VOLUME 81, NO. 2 *THE QUARTERLY REVIEW OF BIOLOGY* JUNE 2006

DEMOGRAPHY AND RECRUITMENT LIMITATIONS OF THREE OAK SPECIES IN CALIFORNIA

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KEYWORDS
Quercus, oak woodland, population, tree, sapling, seedling establishment, long-lived

ABSTRACT

We review published studies on the demography and recruitment of California oak trees and focus on the widespread dominant species of the foothill woodlands, Quercus douglasii, Q. lobata, *and* Q. agrifolia, *to ascertain the nature and strength of evidence for a decline in populations of these species. The vast majority of studies have been of short duration (less than three years), focused on the acorn and seedling life stages, and conducted at few locations within each species' geographic range. We summarize the extensive body of research that has been conducted on the biological and physical factors that limit natural seedling recruitment of oaks. The oak "regeneration problem" has largely been inferred from current stand structure rather than by demographic analyses, which in part reflects the short-term nature of most oak research. When viewed over longer periods of time using field surveys or historical photos, the evidence for a regeneration problem in foothill oaks is mixed.* Q. douglasii *shows very limited seedling or sapling recruitment at present, but longer term studies do not suggest a decline in tree density, presumably because rare recruitment is sufficient to offset low rates of mortality of overstory individuals.* Q. agrifolia *appears to be stable or increasing in some areas, but decreasing in areas recently impacted by the disease* Phytophthora ramorum. *Evidence from the few available studies is more consistent in suggesting long-term declines in foothill populations of* Q. lobata. *Long-term monitoring, age structure analysis, and population models are needed to resolve the current uncertainty over the sustainability of oak woodlands in California.*

The Quarterly Review of Biology, June 2006, Vol. 81, No. 2

0033-5770/2006/8102-0002$15.00

INTRODUCTION

THE OAK GENUS *Quercus,* the largest within the beech family Fagaceae, is widespread throughout the Northern Hemisphere. Oaks, common in temperate and tropical zones within Europe and Asia as well as North and Central America, are often a dominant component of forest, woodland, and shrubland communities in these regions. Thought to be of southeast Asian origin (Melville 1982), *Quercus* has evolved into over 500 species of evergreen and deciduous trees and shrubs that occupy a diverse array of habitat and climate types (Manos et al. 1999).

Oaks serve important functions in both human societies and wildlife communities worldwide. Acorns have provided sustenance to indigenous cultures throughout North America and Europe for centuries; other uses of oaks, acorns, and galls have included medicines, dyes, timbers for shipbuilding, and lumber for fuel, railway ties, furniture, and housing (Keator 1998; Johnson et al. 2002). Numerous wildlife species are dependent on oaks for habitat and rely on acorns or oak leaves as a primary food source (McShea and Healy 2002).

In a number of oak woodlands and savannas throughout the world, stands are composed of large, old adults with few individuals in the smaller, younger classes, which raises concerns that natural recruitment of the oaks may be insufficient to balance adult mortality. Lack of regeneration has been reported in British oak woodlands (Watt 1919; Shaw 1968a,b), oak forests in Asia (Saxena and Singh 1984; Singh et al. 1997; Abrams et al. 1999), and North American oak woodlands in California (Holzman 1993; Swiecki et al. 1993), Texas (Russell and Fowler 1999), and Tennessee (Loftis and McGee 1993).

Oak forests, woodlands, and savannas in California occupy roughly 45,000 km^2, 11% of the state, and nearly one-fourth of its wooded landscapes (Davis et al. 1998) (Figure 1). These communities are among the most diverse in North America, containing more than 1400 species of flowering plants, over 300 species of vertebrates, and thousands of invertebrate species. Despite the importance of oaks as a natural resource, a survey conducted in the mid-1980s found that between 3–5 million of California's original 10–12 million acres of oak woodland habitats had been lost largely due to rangeland clearing, agricultural conversion, and urban development (Bolsinger 1988); as land conversion has continued since that time, acreage of woodland lost to date is certainly higher. Several species, including *Lithocarpus densiflorus, Quercus agrifolia, Q. kelloggii,* and *Q. chrysolepis,* are now threatened by the introduced pathogen *Phytophthora ramorum,* which has caused extensive mortality in coastal and montane forests from Monterey to Mendocino counties (Rizzo et al. 2002).

Compounding the threat to these systems from habitat conversion and the loss of adult trees, natural recruitment of oaks may be insufficient to maintain current densities within extant populations, as has been observed elsewhere. As early as the beginning of the 20th century, researchers observed that California oaks did not appear to be regenerating well (Sudworth 1908; Jepson 1910). However, more recent quantitative assessments of existing oak stands in California have produced conflicting conclusions about the extent of the "regeneration problem." The few large-scale surveys of oaks in California, which focused primarily on blue oak, *Q. douglasii,* found that regeneration is highly site specific, making it difficult to generalize about the extent and urgency of population declines in California's oak woodlands (Muick and Bartolome 1987a; Swiecki et al. 1993).

We review the scientific literature on the demography of nine species of canopy-sized oaks found in California, focusing on three species that have received the majority of study and are widespread in central California's foothill woodlands: blue oak (*Q. douglasii*), valley oak (*Q. lobata*), and coast live oak (*Q. agrifolia*) (Figure 1). We summarize the findings of research concerned with species-specific population distribution and abundance, age and size-class structure, and age-specific patterns of mortality and recruitment. Our objectives are to review the experimental findings on factors limiting establishment of oak seedlings and saplings, and to describe

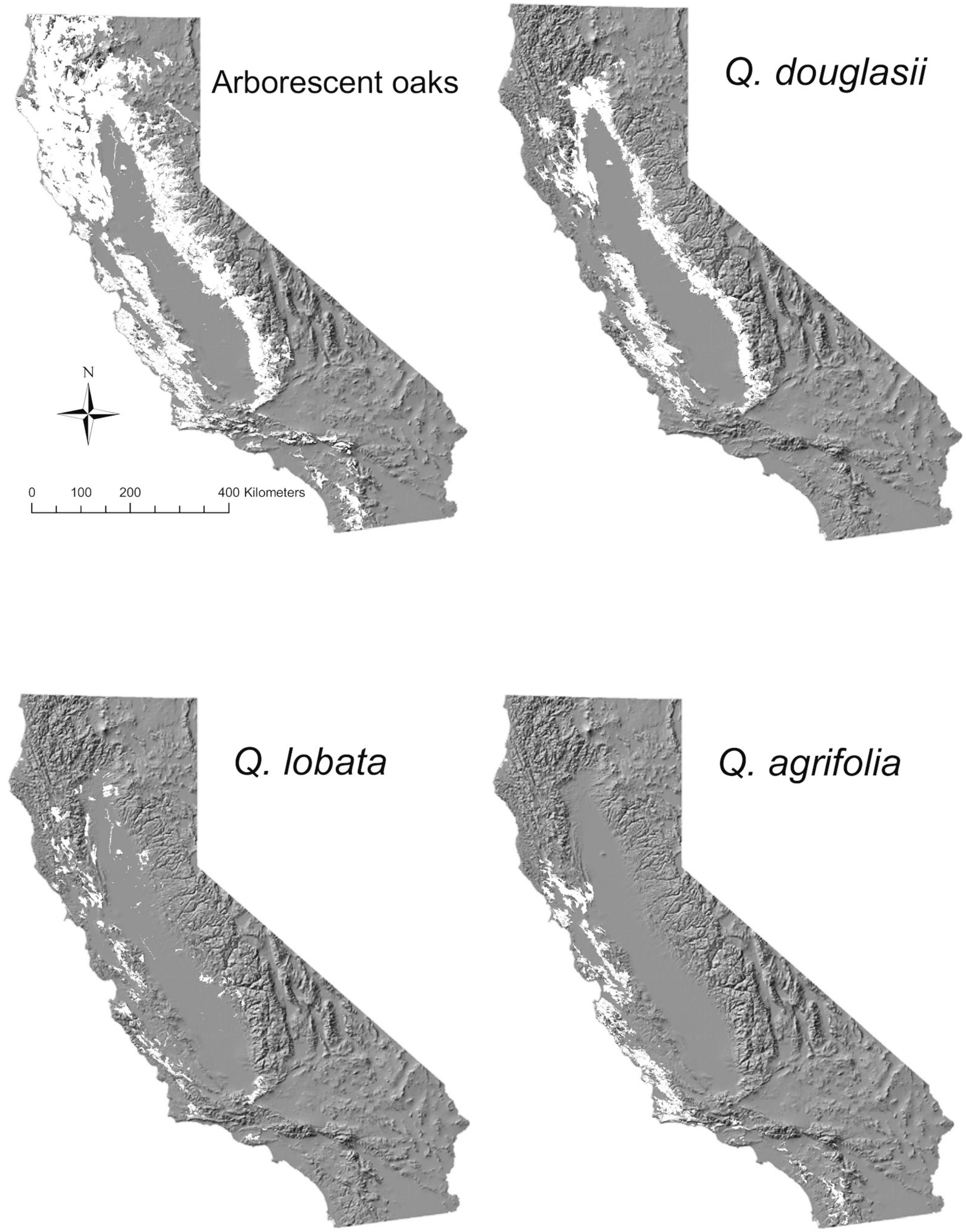

Figure 1. Modern Geographic Distribution of Canopy-Sized Oaks in California (Areas of Occurrence in White)

Data from Davis et al. 1988. A) All nine arborescent species combined; B) *Q. douglassii,* blue oak; C) *Q. lobata,* valley oak; D) *Q. agrifolia,* coast live oak.

and evaluate the evidence for a "regeneration problem," that is, for widespread oak population declines in extant stands. Much of the research on California oaks is presented in graduate theses and dissertations, technical reports, and proceedings from scientific conferences. Thus, a secondary goal of this review is to synthesize the oak literature from California that may not be readily available to the international scientific community in order to facilitate comparative analyses.

CLASSIFICATION OF OAK DEMOGRAPHY AND REGENERATION STUDIES

We reviewed over 150 published sources, and ultimately produced a database of 116 distinct studies that focused on one or more of the arborescent oak species in California and contained results relevant to some aspect of oak demography, including oak population age or size structure, change in population structure over time, or stage-specific survival rates. (A complete listing is available online at http://www.biogeog.ucsb.edu/Data/data.htm). The characteristics of this literature can be summarized as follows (Table 1).

1. Two-thirds of the studies are published in conference proceedings, technical reports to government agencies, theses, and dissertations; only 23 of the sources have been published in peer-reviewed scientific journals.

2. Blue oak (*Q. douglasii*) has received the majority of demography-related research effort (Table 1). Both valley oak (*Q. lobata*) and coast live oak (*Q. agrifolia*) have also received considerable attention, while studies of the remaining species account for less than 20% of published research on California oaks. The blue oak woodland type, which ranks first in terms of total land area (Davis et al. 1998), ranges from open savannas to dense woodlands (Figure 2). Coast live oak and valley oak rank eighth and ninth, respectively, in terms of extent but, like blue oak, are species where observed limited recruitment is a concern (Griffin 1971, 1976; Muick and Bartolome 1987a; Bolsinger 1988). These species occur in habitats ranging from closed riparian forests to open savannas, but recruitment has mainly been an issue in open woodland and savanna systems (Figure 3). All three species have been heavily impacted by habitat conversion to agriculture and residential development, which raises public and scientific concern for their long term viability (Pavlik et al. 1991).

3. The majority of studies have focused on acorns and seedlings, especially on the factors that affect acorn germination success and seedling survival, whereas few studies have been conducted on saplings and adults (Table 1). Most studies were short term (one to two years), and thus we know little about how the effects of these factors vary over time at a site.

4. There is a conspicuous lack of information about the factors that govern the transition from seedlings to saplings, and from saplings to adults, mainly because saplings are infrequent in most species and because long-term study is required. Only four studies focused on the mechanisms that affect survival or recruitment of saplings within populations (Allen-Diaz and Bartolome 1992; Swiecki et al. 1997a; Bartolome et al. 2002; Swiecki and Bernhardt 2002).

5. Little is known about rates of and controls on tree mortality, and only two studies directly measured adult mortality by following individual trees through time (Franco 1976; Brown 1991).

6. A substantial number of studies (22) investigated demography of oaks, but nearly all focused on current population or age structure. Only a few studies used tree rings to examine population dynamics over longer time periods.

7. The majority of studies involved field observation of natural or planted individuals for less than two years. Six of the fifteen studies that extended more than 72 months used historical air photos (Franco 1976; Rossi 1979; Scheidlinger and Zedler 1980; Brown 1991; Davis et al. 1995; Callaway and Davis 1998) (Table 1).

8. Although oak woodlands are widespread in California, most research has been conducted in a few areas associated with research field stations, notably the University of California's Sierra Foothill Research Center (Yuba County), Hastings Natural History Reservation (Monterey County), Sedgwick Re-

TABLE 1

Classification of oak demography and regeneration studies in California

Species studied								
Q. douglasii	*Q. lobata*	*Q. agrifolia*	*Q. wislizenii*	*Q. engelmannii*	*Q. kelloggii*	*Q. chrysolepis*	*Q. garryana*	*L. densiflorus*
75	53	28	11	8	7	7	6	2
Life stage studied								
Acorn	Seedling	Sapling	Adult					
46	87	31	30					
Study type[*]								
Acorn	Emergence	Seedling	Adult	Demography	Grazing	Fire	Change	
16	56	29	4	22	5	10	9	
Study length (months)								
0	1–12	13–24	25–36	37–48	49–60	60–72	>72	
26	30	18	11	13	6	2	15	

[*] Acorn - fate of acorns including germination rates, depredation rates, or damage from other biological factors;
Emergence - processes or agents that affect survival from acorn to seedling or initial emergence/recruitment of seedlings;
Seedling - factors that influence the survival and growth of existing seedlings and saplings;
Adult - fate of adults including sources of mortality, and factors that affect growth and survival;
Demography - quantified population or stand demographics;
Grazing - effects of grazing on population structure or life stage survival rates;
Fire - effects of fire on population structure through changes in survival rates of life stages;
Change - spatial or temporal changes in stand structure, canopy cover, basal area, or abundance
Data are numbers of published studies in each category.

FIGURE 2. BLUE OAK WOODLAND, SEDGWICK RESERVE, SANTA BARBARA COUNTY, CALIFORNIA
Seen hanging from the tree branches is the epiphytic "lace lichen," *Ramalina menziesii*. Photo by C Tyler.

FIGURE 3. FOOTHILL OAK WOODLAND AT SEDGWICK RESERVE, SANTA BARBARA COUNTY, CALIFORNIA
Comprised of equal proportions of *Q. lobata* and *Q. agrifolia*. In the immediate background is coastal sage scrub vegetation with scattered *Pinus sabiniana, Q. agrifolia,* and *Q. douglasii*. Photo by F Davis.

serve (Santa Barbara County), and the Hopland Research and Extension Center (Mendocino County).

Life History of California Oak Species

For context, we provide a brief description of the life history of California foothill woodland oaks, notably *Q. agrifolia, Q. lobata,* and *Q. douglasii.* Details may vary among species, but all oaks share this general life cycle (Figure 4).

FLOWERING AND FERTILIZATION (FROM FLOWER TO ACORN)

Although the reproductive age is not well documented for these species, it is likely that age at first reproduction for naturally established trees is at least several decades (Olson 1974), with maximum production occurring decades later. Mature trees produce flowers during March and April (Nixon 1997). Oaks are monoecious, bearing the long male catkins and the very small female flowers on a single twig. They are wind-pollinated and have limited self-pollination because male flowers generally release their pollen before the stigmas on female flowers of the same tree are receptive (Keator 1998; Sork et al. 2002).

The acorn crop varies widely in quantity from tree to tree and from year to year (Griffin 1971; Koenig et al. 1994). Factors that may influence the number of acorns produced annually by a given tree include weather, tree age, size, and health, the size of the tree's previous year's fruit crop, and perhaps the "neighborhood" conditions, such as distance to and density of neighboring trees (Koenig et al. 1994, 1999; Knapp et al. 2001; Sork et al. 2002).

ACORN DEVELOPMENT AND DISPERSAL (FROM ACORN TO SEEDLING, STAGE 1)

The length of time required for development and maturation of acorns varies among subgenera. Acorns of "white oaks" (subgenus *Lepidobalanus*) ripen within one year, while acorns of most "red oaks" (subgenus *Erythrobalanus*) and "intermediate oaks" (subgenus *Protobalanus*) develop and ripen within two years (Nixon 1997). California oaks that produce acorns within one year are valley, blue, Engelmann, Oregon, and coast live oak (a "red oak"); those that take an additional year to develop acorns are interior live, black, and canyon live oak. Acorn drop occurs between September and November (Griffin 1971). While still on the tree, acorns are susceptible to mortality due to heat, fungus, insects (predominately weevils and moth larvae), birds (including jays, magpies, and acorn woodpeckers), and mammals (including mice, squirrels, deer, pigs, and cattle) (Griffin 1980b; Koenig et al. 2002). No persistent seed bank is formed because acorns do not survive more than one year (Olson 1974).

Most mature acorns that are not eaten or carried away by animals land under or near the canopy of the parent tree. Acorns on the soil surface are likely to be killed by heat, desiccation, or predation (Tietje et al. 1991). In a natural landscape, acorns may become buried. While some seeds may be buried inadvertently (e.g., by wind-blown litter or pocket-gopher tailings), acorn-caching animals, in particular western scrub jays, play a critical positive role in natural seedling establishment in central California's oak woodlands. A single scrub jay may cache up to 5,000 acorns in a season, but only relocate and consume half of this number (Carmen 1988). Other caching animals include magpies, stellars jays, ground squirrels, and deer mice (Grinnell 1936).

ACORN GERMINATION AND SHOOT EMERGENCE (FROM ACORN TO SEEDLING, STAGE 2)

There is no acorn dormancy in most of the white oaks (e.g., blue and valley oaks) (Olson 1974), and germination occurs in the late fall. Germination is delayed until early winter or spring for red oaks such as coast live oak (Griffin 1971; Johnson et al. 2002). During late fall and early winter, the acorn is especially vulnerable to desiccation if it is on the soil surface depending on the timing of early season rainfall. Most of the initial energy stores of the acorn go toward root growth. It can be months before the shoot is fully expanded and visible above ground (Matsuda and McBride 1986). Seed predators, burrow-

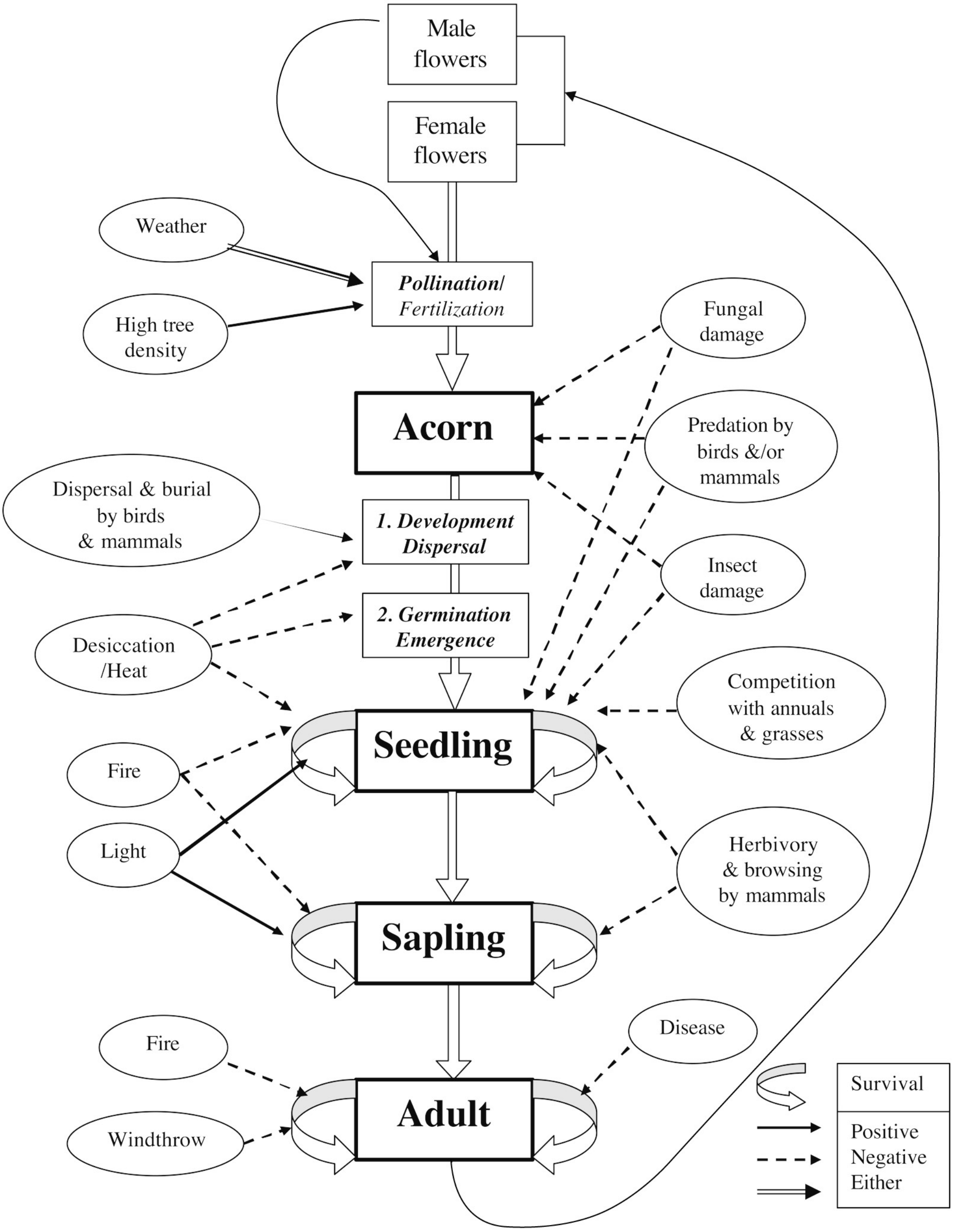

FIGURE 4. CONCEPTUAL MODEL OF THE LIFE-HISTORY STAGES OF OAKS

ing animals that consume plant roots, and fungi continue to add the risk of high mortality at this early life stage.

SEEDLING DEVELOPMENT (FROM SEEDLING TO SAPLING)

Following germination and emergence, seedlings must survive prolonged summer drought, which in the Mediterranean climate of California's foothills may extend more than six months. While it has been suggested that adult valley oak trees have roots that may tap into the water table (allowing trees to survive summer drought), the roots of new seedlings are generally many meters away from perennial water. Water stress experienced by seedlings is significantly greater than that of saplings and trees (Matzner et al. 2003). An additional stress to the young plant is herbivory by insects and mammals. Older saplings with considerable belowground growth may be able to recover from intense herbivory and even complete defoliation, but significant loss of leaves on a new seedling is likely to cause its death. Thus first- and second-year mortality of oak seedlings may be exceptionally high (e.g., Davis et. al. 1991).

SAPLING STAGES TO MATURITY (FROM SAPLING TO TREE)

Unless artificially watered, savanna and woodland oaks in California are relatively slow-growing trees (Sudworth 1908). Competition for light and water in dense stands may reduce growth rates. Sources of mortality at this stage include intensive browsing by deer and cattle as well as those sources that also affect adult tree stages, such as intense fire, disease, and cutting by humans (Griffin 1980a; Swiecki et al. 1997a,b). It is unknown how many years it takes to transition from sapling to tree, but it is probably decades. The life span of oaks varies among species. Valley oak is reported to be the largest and longest-lived oak species in North America, reaching ages of 400 to 600 years (Pavlick et al. 1991). Blue oaks have been aged to more than 400 years old (White 1966; Mensing 1988). Coast live oaks are also long-lived but have shorter life spans, perhaps between 200 and 300 years (Snow 1972).

Factors Limiting Establishment of Oak Seedlings and Saplings

Field surveys of blue oak, valley oak, and in some cases coast live oak, indicate that in many locations the numbers of seedling and sapling recruits are consistently very low. The factors most often cited as limiting oak recruitment are: acorn diseases, acorn predation, herbivory of established seedlings and saplings, competition between oak seedlings and non-native annual grasses for water, soil compaction by cattle, lack of fire, low rainfall in some years, and low tree population density. Below, we examine the current state of knowledge on these biological and physical factors believed to restrict recruitment of oaks in California.

BIOLOGICAL FACTORS

Acorn Diseases and Insect Damage

In an extensive investigation into the impacts of diseases and insect predation, Swiecki et al. (1990) reported a wide array of diseases and insects that damage or kill acorns. They found high incidences of fungi and evidence of boring and ovipositing by insects in blue oak, valley oak, and coast live oak acorns. Comparing the incidence of insect damage on acorns collected from the canopy to those from the ground, they found significantly greater proportions of insect damage on ground-collected acorns (71–96%) opposed to acorns still on the tree (5–29%). Knudsen (1984) found that 58% of valley oak acorns had evidence of insect damage. Griffin (1980b) noted valley oak acorn mortality due to insect damage ranged from 0–31% annually over eight years of observation. Dunning et al. (2002) examined insect damage on coast live oak and Engelmann oak acorns and seedlings. They found that the majority of all ground-collected acorns had some insect damage. The level of insect damage to acorns of both species was slight (less than 20% of the entire acorn), however, and the portions of the acorn most likely to be damaged were the cotyledons (carbohydrate storage) rather than the radicle and epicotyl (growing tips). The degree to which acorn damage reduces germination rates is unclear. Knudsen (1984) reported no difference in growth of seedlings that grew from insect damaged acorns versus those that showed no evidence of insect damage.

Acorn and Seedling Predation

Experimental studies have compared the survival and emergence rates of fully exposed acorns to those protected by cages that exclude birds and mammals. Predation by small mammals, including mice, gophers, voles, and ground squirrels, has been noted as a major source of acorn and seedling mortality for blue oak (Borchert et al. 1989; Callaway 1992; Adams and McDougald 1995), valley oak (Griffin 1971, 1980b; Knudsen 1984; Adams and Weitkamp 1992; Callaway 1992; Tyler et al. 2002), and coast live oak (Hibberd 1985; Plumb and DeLaseaux 1997; Parikh and Gale 1998; Tyler et al. 2002).

Acorn predation has been found to be extremely high in some cases. Griffin (1971) found that within nongrazed savannas, none of 160 sown valley oak acorns produced a seedling. Griffin attributed these substantial losses of acorns and seedlings to both mice and gophers. On Hastings Natural History Reservation, Griffin (1980b) placed 933 valley oak acorns on the ground under the canopy of an adult valley oak. All were within a deer exclosure, and some were protected from birds with mesh screens. After a period of three years, 81% of these acorns had been eaten or carried away. Of the 70 seedlings that emerged, not one survived the continued attacks by rodents. Tyler et al. (2002) conducted field experiments in which approximately 1000 acorns per species per year were planted in four different years to investigate factors that limit seedling establishment of valley oak and coast live oak. They found that maximum rates of seedling emergence (i.e., acorn survival and germination) in locations protected from birds and mammals were 71% in valley oak and 85% in coast live oak, but in locations open to all seed and seedling predators, maximum emergence rates were significantly lower: 30% in valley oak and 32% in coast live oak.

The strong associations between natural oak seedlings and shrub canopies reported for coast live oak (Callaway and D'Antonio 1991) and blue oak (Callaway 1992) are likely a result of protection provided by shrubs from shoot herbivory. Callaway and D'Antonio (1991) surveyed naturally occurring coast live oak seedlings and found that the vast majority were under shrubs, and that these were significantly less browsed than oak seedlings in surrounding open grassland. In field experiments, they determined that acorns planted under shrubs had high emergence and survival rates (up to 55% survival to year two), while no seedlings survived from acorns planted in the open. Herbivory by deer was the suspected cause of mortality for nearly 40% of those dying in the open, as seedlings were removed with no evidence of soil disturbance. Shrubs did not provide protection from acorn predators for blue oaks in similar studies (Callaway 1992); emergence was lower for acorns planted under shrubs caused by excavation by gophers. However, as above, percent survival of emerged shoots was significantly higher under shrubs than in the open, and the majority of mortality in the open was caused by herbivory above the soil surface, most likely by deer. Both studies report that animal activity and damage to acorns and shoots varied between microsites. Acorn and seedling removal under shrubs was caused by gophers, who probably used the shrubs as refuge, whereas deer were presumed responsible for shoot herbivory in the open. Not only do shrubs provide safe-sites by protecting from deer, they also provide shade. In experiments conducted in a dry year with only 50% of average rainfall, the combination of these facilitative mechanisms, as provided by caging and shading, led to highest survival in blue oak seedlings (Callaway 1992). Rock outcrops may similarly serve as natural safe-sites for oak recruitment (Snow 1972).

Herbivory and Browsing of Seedlings and Saplings

The role of insects (McCreary and Tecklin 1994) and small mammals in oak seedling mortality has been demonstrated by a number of studies (Griffin 1971, 1976; Adams et al. 1987, 1997c; Davis et al. 1991; Berhardt and Swiecki 1997; McCreary and Tecklin

1997; Tyler et al. 2002). Leaf defoliation by grasshoppers, root damage by pocket gophers and voles, and bark girdling by mice have all been reported to cause mortality or severe damage to established oak seedlings and saplings. For example, in acorn planting experiments, Davis et al. (1991) found that the proportion of blue oak seedlings that survive three years was reduced by half (22% versus 44%) for seedlings not protected from gophers compared to those that were protected. Higher rates of damage have been reported for valley oak seedlings; gophers were responsible for nearly 90% of the mortality of planted seedlings (Adams and Weitkamp 1992). In addition, browsing by deer has been noted to significantly reduce growth of oak saplings (White 1966; Griffin 1971). Moderate clipping treatments, which simulated defoliation by insects and light herbivore browsing, were found to result in greater mortality in coast live oaks than in blue oak seedlings; average mortality of shaded one-year-old seedlings in clipped treatments compared to controls for coast live oaks was 82% (clipped) versus 55% (control), and for blue oaks was 39% (clipped) versus 35% (control), which suggests that coast live oak seedlings may be especially vulnerable to such attacks (Muick 1995). Welker and Menke (1990) found that survival of blue oak seedlings in response to simulated browsing was greatly reduced when soil water was depleted rapidly, as might occur when oaks grow with exotic annual grasses rather than native perennials.

Livestock grazing has been implicated as a primary cause for failure of natural oak recruitment, but its effects are not straightforward. Several studies that have examined the association of cattle grazing with oak seedling or sapling abundance have yielded conflicting results. Standiford et al. (1997) conducted surveys of blue oak stands in southern Sierra Nevada woodlands and found that livestock grazing was negatively correlated with blue oak seedling presence, but nonsignificantly related to the presence of saplings. Analyses of the effects of environmental factors on blue oak sapling abundance conducted by Swiecki et al. (1997b) found that browsing intensity was negatively associated with blue oak sapling presence. In their statewide survey of oak woodlands, however, Muick and Bartolome (1987a) found that patterns of oak recruitment could not be explained by the presence or absence of cattle grazing. Furthermore, the removal of livestock has not resulted in increased levels of oak recruitment at some sites, even after many decades (e.g., blue oaks, White 1966; valley oaks, Callaway 1992).

Hall et al. (1992) investigated the effects of cattle grazing on blue oak seedling survival, and found that season of grazing played a much greater role in affecting survival than grazing intensity (stocking density) did. Seedlings exposed to spring and summer grazing had significantly more damage and lower survivorship than those exposed only to winter grazing. They also found that controls, which excluded cattle but allowed access to deer and other native grazers, were no different from plots grazed by livestock, which suggests that wildlife had an equivalent effect on oak recruitment. Jansen et al. (1997) examined the effects of two grazing systems, traditional (year-round, low intensity) versus high-intensity-short-duration (HISD), on blue oak sapling growth over four years. They found that effects of these grazing regimes did not differ significantly except that browse utilization (the proportion of twigs that were grazed) was higher in the HISD treatment. Interestingly, grazing by cattle has been shown to have positive indirect effects on oak recruitment by reducing the growth of competing herbaceous vegetation. Bernhardt and Swiecki (1997) found that over a seven year period, while direct effects of cattle on unprotected seedlings were negative, grazing indirectly improved growth and survival of caged valley oak seedlings and saplings.

Competition with Annual Grasses

Native perennial grasses, such as *Nasella pulchra* and *N. cernua,* and exotic annual grasses, such as *Avena fatua* and *Bromus mollis,* use water in different ways, both temporally and spatially (Welker et al. 1991; Holmes and Rice 1996; Hamilton et al. 1999). In California, the exotic annuals grow rapidly in the winter and early spring, depleting surface soil layers of water quickly; these annuals flower and complete their life cycle by mid-summer. In contrast, native perennials have slower growth rates and consume soil water at a slower rate so that the plants maintain photosynthesis well into the summer months while water is still available (Holmes and Rice 1996). The roots of annuals are shallower than those of perennials and are more dense within the topsoil layers (Holmes and Rice 1996; Hamilton 1997). It has been hypothesized that the exotic annual grasses deplete near-surface soil water early in the growing season, which leaves emerging oak seedlings with less water; in contrast, oak seedlings growing among native perennials have access to soil moisture long into the summer. Studies on blue oak and valley oak have demonstrated that seedling emergence, growth, and survival are significantly reduced when grown with exotic annuals as neighbors versus grown without neighbors (Gordon et al. 1989; Danielsen 1990; Gordon and Rice 1993). Oak seedlings grown with exotic annual grasses also exhibited reduced emergence and growth rates compared to those grown with native perennials as neighbors (Danielsen 1990; Welker et al. 1991; Gordon and Rice 2000). The negative effects of annual grasses were attributed to their reducing soil moisture more rapidly than perennial neighbors did.

Lending support to this competition hypothesis, several studies that examined various treatment methods found that reduction of grass cover by clearing or mulching (i.e., "weed control") significantly improved seedling survival and/or growth, most strikingly if the seedlings were also protected from herbivores (Swiecki and Bernhardt 1991; Adams and McDougald 1995; Adams et al. 1997b,c; McCreary and Tecklin 1997). Although the grass species were not identified in these studies, it is safe to assume that they were the exotic annual grasses that dominate California grasslands. To examine survival of oak seedlings with and without grass competition, Griffin (1971) planted acorns in plots, half of which were cleared of the herbaceous layer, and all of which were fenced to exclude large herbivores. In savanna plots, 31% of valley and coast live oak acorns and 88% of blue oak acorns produced seedlings that survived three years within the cleared areas, whereas no seedlings emerged within the uncleared section of the plot. The mechanisms of interaction between oak seedlings and herbaceous plants were not discerned in these studies.

PHYSICAL FACTORS

Soil Compaction

Since the majority of California oak woodlands and savannas are used as rangeland for cattle grazing (Bolsinger 1988; Greenwood et al. 1993), it has been speculated that surface soils within these rangelands have been compacted following decades of cattle presence, resulting in soil conditions that reduce oak establishment. Soil compaction leads to increased soil bulk density, which, in turn, reduces the ability of water to penetrate the soil surface, thus increasing surface runoff (Bezkorowanjnyj et al. 1993; Trimble and Mendel 1995). The compaction has the potential to reduce the ability of roots to penetrate the surface soil layers (Ferrero 1991), which hampers an emerging oak seedling's ability to reach ground water. Research from several systems indicates that the changes in bulk density that occur from grazing vary with the region of study (humid versus arid) as well as season and intensity of grazing (Laycock and Conrad 1967; Van Haveren 1983; Stephenson and Veigel 1987). The rate at which soils recover after grazers are removed has been found to vary from a few to many years (Ratliff and Westfall 1971; Braunack and Walker 1985). To our knowledge, there has been no published experimental research that has investigated the relationship between soil bulk density and the establishment or growth of oak seedlings.

Lack of Fire

Some studies have linked past fire events with periods of above average recruitment within blue oak woodlands. These studies aged populations of oaks and determined dates of fires from fire scars. McClaran (1986) and Mensing (1988) found some correlation between fire events and periods of apparent oak recruitment. However, rather than actual new recruitment, the authors acknowledge that the association of tree ages and fire dates may have resulted from temporal concentration of postfire resprouts. This conclusion was reiterated by McClaran and Bartolome (1989) and Bartolome (1991), who suggested that the correlation between fire and apparent blue oak regeneration was created by removal of older stems by fire and establishment of even-aged stems from resprouting. Contrary to hypotheses about the positive role of fire in oak recruitment, pollen and charcoal evidence suggests that lack of fire (i.e., fire suppression) has led to an increase in coast live oak density in the last 100 years in central coastal California (Mensing 1993).

It has been hypothesized that fire might improve conditions for oak seedling and sapling growth and survival by eliminating herbaceous competitors and by providing a flush of soil nutrients following a burn. Fire has been shown to have variable effects on the survival or growth of existing seedlings, but most studies have not found a stimulatory effect of fire on recruitment or resprouting. The effect of wildfire and prescribed burns on the survival rate of Engelmann and coast live oak seedlings was examined by Lathrop and Osborne (1991) on the Santa Rosa Plateau. For the study period of 18 months (from fire to the final observation), the authors found that seedling survival rates were only slightly higher in the burned areas (61%) compared to seedling survival at unburned sites (55%). Other research has found no positive effect of fire treatments on recruitment, survival, and/or growth of blue oak seedlings (Bartolome and McClaran 1988; Bartolome 1991; Allen-Diaz and Bartolome 1992). Swiecki and Bernhardt (2002) conducted research on the survival and regrowth of naturally occurring blue oak saplings burned in a moderate intensity fire. They discovered that partial or complete topkill from fire did not confer any growth or survival benefits to blue oak saplings, but instead prolonged the period that oak shoots were susceptible to subsequent fires and other damaging agents. In a statewide survey of the distribution of blue oak saplings, Swiecki et al. (1997b) found that frequent fire was negatively associated with sapling recruitment. Infrequent fire was not correlated or only slightly positively associated with sapling recruitment.

Low Rainfall

In multiyear planting experiments, interannual variation in seedling emergence and survival can often be explained by differences in rainfall. Borchert et al. (1989) found that seedling emergence of blue oaks in a wet year was nearly twice that in dry years. Amount of precipitation following planting also influenced rates of emergence and initial establishment of valley oaks (Griffin 1971; Tyler et al. 2002). In savanna plots protected from large mammals, emergence was 68% in a wet year versus 0% in a dry year (Griffin 1971); in similar treatments, Tyler et al. (2002) found that emergence was 45% in a wet year versus 5% in a dry year, and concluded that rainfall in the first year after planting was the decisive factor in recruitment success of both valley oak and coast live oak seedlings.

In years with below average rainfall, there is consistently low emergence and establishment of oaks regardless of caging or weed-control treatments (Griffin 1971; Plumb and Hannah 1991; Adams et al. 1997b), though shading was found to increase survivorship of blue oak (Callaway 1992; Muick 1995) and coast live oak (Muick 1995) seedlings in dry years.

Reduced Fecundity due to Stand Thinning or Habitat Fragmentation

Oak fecundity may be density-dependent at low stand densities. A study of pollen flow in blue oak found a significant positive correlation between individual acorn production and neighborhood density of potential pollen donors (Knapp et al. 2001). Sork et al. (2002) estimated the average distance of pollen dispersal in a valley oak savanna to be 50–150 m, and the effective number of pollen donors to be three to five individuals. As oaks become spaced farther apart in the landscape due to stand thinning or habitat fragmentation, total acorn production and, perhaps, per capita fecundity decline. At present, the demographic consequences of lowered fruit production is poorly understood.

EVIDENCE OF A "REGENERATION PROBLEM"

As in other oak habitats throughout the world, researchers have observed low recruitment rates in California's oak woodlands, raising concerns about population decline. The majority of articles on oak demography make reference to the "oak regeneration problem." This section reviews the evidence related to the hypothesis that extant stands of California's foothill oaks are declining. The majority of the data available focuses on blue oak, valley oak, and coast live oak.

The term "regeneration" has several uses, but as applied here in the context of population dynamics, we use regeneration to describe the process of replacing individuals lost from mortality; thus it represents a balance of the losses due to mortality with the gains from recruitment that maintain a stable population density over time (Harper 1977; Bartolome et al. 1987; Muick and Bartolome 1987b; Johnson et al. 2002). "Recruitment" is the establishment of new individuals into an age- or size-class of a population. Oak recruitment is generally classified into three size-classes: seedling (the successful germination of an acorn and survival of the seedling), sapling, and tree. "Mortality" is the removal (or death) of individuals from a population, and can occur in any age- or size-class. Mortality may be a result of anthropogenic forces (e.g., cutting) or natural forces (e.g., wind throw, disease, old age). To fully and accurately determine whether a regeneration problem exists for a given stand or population, information about both mortality and recruitment is required.

EVALUATION OF STUDY METHODS

We identified 19 studies that provide quantitative information about current stand structure in California's oak woodlands (Table 2). Few studies included data on both recruitment and mortality, however. Four approaches have been used in these studies: (i) age structure analysis of current stands; (ii) size structure analysis of current stands; (iii) comparative analysis of historical and current air photos; and (iv) comparative analysis of historical and current ground surveys. Each of these approaches has its merits and limitations.

Age Structure (Tree Ring) Analyses of Current Stands

In age structure analyses, the age distribution of adults in the stand is determined by coring or sectioning trees and then counting annual growth rings. This approach provides accurate results for species that produce distinct annual rings (e.g., the deciduous species, such as blue oak and valley oak), but is generally not well suited for those species that do not have distinct rings (Cook and Kairiukstis 1990; Cherubini et al. 2003). At the same time, the methods for conducting age structure analyses are quite laborious since oaks generally have very dense wood, which makes coring difficult, and there is considerable time required for preparation and reading of cores (McClaren 1986; Harvey 1989). By describing a stand's age structure, the goals of these analyses are to determine the years in which the present adults recruited, and to relate those recruitment events to past biological or environmental conditions (e.g., rainfall, fire, historical grazing). Additional information derived from this approach can include individual growth rates (by analyzing ring widths) at different ages or sizes and, potentially, their relationship to past environmental conditions.

The main limitation of this, and similarly any static survey, is that the present age structure represents only the age structure and recruitment history of survivors (Harper 1977). There may have been past peaks in recruitment in cohorts that later experienced much higher mortality rates, for example. Also, one cannot know the entire suite of conditions that existed during those recruitment events. A second important limitation of age structure analyses occurs with species that resprout following cutting or damage by fire. In these cases, a given age cohort may actually represent individuals that recruited at many different times, but resprouted simultaneously after the same disturbance. Thus the apparent year of recruitment, as inferred from annual growth rings, may not be the year in which the individual established as a seedling, so conclusions about factors promoting natural establishment can be erroneous. For example, in his study of blue oak demography in

TABLE 2

Studies of age or size structure in blue oak (BO), valley oak (VO), and coast live oak (CLO)

			study measured?		
Source	**Species**	**Study approach**	**Recruitment**	**Mortality**	**Findings**
White 1966	BO	size, agestruct	yes	no	few seedlings; saplings common; little tree recruitment since 1910
Franco 1976	BO	size struct	yes	no	seedlings and saplings abundant in ungrazed site
McClaran 1986	BO	age struct	yes	no	lack of tree recruitment since 1930
Muick and Bartolome 1987a	BO	size struct	yes	no	saplings present in most sites; sapling: tree density> 1:10 for most regions
Bolsinger 1988	BO	size struct	yes	no	seedlings and saplings uncommon to absent in many sites
Mensing 1988	BO	age struct	yes	no	lack of tree recruitment since 1860
Harvey 1989	BO	age struct	yes	no	tree recruit. in past 50 yrs varied among sites from none to abundant
Standiford et al. 1991	BO	size struct	yes	no	many seedlings, saplings rare to abundant
Holzman 1993	BO	plot resurvey	yes	yes	numbers of trees constant or increased at most sites since 1932
Swiecki et al. 1993	BO	size struct	yes	yes	sapling recruits present in low density at 11/15 sites; adult mortality low
Davis et al. 1995	BO	air photo	–	–	tree cover increased at some sites, decreased at others; stable overall
White 1966	VO	size struct	yes	no	no saplings in 2 out of 4 stands; 9 saplings per 306 trees
Franco 1976	VO	size struct	yes	no	seedlings and saplings present but uncommon in ungrazed site
Griffin 1976	VO	size struct	yes	no	seedlings and saplings rare in all grazed sites
Griffin 1976	VO	size struct	yes	yes	seedlings common some years in ungrazed sites; high seedling mortality
Knudsen 1984	VO	size, age struct	yes	no	seedlings and saplings relatively abundant, especially on mesic sites; ungrazed
Muick and Bartolome 1987a	VO	size struct	yes	no	saplings absent from most sites; seedlings present in 4 out of 6 plots
Thomas 1987	VO	size struct	yes	no	seedlings absent from 3, abundant at 1 ungrazed site; saplings uncommon
Bolsinger 1988	VO	size struct	yes	no	seedlings and saplings uncommon to absent in most sites
Brown 1991	VO	air photo	yes	yes	number of trees decreased; no visible recruitment
Snow 1972	CLO	size, age struct	yes	no	younger/smaller classes of trees present but uncommon in most sites
Franco 1976	CLO	size struct	yes	no	seedlings and saplings abundant in ungrazed site
Griffin 1976	CLO	size struct	yes	no	seedlings abundant
Schleidlinger and Zedler 1980	CLO	air photo	–	–	tree cover increased at some sites, decreased at others; decline overall
Muick and Bartolome 1987a	CLO	size struct	yes	no	seedlings abundant, saplings present in most sites
Bolsinger 1988	CLO	size struct	yes	no	seedlings and saplings uncommon to absent in many sites
Holzman 1993	CLO	plot resurvey	yes	yes	tree density increased at most sites since 1932
Callaway and Davis 1998	CLO	size struct	yes	no	saplings common in woodlands with shrubs, uncommon if shrubs rare
Callaway and Davis 1998	CLO	air photo	yes	no	tree density and cover increased in shrublands, decreased in grasslands

the Sierra foothills, McClaran (1986) reported that 70–85% of blue oak trees established after fire; similarly Mensing (1988) found that a large peak of recruitment of blue oaks in the Tehachapi Mountains occurred in 1856. While some ecologists cite this work as evidence that fire stimulates oak recruitment, both authors acknowledge that these large cohorts may likely be the result of resprouting after fire of adults of various ages.

Size Structure Analyses of Current Stands

In size structure analyses, all individuals in a stand are measured and assigned to size classes. It is relatively easy to measure the sizes of trees using diameter at breast height (dbh), and of seedlings and saplings using diameter at base (db) and/or height. The main drawback of this method is that any conclusions about population dynamics and the past or future recruitment or mortality of a stand rely on the assumption that size reflects age. With oaks and many other tree species, it is generally true that the largest individuals are probably old and the youngest individuals are generally small, but it is not always the case that the smallest trees are young. Size and age are not well correlated in blue oaks (McClaran 1986; Harvey 1989), and are weakly correlated in valley oaks (Knudsen 1984). As described in the previous section, some species (including blue oak and coast live oak) resprout following cutting or damage by fire, and thus older individuals that have resprouted may be smaller than expected for their age. Therefore, size can be used as a measure of age only in a very broad sense.

Even given this caveat, there are strong arguments for using size class rather than age class to describe the structure of oak populations and to predict its potential for regeneration. First, mortality risks appear to be more closely associated with size class than age class. For example, although it may take many years for a sapling to reach a height above the browse layer (about 1.5–2 m), it is then less likely to be killed by large grazers (Griffin 1971; Bartolome et al. 2002). Larger seedlings and saplings may also be better able to withstand drought and fire (Swiecki et al. 1997a,b; Swiecki and Bernhardt 2002). Second, as in many other tree species, reproductive behavior is often size- rather than age-related (Johnson et al. 2002). Thus, size may be the most useful parameter for predictions about the future of a given population.

Historical and Current Air Photo Analysis

Sequences of historical aerial photos since about the 1930s were used to determine the change in tree cover and/or density of several areas. After excluding areas completely converted to other land uses, mortality can then be attributed to natural death or isolated cutting. Since these photos were taken at several times in each study area, this approach can provide valuable information about natural mortality rates and recruitment of individuals into the canopy layer. There are several limitations, however. The time period over which mortality and recruitment rates were observed is at most 70 years—a fraction of the life span of an adult oak. Perhaps the main limitation is that in some landscapes, particularly dense woodlands, it may be difficult to accurately determine tree density and species. For example, where valley oak, blue oak, and coast live oak co-occur, the first two deciduous species are easy to distinguish from the latter evergreen species, but may be difficult to distinguish from one another in the aerial photographs. In such cases, and where tree canopies overlap, analyses focus on changes in total tree cover (e.g., Scheidlinger and Zedler 1980; Callaway and Davis 1993; Davis et al. 1995). Without information about changes in density (which would incorporate mortality and recruitment of individuals) of each tree species, conclusions about population dynamics of dense oak stands are limited. This approach may be best suited for use in savanna habitats where the fates of individual trees can be clearly observed (e.g., Brown 1991).

Historical and Current Ground Surveys

The first large-scale mapping of vegetation in California was the Vegetation Type Mapping (VTM) survey directed by A E Wieslander from 1919 to 1945 (Wieslander 1935). A tree species was only recorded if: (i) total tree canopy cover in an assessment area was greater than 20%, and (ii) that species comprised greater than 20% of the relative tree cover. Thus, the estimate of tree abundance and cover from VTM surveys can be considered conservative since rare individuals or small clusters of trees were generally not recorded. The locations of the original VTM plots were marked on topographic maps (30-minute scale). Comparisons of present-day ground surveys in which VTM plots are relocated and sampled to the original VTM dataset provide data on changes in oak woodland cover and tree density in the past 50–60 years (e.g., Holzman 1993). Since the uncertainty about the locations of original plots is on the order of tens to hundreds of meters, the comparisons can indicate only approximate levels of change in these systems (Keeley 2004). However, there are no other techniques that provide comparable data on tree density, and thus recruitment and mortality rates, particularly for oak woodlands.

Two other limitations to this approach are that it is possible to observe changes only over the past 50–70 years, and that due to the sampling criterion of the original surveys (i.e., trees occurring in low densities were not mapped), this method is not well suited for examining change in oak savanna populations, except for stands that formerly had a tree cover of at least 20%.

FINDINGS

Blue Oak

Eleven of the published studies we reviewed contained information about regeneration status in blue oak woodlands (Table 2). Six are field surveys that include information about the current size structure of the populations. Seedlings ranged from absent to few in three studies (White 1966; Muick and Bartolome 1987a; Bolsinger 1988), and abundant in two studies (Franco 1976; Standiford et al. 1991). Whereas the relative abundance of saplings varied among studies, all reported that saplings were present in most stands. Three field surveys included numerous sites throughout the species' distribution; these found that saplings were relatively rare but present in most plots (Muick and Bartolome 1987a; Bolsinger 1988; Swiecki et al. 1993). Other studies reported that saplings were abundant in most plots in central coastal California (White 1966; Franco 1976) and in the Sierra Nevada (Standiford et al. 1991). Several of the field surveys that collected data at more than one site examined the relationship between sapling density and environmental factors (Muick and Bartolome 1987a; Standiford et al. 1991; Swiecki et al. 1993). All found that saplings were more common on mesic sites.

The results of the four studies that examined historical recruitment patterns in blue oak varied. McClaran (1986) and Mensing (1988) found that no trees had established since 1930 and 1864, respectively. White (1966) reported that little recruitment had occurred since 1910. However, Harvey (1989) found that establishment varied among four sites in the past 50 years: one had abundant recruits, one had moderate recruitment, and two had little to none.

The two studies that covered a wide area of the range of blue oak, and included some loss or mortality information in their analyses, found that while some locations had net losses, (i.e., recruitment not balancing mortality), others had increases in tree density or cover, and that most locations had no net change (Holzman 1993; Swiecki et al. 1993). Davis et al. (1995) compared historical to current aerial photographs and found that changes in cover varied among sites and regions, but that decreases in tree cover at some sites were offset by increases at others. While large changes were noted at individual sites, the mean cover over the entire study region remained virtually unchanged from 1940 to 1988.

In summary, blue oak seedlings and saplings are present but relatively rare in many stands, and absent from some. Some stands have no evidence of tree recruitment within the past 50 years. However, mortality rates of adults are also low: estimated to be 2–4% per decade (Swiecki et al. 1993). The only studies that have examined change over time indicate that most locations show no net change in tree cover or density.

Valley Oak

Nearly all of the field studies that inventoried valley oak seedlings and/or saplings (Table 2) found them to be uncommon or absent in most sites and, in multispecies surveys, at the lowest densities of all oak species observed (White 1966; Franco 1976; Griffin 1976; Muick and Bartolome 1987a; Thomas 1987; Bolsinger 1988). Knudsen (1984) was one exception, finding that seedlings and saplings were common at some sites in the Sacramento Valley within a riparian gallery forest. In addition, Griffin (1976) observed high densities of seedlings in some years in areas excluding cattle and deer.

Although there are few studies on natural recruitment in valley oak, several patterns emerge that merit further investigation. First, the studies that report finding some seedlings (Knudsen 1984; Muick and Bartolome 1987a; Thomas 1987) were conducted within a year or two of previously high rainfall years, suggesting that presence or absence of seedlings may depend on the climatic conditions preceding the survey. This is supported by Griffin (1976), who found that presence of seedlings varied considerably among years, from over 316 recruits in 1970 to only 11 recruits in 1973—all under the same valley oak adult. Second, rates of sapling recruitment may vary geographically: one study that reported finding no saplings (Brown 1991) was done at one of the driest sites, at the southern extent of the species' range, while the studies that report at least some sapling recruitment (White 1966; Franco 1976; Knudsen 1984) were conducted in wetter, more northern regions. Interestingly, the latter two surveys were also done in preserves with no cattle grazing.

The one study that measured population dynamics found high tree mortality and no tree recruitment between 1938 and 1989 (Brown 1991). Anthropogenic causes, such as thinning, may contribute to high mortality of valley oak adults in some areas since they occur on land that is usually used for agriculture (Rossi 1979). Given the generally rare occurrence of seedlings and saplings, current data suggest that in extant savanna stands, valley oak regeneration may not be sufficient to maintain populations at their current levels. This conclusion is based on few studies, however, and thus needs to be tested with additional quantitative research of natural recruitment and mortality.

Coast Live Oak

Several field studies noted that coast live oak seedlings were abundant where adult trees were present, and saplings were uncommon but present in nearly all locations (Snow 1972; Franco 1976; Griffin 1976; Muick and Bartolome 1987a). A statewide foresters' survey found that seedlings and saplings were present but rare compared to other evergreen oak species (Bolsinger 1988).

Comparing historical to current aerial photographs, Scheidlinger and Zedler (1980) found that stands dominated by coast live oak varied in the amount of change from 1928 to 1970. They observed an overall decline of 13% cover, but noted that some or all of this loss may have resulted from a temporary reduction in crown cover due to a fire just prior to 1970. In central coast California, Callaway and Davis (1998) compared historical aerial photographs from 1947 to those taken in 1989, and recorded oak canopies that were present only in the latter photographs. They found that recruitment was relatively high in coastal sage scrub habitats and very low in grasslands. Field surveys conducted in oak woodlands at the site revealed that coast live oak seedlings and saplings were common where understories were dominated by shrubs, but uncommon in woodlands with herbaceous understories. Only one large-scale ground survey provided more precise information about change in coast live oak stands over time (Holzman 1993), and this study found that tree cover and density had increased since the 1930s.

To summarize, coast live oak seedlings have been noted to be abundant in some locations, saplings are present in many sites, and adult coast live oaks have increased in some stands (Table 2). There are currently no studies that provide quantitative data on mortality rates. Such information would be useful to better understand the potential impacts of the large-scale loss of coast live oak stands due to Sudden Oak Death syndrome (Garbelotto et al. 2001; McPherson et al. 2002; Rizzo et al. 2002).

SUMMARY: IS THERE A REGENERATION PROBLEM?

Most studies of California's oaks that report a regeneration problem base that conclusion on the rarity of seedlings and/or saplings (Table 2). As several researchers (Bolsinger 1988; Lang 1988; Swiecki et al. 1993) have previously noted, lack of seedlings or saplings suggests, but does not confirm, a regeneration problem. Recruitment of seedlings, in particular, can vary considerably among years, depending on acorn crop, rainfall, and other factors. While sapling densities are low in many stands, both sapling and adult survival rates are high. Similar demographic patterns have been reported for long-lived trees in the tropics (Lieberman and Lieberman 1987; Condit et al. 1995).

At present, there are not sufficient quantitative data, particularly on mortality rates, to support the prevalent belief that oaks in California are suffering from a "regeneration problem." The degree to which oak populations are changing appears to vary among species as well as regionally. Whereas valley oak populations in central California are declining (Brown 1991), blue oak populations appear to be regenerating adequately in many locations (Holzman 1993; Swiecki et al. 1993; Davis et al. 1995), particularly in mesic sites that are not grazed intensively by livestock. Coast live oak may be increasing in some regions as well (Holzman 1993).

Although we currently lack sufficient evidence of widespread decline in extant stands, those responsible for conservation or management of oaks in California's foothill woodlands may well be justified in maintaining preservation and planting efforts for several reasons. First, even with intervention, seedling and sapling establishment and growth rates are low. If it is demonstrated that mortality in a given stand is exceeding natural recruitment, it will take at least 50–100 years to functionally replace the individuals lost. As suggested by Kwit et al. (2004), conservation actions for slow-growing, long-lived species are best pursued before populations decline to a level from which recovery is not possible. Second, evidence suggests that recruitment limitations may be more severe now than in centuries past, due in part to anthropogenic influences (e.g., livestock grazing, stand thinning). Restoration efforts may prove to be challenging and require many years to accomplish. Third, although the major threat to oak woodland habitats is stand loss through conversion to residential development and agriculture, there are other significant human disturbances within extant stands that increase adult mortality, such as the cutting of oaks for firewood or to facilitate agricultural operations.

CONCLUSIONS AND RECOMMENDATIONS

Extensive research has clearly demonstrated what treatments or interventions are necessary to ensure high rates of initial oak seedling establishment. Far less is known about factors limiting establishment of saplings. As discussed by a number of authors, and summarized by McClaran (1986), successful oak recruitment requires a combination of events including abundant acorn production, sufficient rainfall, limited competition for light and water from neighbors, and protection from seed predators, herbivores, and browsers. Any one of these may act as a limiting factor in preventing the recruitment of seedlings and the subsequent transition to sapling and tree. The most significant gaps in our knowledge of seedling and sapling establishment are data on survival rates among size/age classes and how various treatments or locations influence those rates. Longer-term study, including historical aerial photography, ring-based age structure analysis, and monitoring of permanent plots, is required to determine spatial and temporal variation and trends in oak demography, and in particular causes and rates of mortality within the sapling and adult life stages.

Population models are the best means to predicting the long-term consequences of current stage-specific recruitment and mortality rates. Complex, multispecies succession models (i.e., "forest gap models") may not be appropriate for foothill oak populations because the tree layer in oak woodlands is usually comprised of only one or two species, the tree crowns do not interact strongly for light, and there is no evidence of long-term successional replacement of tree dominants in these systems. Instead, single-species stage-based matrix transition models (Caswell 2001) can provide insight into the sensitivity of oak regeneration dynamics to changes in seedling and sapling recruitment, mortality rates, or adult fecundity. With such models, oak population dynamics can be projected under different ecological assumptions or management and restoration strategies. Although these models have limitations, they have been used extensively to model extinction risk for rare plants (Menges 2000; Kwit et al. 2004), and in recent years have been refined to account for variations due to factors such as episodic recruitment, correlation in the variation of stage-specific recruitment rates, and temporal autocorrelation in demographic rates (Fieberg and Ellner 2001; Franco and Silvertown 2004). Spatially explicit "landscape models" that account for individual locations, seed dispersal, site heterogeneity, and species interactions can provide additional insights, although they are more difficult to parameterize and interpret (e.g., Zavala and Zea 2004). Multiple modeling approaches would be welcomed, and the absence of population models for these species is surprising.

A comprehensive understanding of oak demography will ultimately require the integration of observational, experimental, and modeling components. We have recommended general research foci and approaches that we believe will enable the construction of oak population models. These will be necessary to adequately characterize, monitor, and manage California's oak woodlands and savannas for long-term persistence and health, and may contribute to a better understanding of the patterns of regeneration in oak woodlands around the globe.

ACKNOWLEDGMENTS

We gratefully acknowledge support from the David and Lucille Packard Foundation and the Santa Barbara County Energy Division during the writing of this review. We received helpful comments and encouragement from M Borchert, A Carlson, B Mahall, D Odion, and E Zavaleta. We are especially thankful for the detailed critiques provided by D Botkin, J Connell, C D'Antonio, and two anonymous reviewers.

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