TWELVE

Oak Woodlands and Forests

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Introduction

Oak woodlands and savannas occupy 4 million ha in California (Griffin 1977; Bolsinger 1988; FRAP 2003). These areas have an overstory tree canopy, predominantly in the genus *Quercus*. The Latin word is derived from the Celtic words *quer*, meaning fine, and *cuez*, meaning tree (Pavlik et al. 1991). Annual grassland is the major understory vegetation, although shrubs and perennial grasses may be important components in some areas (Griffin 1973; Bartolome 1987; Holmes 1990; Allen et al. 1991). Native perennial grasses are scattered throughout California (Beetle 1947; Bartolome and Gemmill 1981) interspersed within a matrix of annual grasses, forbs, and legumes that are mostly native to the Mediterranean region (Jackson 1985). Oak-dominated communities are bounded by grasslands at lower elevations and conifer forests at higher elevations.

Seven series and 57 subseries have been described within the oak community type (Allen et al. 1989, 1991). Oak types occupy 52 of California's 58 counties and are widely distributed west of the Sierra Nevada (Fig. 12.1). Oak savannas and woodlands are generally 60–700 m elevation (Barbour and Major 1988). The climate is Mediterranean, with precipitation occurring primarily as rain between October and May. Summer drought can result in 2–11 months of water deficit, but it averages 6 months (Pavlik et al. 1991).

Dominant trees in oak woodland and forests include blue oak *(Quercus douglasii)*, valley oak *(Q. lobata)*, interior live oak *(Q. wislizenii)*, coast live oak *(Q. agrifolia)*, Oregon white oak *(Q. garryana)*, and Engelmann oak *(Q. engelmannii)*. These species occur in monospecific to mixed stands (Allen-Diaz et al. 1999). Seventy-three percent of California's oak woodlands and forests are currently privately owned (FRAP 2003), although as much as 90% of California's oak woodlands were privately owned in 1990 (Ewing et al. 1988; Greenwood et al. 1993). Since European settlement of California, oak woodlands have been managed primarily for livestock production. Other economic products include firewood, wildlife, water, and recreation (McClaran and Bartolome 1985; Standiford and Tinnin 1996). This vegetation has taken on a new importance because it has the greatest species richness of any vegetation type in the state, with over 300 vertebrates, 5,000 invertebrates, and 2,000 plants (Barrett 1980; Verner 1980; Garrison 1996).

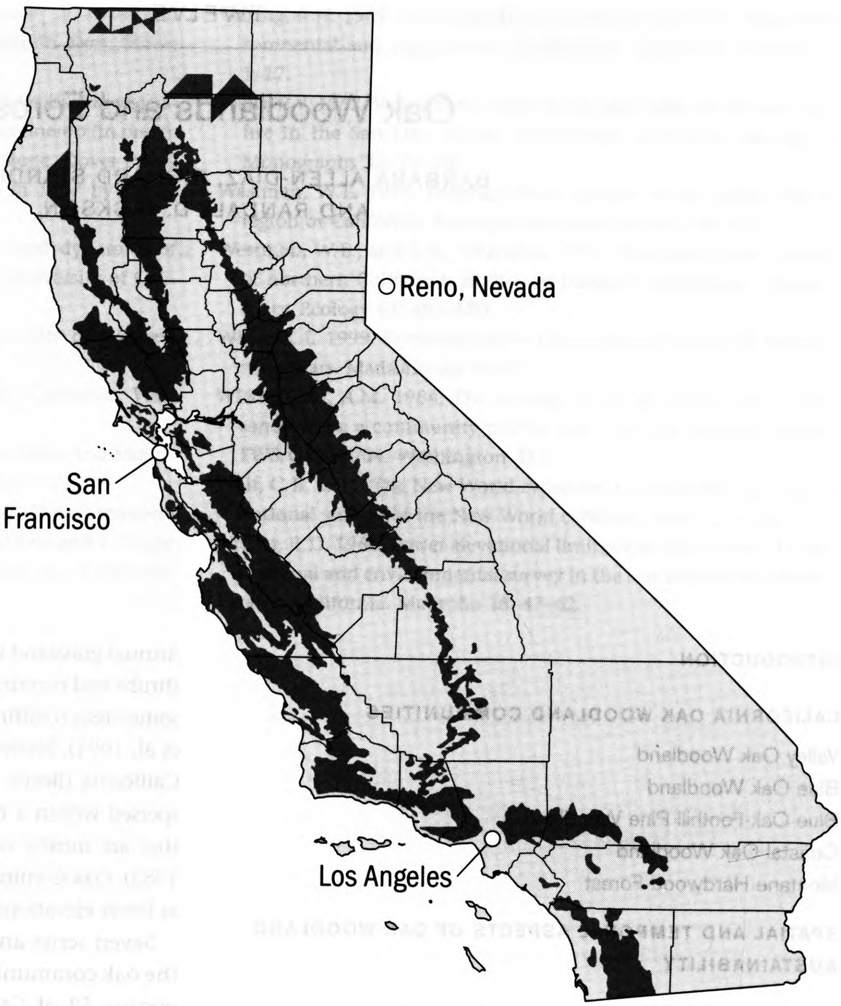

FIGURE 12.1 Distribution of oak woodlands in California. Adapted from FRAP (2003).

California has nine native tree oak species. The five major oak species occurring in the oak woodland include the deciduous white oak species blue oak, valley oak, and Engelmann oak; and the evergreen oaks, coast live oak and interior live oak. Three additional species of oak are found primarily in oak forests where mixtures of tree oak and conifer species coexist. These species are California black oak *(Quercus kelloggii)*, Oregon white oak, and canyon live oak *(Quercus chrysolepis)*; they are more typically found on moister, more productive sites. A ninth tree species of oak is Island oak, *Quercus tomentella*, the rarest of California's tree oaks occurring only on the Channel Islands and on Guadalupe Island southwest of San Diego (Pavlik et al. 1991).

These eight major tree oak species (Table 12.1, Fig. 12.2) will be the focus of this chapter. The term *oak woodland* will be used to include oak woodlands and forests, although clear distinctions will be evident in the description of individual community types.

California Oak Woodland Communities

A variety of systems have been used to classify oak woodlands in California based on the distribution, density, and abundance of the various oak species, together with other tree, shrub, and herbaceous species (Allen et al. 1991; Griffin 1977; Munz and Keck 1973; Kuchler 1988; Eyre 1980). Table 12.2 provides a comparison crosswalk among the several systems. Allen et al. (1991) has the most detailed system, and it is based on analyses of plant species composition from plot data. However, that system is incomplete because the plot data used in the analyses did not cover all oak woodland types. Sawyer and Keeler-Wolf (1995) integrate both plot-based and experience-based analyses and provide complete coverage of California's oak-dominated communities. Mayer and Laudenslayer's work (1988) is useful because it is a direct link to wildlife presence/absence data maintained by the California Department of Fish and Game in the Wildlife Habitat Relations (WHR) database.

In this chapter, we use WHR headings from Mayer and Laudenslayer (1988), but with additional details from Allen et al. (1989, 1991) and Sawyer and Keeler-Wolf (1995). For Oregon White oak types, we use Bolsinger (1988).

Valley Oak Woodland

Valley oak is endemic to California (Griffin and Critchfield 1972). Once widespread, valley oak woodland now

TABLE 12.1

General Characteristics of California's Important Hardwood Rangeland Oak Species

Characteristics	*Blue Oak*	*Interior Live Oak*	*Coast Live Oak*	*Valley Oak*
Scientific name	*Quercus douglasii* Hook. & Arn.	*Quercus wislizenii* A. DC.	*Quercus agrifolia* Nee	*Quercus lobata* Nee
Common names	Blue, white, mountain, rock, iron, post, jack, Douglas	Interior live oak, highland live oak, Sierra live oak	Coast live oak, California live oak, encina	Valley, white, Calif. white, mush, water, swamp, roble
Height	Usually 6–18 m; tallest over 27 m	Usually 9–23 m,. shrub form 2.5–3 m.	Usually 6–12 m.; may reach 24 m.	12–36 m.
Mature Tree DBH	Less than 0.3 m, up to 0.6 m; largest >1.8 m	0.3–1.0 m	.3–1.2 m	0.3–1.2 m; largest >2.4 m
Longevity	Long-lived, 175–450 yrs.	150–200 yrs.	Long-lived, 125–250 yrs.	Long-lived, 200–250 yrs.
Sprouting	Variable sprouter; not vigorous on dry sites	Very vigorous sprouter	Very vigorous sprouter	Not a vigorous sprouter
Acorn	Matures first year; variable in shape; warty scales; cup very shallow	Matures second year; very slender, pointed, 2.5 cm long; cup over half the nut	Matures first year; 2–7 cm; cup over 1/3 of nut and not warty	Matures first year, variable but large and tapered, cup over 1/3 of nut, warty
Foliage	Deciduous; blue-gray color; smooth or slightly to deeply lobed edges; 2.5–7.6 cm. long and 1.2–5 cm wide	Evergreen with smooth to very spiny-toothed; dark green above and lighter below with waxy/shiny surface 2.5–10 cm; flat	Evergreen; 2.5–7.5 cm; roundish; dark and shiny above with gray or rusty fuzz underneath; cupped or spoon-shaped	Deciduous; leaves leathery with shiny, dark green-yellow above and grayish below; deep irregular lobes; 5–10 cm.
Shade Tolerance	Seedlings not tolerant	Somewhat shade tolerant	Shade tolerant throughout life	Seedlings somewhat tolerant, mature trees intolerant
Fire Tolerance	Tolerates grass fires; not hot brush fires	Not very tolerant, but sprouts well after fire	Very tolerant of hot fires due to thick bark	Not tolerant of fires
Elevation	150–600 m in north; up to 1,500 m in south	Below 600 m in north and above 1,800 m in south	Below 900 m. in north and up to 1,500 m in south	150–240 m in north; up to 1,700 m in south
Associates	Grades into open valley oak stands at low elevations; into denser live oak stands at higher elev.; foothill pine common	In pure stands or mixed with blue and/or coast live oak, and valley oaks in So. California	Forms pure stands; also grows with interior live oak and coast live oak	Blue and Oregon white oak; sometimes interior live oak
Sites	Hot, dry sites with rocky soils, 30–100 cm deep; can't compete with live oak on better sites	Wide range, from valleys to foothills; moister areas than blue oak	Common on valley floors or not-too-dry fertile slopes	Prefers fertile, well-drained bottomland soils, streambeds, and lower foothills
Notes	Confused with valley oaks when leaves are dusty	Confused with coast live oaks; distinguished by flat leaves	Confused with interior live oak but rounded and cupped leaves	Confused with Oregon white oak but acorns pointed with warty cups

(continued)

TABLE 12.1 (continued)

Characteristics	*Engelmann Oak*	*California Black Oak*	*Oregon White Oak*	*Canyon Live Oak*
Scientific name	*Quercus engelmannii* Greene	*Quercus kelloggii* Newb.	*Quercus garryana* Dougl.	*Quercus chrysolepis* Liebm.
Common names	Engelmann, mesa	Black, California black oak	Garry oak, white oak, Oregon oak	Canyon live oak, canyon oak, gold cup oak, live maul, maul oak, white live oak
Height	6–15 m	18–27 m	15–24 m	18–24 m
Mature Tree DBH	0.3–0.6 m	0.3–1.2 m.	0.6–1.0 m; largest over 1.5 m	.3–1.2 m; largest over 1.5 m
Longevity	100–200 yrs.	100–200 yrs., occasionally up to 500 yrs.	100–200 yrs.	Up to 300 yrs.
Sprouting	Variable sprouter	Excellent sprouter	Excellent sprouter	Variable sprouter
Acorn	Matures first year	Matures second year; 3.8 cm long; thin cup over half the nut	Matures first year; 2.5 cm long with shallow cup	3.8 cm long; thick, shallow cup
Foliage	Considered deciduous but foliage may persist during winter; similar to blue-gray color of blue oak	Deciduous; 13 cm long; 5–7 lobed; spiny leaf tips; dark yellow-green above and pale yellow-green below	Deciduous; 10–15 cm– long; evenly and deeply lobed with rounded leaf tips; lustrous dark-green and shiny above and pale green below	Evergreen; 7.5 cm– long; persist 3 or 4 seasons on tree; usually not lobed; leathery
Shade Tolerance	Seedlings tolerant, mature trees intolerant	Intermediate tolerance as seedling and intolerant as tree matures	Intermediate tolerance as seedling and intolerant as tree matures	Tolerant of shade
Fire Tolerance	Very tolerant of hot fires	Very sensitive to cambium being killed in hot fires	Maintained in open stands by regular, low-intensity fires	Sensitive to hot fires
Elevation	Under 1,200 m	60–1,800 m	150–900 m	90–1,500 m
Associates	In pure stands and with coast live oak	Most common with tanoak, madrone, mixed conifer forest species;, also with coast live oak, interior live oak, and blue oak	Douglas-fir and mixed evergreen forests; Pacific madrone and tanoak	Found with mixed conifer, chaparral, and woodland species; tanoak, Douglas-fir, Pacific madrone, coast live oak
Sites	Warm, dry fans and foothills	More common on forest sites; found on moister hardwood rangelands; well-drained soils	Cool humid sites near coast to hot, dry sites inland	Most widely distributed oak on CA.; sheltered north slopes and steep canyons
Notes	Very limited range in southern California makes protection a high priority	Protected by Forest Practice Act on timberlands; commercial properties for finished lumber	Protected by Forest Practice Act on timberlands	Both a shrubby and tree form; very dense wood

NOTE: Adapted from Pavlik et al. 1991 and Standiford 2001.

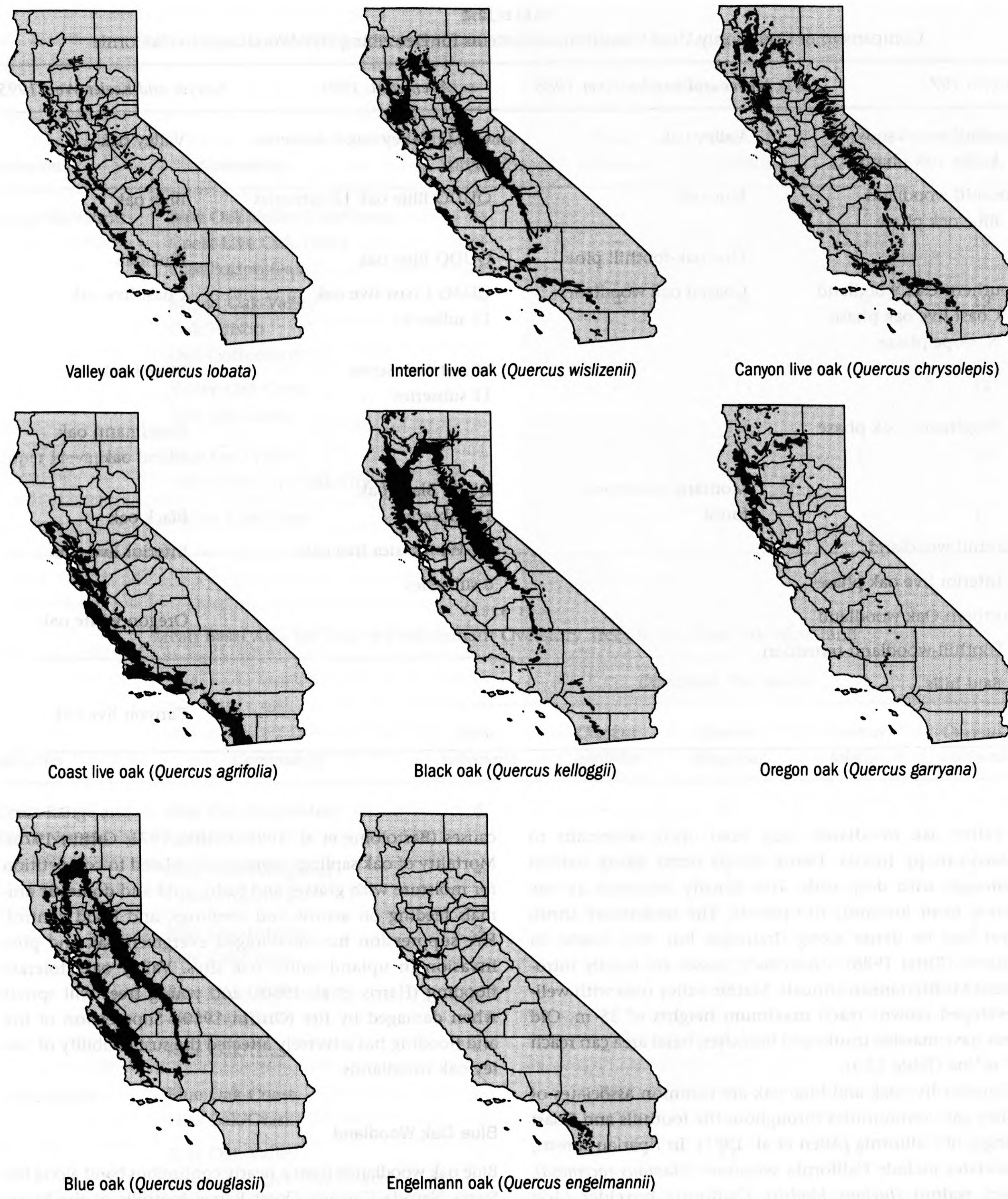

FIGURE 12.2 Geographic distribution of oak tree species.

occupies only 2.7% of the state (Bolsinger 1988). The woodland has a patchy distribution adjacent to most major lowland valleys with deep soils below 740 m elevation from Los Angeles County northward to Shasta Lake (Allen et al. 1991). The patches are embedded in a matrix of agricultural, urban, and suburban land, annual grasslands, riparian forests, and other oak woodland types (Knudson 1987). Conversion of valley oak woodlands to irrigated agricultural land has had the largest effect on the acreage decline of this type (Jensen, Tom, and Harte 1990). Valley oak trees may occur up to 1,700 m as components of other vegetation types (Griffin 1977).

TABLE 12.2
Comparison of Commonly Used Classification Systems for Describing Oak Woodlands in California

Griffin 1977	*Mayer and Laudenslayer 1988*	*Allen et al. 1991*	*Sawyer and Keeler-Wolf 1995*
Foothill woodland Valley oak phase	Valley oak	QULO Valley oak 6 subseries	Valley oak
Foothill woodland Blue oak phase	Blue oak	QUDO Blue oak 12 subseries	Blue oak
	Blue oak-foothill pine	QUDO Blue oak	Blue oak
Southern Oak woodland Coast live oak phase N. slope phase	Coastal oak woodland	QUAG Coast live oak 15 subseries	Coast live oak
		Mixed Oak Series 11 subseries	Mixed oak
Engelmann oak phase			Engelmann oak Island oak
	Montane hardwood forest	QUKE Black oak 13 subseries	Black oak
Foothill woodland Interior live oak phase		QUWI Interior live oak 6 subseries	Interior live oak
Northern Oak woodland Foothill-woodland transition Bald hills			Oregon white oak
			Canyon live oak

Valley oak woodlands vary from open savannahs to closed-canopy forests. Dense stands occur along natural drainages with deep soils. Tree density decreases as one moves from lowlands to uplands. The understory shrub layer can be dense along drainages but very sparse in uplands (Ritter 1988). Understory grasses are mostly introduced Mediterranean annuals. Mature valley oaks with well-developed crowns reach maximum heights of 35 m. Old trees have massive trunks and branches; basal area can reach 17 m^2/ha (Table 12.3).

Interior live oak and blue oak are common associates of valley oak communities throughout the foothills and Coast Ranges of California (Allen et al. 1991). In riparian forests, associates include California sycamore *(Platanus racemosa)*, black walnut *(Juglans hindsii)*, California boxelder *(Acer negundo)*, Fremont cottonwood *(Populus fremontii)*, tree willows (*Salix* spp.), and Oregon ash *(Fraxinus latifolia)*. California black oaks and pines often occur with valley oaks at higher elevations (Griffin 1977). In communities with coast live oak, mean stand basal area can reach >60 m^2/ha.

Valley oaks are among the oldest and largest oaks in North America (Pavlik et al. 1991). Tree age can exceed 500 years (Allen-Diaz et al. 1999). In many areas, there is little valley oak recruitment, due to both natural and human causes (Bartolome et al. 1987; Griffin 1971; Griffin 1976). Mortality of oak saplings seems to be related to competition for moisture with grasses and forbs, wild and domestic animals feeding on acorns and seedlings, and flood control. Fire suppression has encouraged evergreen oak and pine invasion in upland valley oak sites. Valley oaks tolerate flooding (Harris et al. 1980), and young trees will sprout when damaged by fire (Griffin 1980). Suppression of fire and flooding has adversely affected the sustainability of valley oak woodlands.

Blue Oak Woodland

Blue oak woodlands form a nearly continuous band along the Sierra Nevada–Cascade–Coast Range foothills of the Sacramento and San Joaquin Valleys (Fig. 12.2; Griffin and Critchfield 1972), typically between 300 and 760 m in elevation in the north, rising to 1,500 m in the south. At lower elevations on gentle slopes, blue oak woodlands typically occur as large blocks with highly variable canopy cover. On steeper ground, blue oak woodlands occur in small patches within other vegetation such as annual grassland, chaparral, riparian forest, and other types of oak woodland. Blue oak woodlands occur on a wide range of soils; however, they are often shallow,

TABLE 12.3

Mean Basal Area (m^2/ha) of Predominant Overstory Trees in the Valley Oak Woodland

		Dominant Tree Species				
Subseries	*Community*	*Arbutus californica*	*Pinus sabiniana*	*Quercus agrifolia*	*Quercus douglasii*	*Quercus lobata*
Lower Elevation	Blue Oak-Valley Oak/Grass	–	–	–	7	4
	Coast Live Oak-Valley Oak/Poison Oak	–	–	21	–	10
	Mixed Oak-Valley Oak/Poison Oak-Coffeeberry	5	4	25	6	19
	Valley Oak-Coast Live Oak/Grass	–	–	11	–	14
Upper Elevation	Blue Oak-Valley Oak-Coast Live Oak/Grass	–	–	5	11	14
	Valley Oak/Grass	–	–	–	–	17

TABLE 12.4

Mean Basal Area (m^2/ha) of Predominant Overstory Trees in the Blue Oak Woodland

		Dominant Tree Species				
Subseries	*Community*	*Pinus sabiniana*	*Quercus agrifolia*	*Quercus douglasii*	*Quercus lobata*	*Quercus wislizenii*
Coast Range and Sierra Nevada	Blue Oak/Narrowleaf Goldenbush	6	–	6	–	
	Blue Oak/Wedgeleaf Ceanothus/Grass	4	–	5	–	3
	Blue Oak-Interior Live Oak/Grass	2	–	5	–	4
	Blue Oak-Understory Blue Oak/Grass	–	–	11	–	–
	Blue Oak/Grass	–	–	11	–	–
Coast Range	Blue Oak-Coast Live Oak/Grass	–	3	9	–	–
	Blue Oak-Valley Oak-Coast Live Oak/Grass	–	5	11	14	–
	Blue Oak-Valley Oak/Grass	–	–	7	4	–

rocky, infertile, and well drained. There is considerable climatic variation, with annual precipitation ranging from 25 to 150 cm, and averaging 52 cm (Barbour and Minnich 2000).

Blue oak woodlands are highly variable (Table 12.4), with blue oak comprising 80% to 100% of the trees present. The rounded tree canopy, 7–20 m in height, is characterized by distinctive blue-green leaves. Foothill pine *(Pinus sabiniana)*, California buckeye *(Aesculus californica)*, valley oak, interior live oak, canyon live oak, and California black oak are common associates (Allen et al. 1989; Ritter 1988a; Neal 1980).

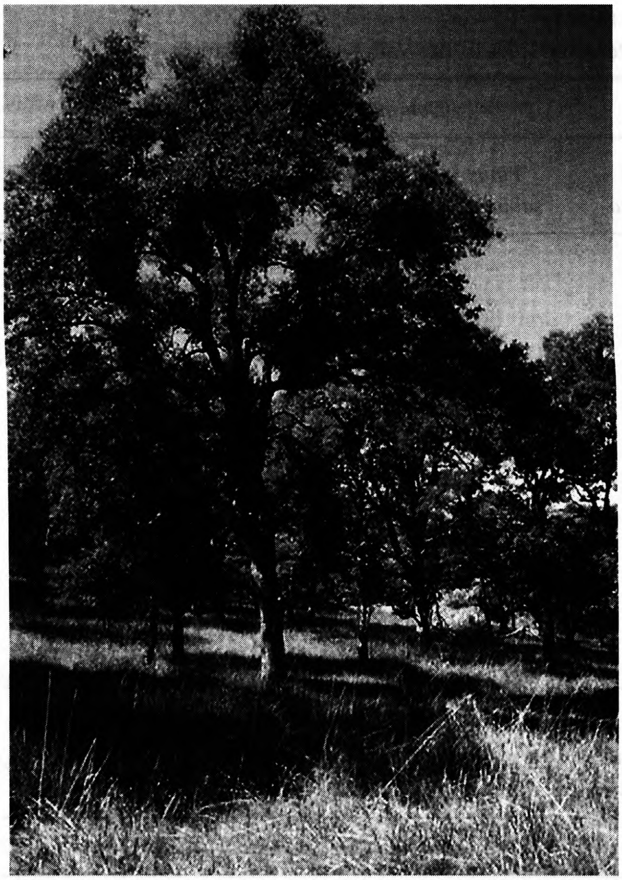

FIGURE 12.3 Blue oak woodlands are highly variable. Tree canopies are characterized by distinctive blue-green, deciduous leaves. Often there is little seedling recruitment, and annual grasses create most of the understory cover in open woodlands.

The overstory of blue oak woodland ranges from sparsely scattered trees on poor sites to nearly closed canopies on good quality sites. Blue oak basal area varies from association to association (Table 12.4), from as low as 5 m^2/ha to as high as 11 m^2/ha. Stand basal area for all tree species combined can be >28 m^2/ha.

Annual grasses create most of understory cover in open woodlands. Common species include *Bromus hordeaceus*, *Lolium multiflorum*, *Bromus diandrus*, and *Hordeum leporinum*. Common forbs include *Daucus pusillus*, *Geranium molle*, *Madia* spp., and *Trifolium* spp. Characteristic shrub species include poison-oak *(Toxicodendron diversilobum)*, California coffeeberry *(Rhamnus californica)*, and several species of *Ceanothus* and *Arctostaphylos* (Allen-Diaz et al. 1991; Sawyer and Keeler-Wolf 1995).

Blue oaks are relatively slow-growing, long-lived trees (McDonald 1990) endemic to California (Allen-Diaz et al. 1999). Most blue oak stands exist as groups of medium-to-large trees with few or no young oaks (Fig. 12.3), which may indicate a regeneration problem (Muick and Bartolome 1987). There is concern that blue oak woodlands may be slowly changing into savannas and grasslands as trees die and are not replaced. Fire is an important environmental factor (McClaran and Bartolome 1989), because young blue oaks can stump sprout readily, but older, decadent trees cannot (McDonald 1990; McCreary et al. 1991, 2002). Therefore, younger stands are more likely to regrow after fires.

Poor blue oak recruitment from acorns occurs for several reasons. Introduced annual grasses out-compete blue oak seedlings for soil moisture (Gordon et al. 1989). In addition, acorns and seedlings are eaten or damaged by insects, domestic livestock, and wildlife (Griffin 1971). Blue oak also appears to be somewhat intolerant of shade and is unable to survive under dense overstory canopies (Muick 1997). Most recent work suggests that recruitment is not limited by reproduction (number of acorns), but by the establishment and survival of saplings. Various studies have shown that grazing by vertebrates reduces growth and survival of blue oak (e.g., Borchert et al. 1989; Adams et al. 1992) and thus protection of seedlings is important for successful regeneration (Allen-Diaz and Bartolome 1992; Hall et al. 1992; Tecklin et al. 2002).

Blue oak trees have a significant effect on understory composition and productivity depending on density of oak species and annual precipitation. Where precipitation is >50 cm annually, the canopy suppresses understory biomass throughout the growing season. The degree of suppression depends on canopy density and site characteristics and is generally greater with evergreen species than with deciduous oak species (Allen-Diaz et al. 1999; Pitt and Heady 1978). In one study at UC's Hopland Research and Extension Center in the Coast Ranges of Mendocino County, grassland above-ground biomass averaged 2,300 kg/ha in open grassland and 1,300 kg/ha under blue oak canopies (Bartolome and McClaran 1992; Murphy 1980).

On drier sites in the blue oak woodland, the opposite effect occurs. Grassland productivity under blue oak canopies can be twice that of open grassland (Holland 1980). Other researchers have reported similar results, although once trees die, the level of productivity gradually declines to that of open grassland (Allen-Diaz et al. 1999).

Blue Oak-Foothill Pine Woodland

Blue oak-foothill pine woodlands are found on steeper, dryer slopes with shallower soils than blue oak woodlands. At lower elevations on gentle slopes, these two communities intermix with grasslands (Holmes 1990; Bartolome 1987). At higher elevations on steeper slopes, the communities are mixed with grasslands and shrublands. Riparian woodlands may bisect these mosaics along permanent and intermittent watercourses. Blue oak-foothill pine woodlands are found throughout the range of blue oak and form a nearly continuous band along the Sierra Nevada-Cascade foothills of the Sacramento-San Joaquin Valley, except for a gap in Tulare and southern Fresno counties. The upper elevation limit ranges from 150 m in the north to 900 m in the south. This woodland type occurs on a variety of well-drained soils.

Foothill pine is taller and dominates the overstory, but is shorter-lived (at approximately 80 years) than blue oak

TABLE 12.5

Mean Basal Area (m^2/ha) of Predominant Overstory Trees in the Blue Oak-Foothill Pine Woodland

		Dominant Tree Species					
Subseries	Community	*Pinus ponderosa*	*Pinus sabiniana*	*Quercus agrifolia*	*Quercus douglasii*	*Quercus lobata*	*Quercus wislizenii*
Coast Range and Sierra Nevada	Blue Oak-Foothill Pine/Grass	–	6	–	8	–	–
	Blue Oak-Foothill Pine/Wedgeleaf Ceanothus-Mt.mahogany	–	4	–	6	–	–
	Interior Live Oak-Blue Oak- Foothill Pine	–	7	–	7	3	9
Coast Range	Mixed Oak-Foothill Pine/Grass	–	7	8	10	11	
Sierra Nevada	Blue Oak-Foothill Pine/Whiteleaf Manzanita/Grass	–	6	–	7	–	1
	Mixed Oak-Interior Live Oak-Foothill Pine	8	3		4	–	4

(150–250 years; Allen-Diaz and Holzman 1991). Blue oak is usually the more abundant of the two trees (Table 12.5, Verner 1988), but foothill pine contributes as much basal area as blue oak, averaging 4–7 m^2/ha. In the Sierra Nevada foothills, interior live oak and California buckeye may be associated with foothill pine and blue oak. Interior live oak becomes more abundant on steeper slopes, shallower soils, and at higher elevations. Shrub associates include several ceanothus and manzanita species, poison-oak, and California redbud *(Cercis occidentalis)*, and they are usually clumped in areas of full sunlight. Blue oak-foothill pine woodlands have a diverse mix of hardwoods, conifers, and shrubs, and widely variable overstories.

Foothill pine tends to grow faster than blue oak; thus it is important in the path of succession (McDonald 1990). Historically, fire was a frequent occurrence (McClaran and Bartolome 1989). Foothill pine and blue oak are both adapted to fire, with cones remaining on the pine for several years, and vigorous sprouting in young oaks after fire (McCreary et al. 1991, 2002). Younger stands of oaks are more likely to replace themselves after fires, whereas foothill pine must depend on regeneration from seed.

Coastal Oak Woodland

Coastal oak woodlands include woodland types with Engelmann oak, coast live oak, or Oregon white oak as dominants, and occur along California's coastal foothills and valleys (Holland 1988). Engelmann oak has a very limited range, occupying about 15,700 ha in southern California and Baja (Fig. 12.2). Elevations range from sea level to around 500 m (Allen et al. 1991). Coast live oak occupies habitats within 100 km of the coast (Fig. 12.2), largely within the coast fog belt (Allen-Diaz et al. 1999). On steep slopes, coast live oak occurs as relatively small woodland patches in mosaics with annual grasslands, shrublands, and riparian habitats. Blue oak woodland and montane hardwoods are the more interior and higher elevation coastal oak woodlands; Oregon white oak woodland is to the north (Fig. 12.2), beginning in Sonoma county, and is described in the Montane Hardwood Forest section later. Coastal oak woodlands typically occur on moderately to well-drained soils that are moderately deep and have low to medium fertility. As with other oak woodlands, considerable climatic extremes exist.

Coastal oak woodlands are highly variable because of their latitudinal distribution (Fig. 12.2). Basal area of coast live oak ranges from about 5 m^2/ha in middle-elevation xeric communities to as much as 60 m^2/ha in coast live oak/grass communities (Table 12.6). In some coastal oak woodlands, three or more species of oaks occur (Allen et al. 1991).

Coast live oak occurs with valley oak, blue oak, and foothill pine on drier sites. Species associated with coast live oak on moister sites are Pacific madrone *(Arbutus menziesii)*, California bay *(Umbellularia californica)*, tanoak *(Lithocarpus densiflorus)*, and canyon live oak. In southern California, coast live oak is associated with interior live oak, valley oak, California

TABLE 12.6

Mean Basal Area (m^2/ha) of Predominant Overstory Trees in the Coast Live Oak Subseries of the Coastal Oak Woodland

Subseries	Community	Dominant Tree Species: *Quercus agrifolia*	Dominant Tree Species: *Quercus engelmanii*	*Mean % Grass*
Lower Elevation	Coast Live Oak/ Blackberry/ Bracken Fern	4	–	15
	Coast Live Oak-Madrone/Hazelnut-Blackberry	28	–	4
	Coast Live Oak/ Poison Oak	31	–	3
Middle Elevation	Coast Live Oak/ Coast Sagebrush/ Grass	17	–	48
	Coast Live Oak/ Poison Oak/Grass	28	–	19
	Coast Live Oak/ Grass	10	–	83
	Coast Live Oak/ Chamise-Black Sage	6	–	6
	Coast Live Oak	59	–	–
	Coast Live Oak/ Toyon-Poison Oak	20	–	25
	Coast Live Oak/ Toyon/Grass	11	–	28
Upper Elevation	Coast Live Oak/ Coffeeberry-Toyon	21	–	42
	Coast Live Oak/ Ocean Spray-Snowberry	38	–	–
	Coast Live Oak-California Bay/ Toyon-Scrub Oak	9	–	6
	Coast Live Oak-Maple/Coffeeberry-Ocean Spray	39	–	19
Engelmann Oak	*Quercus engelmannii*		15	

FIGURE 12.4 Typical dense canopy of coast live oak woodland interspersed with grassland and coastal chaparral habitats.

black walnut *(Juglans hindsii)*, and Coulter pine *(Pinus coulteri)*. Overstories range from open to nearly closed, resulting in variable cover and richness of understory shrubs, grasses, and forbs. Annual grasses form most of the understory in open woodlands but are almost nonexistent in very dense woodlands. Coast live oak savannas typically occur adjacent to grassland habitats (Fig. 12.4). Shrubs in closed-canopy situations tolerate shade and include toyon *(Heteromeles arbutifolia)*, poison-oak, California coffeeberry *(Rhamnus californica)*, and several species of *Ceanothus* and *Arctostaphylos*.

Where Engelmann oak dominates, it may occur with coast live oak or in almost pure stands. Tree density is 27–56/ha, with basal areas averaging 15 m^2/ha (Griffin 1977). Although Engelmann oak occurs along the coast of California and thus could be considered part of the coastal oak woodland, Griffin (1977) views this type as a southern California version of the blue oak woodland.

Coast live oaks are relatively long-lived (125–250 years), slow-growing trees, requiring 60–80 years to mature under good conditions (Griffin 1977). Historically, fires frequently occurred in these woodlands. Mature Engelmann and coast live oaks are resistant to low-intensity ground fires due to their thick bark, whereas some mortality occurs among seedlings and saplings (Plumb and Gomez 1983). Coast live oak is also fairly resistant to grazing pressure, and it appears to be replacing the less resistant deciduous oaks in areas with intense grazing. Its regeneration is generally good. Adequate regeneration of Engelmann oak is not occurring for many of the same reasons affecting blue oaks.

The recent appearance of the pathogen *Phytophthora ramorum*, which causes sudden oak death (SOD), is creating

TABLE 12.7

Mean Basal Area (m^2/ha) of Predominant Overstory Trees in the Black Oak Subseries of the Montane Hardwood Forest

		Dominant Tree Species				
Subseries	*Community*	*Arbutus menziesii*	*Pseudotsuga menziesii*	*Quercus agrifolia*	*Quercus chrysolepis*	*Quercus kelloggii*
Coast Range	Black Oak-Madrone-Coast Live Oak	8	16	5	–	11
	Mixed Oak-Coast Live Oak/Poison Oak	2	–	12	–	9
	Black Oak-Coast Live Oak-Beach Pine/Ocean Spray	4	–	14	3	12
	Black Oak-Valley Oak/ Grass		9	9	–	10
Sierra Nevada	Black Oak/Poison Oak-Calif. Storax/Grass-nut	–	3	–	–	11
	Black Oak/Deerbrush-Poison Oak/Bracken Fern	–	–	–	–	14
	Black Oak/Deerbrush	–	–	–	–	9
	Black Oak/Greenleaf Manzanita	–	–	–	–	4
Coast Range & Sierra Nevada	Black Oak/Poison Oak	–	–	–	–	26
	Black Oak/Poison Oak/Grass	–	–	–	1	19
	Black Oak-Canyon Live Oak/Poison Oak	–	–	–	11	16
	Black Oak/Grass	–	–	–	–	22

widespread mortality of coast live oak (see Conservation and Restoration Issues later), and it will surely affect ecological processes in the future (Rizzo and Garbelotto 2003).

Montane Hardwood Forest

Associations within the montane hardwood forest (synonymous with "mixed evergreen forest") are diverse. Oak-dominated communities occur on slopes ranging from gentle to steep, and elevations of 349–1,700+ m (Table 12.7). Relatively large California black oak stands occur in mountain valleys on alluvial soils. Exposures tend to be south, west, and east, with conifers dominating on northern exposures. Climates are Mediterranean, but extremely variable given the wide distribution of this type (Fig. 12.2). Average summer temperatures are moderate, whereas average winter temperatures range from near freezing to 10°C. Snow occurs in the winter at higher elevations, but does not remain as long as on adjacent conifer-dominated habitats. Annual precipitation averages 100 cm (Barbour and Minnich 2000).

Montane hardwood forests are the most variable oak type (Table 12.7). The dominant oak species vary by topography, soil, and elevation. Montane hardwood forests typically lack blue and valley oaks (although mixed oak-interior live oak-foothill pine in the Sierra Nevada at elevations averaging 580 m includes these species). Characteristic oaks include canyon live, interior live, California black, and Oregon white oak (Mayer and Laudenslayer 1988; McDonald 1988; Sawyer and Keeler-Wolf 1995). Many areas of montane hardwood forest are located on productive forest soils and are classed as commercial hardwood forests. Montane hardwoods have a pronounced hardwood tree layer with poorly developed shrub and herbaceous layers (McDonald 1988).

California black oak tends to dominate on gentle topography at higher elevations. It is 20–24 m at maturity, with long, straight trunks in closed-canopy situations. In open forests, it has large, spreading branches (McDonald 1990a). It is winter-deciduous. Basal area of coastal black oak communities is 9–12 m^2/ha, whereas Sierra Nevada communities have two to three times as much basal area (Table 12.7).

Oregon white oak occurs along the moister north coast as well as in northern inland regions (see Fig. 12.2). Stand basal area ranges from <5 m^2/ha to over 23 m^2/ha (Fig. 12.5), with one site of pure Oregon white oak reaching 41 m^2/ha (Bolsinger 1988). It is 15–24 m at maturity; crowns

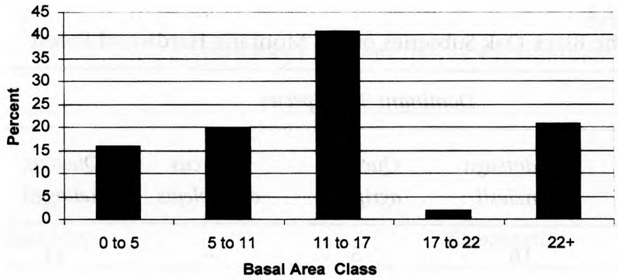

FIGURE 12.5 Oregon white oak (montane hardwood forest) stand structure

are rounded in open conditions, narrow in closed conditions. Associated trees include California black oak, canyon live oak, Pacific madrone, and interior live oak. Other associated species in the drier eastern part of its range include *Artemisia tridentata, Cercocarpus ledifolius, Purshia tridentata,* and *Ribes cereum* (Bolsinger 1988).

Canyon live oak forms almost pure stands on steep canyon slopes and rocky ridgetops throughout the Sierra Nevada and Klamath Mountains. The trees have tremendously variable growth forms, ranging from shrubs with multiple trunks on rocky, steep slopes, magnificently spreading to 18- to 20-m tall trees on deeper soils in moister areas (Thornburgh 1990). It is evergreen.

Interior live oak often dominates stands (Table 12.8) or it may occur with canyon live oak on steep canyon slopes and rocky, steep slopes throughout the Sierra Nevada. Its growth form varies much like that of canyon live oak; it is an evergreen with a dense canopy. Basal areas of interior live oak communities vary from 2 m^2/ha on dry sites to 15+ m^2/ha on higher elevation mesic sites. Common associates include black oak, blue oak, and foothill pine, depending on elevation (Allen et al. 1991).

The oaks of the montane hardwood forests are widely distributed throughout much of the Sierra Nevada, North Coast, and Klamath region. Associates of montane hardwood communities at higher elevation on good-quality sites include ponderosa pine *(Pinus ponderosa),* Douglas fir *(Pseudotsuga menziesii),* Pacific madrone, Jeffrey pine *(Pinus jeffreyii),* sugar pine *(Pinus lambertiana),* incense-cedar *(Calocedrus decurrens),* and white fir *(Abies concolor).* In southern California, big cone Douglas fir *(Pseudotsuga macrocarpa)* and Coulter pine are common associates (Barbour and Minnich 2000). At lower elevations and on poor sites with steep slopes, associates include foothill pine, knob-cone pine *(Pinus attenuata),* tanoak *(Lithocarpus densiflorus),* and Pacific madrone. Blue oak and valley oak can be associates at lower elevations. Understory shrub species include poison-oak, ceanothus, manzanita, mountain-mahogany, coffeeberry, wild currant (*Ribes* spp.), and mountain misery *(Chamaebatia foliolosa).* Forbs and grasses are not as prevalent as on lower elevation hardwood rangeland types.

Because oaks of montane hardwood communities are long-lived and slow-growing, the community is rather stable and persistent. As with all oaks, initial tree establishment is by acorn. Once established, the four dominant oaks can sprout vigorously from stumps, allowing rapid reestablishment after a fire (McDonald 1988). Frequent fires over relatively small areas result in a variety of age classes across the landscape (Stephens 1997). The large number of hardwood and conifer species allows this type to occupy many environments and locations. The elevation and general inaccessibility of these habitats has historically protected them from transhumance livestock grazing, commercial timber harvesting, fuelwood cutting, and residential development, but that is now changing. Table 12.9 shows the number of hectares of California oak woodland habitats in various regions of the state (Greenwood et al. 1993).

Spatial and Temporal Aspects of Oak Woodland Sustainability

California has one of the most rapidly growing human populations in the world: from less than 100,000 people in 1850, to over 35 million people today (an average annual rate of growth of 3.4%), to a projected 63 million people in the next 50 years (Medvitz and Sokolow 1995). This growth is having an impact on oak woodlands. A survey of oak woodland owners showed that the majority now live <13 km from a subdivision (Huntsinger and Fortmann 1990; Huntsinger 1997), that approximately one-third of the properties changed owners between 1985 and 1992, and that 5% were subdivided for residential development. The urban interface with oak woodlands, once confined to the major population centers of the San Francisco Bay, Sacramento, and the Los Angeles basin, now extends throughout the entire state.

Landscape factors affecting oak woodland distribution include long-term climatic factors (Byrne et al. 1991) and, more recently, human-caused events such as clearing and the introduction of exotic pathogens. Over the past 40 years, California's oak woodlands have decreased by over 400,000 ha (Bolsinger 1988). Major losses from 1945 through 1973 were from rangeland clearing for enhancement of forage production. Major losses since 1973 were from conversions to residential and industrial use. Regionally, some oak woodlands have decreased due to urban expansion (Saving and Greenwood 2002), firewood harvesting (Standiford et al. 1996), range improvement (Bolsinger 1988), and conversion to intensive agriculture (Merenlender 2000). Habitat fragmentation, increased conflicts between people with different value systems, predator problems, and soil and water erosion have resulted from human uses of the oak woodland.

Specific oak woodland types show similar trends. From 1932 to 1992, blue oak woodland canopy density and basal area increased under typical livestock grazing and fire-exclusion policies (Holzman 1993). This indicates that many oak stands are stable-to-increasing over a moderately long period, despite perceived natural regeneration problems (Muick and Bartolome 1987; Bolsinger 1988; Swiecki et al. 1997). However, >20% of the study sites were converted to other land uses, primarily residential subdivisions, during this period

TABLE 12.8

Mean Basal Area (m^2/ha) of Predominant Overstory Trees in the Interior Live Oak Subseries of the Montane Hardwood Forest

		Dominant Tree Species				
Subseries	*Community*	*Arbutus menziesii*	*Pinus sabiniana*	*Quercus douglasii*	*Quercus kelloggii*	*Quercus wislizenii*
Coast Range and Sierra Nevada	Interior Live Oak-Blue Oak-Foothill Pine	–	7	7	–	9
	Interior Live Oak-Madrone/Poison Oak	7	–	–	2	15
Sierra Nevada	Interior Live Oak/Toyon	–	1	1	1	4
	Interior Live Oak/Whiteleaf Manzanita	–	2	–	2	4
	Interior Live Oak/Yerba Santa/Grass	–	2	2	–	2
	Interior Live Oak-Foothill Pine/Manzanita	–	6	2	–	5

TABLE 12.9

The Area and Extent in Hectares of California Oak Woodland Habitats in Various Regions of the State

Habitat Type (CWHR)	*Central Coast*[a]	*San Joaquin Valley/ Eastside*	*Sac. Valley/ North Interior*	*Central Sierra*	*North Coast*	*So. California*	*TOTAL*
Blue oak woodland	443,951	436,299	382,510	148,088	30,717	13,760	1,455,325
Blue oak- foothill pine woodland	114,603	134,397	185,604	93,295	0	0	527,899
Valley oak woodland	22,097	6,827	712	0	902	405	30,943
Coastal oak woodlands	517,057	10,000	8,414	0	88,083	161,475	785,029
Montane Hardwood	256,127	313,824	440,277	412,758	218,141	34,804	1,675,931
TOTAL	1,353,835	901,348	1,017,517	654,141	337,844	210,444	4,475,128

NOTE: Adapted from Greenwood et al. 1993

[a]Description of regions: Central Coast: Alameda, Contra Costa, Lake, Marin, Monterey, San Benito, San Luis Obispo, San Mateo, Santa Barbara, Santa Clara, Santa Cruz, Solano, Sonoma, Ventura Counties. San Joaquin Valley/Eastside: Fresno, Kern, Kings, Madera, Merced, San Joaquin, Stanislaus, Tulare Counties. Sacramento Valley/North Interior: Butte, Colusa, Glenn, Lassen, Modoc, Plumas, Sacramento, Shasta, Sierra, Siskiyou, Solano, Sutter, Tehama, Trinity, Yolo, Yuba Counties. Central Sierra: Amador, Calaveras, Eldorado, Mariposa, Nevada, Placer, Tuolumne Counties. North Coast: Del Norte, Humboldt, Mendocino Counties So. California: Imperial, Los Angeles, Orange, Riverside, San Diego, San Bernardino Counties.

(Holzman 1993). A similar study of changes in tree and total woody cover of foothill oak woodlands from 1940 to 1988 found these areas were relatively stable (Davis 1995).

Pollen analysis studies document the dynamics of oak woodland composition over a very long-term period and highlight the changing influence of human populations (Byrne et al. 1991). Oak woodlands were relatively stable during the long period of use by Native Americans. Following European settlement, approximately 200 years ago, livestock introduction and clearing for intensive agriculture caused significant declines in oak pollen. Exotic annuals first show up in the pollen record at this same time. Since this initial exploitation, oak pollen has increased dramatically. Current oak pollen deposition is at its highest level, probably due to fire-exclusion policies of the last 80 years, and low-intensity management practices associated with ranching.

Oak Woodland Ecosystem Processes

Pre-European Settlement: Herbaceous Flora and Historic Change

Most of the tree species of oaks occupied their current distributions by about 10 million years before the present (BP) in California (Allen et al. 1999). The California Mediterranean climate, with its dry summers, was probably well in place by 5 million years BP (Rundel 1987). Byrne et al. (1991) suggested that the woodland oak species (e.g., blue and valley) moved to higher elevations in the Sierra between 10,000 and 5,000 years ago, based on pollen evidence, but by the mid-1800s, woodland species had retreated to their present locations at lower elevations in the Sierra and Coast Ranges.

The species composition of herbaceous vegetation in oak woodlands prior to European contact is unknown. Many believe native perennial grasses, particularly the bunchgrass *Nassella pulchra*, once enjoyed a more widespread distribution (Clements 1934; Heady 1977). Hamilton (1998) has rather convincingly argued against overuse of this paradigm, suggesting that native annual forbs were once dominant, especially in drier parts of the woodland. Holstein (2001) suggested the rhizomatous perennial grass, *Leymus triticoides*, dominated the pre-agricultural Central Valley floor. (However, his analysis relied on the relict method for which he and others criticize Clements.)

Two studies provide physical evidence of pre-European settlement composition. Bartolome et al. (1986) found greater abundance of distinctive opal phytoliths (silica bodies that are resistant to decay with shapes specific to certain taxonomic groups) at soil depths corresponding to >150 years ago. The shapes these phytoliths took were specific to those found in perennial grasses, indicating their greater abundance in the past at that particular site (Jepson Prairie near Davis, CA).

Mensing and Byrne (1999) offer some physical evidence of the pre-European flora. They examined pollen in sediment cores from the Santa Barbara channel and determined that the presence of the exotic annual, *Erodium cicutarium*–now ubiquitous in much of California—pre-dated European settlement and livestock introduction. They show patterns suggesting it invaded from Baja California prior to the Mission Period.

Beginning with the introduction of domestic livestock and exotic annuals by European settlers, oak woodland ecosystems have changed dramatically. Herb cover has shifted from perennial to annual (Holmes 1990). Fire interval and intensity have increased (McClaran and Bartolome 1989). Overstory cover has generally increased (Holzman and Allen-Diaz 1991). Soil moisture late in the growing season has decreased, and soil bulk density has increased due to compaction from large herbivore numbers (Gordon et al. 1989). Riparian zones are now less dense and diverse (Tietje et al. 1991). A general summary of the changes in ecosystem inputs from presettlement conditions to the current time is shown in Table 12.10. These ecosystem changes are discussed below.

The pre-European herbaceous oak woodland understory included native perennial bunchgrasses, annual grasses and annual and perennial forbs (Holmes 1990). Native species were reduced in cover with multiple introductions of alien annual species from Europe, Asia, Africa and South America (Burcham 1970; Heady et al. 1992). Species extinctions were few (Solomeshch and Barbour 2006).

Species composition differences between oak understory and open grassland have been demonstrated by several authors (Saenz and Sawyer 1986; Jackson et al. 1990; Davis et al. 1991; Maranon and Bartolome 1994). Some species appear to be strongly controlled by this dichotomy, but generalizations for California's oak woodlands are tenuous. A given species may be strongly associated with tree canopy cover at one site but with open grassland in another. For instance, *Nassella pulchra* is thought to be an open grassland species, but it has been observed scattered beneath relatively continuous oak canopy in the Sierran foothills (Jackson and Bartolome 2002). Alternatively, *Cynosurus echinatus* is rare in open grassland but very common beneath oak canopy throughout the state. Rice and Nagy (2000) sought the mechanism for the spatial separation of *Bromus diandrus* (found under canopy) and *Bromus hordeaceus* (found in open) and reported that interspecific competition was important in the high-resource soils beneath oak canopy, but only *B. hordeaceus* could tolerate the harsher physical conditions of open grassland (i.e., there was little evidence of competition between these species in the open). Working (2002) found that aspect, measured at the 10- to 100-m^2 scale, was a more important determinant of species composition than canopy cover. Hence, species composition of the herbaceous understory is a result of a complicated mix of time, site, and abiotic and biotic interactions. Generalizations are tenuous.

Plant species richness was shown to be highest at intermediate (35–57 g/m^2) herbaceous biomass levels (Heady et al. 1992; Maranon and Bartolome 1994) following the model of Grime (1979) and discussed by Maranon and Garcia (1997) and Garcia et al. (1993). They suggested that maintaining an oak overstory component provides for maximal landscape diversity, owing to different plant assemblages under canopy and in the open.

Grazing Processes and Forage Production

Livestock grazing has had a major impact on California's oak woodlands. By 1880, Spanish coastal missions had 4 million sheep and 1 million cattle (Holmes 1990), fostering a large demand for forage and oak browse. Currently, two-thirds of all woodlands are grazed (Huntsinger 1997). In addition to domestic livestock grazing, feral hogs consume acorns, as do ground squirrels and pocket gophers.

TABLE 12.10

Comparison of Oak Woodland Conditions Before European Settlement, During Extensive Ranching Period, and in Urban Interface Areas

Pre-European Settlement Conditions	*Extensive Ranching Period*	*Current Urban Influence*
Perennial herbaceous layer	Exotic annual invasion	Increasing annual invasion, especially noxious weeds
Regular fire interval	Continuation of regular fire interval	Fire suppression policies and long fire interval and increased intensity
More open overstory layer	Rangeland clearing and tree thinning	Increased multi-species overstory layer of unconverted stands
Soil moisture higher later into growing season	Soil moisture less late into the growing season due to exotic annuals	Decreased soil moisture late in growing season due to exotic annuals
Lower soil bulk density	Increased soil bulk density	Increased soil bulk density
Snags, large woody debris	Snags, woody debris cleaned up in typical management activities	Less attention to clean-up; increased snags and woody debris
Dense, diverse riparian zone	Riparian zones less dense and diverse	Higher human use of riparian zones, and increased storm runoff from urban areas
Lower herbivore densities	Higher herbivore density, primarily domestic livestock	Decrease in numbers of domestic livestock and wildlife

NOTE: Adapted from Standiford 2001.

Grazing has both positive and negative effects on oak woodland sustainability. Positive grazing effects include reduced moisture competition between oaks and herbaceous material (Hall et al. 1992); reduced leaf area in grasses, which may help conserve moisture late in the growing season (Welker and Menke 1990); reduced habitat for rodents that consume acorns and young seedlings; and elimination of fuel ladders, reducing the probability of crown fires. Some of the negative effects of livestock grazing include consumption of oak seedlings and acorns (Davis et al. 1991; Adams et al. 1992; Hall et al. 1992; Swiecki et al. 1997); increased soil compaction, making root growth for developing oak seedlings more difficult (Gordon et al. 1989); and reduced soil organic matter.

The oak canopy has an effect on forage production, composition, and quality; the magnitude of the effect depending on precipitation, oak species, and amount of overstory cover (Table 12.11). Oaks compete with the understory for moisture, and they alter the nutrient status of the site because of their deep-rooting habit and litter quality.

Oak removal was historically recommended as a means of increasing forage production on hardwood rangelands (George 1987). For the deciduous blue oak, most studies have demonstrated increased forage production following tree removal on areas previously containing over 25% canopy cover and receiving >50 cm of rain (Kay 1987; Jansen 1987). Conversely, where there is <50 cm of rain, areas with low (<25%) blue oak canopy consistently had higher forage yields than adjacent open areas (Holland and Morton 1980; Frost and McDougald 1989; Camping et al. 2002). In areas with moderate blue oak canopy cover (25%–60%), there was a variable canopy effect on forage production (McClaran and Bartolome 1989a; Table 12.11).

Blue oak, in the southern and central portion of its range, provides green understory forage earlier (with adequate rainfall) and in higher quantities compared to the forage in open areas (Holland 1980; Frost and McDougald 1989; Ratliff et al. 1991). The difference in forage quality and quantity may be even more pronounced during drought, due to shading by tree canopies and the consequent reduction in moisture loss through evapotranspiration (Frost and McDougald 1989).

In evergreen live oak stands, the few studies that have been carried out show a larger competitive effect of oaks on understory production (Ratliff et al. 1991). In general, live oaks stands with >25% canopy cover will have less forage growth than cleared areas. One study of drought years in the Southern Sierra Nevada foothills, showed that live oak shade helped conserve soil moisture, resulting in higher understory production than on open sites (Frost and McDougald 1989).

Production increases beneath blue oak canopies (or in areas previously beneath blue oak canopies) is attributed, in part, to increased soil fertility due to leaf fall and decomposition (Jackson et al. 1990; Frost and Edinger 1991; Firestone 1995). Enhanced soil fertility also improved forage quality. Because the nutrient input from leaf litter ceases after tree removal, herbaceous production gradually declines to the levels of adjacent open areas (Kay 1987; Camping et al. 2002).

TABLE 12.11
The Effect of Oak Canopy on Hardwood Rangeland Forage Production

Canopy Cover	*Winter Forage Production*	*Spring Forage Production*
Live oaks		
Scattered (<10% cover)	– / +	– / +
Sparse (10%–25% cover)	– / +	– / +
Moderate (25% –60% cover)	–	–
Dense (over 60% cover)	–	–
Deciduous oaks		
Scattered (<10% cover)	+	+
Sparse (10%–25% cover)	+	+
Moderate (25%–60% cover)	– / +	– / +
Dense (over 60% cover)	–	–

NOTE: a "+" indicates that forage production is enhanced by oak canopy, and a "–" indicates that forage production is inhibited by oak canopy. Adapted from Allen-Diaz et al. 1999.

Oak canopies also have an effect on forage species composition. Studies have found that understories of both blue and live oak stands favor later-successional herbaceous species such as wild oats *(Avena fatua)*, soft chess *(Bromus hordeaceus)*, and ripgut brome *(Bromus diandrus)*. Clovers (*Trifolium* spp.), annual fescues (*Vulpia* spp.), filaree (*Erodium* spp.), and soft chess account for more of the total herbage biomass in open areas than under oak canopy (Holland 1980; Ratliff et al. 1991).

Current oak management guidelines for ranchers are (Standiford and Tinnin 1996):

- There is little or no value in removing blue oaks in areas with <50 cm of annual precipitation.
- On areas with >50 cm of annual rainfall, thinning oaks where the canopy cover is >50% will have the greatest positive effect on herbaceous production.
- In areas thinned for forage enhancement, residual tree canopy cover of 25%–35% is able to maintain soil fertility and wildlife habitat, and minimize erosion processes.
- Tree removal should always consider all values of the trees, including wildlife habitat, soil stability, and so forth in addition to possible forage production benefits.

Soil Processes and Nutrient Cycling

Frost and Edinger (1991) found higher organic carbon levels, greater cation-exchange capacity, lower bulk density, and greater concentrations of some nutrients (at a soil depth of 0–5 cm) under blue oak canopies than in open grassland. Organic matter input from blue oak leaf litter primarily accounts for this finding, and leaching of nutrients from rainwater drip may also make a significant contribution. The soil conditions beneath interior live oak and blue oak are similar; more intensive shading from the evergreen canopy, therefore, is thought to primarily account for the reduced total annual herbage production under interior live oaks growing in moderate environmental conditions (Frost and Edinger 1991).

Oak woodlands with perennial grasses retain soil moisture later in the growing season than woodlands with annual grasses (Gordon et al. 1989). This difference in soil moisture may partially explain the observed lack of sapling recruitment in oak woodlands containing an annual grass understory. Evaluation of hardwood rangeland soil bulk density shows that areas with livestock grazing have a higher bulk density than ungrazed areas.

Jackson et al. (1990) found that soils under blue oak canopies have higher nitrogen turnover rates and inorganic nitrogen contents than surrounding open grassland soils, due primarily to the higher nitrogen content from mineralization of oak leaf litter. There was no difference in soil water potential between the understory and the open grassland. The increased fertility under blue oak canopy did not result in enhanced forage productivity.

In general, grazing accelerates carbon and nutrient cycling by effectively bypassing the microbial decomposition pathway. Livestock mineralize plant organic material much more quickly than microbes and return it to the soil and atmosphere as feces, urine, and gas. In perennial grasslands of the Midwest, accelerated nutrient cycling is credited for stimulating net primary productivity (Frank and McNaughton 1993; Frank et al. 1994; Frank and Evans 1997). However, similar grazing effects on nutrient dynamics in California annual grassland were not evident (Davidson et al. 1993; Dahlgren et al. 1997). Nitrogen quickly cycles within annual-dominated

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Dahlgren et al. (1997) describe soils beneath oak canopy as "islands of fertility" because of greater carbon, nitrogen, and phosphorous stocks, compared to adjacent open grasslands sites. The patchiness of oak woodland canopy may be enhanced by the ability of oaks to garner water and nutrients from beyond the canopy perimeter, from the open grassland spaces between them and their neighbors, and then preferentially returning leaf litter below the existing canopy, thereby redistributing ecosystem resources.

Conservation and Restoration Issues

Oak Regeneration and Recruitment Processes

One of the key concerns that landowners, policymakers, and the public have about oak woodlands is whether oak regeneration is adequate to sustain current woodlands and savannas. Several surveys of oak regeneration (White 1966; Griffin 1973; Bartolome 1987; Bolsinger 1988; Bernhardt and Swiecki 1991; Danielsen and Halverson 1991; Standiford et al. 1991; Swiecki et al. 1997) have shown a shortage of saplings for certain species (especially blue oak, Engelmann oak, and valley oak) in certain regions of the state (sites at low elevation, on south- and west-facing slopes, on shallow soils, and with high populations of natural or domesticated herbivores). If this shortage of small trees continues over time, then the oak stands may gradually be lost as natural mortality or tree removal decrease the number of large, dominant trees, and woodlands convert to other vegetation types such as brushfields or grasslands.

Deciduous oaks have reproduced poorly in the past 50+ years (Griffin 1977; Muick and Bartolome 1987). Although seedlings become established, few develop into saplings. Live oaks, whose seedlings may be more resistant to grazing and browsing, have produced saplings with more success than have deciduous oaks. Pocket gophers, a significant seedling predator, may prefer deciduous oak roots to those of live oaks. Where there has been a failure of deciduous oak seedling establishment, the cause may be attributed to damage to acorns and seedlings by insects, cattle, deer, and rodents (Griffin 1977; Borchert et al. 1989).

Older individuals dominate most extant blue oak populations (Davis 1995; Swiecki et al. 1997). Recruitment of valley and blue oak saplings is not sufficient to maintain existing stands according to Muick and Bartolome (1987) but Tyler et al. (2006) disagree and others think stump sprouting may reduce the concern about sustainability (McCreary et al. 1991, 2002; Standiford et al. 1996).

Riparian Ecosystem Processes

Although a small percentage of the state's water supply originates on hardwood rangelands, virtually all of it flows through oak woodland riparian zones (Ewing et al. 1988). Also, most of the state's major reservoirs are located within oak woodlands. Riparian zones provide important habitat for wildlife and aquatic organisms. Management activities influence water quality and wildlife and fisheries habitat. Yet, removal of up to one-third of the oak canopy had little effect on water quality and yield in one regional study (Epifanio et al. 1991). New efforts have been started to develop rangeland management practices that will minimize erosion and improve water quality. In urban interface areas, riparian zones are often subject to very high levels of human use for recreational purposes. Scott and Pratini (1997) documented how urban development increases human use of riparian areas, lowering the habitat value for various wildlife species and decreasing overall biological diversity.

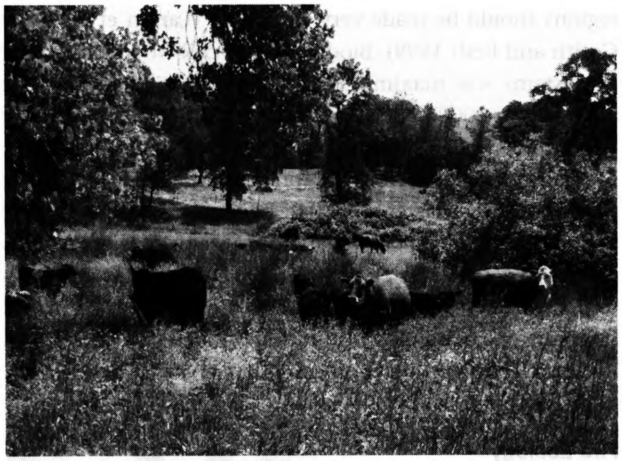

FIGURE 12.6 Typical spring-fed wetland in the blue oak-foothill pine type in the Sierra foothills near Marysville, CA. Spring-fed wetlands are a high quality source of forage and water for domestic and wild animals.

Spring-fed wetlands and riparian areas are often the only sources of summer water in oak woodlands and they are heavily utilized by grazing animals (Fig. 12.6). However, light-to-moderate, autumn/winter grazing had little effect on Sierra Nevada foothill spring-fed vegetation, even after 10 years of treatment (Allen-Diaz et al. 2004; Allen-Diaz and Jackson 2000). Continued monitoring of these systems under experimental treatments has shown that, by years 7 through 10, moderate grazing reduced herbaceous cover, light grazing had minimal effect, and grazing removal significantly increased cover (Jackson 2002). However, the increased cover brought with it an undesirable accumulation of plant litter that suppressed subsequent plant productivity.

Studies examining grazing effects on vegetation in riparian systems other than spring-fed wetlands are few. Intensive grazing can negatively affect water quality, plant biodiversity, productivity, wildlife habitat, wildlife species biodiversity, and nutrient cycling in riparian areas in regions with continental-type climates (Kauffman et al. 1983; Kauffman and Krueger 1984; Fleischner 1994; Clary 1995; Belsky et al. 1999), but extrapolation to Mediterranean-type *regions should be made very cautiously (Larsen et al. 1998;* Gasith and Resh 1999). Biodiversity in oak woodland spring ecosystems was maximized with light grazing (Allen-Diaz and Jackson 2000). Nitrate release in spring waters, contrary to common belief, increased with removal of cattle grazing. Methane production from the springs was reduced by grazing removal (Allen-Diaz et al. 2004). Effects of livestock grazing and grazing removal on wetland ecosystems of these regions are varied (Allen-Diaz et al. 1998, 2004; Allen-Diaz and Jackson 2000). Research shows that the timing of grazing and sampling of grazing affects must be considered to understand livestock–ecosystem relationships (Tate et al. 1999).

Fire Ecology

Fire is an important ecosystem process and management tool in oak woodland. Fire affects oak woodland stand structure, oak regeneration, wildlife habitat, nutrient cycling, and livestock grazing. The ecological effects of fire depend on fire frequency, timing, intensity, and complexity. Adjacent vegetation types, such as chaparral and montane forests, influence oak woodland fire regimes. Recent increases in the acreage of stand-destroying fires in oak woodlands point to the need to include fire in management plans in order to sustain the economic and ecological values of oak woodlands.

Because of the long period of human habitation of oak woodlands, it is extremely difficult to define the "natural" fire regime. Lightning-caused fires originating from major storms coming northward from Mexico have helped shape oak woodlands. It is speculated that decades may pass between lightning-caused fire events in oak woodland (Griffin 1977). Mature oaks can survive regular low-intensity surface fires, and most woodland oak species have the capacity for young trees to resprout after being top-killed by fire.

Native Americans used fire in their stewardship of oak woodlands (Holmes 1990). There are numerous accounts of burning by Native Americans in woodlands to enhance habitat for game species, to improve access for hunting and gathering of acorns, to reduce insect pest populations, and to maintain plant materials in an appropriate growth form for crafts (Jepson 1910; Cooper 1922; Anderson 2005). However, it is difficult to document the frequency, intensity, and extent of burning by Native Americans.

The first European settlers continued to use fire as a management practice to keep stands open for livestock production and to encourage forage production. Surveys indicated oak woodland burning intervals of 8–15 years by ranchers (Sampson 1944). Local prescribed burning associations were set up in various locations around the state, where neighbors came together annually to help conduct burns in the highest priority areas.

The use of prescribed burning as a management tool, to mimic the effects of nature, ceased on the state's conifer forest lands in the early 1900s. However, ranchers continued the extensive use of prescribed burning on oak woodlands until the 1950s. Since then, fire use declined, driven by negative urban attitudes toward fire, increasing housing density in rural areas of the state, and concerns about liability and air quality. Fire suppression eventually became the standard management policy.

McClaran and Bartolome (1989) evaluated fire frequency in Sierran foothill oak woodlands. Fire-return interval was around 25 years prior to settlement by Europeans in the mid-1800s. After settlement, the fire-return interval shortened to 7 years. No fires were observed from 1950 to the mid-1980s, when fire suppression was the dominant practice. Stephens (1997) observed similar fire-return intervals in the Sierra Nevada.

Shorter fire-return intervals in the past may have created conditions more conducive for oak regeneration. McClaran and Bartolome (1989) compared oak stand age structure with fire history and showed that oak recruitment was associated with fire events. Most oak recruitment in their Sierran foothill study area occurred during periods of high fire frequency in the 1880s to 1940s. Oak recruitment has been rare since fire suppression.

The factors leading to enhanced oak regeneration from higher fire frequencies are not entirely clear. Allen-Diaz and Bartolome (1992) evaluated blue oak seedling establishment and mortality with grazing and prescribed burning treatments in coastal oak woodlands dominated by blue oak. Neither of these treatments significantly affected oak seedling density nor the probability of mortality, when compared to unburned and ungrazed areas. Lawson (1993) evaluated prescribed fire effects on coast live oak and Engelmann oak in southern California and found higher seedling mortality in areas of prescribed fire.

Perhaps the importance of fire for oak regeneration is explained by enhanced postfire oak sprout growth documented by Bartolome and McClaran (1989). Other factors affecting oak regeneration, which would be influenced by the timing of fire, include modifications to the seedbed, decreased competition for moisture from herbaceous species, and the size of wildlife populations that feed on acorns and seedlings.

Fire also has an effect on oak woodland stand structure and composition. Lawson (1993) showed differential postfire effects on coast live and Engelmann oaks, coast live oak having a higher mortality and Engelmann oak having greater height growth following fire. The thicker bark of Engelmann oak provided more protection. Declines in Engelmann oak habitats in Southern California might be mitigated by reintroduction of fire. Fry (2002) found high survival of blue oaks following prescribed burning in central coastal California, and Horney et al. (2002) and Dagit (2002) documented high blue and coast live oak survival after wildfire.

Fire also kills diseases and pests, such as the filbert weevil *(Cucurlio occidentalis)* and the filbert worm *(Melissopus latiferreanus)*, which can infest acorns (Lewis 1991). Fire also reduces fuel ladders under oak canopies, preventing high-intensity crown fires.

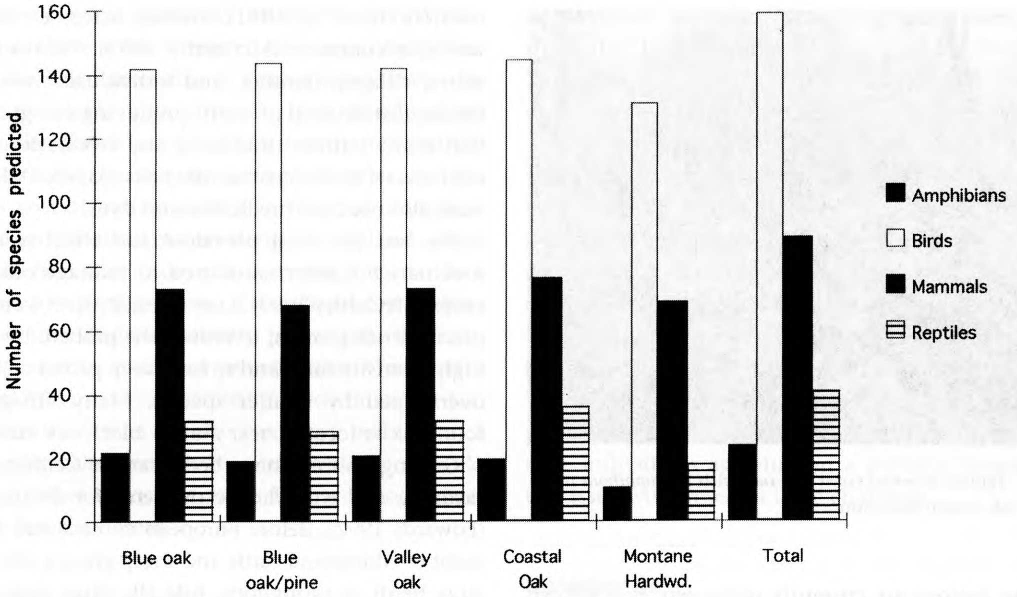

FIGURE 12.7 Number of vertebrate species by Wildlife Habitat Type (adapted from Mayer and Laudenslayer 1988).

Wildlife Habitat and Biodiversity Processes

California's oak woodlands provide habitat for over 300 vertebrate species, more than 2,000 plant species, and an estimated 5,000 species of insects. Figure 12.7 shows vertebrate wildlife diversity predicted by the California Wildlife Habitat Relationships (CWHR) model for the five major oak woodland communities (Mayer and Laudenslayer 1988).

In a 3-year study of nongame wildlife populations in the Sierra Nevada, Block and Morrison (1990) found 113 bird species (at least 60 of which bred at the site), much of the bird species richness being directly related to plant richness. Hutton's vireos *(Vireo huttoni)*, orange-crowned warblers *(Vermivora celata)*, and Wilson's warblers *(Wilsonia pusilla)* are closely associated with interior live oak. White-breasted nuthatches *(Sitta carolinensis)* and western bluebirds *(Sialia mexicana)* are closely associated with blue oak (Block 1990). The specific habitats utilized by the birds change seasonally. For example, many resident woodland birds obtained insects from the foliage of blue and interior live oaks during the breeding season and shifted to live oaks when the blue oaks were leafless.

Favorable oak woodland habitats supply food, water, and cover to sustain wildlife species. The absence of a particular element in a habitat may limit species diversity. Important habitat elements in oak woodlands include riparian zones, vernal pools, wetlands, dead and downed logs, and other woody debris, brush piles, snags, rock outcroppings, and cliffs.

Riparian habitat elements are used by almost 90% of all oak woodland wildlife species, illustrating the importance of conserving this habitat. Over one-third of all woodland bird species use snags, suggesting that management strategies maintaining an appropriate snag density will result in greater wildlife species richness. Downed coarse woody debris provide valuable habitat for most reptiles and amphibians and for many bird species. Oak woodland wildlife management must include trees in various stages of vigor (Block et al. 1990). Mid-elevation habitats, with several oak species, vertical diversity in vegetation structure, and diverse riparian zones, have the highest wildlife diversity (Motroni et al. 1991).

Currently the threats to continued high biodiversity on oak woodlands include (1) fragmentation of large blocks of extensively managed oak woodlands; (2) reduction in important habitat elements such as snags, woody debris, and diverse riparian zones; and (3) increasing encroachment of urban areas, bringing household pets, humans, and fire suppression policies into contact with woodland habitats. These threats can be reduced by encouraging cluster housing development and maintaining connecting corridors between large oak woodland blocks (Merenlender et al. 1998).

Exotic Pathogens

Beginning in 1995, tanoaks *(Lithocarpus densiflorus)* in coastal forests and woodlands showed widespread and unexplained mortality. By 1998, similar patterns were noted in coast live oak and California black oak in the area just north and south of San Francisco Bay (Svihra 1999). In 2000, the causal agent for this disease, popularly known as "sudden oak death" (SOD), was determined to be a pathogen new to science, *Phytophthora ramorum* (Rizzo and Garbelotto 2003). This same pathogen has since been isolated from ornamental rhododendrons in Europe and coastal California (Werres et al. 2001). Mortality is currently widespread on coast live and black oak species, as well as on tanoak throughout coastal California.

This pathogen is apparently an introduced organism, based on preliminary evaluations of its genetic structure (Garbelotto et al. 2002). The mechanisms for the spread

FIGURE 12.8 Typical downed coast live oak with *Phytophthora ramorum* (Sudden Oak Death) infection.

and infection biology are currently unknown. It is known that *P. ramorum* is found on the leaves of a wide variety of plant species in coastal oak woodlands, and it has also been isolated in rain splash, watercourses, and soil that may contribute to its movement (Davidson et al. 2002)

Sudden oak death represents a major threat to ecosystem health of California's oak woodlands (Fig. 12.8). Work on silvicultural and arboricultural management techniques are underway. The potential for genetic resistance is being evaluated, as well as the risk factors for various woodland stand structures and site conditions.

Economic Values and Utilization of Oak Woodlands

Oak woodlands have been important to humans living in California for centuries. Recent trends in human use, however, are leading to conversion from ranching to agriculture, residential development, and industry. Some of the economic and utilization issues facing oak woodlands are discussed later.

The original oak woodland human inhabitants were Native Americans. Acorns were the dietary staple and sustained the cultures of those that lived among the oak woodlands (Pavlik et al. 1991). Virtually all tribes west of the Sierra Nevada harvested acorns for food. Acorns are estimated to have been the primary diet for more than three fourths of all Native Americans in California (McCarthy 1993). Black oak was the preferred species in many regions. Each tribe had special mechanisms for acorn gathering, storing, hulling, drying, leaching, pounding, and cooking. The bark, roots, wood, small branches and galls of oaks were also utilized.

Acorns were second to salt among the most frequently traded foods or condiments among Native Americans. The trade in acorns flowed from west to east. For example, Miwoks gathered black oak acorns from the western Sierra and trading with the Mono Lake Paiute for pinyon pine nuts (Pavlik et al. 1991). Trading across elevational zones was also common (McCarthy 1993). Territorial claims of tribes, villages, families, and individuals were often based on the distribution of acorn-producing oak groves. The fact that many cultural traditions and celebrations focused on oaks attests to the central role oaks played. Oaks and acorns were also used for medicines and dyes.

Fire was the most prevalent and effective management tool native Californians used to manage oaks and acorn crops (McCarthy 1993). Low-intensity fires were also used to promote oak growth, to reduce the probability of damaging high intensity fires, and to help keep prized oaks from being overtopped by conifer species. Many village sites were found to be located near mature black oak stands.

Grazing animals have been part of California grassland, savanna, and woodland ecosystems for thousands of years (Edwards 1992). Before European contact and the establishment of widespread cattle and sheep grazing (Burcham 1957), large herds of pronghorn, tule elk, mule deer, and rodents grazed these grasslands, savannas, and wetlands (Edwards 1997). Many grassland species have habits (e.g., prostrate growth) and structures (e.g., basal meristems) that mitigate the damage from grazing or surface fire (Briske 1991).

Since the 1800s, California's oak woodlands have been used mainly for livestock grazing. Today, two thirds of California's oak woodlands are grazed by livestock (Ewing et al. 1988; Huntsinger and Fortmann 1990). Dramatic annual fluctuations in livestock markets, coupled with risk from forage shortages due to high variability in annual rainfall, make many livestock operations marginal. Uncertainty about federal grazing policies (many rangeland operators lease summer forage on Federal land) also hinders economic viability of oak woodland livestock enterprises (Sulak and Huntsinger 2002). Low profitability and high risk have accelerated conversion of extensively managed private ranches to suburban developments and intensive agriculture (e.g., vineyards).

Traditional efforts to increase profitability of oak woodlands have focused almost exclusively on enhancing forage production through removal of oaks (George 1987). This simplification of the ranch ecosystems did pay short-term dividends in improved forage yields, but the same risk from fluctuating markets and weather continued to make ranching a low profitability enterprise.

New markets have developed in the last 20 years for oaks for firewood, furniture (as new techniques have allowed for economic utilization of small-diameter logs), and as habitat for commercial hunting enterprises. This diversified economic portfolio has helped to enhance the economic sustainability of these areas by spreading risk out over several enterprises, increasing overall returns per acre, and providing an economic incentive to conserve more diverse woodlands (Standiford and Howitt 1992, 1993). Diversified markets have reduced tree harvesting and intensity of livestock use.

Historically, the market value of oak woodlands for subdivisions near urban areas has exceeded their value for amenities and ecological functions. Recent human population increase in these areas, however, has raised the potential value of woodland amenities to a point where they may be a financially viable alternative to land development (Scott 1996). Woodlands provide a large component of the quality-of-life sought by many relocating industries, and the relatively low cost of industrial sites in these woodlands is equally appealing. Woodland owners along the wildland–urban interface often find that their management options track public demand for specific values. If woodland conversions trigger a public demand for amenity protection, the solutions typically must be found on private lands. Open space easements and other deed restrictions provide financial, tax, or development incentives for the voluntary maintenance of public amenity values on private lands. Mitigation banking provides another economic value for hardwood rangeland in urban interface areas.

Areas for Future Research

Research must address political and economic forces shaping human conversion of oak habitats as well as biological issues related to long-term habitat sustainability under pressures from climate change, invasive species (e.g. SOD), and regeneration problems. Research focused at the whole-ecosystem scale, including development of viable economic alternatives for land use, will be most productive in ensuring the long-term preservation of California oak savannas.

Much of the recent work in oak savanna has focused on reproduction, incorrectly assuming that it is synonymous with recruitment. Future research will have to focus on recruitment success, which appears to vary with species, past stand structure, and tree mortality, and seems to vary at multiple spatial and temporal scales.

Management of savanna understory species composition and productivity has been assumed to fit the residual dry-matter model, which has been successfully applied to grasslands (George et al. 1985). This model assumes that if land managers leave recommended levels of mulch at the end of the dry season, the best combination of positive effects to the grassland ecosystem as a whole will result, such as optimum forage production, optimum biodiversity, optimum protection from soil erosion, and optimum wildlife habitat. However, there is little research to back up this assumption. Because of the highly variable nature of canopy effects on understory composition and productivity, many more site-specific studies are needed to fully examine ecosystem response and management options.

Protection of ecosystem services is of concern due to rapid population growth, and the resulting conversion and fragmentation of woodland habitats. A large number of counties have started the process of adopting local conservation strategies to conserve oak woodlands. Education and research have played a major role in conservation. Major accomplishments have been made in rural areas of the state, where livestock and natural resource management are the predominant land use. Where individual landowners have the ability to implement management activities that affect large acreage, education and research has contributed to decisions that favor conservation of oak woodlands.

However, for much of California, conversion of oak woodland habitats to urban or suburban use is having the largest impact on sustainability of resource values. Incorporation of ecologically-based material into land use plans adopted by the county government is only beginning. Since conversion to residential and industrial uses is ultimately a land-use decision, it is a political process involving action by elected officials with input from different constituencies. The political and economic forces vary greatly in different parts of the state. Since "success" in this area involves multiple individuals agreeing on a political course of action, this issue will present a large challenge.

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