2006. Impact of a high-intensity fire on mixed evergreen and mixed conifer forests in the Peninsular Ranges of southern California, USA. *Forest ecology and management* 235:18-29.
- Franklin, J. F. and T. A. Spies. 1991. Ecological definitions of old-growth Douglas-fir forests. Ruggiero. LF; Aubry, KB; Carey, AB:61-69.
- Frost, W. E. and S. B. Edinger. 1991. Effects of tree canopies on soil characteristics of annual rangeland. *Journal of Range Management*:286-288.

- Fryer, J. L. 2007a. *Quercus douglasii*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory.
- Fryer, J. L. 2007b. *Quercus kelloggii*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory
- Fryer, J. L. 2008. *Lithocarpus densiflorus*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory
- Fryer, J. L. 2012. *Quercus wislizeni*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory
- Fuchs, M. A., P. G. Krannitz, and A. S. Harestad. 2000. Factors affecting emergence and first-year survival of seedlings of Garry oaks (*Quercus garryana*) in British Columbia, Canada. 137:209-219.
- Gaman, T. and J. Firman. 2006. Oaks 2040: The status and future of oaks in California. California Oak Foundation Oakland, CA, USA:.
- Garrison, B. A., R. L. Wachs, T. A. Giles, and M. L. Triggs. 2002. Dead branches and other wildlife resources on California black oak (*Quercus kelloggii*). *Laudenslayer, William F. Jr.; Shea, Patrick J*:2-4.
- Gonzalez, P., R. P. Neilson, J. M. Lenihan, and R. J. Drapek. 2010. Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. *Global Ecology and Biogeography* 19:755-768.
- Gordon, D. R., J. M. Menke, and K. J. Rice. 1989. Competition for soil water between annual plants and blue oak (*Quercus douglasii*) seedlings. *Oecologia* 79:533-541.
- Gordon, D. R. and K. J. Rice. 1993. Competitive effects of grassland annuals on soil water and blue oak (*Quercus douglasii*) seedlings. *Ecology*:68-82.
- Gordon, D. R. and K. J. Rice. 2000. Competitive suppression of *Quercus douglasii* (Fagaceae) seedling emergence and growth. *American Journal of Botany* 87:986-994.
- Griffin, J. R. 1977. Oak woodland. Pages 383-416 in M. G. Barbour and J. Major, editors. *Terrestrial vegetation of California*. John Wiley & Sons, New York.
- Griffin, J. R. and W. B. Critchfield. 1972. The distribution of forest trees in California. Pacific Southwest Forest and Range Experiment Station.
- Gruell, G. E. 2001. Fire in Sierra Nevada forests: a photographic interpretation of ecological change since 1849. Mountain Pr.
- Gucker, C. L. 2007. *Quercus garryana*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory
- Heady, H. F. 1977. Valley grassland. Pages 491-514 in B. M. and M. J., editors. *Terrestrial vegetation of California*. Wiley, New York
- Hobbs, N. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* 60:695-713.
- Holland, R. F. 1986. Preliminary descriptions of the terrestrial natural communities of California. State of California, The Resources Agency, Department of Fish and Game.
- Holmes, K. A., K. E. Veblen, T. P. Young, and A. M. Berry. 2008. California oaks and fire: a review and case study. Pages 551-565 in *Proceedings of the sixth California oak symposium: Today's challenges, tomorrow's opportunities*. USDA Forest Service, Pacific Southwest Research Station.
- Holmes, T. H. 1990. Botanical trends in northern California oak woodland. *Rangelands* 12:3-7.

- Holzman, B. A. and B. H. Allen-Diaz. 1991. Vegetation change in blue oak woodlands in California. USDA For. Serv. Gen. Tech. Rep. PSW-126:189-193.
- Hunter, J. C. and M. G. Barbour. 2001. Through-growth by *Pseudotsuga menziesii*: A mechanism for change in forest composition without canopy gaps. *Journal of Vegetation Science* 12:445-452.
- Jepson, W. L. 1910. The silva of California. University of California Mem.
- Jepson, W. L. 1921. The fire-type forest of the Sierra Nevada. *The Intercollegiate Forestry Club Annual* 1:7-10.
- Kauffman, J. B. and R. E. Martin. 1987. Effects of fire and fire suppression on mortality and mode of reproduction of California black oak (*Quercus kelloggii* Newb.). USDA Forest Service general technical report PSW United States, Pacific Southwest Forest and Range Experiment Station.
- Keeley, J. E., D. Lubin, and C. J. Fotheringham. 2003. Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecological applications* 13:1355-1374.
- Kie, J. and B. Boroski. 1996. Cattle distribution, habitats, and diets in the Sierra Nevada of California. *Journal of Range Management* 49:482-488.
- Kinney, W. C. 1996. Conditions of Rangelands before 1905. Pages 31-45 *Sierra Nevada Ecosystem Project: Final report to Congress, Vol. II, Assessments and scientific basis for management options*. University of California, Davis: Centers for Water and Wildland Resources.
- Klinger, R. C., M. J. Kutilek, and H. S. Shellhammer. 1989. Population responses of black-tailed deer to prescribed burning. *The Journal of wildlife management*:863-871.
- Knops, J. M. H. and W. D. Koenig. 1994. Water use strategies of five sympatric species of *Quercus* in central coastal California. *Madrono* 41.
- Kuhn, B. and B. Johnson. 2008. Status and Trends of Black Oak (*Quercus kelloggii*) Populations and Recruitment in Yosemite Valley (aka Preserving Yosemite's Oaks).
- LANDFIRE. 2007. LANDFIRE Rapid Assessment. . Rapid assessment reference condition models. In: (Producers). Available: [66533]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Lab; U.S. Geological Survey; The Nature Conservancy
- Laudenslayer, W. F. 1999. Cavity-nesting bird use of snags in eastside pine forests of northeastern California. Pages 2-4 in *Proceedings of the symposium on the ecology and management of dead wood in western forests*. Laudenslayer, WF, PJ Shea, VE Valentine, CP Weatherspoon, and TE Lisle (tech. coord.).
- Lawrence, G. and H. Biswell. 1972. Effect of forest manipulation on deer habitat in giant sequoia. *The Journal of Wildlife Management*:595-605.
- Leach, H. R. 1956. Food habits of the Great Basin deer herds of California. *California Fish and Game* 42:243-308.
- Leiberg, J. B. 1902. Forest conditions in the northern Sierra Nevada, California. Page 194 *United States Geological Survey, Professional Paper Number 8, Series H, Forestry*. Government Printing Office, Washington, D.C.
- Lewis, H. T. 1993. Patterns of Indian burning in California: ecology and ethnohistory. Pages 56-115 in T. C. Blackburn and K. Anderson, editors. *Before the wilderness: environmental management by native Californians*. Ballena, Menlo Park, California.
- Loft, E. R., J. W. Menke, and J. G. Kie. 1991. Habitat shifts by mule deer - the influence of cattle grazing. *Journal of Wildlife Management* 55:16-26.
- Mackey, E. M. and D. G. Sullivan. 1986. A 10,000 year palynological and stratigraphic record from Gabbot Lake, Alpine County, California. *Ninth AMQUA Programs and Abstracts* 95.

- Marshall, L. G. 1988. Extinction. Pages 219-254 *Analytical Biogeography*. Springer.
- McClaran, M. P. 1986. Age structure of *Quercus douglasii* in relation to livestock grazing and fire. University of California, Berkeley.
- McClaran, M. P. and J. W. Bartolome. 1989. Fire-related recruitment in stagnant *Quercus douglasii* populations. *Canadian Journal of Forest Research* 19:580-585.
- McCorquodale, S. 1999. Landscape and patch scale habitat use by migratory black-tailed deer in the Klickitat Basin of Washington.
- McCullough, D. R. 1969. The tule elk: its history, behavior, and ecology. University of California Press Berkeley.
- McDonald, P. M. 1969. Silvical characteristics of California black oak (*Quercus kelloggii* Newb.). Pacific Southwest Forest and Range Experiment Station.
- McDonald, P. M. 1979. Growth of thinned and unthinned hardwood stands in the northern Sierra Nevada... preliminary findings. Pages 119-127 in *Proceedings, Symposium on the Ecology, Management, and Utilization of California Oaks*.
- McDonald, P. M. 1990. *Quercus douglasii* Hook. & Arn. *Silvics of North America: Hardwoods*. USDA Forest Service Handbook:631e639.
- McDonald, P. M. and D. W. Huber. 1994. California's hardwood resource: current status of the industry and an ecosystem management perspective. Page 24 *Gen. Tech. Rep. PSW-GTR-153*. Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture
- McDonald, P. M. and D. W. Huber. 1995. California's hardwood resource: managing for wildlife, water, pleasing scenery, and wood products., Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, CA.
- McDonald, P. M. and J. C. Tappeiner. 1987. Silviculture, ecology, and management of tanoak in northern California. USDA Forest Service general technical report PSW-United States, Pacific Southwest Forest and Range Experiment Station.
- McDonald, P. M. and J. C. Tappeiner. 1996a. Silviculture-ecology of forest-zone hardwoods in the Sierra Nevada. Pages 621-636 *Sierra Nevada Ecosystem Project: Final Report to Congress, Vol. II, Assessments and scientific basis for management options*. University of California: Centers for Water and Wildland Resources, Davis, California.
- McDonald, P. M. and J. C. Tappeiner. 1996b. Silviculture-ecology of forest-zone hardwoods in the Sierra Nevada. Pages 621-636 in *Sierra Nevada Ecosystem Project: Final Report to Congress*.
- McKelvey, J. V. K. S., B. R. Noon, R. J. Gutierrez, G. I. Gould Jr, and T. W. Beck. 1992. Assessment of the Current Status of the California Spotted Owl, with Recommendations for Management. *The California spotted owl: A technical assessment of its current status* 133:3.
- Mensing, S. 2005. The history of oak woodlands in California, Part I: The paleoecologic record. *The California Geographer* 45:1-38.
- Mensing, S. 2006. The History of Oak Woodlands in California, Part II: The Native American and Historic Period. *The California Geographer* 46:1-31.
- Mensing, S. A. 1992. The impact of European settlement on blue oak (*Quercus douglasii*) regeneration and recruitment in the Tehachapi Mountains, California. *Madroño* 39:36-46.

- Millar, C. I. 1996. Tertiary vegetation history. Pages 71-122 Sierra Nevada Ecosystem Project: final report to congress Volume II. Assessments and scientific basis for management options. University of California, Davis, Centers for Water and Wildland Resources, Davis, California.
- Millar, C. I. and W. B. Woolfenden. 1999. Sierra Nevada forests: Where did they come from? Where are they going? What does it mean. Pages 206-236 in Transactions of the North American Wildlife and Natural Resources Conference, San Francisco, California.
- Minnich, R. A. 1988. The biogeography of fire in the San Bernardino Mountains of California: a historical study. Univ of California Press.
- Moratto, M. J., T. F. King, and W. B. Woolfenden. 1978. Archaeology and California's climate. *Journal of California Anthropology*:147-161.
- Motroni, R. S., D. A. Airola, R. K. Marose, and N. D. Tosta. 1991. Using wildlife species richness to identify land protection priorities in California's hardwood rangelands. Pages 110-119 in Proc. Symp. Oak Woodlands and Hardwood Rangeland Management. USFS Gen. Tech. Rep. PSW-126.
- Muick, P. C. and J. W. Bartolome. 1986. Oak regeneration on California's hardwood rangelands. *Transactions of the Western Section of the Wildlife Society* 22.
- Muir, J. 1901. *Our national parks*. Houghton Mifflin.
- Niemiec, S. S., G. R. Ahrens, S. Willits, and D. E. Hibbs. 1995. Hardwoods of the Pacific Northwest. *Western Hardwoods*:32.
- Nowacki, G. J., D. W. MacCleery, and F. K. Lake. 2012. Native Americans, ecosystem development, and historical range of variation. Pages 76-91 in J. Wiens, G. Hayward, H. Safford, and C. Giffen, editors. *Historical environmental variation in conservation and natural resource management*. John Wiley and Sons, Sussex, UK.
- Parsons, D. J. 1981. The historical role of fire in the foothill communities of Sequoia National Park. *Madroño* 28:111-120.
- Pavlik, B. M. 1991. *Oaks of California*. Cachuma Press, Los Olivos, California.
- Paysen, T. E., R. J. Ansley, J. K. Brown, G. J. Gottfried, S. M. Haase, M. G. Harrington, M. G. Narog, S. S. Sackett, and R. C. Wilson. 2000. Fire in western shrubland, woodland, and grassland ecosystems. *Wildland fire in ecosystems: Effects of fire on flora*. Gen. Tech. Rep. RMRS-GTR-42-vol 2:121-159.
- Plumb, T. R. 1979. Response of oaks to fire. Pages 205-215 in *Proceedings of the symposium on the ecology, management, and utilization of California oaks*.
- Plumb, T. R. and A. P. Gomez. 1983. *Five southern California oaks: identification and postfire management*.
- Ratliff, R. D. 1985. *Meadows in the Sierra Nevada of California: state of knowledge*. Gen. Tech. Rep. PSW-84. 52 p. US Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, CA.
- Reynolds, R. D. 1959. *Effect of natural fires and aboriginal burning upon the forests of the central Sierra Nevada*. University of California, Berkeley.
- Riegel, G. M., R. F. Miller, C. N. Skinner, and S. E. Smith. 2006. Northeastern plateaus bioregion. in N. Sugihara, J. van Wagtendonk, J. Fites-Kaufmann, K. Shaffer, and A. Thode, editors. *Fire in California's ecosystems*. University of California Press, Berkeley.
- Ripple, W. J. and R. L. Beschta. 2008. Trophic cascades involving cougar, mule deer, and black oaks in Yosemite National Park. *Biological Conservation* 141:1249-1256.

- Rossi, R. S. 1980. History of cultural influences on the distribution and reproduction of oaks in California. Pages 7-18 in Proceedings of a symposium on the ecology, management, and utilization of California Oaks. Gen. Tech. Rep. PSW-44. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, US Department Agriculture.
- Roy, D. G. and J. L. Vankat. 1999. Reversal of human-induced vegetation changes in Sequoia National Park, California. *Canadian Journal of Forest Research* 29:399-412.
- Sampson, A. W. 1944. Plant succession on burned chaparral lands in Northern California. Bull. 685 Calif. Agric. exp. Stn. March 1944.
- Sessions, J., P. Bettinger, R. Buckman, M. Newton, and J. Hamann. 2004. Hastening the return of complex forests following fire: the consequences of delay. *Journal of Forestry* 102:38-45.
- Skinner, C. N. and C. Chang. 1996. Fire regimes, past and present. Pages 1041-1069 Sierra Nevada Ecosystem Project, Final Report o Congress. Volume II: Assessments and scientific basis for management options. . Centers for Water and Wildland Resources, University of California, Davis, California.
- Skinner, C. N., A. H. Taylor, and J. K. Agee. 2006. Klamath mountains bioregion. Fire in California's Ecosystems. University of California Press, Berkeley.
- Smith, J. S. and G. R. Brooks. 1978. The southwest expedition of Jedediah S. Smith: His personal account of the journey to California, 1826-1827. Arthur H. Clark Company.
- Smith, S. J. and R. S. Anderson. 1992. Late Wisconsin paleoecologic record from Swamp Lake, Yosemite National Park, California. *Quaternary Research* 38:91-102.
- Spero, J. G. 2001. Development and fire trends in oak woodlands of the northwestern Sierra Nevada foothills. US Forest Service General Technical Report PSW-GTR-184. Available online at: <http://danr.ucop.edu/ihrmp/proceed/spero.pdf>.
- Standiford, R., N. McDougald, W. Frost, and R. Phillips. 1997. Factors influencing the probability of oak regeneration on southern Sierra Nevada woodlands in California. *Madrono* 44:170-183.
- Standiford, R., N. McDougald, R. Phillips, and N. A. 1991. South Sierra oak regeneration weak in sapling stage. *California Agriculture* 45:12-14.
- Standiford, R. B. 1996. Growth of blue oak on California's hardwood rangelands. Pages 169-176 in Proc Symp Oak Woodlands: Ecology, Management, and Urban Interface Issues.
- Standiford, R. B., J. Klein, and B. Garrison. 1996a. Sustainability of Sierra Nevada hardwood rangelands. in Sierra Nevada Ecosystem Project: final report to Congress.
- Standiford, R. B., J. Klein, and B. Garrison. 1996b. Sustainability of Sierra Nevada hardwood rangelands. Sierra Nevada Ecosystem Project: final report to Congress, vol. III, Assessments and scientific basis for management options. Centers for Water and Wildland Resources, University of California, Davis, California.
- Standiford, R. B., R. L. Phillips, and N. K. McDougald. 2012. Fire history in California's southern Sierra Nevada blue oak woodlands. *Fire Ecology* 8:163-167.
- Steger, G. N., G. E. Eberlein, T. E. Munton, and K. D. Johnson. 1997. Characteristics of California spotted owl nest sites in foothill riparian and oak woodlands of the southern Sierra Nevada, California. Pages 19-22 in Pillsbury, Norman H.; Verner, Jared; Tietje, William D., technical coordinators. Proceedings of a symposium on oak woodlands: ecology, management, and urban interface.
- Stein, W. 1980. Oregon white oak 233. Forest cover types of the United States and Canada. Soc. Amer. For., Washington DC:110-111.

- Stein, W. I. 1990. *Quercus garryana* Dougl. ex Hook. RM Burns and BH Honkala, tech. coords. *Silvics of North America* 2:650-660.
- Stephens, S. L. 1997. Fire history of a mixed oak-pine forest in the foothills of the Sierra Nevada, El Dorado County, California. Pages 191-198 in *Proceedings, Symposium on Oak Woodlands: Ecology, Management, and Urban Interface Issues*. USFS GTR-PSW GTR-160.
- Stephens, S. L. and B. M. Collins. 2004. Fire regimes of mixed conifer forests in the north-central Sierra Nevada at multiple spatial scales. *Northwest Science* 78:12-23.
- Stephenson, N. L. 1990. Climatic control of vegetation distribution: the role of the water balance. *American Naturalist*:649-670.
- Stephenson, N. L., D. J. Parsons, and T. W. Swetnam. 1991. Restoring natural fire to the sequoia-mixed conifer forest: should intense fire play a role. Pages 321-337 in *Proceedings of the Tall Timbers Fire Ecology Conference*.
- Stuart, J. D. 1987. Fire history of an old-growth forest of *Sequoia sempervirens* (Taxodiaceae) forest in Humboldt Redwoods State Park, California. *Madrono* 34:128-141.
- Stuart, J. D. and S. L. Stephens. 2006. North coast bioregion. *Fire in California's ecosystems*. University of California Press, Berkeley, California, USA:147-169.
- Sudworth, G. B. 1900. Stanislaus and Lake Tahoe Forest Reserves, California, and adjacent territories. Pages 505-561 *Twenty-first annual report of the US Geological Survey, Part 5, Forest Resources*. Government Printing Office, Washington, DC.
- Sugihara, N. G., J. W. Van Wagtenonk, and J. Fites-Kaufman. 2006. Fire as an ecological process. *Fire in California's ecosystems*:58-74.
- Swiecki, T. J. and E. Bernhardt. 1998. Understanding blue oak regeneration. *Fremontia* 26:19-26.
- Swiecki, T. J. and E. Bernhardt. 2001. Effects of fire on naturally occurring blue oak (*Quercus douglasii*) saplings. Pages 251-259 in *Proceedings of the Fifth Symposium on Oak Woodlands: oaks in California's changing landscape*. Pacific Southwest Research Station, San Diego, California.
- Swiecki, T. J., E. A. Bernhardt, and R. A. Arnold. 1997a. The California oak disease and arthropod (CODA) database. Pages 543-552 in *Proceedings of a Symposium on Oak Woodlands: Ecology, Management, and Urban Interface Issues*. Gen. Tech. Rep. PSW-GTR-160. USDA Forest Service Pacific Southwest Research Station, Albany, CA. Zusammenfassung. Die Attacken des Eichenambrosia.
- Swiecki, T. J., E. A. Bernhardt, and A. Arnold Richard. 1991. Monitoring insect and disease impacts on rangeland oaks in California. Notes.
- Swiecki, T. J., E. A. Bernhardt, and C. Drake. 1993. Factors Affecting Blue Oak Sapling Recruitment and Regeneration. *Forest and Rangeland Resources Assessment Program (FRRAP) California*.
- Swiecki, T. J., E. A. Bernhardt, and C. Drake. 1997b. Factors affecting blue oak sapling recruitment and regeneration. Pages 157-167 in Pillsbury NH, Verner J, Tietje WD (tech. coords.). *Proc Symp Oak Woodlands: Ecology, Management, and Urban Interface*.
- Swiecki, T. J., E. A. Bernhardt, C. Drake, N. H. Pillsbury, J. Verner, and W. D. Tietje. 1997c. Stand-level status of blue oak sapling recruitment and regeneration. Pages 147-156 in Pillsbury NH, Verner J, Tietje WD (tech. coords.). *Proc Symp Oak Woodlands: Ecology, Management, and Urban Interface*.
- Tappeiner, J. C., P. M. McDonald, and D. F. Roy. 1990. *Lithocarpus densiflorus* (Hook. & Arn.) Rehd. Tanoak. Burns RM, Haonkala BH,(tech cords) *Silvics of North America* 2:417-425.

- Tate, K. W., D. M. Dudley, N. K. McDougald, and M. R. George. 2004. Effect of canopy and grazing on soil bulk density. *Rangeland Ecology & Management* 57:411-417.
- Taylor, A. H. and C. N. Skinner. 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. *Ecological Applications* 13:704-719.
- Thornburgh, D. A. 1990. *Quercus chrysolepis* Liebm. canyon live oak. *Silvics of North America* 2:618-624.
- Thorne, J. H., B. J. Morgan, and J. A. Kennedy. 2008. Vegetation change over sixty years in the Central Sierra Nevada, California, USA. *Madronno* 55:223-237.
- Tietje, W. D., T. C. Berlund, S. L. Garcia, C. G. Halpin, and W. A. Jensen. 1997. Contribution of downed woody material by blue, valley, and coast live oaks in central California. Pages 423-430 in Pillsbury et al. *Proceedings of a symposium on oak woodlands: ecology, management, and urban interface issues*. Gen. Tech. Rep. PSW-GTR-160.
- Tietje, W. D., K. L. Waddell, J. K. Vreeland, and C. L. Bolsinger. 2002. Coarse woody debris in oak woodlands of California. *Western Journal of Applied Forestry* 17:139-146.
- Tollefson, J. E. 2008. *Quercus chrysolepis* U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory
- Tyler, C. M., B. Kuhn, and F. W. Davis. 2006. Demography and recruitment limitations of three oak species in California. *The quarterly review of biology* 81:127-152.
- Van de Water, K. M. and H. D. Safford. 2011. A summary of fire frequency estimates for California vegetation before Euro-American settlement. *Fire Ecology* 7:26-58.
- Van Dersal, W. R. 1940. Utilization of oaks by birds and mammals. *The Journal of Wildlife Management* 4:404-428.
- Van Wagtendonk, J. W. and J. Fites-Kaufman. 2006. Sierra Nevada bioregion. *Fire in California's ecosystems*. University of California Press, Berkeley, USA:264-294.
- Vankat, J. L. and J. Major. 1978. Vegetation changes in Sequoia National Park, California. *Journal of Biogeography*:377-402.
- Verner, J. and A. S. Boss. 1980. *California wildlife and their habitats: western Sierra Nevada*. US Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station.
- Wagner, F. H. 1989. Grazers, past and present. *Tasks for vegetation science*. 20:151.
- Webb, S. D. and A. D. Barnosky. 1989. Faunal dynamics of Pleistocene mammals. *Annual Review of Earth and Planetary Sciences* 17:413.
- Weeks, D., A. E. Wieslander, and C. L. R. Hill. 1934. *The Utilization of El Dorado County Land*. University of California [Press.
- White, S. D. and J. O. Sawyer Jr. 1994. Dynamics of *Quercus wislizenii* forest and shrubland in the San Bernardino Mountains, California. *Madroño* 41.
- Wohlgemuth, E. 1996. Resource Intensification in Prehistoric Central California: Evidence from Archaeobotanical Data. *Journal of California and Great Basin Anthropology* 18.
- Wolf, C. B. 1945. *California wild tree crops*. Rancho Santa Ana Botanic Garden, Claremont, California.
- Zielinski, W. J., R. L. Truex, G. A. Schmidt, F. V. Schlexer, K. N. Schmidt, and R. H. Barrett. 2004. HOME RANGE CHARACTERISTICS OF FISHERS IN CALIFORNIA. *Journal of Mammalogy* 85:649-657.

TABLES

Table 1. Differences in geographic, physical, and ecological attributes of primary hardwood species addressed in this assessment.

Dominant Species	Elevation Range: (feet)	Associated Species	Mean Annual Precipitation (mm)	Mean Maximum Temperatures (° F)	Mean Minimum Temperatures (° F)	Soils
Blue Oak ¹	165-5,900	Gray pine, California buckeye, valley oak, interior live oak	510-1,020 mm	90°	30°	Shallow, infertile, moderate to excessively well drained
Canyon Live Oak ²	300-9000	Blue oak, gray pine, California black oak, interior live oak, Ponderosa pine, Douglas fir	300-2,790 mm	73°	43°	Deep, rich to shallow, infertile, well drained
Interior Live Oak ³	1,000-6,200	Canyon live oak, valley oak, blue oak, gray pine,	380-1,300 mm			Deep, rich to shallow, infertile, moderately to poorly drained
Black Oak ⁴	200-8,000	Ponderosa pine, Douglas fir, tanoak, Pacific madrone	300-2540 mm	74°	38°	Deep, well drained
Tanoak ⁵	1,900-6,500	Douglas fir, tedwood, Pacific madrone,	1,020-2,540 mm	67°	39°	Deep, well to moderately drained
Oregon White Oak ⁶	980-5,900	Douglas fir, Pacific madrone,	510-1,300 mm	72°	32°	Deep to shallow, moderately to poorly drained

Data sources: (1) (McDonald 1990); (2) (Thornburgh 1990); (4) (McDonald 1990); (5) (Tappeiner et al. 1990); (6) (Stein 1990)

Table 2 Comparison of total basal area, tree density, mortality, and seedling and sapling density of California black oak between 1969 and 1996 on unburned and burned plots in Sequoia National Park (Roy and Vankat 1999).

Stand Structure Variable	Unburned		Burned	
	1969	1996	1969	1996
Basal area (m ² /ha)	18	15	5	2
Density (trees/ha)	475	150	380	350
Mortality (trees/ha)	NA	110	NA	320
Seedlings/sapling (#/ha)	NA	0	NA	290

Table 3. Comparison of changes in frequency (percent of plots) and tree densities (trees/ha) for three size classes between Vegetation Type Mapping plots (ca. 1930) and Forest Inventory and Analysis plots (ca. 2000). From Dolanc et al. (in review).

Species	VTM frequency (% of plots)	FIA frequency (% of plots)	Size Class (cm dbh)	Ca. 1930 (trees/ha)	Ca. 2000 (trees/ha)
Tanoak	0.5	2.8	10.2-30.4	66.5	178.6
			30.5-60.9	NA	NA
			≥61.0	NA	NA
Canyon live oak	4.1	13.6	10.2-30.4	88.7	226.7
			30.5-60.9	28.4	59.1
			≥61.0	NA	NA
Blue oak	9.9	9.2	10.2-30.4	102.4	105.7
			30.5-60.9	29.6	33.7
			≥61.0	NA	NA
California black oak	21.3	20.5	10.2-30.4	56.2	104.0
			30.5-60.9	26.1	37.3
			≥61.0	29.8	20.6
Interior live oak	12.2	10.3	10.2-30.4	94.0	230.4
			30.5-60.9	28.3	26.8
			≥61.0	NA	NA

Table 4. Estimated CWD logs (total million ft²) on unreserved woodlands outside National Forests, California 1991-1994. From (Tietje et al. 2002).

Species	Northern Sierra Nevada	Central Sierra Nevada	Plots with no CWD (%)
Blue oak	6.3	39.3	65
California black oak	3.9	5.0	67
Canyon live oak	2.9	0	78
Interior live oak	2.4	19.7	58
Oregon white	2.2	0	59

Table 5. Historic fire regimes in major hardwood vegetation types in the Sierra Nevada.

Vegetation Type	FRI Median¹	FRI Minimum¹	FRI Maximum¹	Percent Low/Mixed/Replacement Fire²	Size³	Complexity³	Type³	Seasonality³
Blue oak–gray pine	12	5	45	8/2/91	Large	Low	Surface	Summer-fall
Black oak-Ponderosa pine	7	5	40	5/17/78	Large	Low	Surface	Summer-fall
Mixed Evergreen/Tanoak	13	15	80	10/58/32	Medium	Multiple	Multiple.	Summer, Fall, <i>occasionally</i> Winter, Spring
Canyon Live/Interior Live Oak	<35			NA	Medium-Large	Multiple	Multiple	Summer-fall
Oregon White Oak	14	3	30	3/19/78				

Data from Van de Water and Safford (2011)¹, Landfire (2007)², and Van Wagtendonk and Fites (2006)³.

Table 6. Fire sensitivity of mature trees, mixed age, saplings and seedlings for hardwood species addressed in this assessment. Table from (Holmes et al. 2008)

Species	#	Fire Type/Season	Dead	Top Killed ^a	Citation
Mature Trees					
Q. douglasii					
Q. kelloggii	208	prescribed, June	1% b	none noted	Fry 2002
Q. lobata					
Q. douglasii	119	Wildfire, June	6%	8%	Haggerty 1994
Q. wislizeni	29	wildfire, June	11%	24%	Haggerty 1994
Mixed Age					
Q. chrysolepis	239	prescribed, Nov	>15cm dbh 10% c <15cm dbh 47% c	included in dead	Paysen and Narog 1993a
<i>Q. chrysolepis</i> (>7.5cm dbh)	156	wildfire, Nov	2%	63%	Plumb 1980
Q. douglasii	100	wildfire, summer	2% b	seedling 50% others 8%	Horney and others 2002
Q. garryana	874	prescribed, spring prescribed, fall prescribed, 2x	spring 94/ha c fall 91/ha c 2x 523/ha c	included in dead	Regan and Agee 2004
Q. kelloggii	?	prescribed, various	high fuel 55-91% mod. fuel 22-65%	none noted	Kauffman and Martin 1987
Q. kelloggii	72	wildfires, various	13%	24%	Plumb 1980
Saplings					
Q. chrysolepis	10	wildfire, Nov	10%	90%	Plumb 1980
Q. douglasii	38	prescribed, Oct	<5%	78%	Tietje et al. others 2001
Q. douglasii	67	wildfire, Sept	9%	82%	Swiecki and Bernhardt 2002
Q. douglasii	48	prescribed, July	<10%	>90%	Bartolome et al. 2002
Seedlings					
Q. douglasii	558	wildfire, July	17%	5% ^{b d}	Schwan et al. 1997

^a Death of all above-ground stems, followed by recovery via sprouting of basal shoots.

^b Study addressed either multiple species or multiple sizes of oaks; results not provided individually.

^c Topkilled trees included in numbers reported for dead trees.

FIGURES

Figure 1. Pollen abundances of different genera from Lake Moran, elevation 2107 m in the north fork of the Stanislaus River, Sierra Nevada. Data from (Edlund and Byrne 1991). Figure from (Byrne et al. 1991).

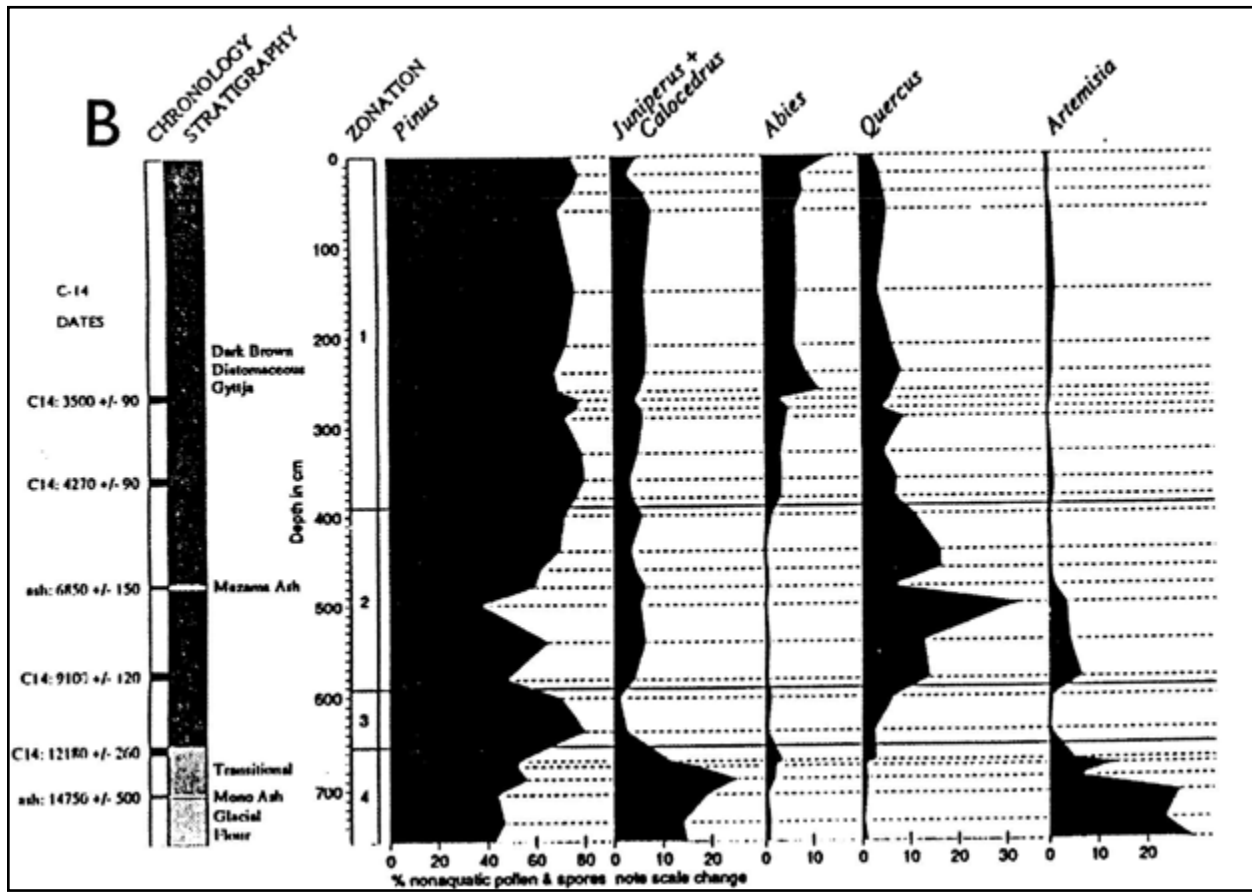


Figure 2. Distribution of oak pollen from five sites in the Sierra Nevada showing an increase in oak abundance between 5,000 and 10,000 ybp. Figure from (Mensing 2005)

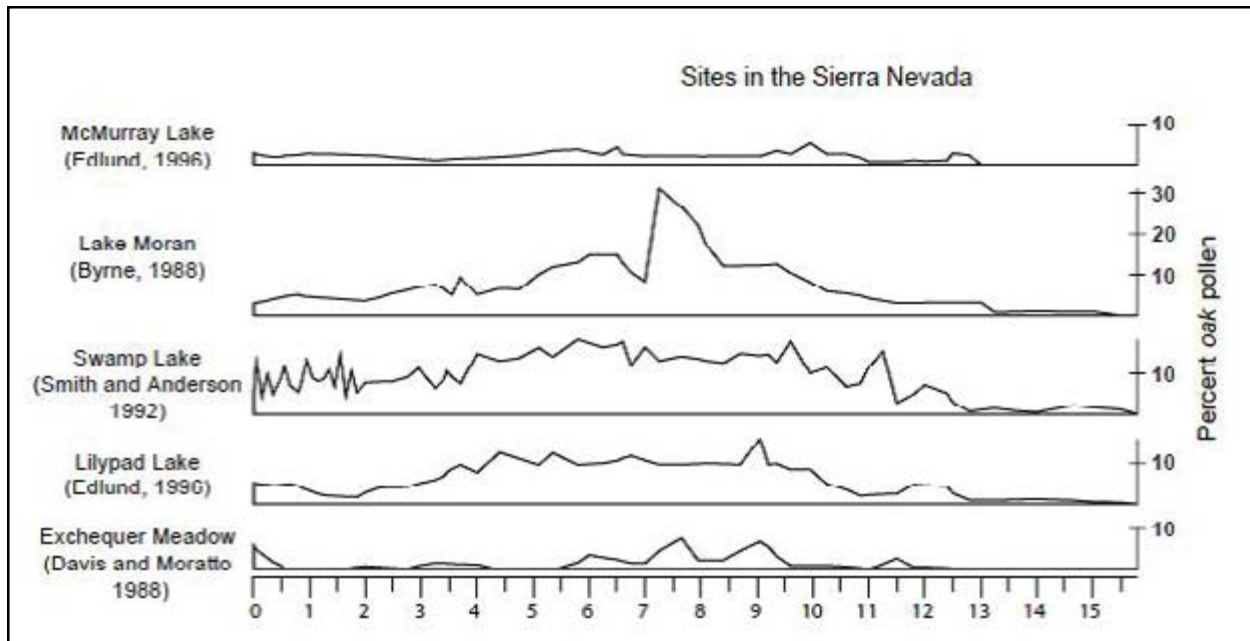


Figure 3. Diagram showing movement of oak taxa along elevational gradients over time, as represented by percent pollen at seven sites in the central and south-central Sierra Nevada. Data from (Anderson and Smith 1994). Figure from (Millar and Woolfenden 1999).

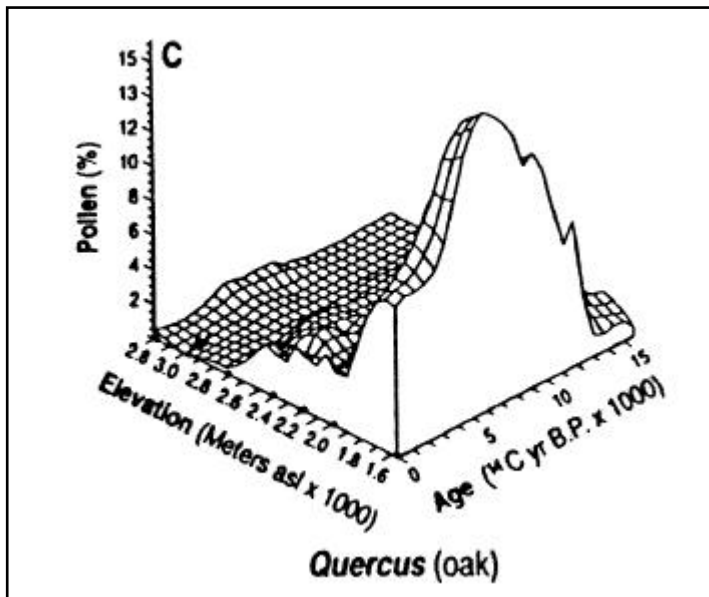


Figure 4. Composite charcoal record over the last 11,000 years based on sums from seven meadows in the central and southern Sierra Nevada. Data from (Anderson and Smith 1997). Figure from (Millar and Woolfenden 1999).

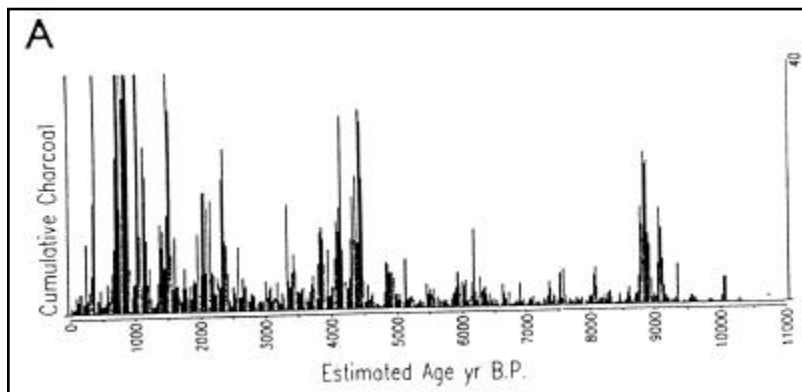


Figure 5. Pleistocene age pollen diagrams for sites in California recording oak. Filled circles represent packrat midden samples with oak pollen and open circles represent samples with no oak pollen. Gray bands identify cold periods (stadials and glacial maxima) when percent oak pollen was generally very low. Figure from (Mensing 2005).

