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Hardwoods occupy about 25% of the total forest area in California (Bolsinger 1988). Predominant among the hardwoods are oaks (Table 1). Over the past 10 years, concerns have been raised about the ability of some oak woodland stands to replace themselves. These concerns have focused on 2 distinct management dilemmas. The first involves the gradual loss of oak woodland acreage due to human activities. These activities often involve some type of conversion, such as the clearing of trees for rangeland improvement, production agriculture, or residential development (Schmidt and Tietje 1987). The rapid increase in California's population means more pressure on oak woodlands and hardwood rangelands to convert them into housing developments. Over the past 15 years, 85% of the oak woodland acreage lost has been due to urbanization and road building (Bolsinger 1988). Over 50% of the woodland area converted since 1973 has been the blue oak type. There are 29 million people in California today. By the year 2000, the population is expected to reach 31 million, and by the year 2020, 37 million (Ewing 1987). Pressure on oak woodlands undoubtedly will increase, and policies for reducing or mitigating this loss need to be developed. In addition, utilization of oak biomass for fuelwood consumption is expected to follow a similar increasing trend.

The second oak management dilemma involves the biological processes relating to regeneration. Three species, valley oak, blue oak, and Engelmann oak, have been recognized as suffering from poor regeneration on a statewide basis, although there are regional and site-specific concerns for other species. The actual mechanisms resulting in the poor regeneration of blue, valley, and Engelmann oaks are unknown, although a number of factors, acting in concert or alone, are presumed responsible (Holmes 1990). These factors include rodent, bird, pig *(Sus scrofa),* and deer *(Odocoileus hemionus)* predation on acorns; rodent, rabbit *(Lepus* and *Sylvilagus* spp.), and deer browsing on seedlings; livestock consuming acorns and seedlings; competition for water and nutrients with annual grasses; and modified soil and fire dynamics.

For a discussion of how vertebrates can affect the regeneration of oak stands, it is useful to divide the life history of oak trees into four stages: 1) acorn,

Table 1. List of oaks (genus *Quercus)* native to California (Tucker 1980).

Common name	Scientific name
White oaks (Subgenus *Quercus)*	
Blue oak	*Quercus douglasii*
Scrub oak	*Q. dumosa*
Leather oak	*Q. durata*
Engelmann oak	*Q. engelmannii*
Oregon oak	*Q. garryana*
Valley oak	*Q. lobata*
Deer oak	*Q. saderiana*
Desert scrub oak	*Q. turbinella*
Intermediate oaks (Subgenus *Protobalanus)*	
Canyon live oak	*Q. chrysolepis*
Dunn oak	*Q. dunnii*
Island oak	*Q. tomentella*
Huckleberry oak	*Q. vaccinifolia*
Black or Red oaks (Subgenus *Erythrobalanus)*	
Coast live oak	*Q. agrifolia*
California black oak	*Q. kelloggii*
Interior live oak	*Q. wislizenii*

2) seedling, 3) sapling, and 4) mature, acorn-producing tree. A tree needs to pass through all 4 of these stages to produce offspring, and each stage provides new food resources for a different set of vertebrates.

Acorns are consumed by a wide variety of bird and mammal species. The exact mix of species has changed over the past 300 years. Deer populations are probably higher, wild pigs have been introduced and now are common, and new assemblages of rodents and birds, adjusting to human influences on the landscape, inhabit oak woodlands. However, there is no evidence that consumption of acorns is a primary cause of poor regeneration. Normally, some acorns will remain in the seedbank.

Seedlings are browsed aboveground by rabbits, ground squirrels *(Spermophilus* spp.), various rodents, livestock, and deer. Below ground, pocket gophers *(Thomomys* spp.) are known to clip the tap root. Vertebrates are significant sources of mortality for young trees at this stage (up to 30 cm in height).

The terminal and lateral buds of saplings can be browsed back by deer and livestock until they exceed 150 cm in height. Rabbits and rodents can still girdle the young trees.

Probably the most serious effects of vertebrates on mature trees is 1) compaction of the root zone, especially by livestock, and 2) desiccation of the root system by ground squirrel burrows at the base of the tree.

There appears to be no simple solution, such as removing livestock from an area, that assures natural regeneration of these species of oaks. Artificial regeneration techniques will need to be developed (Schmidt 1987). These techniques include repellents for protecting acorns, seedlings, and saplings, exclusion (barrier) devices for protecting seedlings and saplings, and coordinated planting systems that take into account potential mortality sources and plan for them (e.g., planting seedlings instead of acorns when ground squirrels are present). It is doubtful that standard vertebrate pest control materials and strategies (e.g., reducing populations of voles *[Microtus* spp.] with toxic baits) will be either practical or cost-effective, but this research has not been accomplished.

There is surprisingly little attention focused on improving the technologies available for managing this source of oak mortality. Species responsible for the damage are often not identified. Assessment methods for determining the degree and severity of the damage are not developed. Screening technologies are not being improved. Finally, persons involved in restoration work are not sharing information with those involved in animal damage control work (and vice versa), resulting in a limited bag of tricks for managing the vertebrates responsible for oak mortality.

ACORN AND SEEDLING MORTALITY

Acorns are an important source of food for many insects, birds, and mammals in California. For example, Bowyer and Bleich (1980:294) observed that 85% of the California black oak acorns dropped in 1978 on the Cuyamaca Mountains were consumed by wildlife over a 3 week period, with 94% of these acorns consumed by mule deer. This pattern is repeated throughout California for all species of oaks, although the relative proportion of the acorn crop eaten by the various acorn predators may differ. Acorns provide a concentrated source of energy to the consumer, and animals ranging in size from black bears *(Ursus americanus)* to deer mice *(Peromyscus* spp.) utilize them to varying degrees (Schmidt 1991).

Oak seedlings are also consumed by a variety of herbivores. At the Hopland Field Station in Mendocino County, Menke and Fry (1980:303) found that black-tailed deer diets were composed of 40% oak browse (leaves and twigs) in the summer months (oak browse plus acorns made up 59% of the diet). They noted that year-long consumption of oak browse averaged 21.5% per month. Nitrogen levels in both blue and California black oaks peaked in the spring (May), and they speculated that oak browse was a significant source of crude protein for deer. Although the majority of this browse must have been leaves and twigs from the lower branches of larger trees, oak seedlings within the reach of deer are no doubt consumed also. Other animals, such as pocket gophers and sheep, consume seedlings as well.

Thus, it comes as no surprise that professionals involved in the planting of oaks in wildlands invariably include some management strategy which is directed toward reducing predation or herbivory on planted acorns and seedlings. The same mortality sources which affect naturally planted acorns are present in the environment for impacting human-planted trees. In order to maximize survival and minimize replanting costs, appropriate protection methods must be utilized.

ACORN MORTALITY SOURCES

Zimmerman (1982) noted that "the ultimate effect of vertebrate animals on acorn availability will be mediated by then-dual role as acorn predators and acorn dispersers." This is pointedly true in California with two birds in particular, scrub jays *(Aphelocoma coerulescens)* and acorn woodpeckers *(Melanerpes formicivorus),* acting as both predators and dispersers of acorns. Griffin (1980) measured the removal of valley oak acorns by scrub jays and determined that removal rates exceeded 400 acorns per hour. He did note that "...the numerous acorns which are not found and eaten later are effectively 'planted'" (p. 242). Johnson and Adkisson (1986) measured the number of pin oak acorns transported by blue jays *(Cyanocitta cristata)* in Virginia. In 28 days, about 50 blue jays transported and cached 150,000 acorns, or about 58% of the total acorn crop. They noted that "...the ease with which [blue] jays move about in human-dominated landscapes fosters oak regeneration in old fields, vacant lots, fencerows, and other untended land isolated from seed-bearing oaks." (p. 46). Schmidt (1991) estimated that scrub jays cached over 1 billion acorns every year in California.

Verner (1980) listed 30 species of birds in California which utilize acorns as food. He also noted that birds consume acorn insects.

Birds are rarely noted as specific problems in wildland oak plantings. In reality, the attention given to solving acorn predation problems from rodents probably is also effective in preventing avian predation.

That mammals are significant predators of acorns is accented by the number of oak planting-related papers that highlight early collection and protection as items critical to the success of a planting program. Johnson and Krinard (1985) pointed out that "acorn collection must not be delayed, as most acorns will be devoured within a few days by animals..." (p. 58).

McElwee (1970) pointed out that destruction of acorns by rodents had been the chief cause of failure in direct seeding programs in North Carolina. Adams et al. (1987) had more than 5,000 acorns in Madera County, California, depredated, and they assumed the culprits were ground squirrels, although scrub jays, pocket gophers, and other rodents were undoubtedly present.

Barrett (1980) calculated that at least 37 (22%) of California's terrestrial mammals are known to utilize acorns. He stated that, "Acorn utilization usually approaches 100 percent where deer, pigs, or bear occur." (p. 277).

Bowyer and Bleich (1980:294)), for their study area in San Diego County, observed that, "only when [California black oak] acorns germinate within dense patches of squaw bush or snowberry are they not substantially damaged or completely consumed by deer."

Griffin (1980) noted that valley oak acorns on the ground in January were rare at the Hastings Natural History Reservation in Monterey County. When cattle and deer were eliminated as potential predators with exclosures, one experimental plot lost 56% of the 233 planted acorns, presumably to pocket gophers *(Thomomys bottae).* Additional studies revealed predation to planted acorns by deer mice. Summarizing his various experiments, Griffin recorded 756 of 933 planted acorns (81%) eaten or carried away by both avian and mammalian predators.

Johnson and Krinard (1985) found that site-prepared forest openings of 0.83 ha or more and agricultural fields had much less rodent damage than those planted under a full forest canopy. They worked with oak species native to the Mississippi area, predominantly Nuttall *(Quercus nuttalii),* Shumard *(Q. shwnardii),* cherrybark *(Q. falcata),* and water oak *(Q. nigra).* They reported that, "squirrels and chipmunks" were the greatest deterrent to direct seeding. Knudsen (1987:40) concluded that house mice *(Mus musculus)* and California voles *(Microtus californicus)* were the primary small-rodent predators on planted valley oak acorns in his Sutter County, California, study area.

SEEDLING MORTALITY SOURCES

Damage to oak seedlings by birds is not a common occurrence. Verner (1980) listed 110 breeding bird species associated with oak habitats in California. None were reported to consume seedlings, although he noted that band-tailed pigeons *(Columba fasciata)* had been reported to consume new leaf buds, and pine siskins *(Carduelis pinus)* had been reported to consume "foliage." Black-headed grosbeaks *(Pheucticus melanocephalus)* eat oak catkins. However, Verner noted that 35 species of birds eat foliage insects, and 11 species of birds consume bark or wood insects. Knudsen (1987:41) reported scrub jays pulling on valley oak seedlings on 2 occasions.

The Heritage Oaks Committee (1976:56) wrote that, "gophers, jack rabbits [sic], pets, human foot steps and other hazards must be kept away from the little oak trees." Hannah (1987) noted that eastern oaks (in general) have the ability to persist despite browsing, because of their sprouting potential, but that sprouts may be even more desirable (as deer browse) than unbrowsed seedlings. He stated that current-year shoot growth on oaks was highly preferred by deer, and that rabbits also browsed twigs and stems. Hannah speculated that high deer populations were "...one of the principal hindrances to revegetation of the preferred hardwoods including oaks." (p. 98). He added that even when oaks are at low densities and well mixed with other species, they experience "intense" browse pressure because of the preference deer and rabbits have for oaks. Barrett (1980:276) noted that voles, pocket gophers, and deer all forage on the leaves and twigs of oaks, "...especially young seedlings." Bowyer and Bleich (1980) found that California black oak seedlings in San Diego County, measured at a density of 6/ha in the spring, disappeared in early July in areas of heavy mule deer use.

Griffin (1980) pointed out that browsing by brush rabbits *(Sylvilagus bachmani)* contributed to the deaths of many valley oak seedlings in some of his plots. In 1 plot, after 5 seasons, 5 heavily browsed valley oak seedlings remained out of 320 planted, the tallest 7 cm. He noted that seedling supply seldom exceeds the capacity of rodent predators to eat them. At the Hastings Reservation, pocket gophers were identified as the major rodent mortality source. Griggs (1987) reported Engelmann oak seedlings up to 40 cm high were being killed by pocket gophers, but these events were rare.

Alfano (1980:182) observed 18.9-1 (5-gallon) container canyon live oak seedlings planted on a 4 ha site in Los Padres Forest, and reported that the roots "...provided succulent dinners for hundreds of ground squirrels in the area." In future plantings, roots were covered with a 2.5 cm wire mesh (dimensions unknown). However, if the roots were indeed damaged, the culprit was probably pocket gophers, not ground squirrels. Hickman and Caprile (1988) reported evidence that California voles were responsible for 80% mortality of planted valley oak seedlings in San Joaquin County.

Rossi (1980:12) reviewed literature on the impact of livestock on oak regeneration.

Barrett (1980:276) noted that, "the browsing domestic livestock and deer may be the most significant factor inhibiting the regeneration of oaks on California rangelands..." Duncan and Clawson (1980:308) concluded that, "there is no doubt that consumption of acorns by domestic livestock...reduces the number of acorns that might possibly become trees." Griggs (1987) recommended that managing cattle in Riverside County oak woodlands through timing of grazing was the most obvious mean of influencing the survival of Engelmann oak seedlings, since his observations indicated that cattle were not seeking out the seedlings as food as much as eating them because they were mixed in with the grasses.

While surveying oak regeneration in California, Muick and Bartolome (1987:89) determined that no significant relationship between livestock grazing and oak regeneration emerged. Martin (1987:109) summarized the impact of large vertebrates on hardwood regeneration. He noted that trees can be affected by consumption of seeds and by trampling and browsing seedlings, but that trampling may also provide a textured microclimate and the physical planting of seeds. McClaran (1987:358) reviewed the hypotheses associated with the impact of livestock and oak regeneration. Several authors had proposed that livestock browsing, acorn consumption, and trampling limit oak recruitment, while others suggest that livestock grazing favored successful recruitment of blue oak through a grazing regime which reduced herbaceous competition and lowered fire frequencies. McClaran sampled ungrazed, lightly grazed, and moderately grazed sites in Tulare County for blue oak regeneration. Age structure was negatively correlated with grazing (trees in ungrazed plots were older than those in lightly grazed plots, and trees in lightly grazed plots were older than those in moderately grazed plots). Seedling density was highest on lightly grazed plots. He concluded that no single event could assure recruitment and any number of factors could limit recruitment, and that successful blue oak establishment was more complicated than simply the presence or absence of livestock.

ACORN PROTECTION

Johnson and Krinard (1985) noted that no suitable repellent was available for squirrels and chipmunks for use during direct seeding of acorns. Williams and Hanks (1976) recommended hardware cloth (no size specified) as protection against seed pilfering by moles, chipmunks, and squirrels. McElwee (1970) pointed out that repellents, screens, and other protective measures had proven necessary in some instances and not in others, "...depending upon the size and tenacity of the rodent population" (p. 23). Tappeiner and McDonald (1980) recommended "...pinned-down cone screens..." to protect planted California black oak acorns "...from rodents, especially squirrels" (p. 109). They noted that protection from pocket gophers, deer, and cattle would aid in seedling establishment. Knudsen (1987:40) reported that a 1.3 cm galvanized hardware cloth, buried 1 m in the ground (extending aboveground an unknown distance) was hypothesized to have prevented rabbit and small rodent damage to valley oak acorns and seedlings.

McCreary and Schmidt (1989) and McCreary (1989) recommended using protective cages of aluminum screening to protect newly planted acorns. McCreary (1989) recommended a 46 X 46 cm aluminum screen formed into a 13 cm diameter cylinder and stapled to a 2.5 X 5 X 61 cm stake. The cylinder is folded closed at the top, and the stake is driven into the ground so that the screen cage covers the acorn.

Bush and Thompson (1989) described in detail the "collar and screen" technique for protecting oak tree acorns (and seedlings). They have planted thousands of oak trees with good success. The technique involves wrapping a piece of aluminum screening around a plastic, bottomless container (like a 0.9 1 [1 quart] cottage cheese container without a bottom). The acorn or seedling is planted inside the container, then the screen is wrapped around the top edge of the container, where it is attached with a piece of wire.

Williams and Hanks (1976) suggested hardware cloth screens as protection from seed-eating birds in nursery environments.

SEEDLING PROTECTION

Since avian damage to seedlings is rare, protective strategies for preventing bird damage have not been developed. As for acorns, caging seedlings to keep out rodents probably serves as a barrier for birds also.

Williams and Hanks (1976) recommended that a 3 m high fence might be necessary to prevent white-tailed deer *(Odocoileus virginianus)* damage to oaks in nurseries (and presumably out-plantings). They noted that rabbits could be excluded with a 1.8 m high fence with a 2.5-5 cm mesh, or they could be trapped or shot. Pocket gophers (presumably *Geomys* spp.) could be trapped or killed with poison bait, and they noted that controls were most effective during the spring and fall when gophers were most active. Finally, they reported that "mice" could be trapped or poisoned.

Utilizing rigid mesh plastic protectors, Adams et al. (1987) increased survival of valley and blue oak seedlings from 1/3 to 13 times that without protection. At these locations, they identified problem animals as jackrabbits, cottontail rabbits, squirrels, and pocket gophers. They noted that the rigid mesh plastic protectors were not effective against pocket gophers.

Pancheco (1987:146) reviewed the success of 2 valley oak planting operations in the Santa Monica Mountains National Recreation Area. They initially used an aboveground protective cage made of 2.5 cm poultry wire, plus an underground "pocket" made of 1.3 cm aviary mesh. The upper cage was held in place with a heavy gauge wire formed in a "U" shape. This procedure seemed to work well for small browsers, but cattle readily pushed the screens over and damaged the seedlings. The second planting operation used a similar screen except that the upper cage was extended downward so it could be buried 2 cm or so below the surface or held down with rocks. Cattle were not present at this site. Pancheco noted that damage from browsers to both sites was high, and that many of the surviving seedlings had multiple stems.

Many of the caging techniques listed above for protecting acorns from predation are also effective for protecting seedlings. The Heritage Oaks Committee (1976:56) reported that permanent fences would be needed in the presence of grazing animals. New developments in protecting seedlings include a rigid, semi-translucent plastic tube of varying diameters and heights (Tubex Treeshelter, St. Paul, MN), and a low-cost, pre-fabricated tent made of plastic mesh with a metal support wicket (Hopland Tent, Quadel Industries, Coos Bay, OR).

Selection of a proper caging or fencing design depends on a variety of economic and biological considerations. Economic considerations include the cost of labor and materials for installation, maintenance, and disposal. Biological considerations include how long a seedling needs to be protected (rate of tree growth), how caging is effective for a variety of vertebrate mortality factors, and tree growth response within fencing or caging. There is evidence that some types of cages actually enhance tree growth (Costello et al. 1991). Enhanced growth would be useful in shortening the period in which seedlings, by nature of their size, are vulnerable to severe vertebrate herbivory. In northern California, trees remain within the reach of black-tailed deer and sheep until the trees exceed 150 cm in height (Fig. 1). Note the variation between sheep and deer, and between blue oak and live oak. Blue oak, being a preferred browse species (Longhurst et al. 1979), requires more protection than does interior live oak.

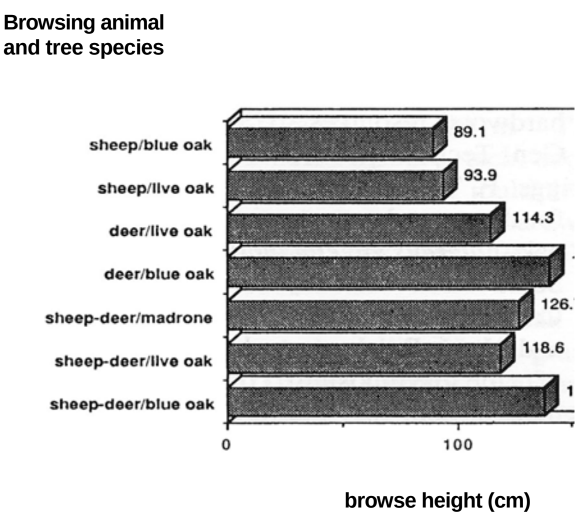

Fig. 1. Mean browse line heights with black-tailed deer and sheep in Mendocino County, California, for blue oak, interior live oak, and madrone. Trees measured had very distinct browse lines, and each tree was measured at 4 locations spaced equally around the perimeter of the canopy's drip line. Number of trees sampled for each treatment ranged from 4 to 20.

General references on controlling damage from rodents and larger browsing animals to oaks, agricultural crops, and structures include Timm (1983) and Clark (1986). Most articles on animal damage management in California can be found in the 14 volumes of the *Proceedings of the Vertebrate Pest Conference.* Although none of these articles are written explicitly for oak regeneration, many of the animal management tools have applicability to protection of acorns and seedlings from mammals and birds.

CONCLUSIONS

This review makes it clear that any serious revegetation program for oaks must incorporate planning, resources, and commitment to preventing insect, bird, and mammal damage to planted acorns and seedlings. This input must persist beyond the first 1 or 2 years. There are a number of areas that this review found data lacking, however. These include:

- comparative efficacy of alternative screening mechanisms
- data on the cost-effectiveness of damage prevention programs
- accurate and specific identification of insect, bird, or mammal involved in damage
- specific details of damage mechanisms
- species-specific responses to varying degrees of damage from different agents
- benefits of insects, birds, and mammals in reducing competition, and through their planting activities

In addition, there were numerous unsubstantiated claims of protection without adequate controls, and identification of damage vectors based on presence at a site, not on actual observation or experimental manipulation. In short, although we can recognize that damage factors must be considered, the level of sophistication in understanding damage processes and in refining damage control systems is low.

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