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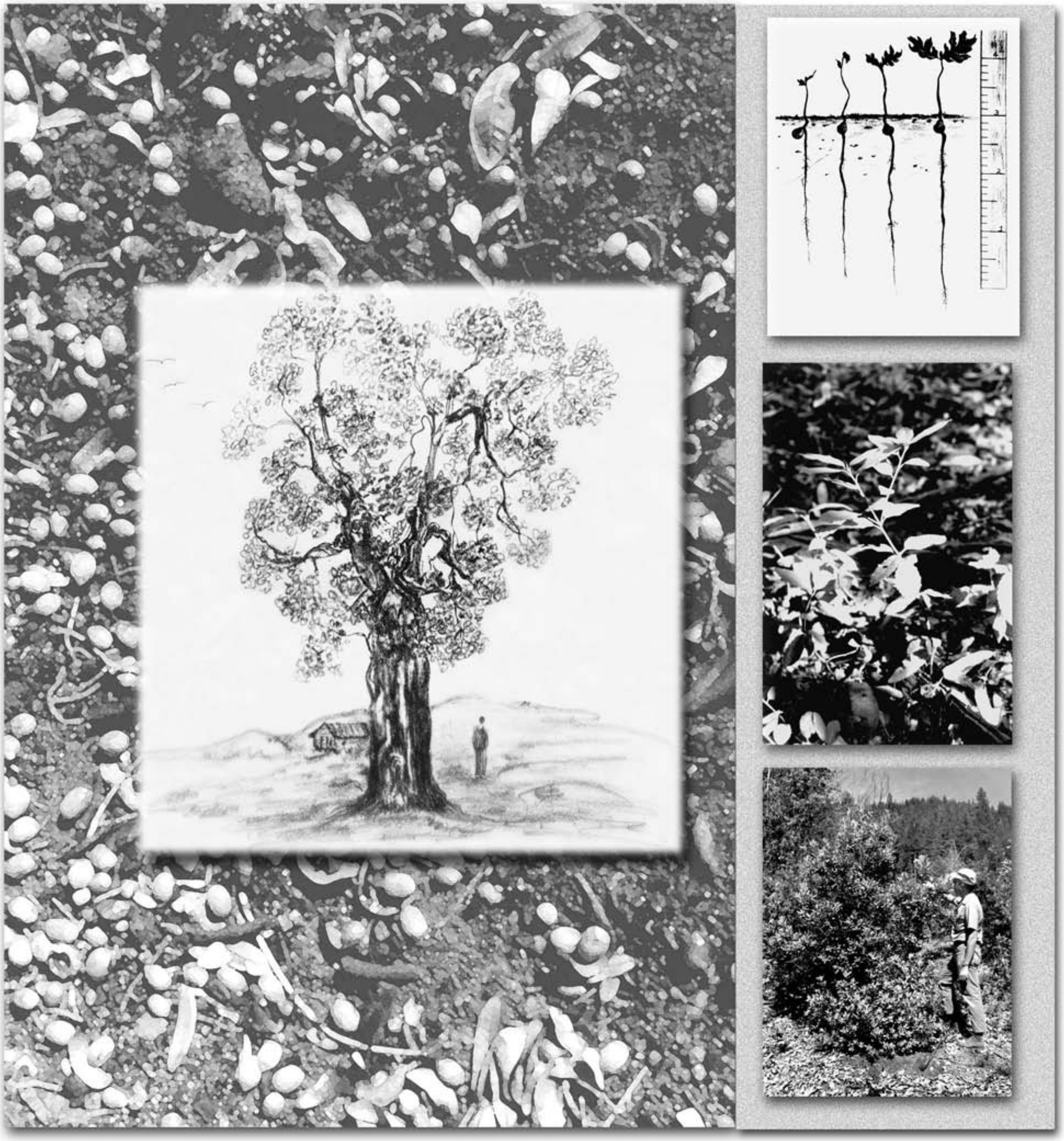
PSW-GTR-185

California's Hardwood Resource: Seeds, Seedlings, and Sprouts of Three Important Forest-Zone Species

Philip M. McDonald **John C. Tappeiner, II**



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Abstract

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Although California black oak, tanoak, and Pacific madrone are the principal hardwood species in the forest zone of California and Oregon and are key components of many plant communities, their seed production, regeneration, and early growth requirements have received little study. Information is presented on seed production, storage, and germination, and on the density, survival, and growth of three types of hardwood reproduction: seedlings, seedling-sprouts, and root-crown sprouts. Many trials showed that establishing planted seedlings in conventional sunlit plantations is difficult. Although initial stocking levels were high, height growth was poor. Dieback and death were common. Application of fertilizer and water and concomitant foliar analysis and tests of xylem sap tension indicated that internal moisture levels were inadequate to sustain seedling height growth. Thus, manipulating seedling-sprouts and root-crown sprouts currently are the silviculturist's best techniques for establishing new stands. On a good site, root-crown sprouts of California black oak and tanoak were 20 feet tall in 10 years and those of Pacific madrone were 22 feet tall in the same time span. However, more information is needed on overstory-understory relationships for promoting the growth of seedling-sprouts and more knowledge is needed on clump density and thinning regimes for root-crown sprouts.

Retrieval Terms: California black oak, ecology, growth, Pacific madrone, regeneration, tanoak, vegetative propagation

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In Brief . . .

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California black oak, tanoak, and Pacific madrone are California's most widespread and most valuable forest-zone hardwoods. They are found throughout California and in part of Oregon and grow from near sea level to the 7,500-foot elevation. They occur as pure hardwood stands, as components of mixed hardwood and conifer stands, and as occasional trees, clumps, and groves within the conifer forest. Their ecosystems are both numerous and complex. More than 300 species of wildlife use these hardwood-dominated habitats for reproduction, many people enjoy the contrast and beauty of these hardwoods in spring and fall, and many acre-feet of water originate in the hardwood forest.

In spite of their recognized value as habitats and important components of ecosystems, these hardwood species are scarcely utilized and virtually unmanaged. Currently, the best "management" they receive is not cutting them. In some areas, these species have been eliminated in favor of other species or uses, and managers now want to reestablish them. In other areas, the old trees that are present have lost their ability to sprout, and seedlings are not present to replace them. In still other areas, small seedlings are plentiful, but never seem to grow larger. Plainly, silviculturists need to know how to successfully regenerate the hardwood forest. More specifically, they need to be able to secure regeneration, however initiated, that will be reliable and consistent and that will rapidly grow and become trees. This paper presents what is known on the reproductive silviculture of California black oak, tanoak, and Pacific madrone in the forest-zone of California and southwest Oregon.

California black oak, tanoak, and Pacific madrone regenerate via three reproductive modes to form seedlings, seedling-sprouts, and root-crown sprouts. Seedlings, like their name suggests, originate from seed and their tops have never died back to the root crown (burl); seedling-sprouts also originate from seed, but their tops have died back and sprouted from small burls at least once; root-crown sprouts originate from larger burls on top-killed trees, and although they die, they seldom die back. Each reproductive type is unique, and the individual seedlings, single sprout stems, or multiple sprout stems develop differently and have different growth potentials.

Although we present information on seed production, storage, germination, and direct seeding, we collected even more information on the three types of reproduction. In general, where a seed source is present, the seedlings of each of these three species can number 1,000 or more per acre. Some remain as single stems, but many die back one or more times, depending on the amount of light and other factors, to become seedling-sprouts. Populations of seedling-sprouts beneath tree crowns constitute an in-place resource that can be managed to form new stands. Research is needed on manipulating the overstory and in thinning the number of seedling-sprouts to provide adequate site resources for enhanced growth. Root-crown sprouts, which benefit from existing portions of parent-tree root systems, are another established resource that can be manipulated to form stands of these hardwood species. Much is known on root-crown sprout density, number per stump, and growth rates in various environments. Equations are available for projecting this information.

Artificial regeneration with planted seedlings is a reproduction mode that needs more work. Although some research has been done in conventional sunlit plantations, and results from trials with fertilizer, water, and shading are available, knowledge on seedling growth in partially shaded plantations is needed.

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The Forest Service, U.S. Department of Agriculture, is responsible for Federal Leadership in forestry. It carries out this role through four main activities:

- Protection and management of resources on 191 million acres of National Forest System lands;
- Cooperation with State and local governments, forest industries, and private landowners to help protect and manage non-Federal forest and associated range and watershed lands;
- Participation with other agencies in human resource and community assistance programs to improve living conditions in rural areas; and
- Research on all aspects of forestry, rangeland management, and forest resources utilization.

The Pacific Southwest Research Station

- Represents the research branch of the Forest Service in California, Hawaii, American Samoa, and the western Pacific.

Introduction

In 1992, a series of publications was initiated on California's hardwood resource in the forest zone. In the first publication, Huber and McDonald (1992) began by detailing the history of use for three species of economically important hardwoods, especially for wood and wood products, and presented 22 reasons why the industry had not been sustained. In a second publication, they followed the progress of the industry and cautiously suggested that a viable wood processing industry was possible in the near future (McDonald and Huber 1994). By developing this industry, demand for products from the hardwood forest would be created, which would lead to active management of the resource. McDonald and Huber (1994) also recognized that wood products were just one of four major "yields" from the land and that wildlife, water, and pleasing scenery were currently more valuable than wood products. This led to an ecosystem management perspective that was followed a year later by a philosophy and guidelines for managing for these four yields in the general forest zone, as well as in an agroforestry and urban interface setting (McDonald and Huber 1995). These three publications (Huber and McDonald 1992; McDonald and Huber 1994, 1995) provided an overview and framework for managing California hardwoods, but lacked specifics on the reproductive biology and silvicultural practices necessary for regenerating the stands. This paper addresses these specifics and as such constitutes the fourth volume of the series on hardwoods.

Native hardwoods in the forest zone of California's mountains constitute a major resource that currently has great potential, but about which critical information is absent or fragmented. In old-growth stands, the hardwoods are decadent and dying, but little regeneration is present to replace them. In some locales, acorns and berries fall by the thousands, but seedlings do not result. In other areas, small hardwoods seem to always be present, but they never grow larger. In still other areas, planted hardwood seedlings either die outright or die back again and again and never become trees. Plainly, more information is needed on the establishment and development of early hardwood stands.

Unfortunately, research on the reproduction of forest-zone hardwoods in the mountains of California is scant. When knowledge from research in the foothill-woodland zone of California and the Cascade Mountains of southwestern Oregon is included, several gaps are filled, but the overall research base remains small. Most of the work has been concentrated at a few locations where trials have been mostly case histories. While most of the major components of hardwood reproduction have been studied, they have not been examined in depth. However, studies in both California and Oregon, where replicated, have shown similar trends. Furthermore, findings on western species of *Quercus* show similarity in several areas to findings on related species of *Quercus* in the northern and central United States. Thus, the silvicultural concepts and principles examined in this paper are supported by previous studies, but the data are unreplicated and site-specific in many instances.

The objectives of this paper are to bring together available information on the full spectrum for regenerating selected native California hardwoods, including information on seed production, the gathering and storing of acorns and berries, natural seedlings and seedling-sprouts, the survival and growth of artificially reproduced seedlings, and the density and development of root-crown sprouts.

Species, Occurrence, and Physical Environment

The indigenous hardwoods of California can be divided into two major groups: those that grow in the forest-zone at higher elevations, and those that grow in the foothills and woodlands at lower elevations. Red alder (*Alnus rubra* Bong.), which grows best at low elevations along California's north coast, is a separate, but relatively minor group. Although data from hardwood species at lower elevations in California or from other States are included to support a point or illustrate a technique, only those species that grow in the forest zone, primarily on upland sites, are discussed in this paper. In addition, only the three species that are the best studied, most abundant, and have a fairly large natural range, are presented. These are California black oak (*Quercus kelloggii* Newb.), which is a member of the red oak subsection of *Quercus;* tanoak (*Lithocarpus densiflorus* [Hook. & Arn.] Rehd.), which is not a true oak, but considered to be intermediate between the chestnuts *(Castanea*) and the oaks (*Quercus*) (McMinn 1939); and Pacific madrone (*Arbutus menziesii* Pursh) (*fig. 1*). Black oak is deciduous and tanoak and Pacific madrone are evergreen. All three species have an established history of utilization for wood products and other yields (Economic Development Administration 1968) and as food and raw material for people (Wolf 1945), especially Native-Americans (Baumhoff 1963).

Other forest-zone hardwood species that have a wide distribution or are locally abundant are canyon live oak (*Quercus chrysolepis* Liebm.), bigleaf maple (*Acer macrophyllum* Pursh), and giant chinkapin (*Castanopsis chrysophylla* [Dougl.] A. DC.). Although potentially important, little is known about their reproduction, and they are not covered in depth in this paper.

The north-south range of California black oak is about 780 miles (McDonald 1990). In Oregon it is found directly north of Eugene and southward along the lower slopes of the Klamath and Cascade Mountains. In California, black oak is present in the northern Coast Range from the Oregon State line to Marin County and then intermittently to the Santa Cruz and Santa Lucia Mountains. In southern California, the species becomes more common in the San Bernardino, San Jacinto, and Agua Tibia Mountains, extending a little south of Mt. Laguna. At least one small stand has been found in Baja California (Rodriguez 1987). In California's Sierra Nevada, this oak grows abundantly along the west side from south of Lassen Peak to near Kings Canyon. California black oak then becomes intermittent southward to the Tehachapi Mountains, where it again increases in abundance. A few stands also are found along the east side of the Sierra Nevada range.

Other than a disjunct stand north of the Umpqua River in southwestern Oregon, the general northern limit of tanoak is farther south in the Coquille River drainage (Tappeiner and others 1990). This species then extends southward to the California State line. Its eastern limit in Oregon extends from west of Roseburg to Grants Pass and then southwesterly into the Applegate River drainage. In California, tanoak extends southward in the Coast Ranges to the Santa Ynez Mountains northeast of Santa Barbara. Its range also extends northeastward from the Humboldt Bay region to the lower slopes of Mount Shasta, then intermittently southward along the western slopes of the Sierra Nevada as far as Mariposa County.

Pacific madrone ranges from the east coast of Vancouver Island and the immediate mainland of British Columbia southward to near Palomar Mountain in San Diego County, California—a north-south distance of about 1,170 miles (McDonald and Tappeiner 1990). The species is common along the western slopes of the Coast Ranges in Washington, Oregon, and California, southward to San Luis Obispo County, California. It is abundant throughout much of the Klamath Mountains of Oregon and California, and from Yuba County, California southward through Calaveras County in the Sierra Nevada.

Figure 1—Well developed trees of California black oak (A), tanoak (B), and Pacific madrone (C) in northern and central California.

The physical environment where California black oak, tanoak, and Pacific madrone reside is best described as moderate and variable. Within their natural ranges, all three species are found in a fairly broad range of slopes, aspects, elevations, soils, temperatures, and amounts of precipitation. Growth is best in areas having deep, well drained soils, moderate slopes, and a growing season of 200 days or more. Rarely are these species found in areas having less than 15 inches of annual precipitation, poorly drained soils, or a growing season of less than 100 days. Tanoak has more restrictive site requirements than California black oak or Pacific madrone. In general, it is found in more moist environments such as areas of frequent fog, high relative humidity, and high annual precipitation. Tanoak foliage also is damaged from sudden exposure to bright sunlight, and the crowns of recently exposed trees will steadily die back to a point on the bole where they receive shade. Of the three species, California black oak has the widest elevational range (200 to 8,000 feet), Pacific madrone the narrowest (0 to 4,700 feet), and tanoak intermediate (0 to 6,500 feet).

These hardwood species, either alone or together, seldom occupy entire mountain sides. Most often they are found as single trees, in clumps or groves, or occupying a given aspect in areas of up to 100 acres. Exceptions can occur, however, where extensive cutting and burning of conifer associates has allowed hardwood species to dominate over much larger areas. Each of these species seldom grows in pure stands, and rarely are the three species found growing together. Tanoak, Pacific madrone, and California black oak are most commonly found as associates in the northern Sierra Nevada. Black oak and canyon live oak sometimes intermingle on poorer sites throughout their range. Both California black oak and tanoak have a shrub form that grows on poorer sites and extends the species natural range to higher elevations. Shrub tanoak (*Lithocarpus densiflorus* var. *echinoides*), whose form is stunted and upright, is found in this environment. However, another form, which is not upright and sprawls along the ground, is found on above-average sites in the northern Sierra Nevada (McDonald [In press]). Although it never becomes a tree, it is not recognized as a variety.

The three hardwoods in this paper are rarely found without conifer associates. In the Coast Ranges, the most common associates are Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), redwood (*Sequoia sempervirens* [D. Don] Endl.), and western hemlock (*Tsuga heterophylla* [Raf.] Sarg.). In the Klamath Mountains and northern Sierra Nevada, Douglas-fir is an important species. In the Sierra Nevada and southern California ranges, ponderosa pine (*Pinus ponderosa* Dougl. ex Laws var. *ponderosa*), is most common, with California white fir (*Abies concolor* var. *lowiana* [Gord.] Lemm.), incense-cedar (*Libocedrus decurrens* Torr.), and sugar pine (*Pinus lambertiana* Dougl.) less abundant.

Shrub species that associate with these hardwoods tend to be few and to vary inversely in species richness, density, and cover with overstory tree density. Some common shrub genera include *Adenostoma, Arctostaphylos, Castanopsis, Ceanothus*, *Chamaebatia, Corylus, Prunus, Rhamnus,* and *Toxicodendron*. Forbs and grasses, like the shrubs, vary tremendously beneath the hardwoods. They can be almost totally absent in the shade beneath dense stands or quite diverse and abundant in more open stands.

Adaption and Ecology

Through natural selection (Chaney 1925), California black oak, tanoak, and Pacific madrone have been adjusting to major and minor changes in their environment for millions of years. The fossil record reveals that they have lineage to the Mascall flora of the Miocene epoch of 12 to 26 million years ago. Consequently, they have survived such major geologic events as glaciation, volcanism, upthrusting, and subsidence.

Figure 2—Rapidly growing root-crown sprouts of tanoak give the species a strong presence after a forest fire, northern California.

Specifically, they are well adapted to a broad range of biotic agents and abiotic events (Cooper 1922, Keeley 1977, Kummerow 1973, Mooney and Dunn 1970). The adaptations are both morphological and physiological. Morphological features include special structures and coatings on leaves and stems to inhibit moisture loss, smooth upper-stem bark to facilitate the transport of water to the base of the tree via stem flow, a deep and extensive root system, capability to form a burl at an early age, and capacity to produce both an enormous amount of seed and large numbers of rapidly-growing root-crown sprouts (*fig. 2*). Physiological processes involve photosynthesis, transpiration, and respiration, which govern plant metabolism, energy intake, water losses, and eventually dominance potential (McDonald 1982). Photosynthesis can take place at low internal moisture levels and may provide an energy input. It also can happen quickly after the onset of favorable conditions. For example, positive net photosynthesis can occur early in the morning of a hot summer day and, even if for an hour, contributes to the plant's well being at an opportune time.

In a study on the internal water relationships of young tanoaks, Hanson (1977) noted the presence of "an internal controlling mechanism" that responded to environmental factors and served to "make tensions less negative to maintain the survival of the seedling." Mooney and Dunn (1970) called this mechanism a "fail-safe" for lowering respiration when internal moisture levels are low and internal temperatures are high. Being able to internally monitor and control respiration keeps the plant from using all its energy reserves during the hot, dry, windy days of summer. A major limitation to the dominance of these forest-zone hardwood species, however, is tree height. None of these hardwoods grow as tall as their conifer associates. Because of their shorter stature, the hardwoods need periodic disturbance to retain their place in the stand. As Atzet and Martin (1992) noted: "Disturbance brings change that helps maintain compositional, structural, and functional diversity, helps to select adapted, resilient individuals, and helps to dampen the effects of minor environmental oscillations and extremes. Change is an essential ingredient of healthy ecosystems" (p. 40). These hardwoods depend primarily on fire, logging, blow-down, insect devastation, or mass soil movement to provide the disturbed and temporarily vegetation-free ground needed for establishment and growth (McDonald and others 1983).

The size and intensity of the disturbance affects the amount and growth of the ensuing reproduction. Natural mortality of California black oak, tanoak, and Pacific madrone most often consists of the death of single trees or perhaps the death of a clump of trees, rather than the death of a stand. With a low level of disturbance, many seedlings of all three species die and others die back and sprout. Growth tends to be slow. With moderate disturbance like that from a ground fire, which typically involves a larger area and a more intense form of damage, some trees suffer topkill and sprout from the root crown. Most of the seedlings on the forest floor either are killed or put forth a few sprouts from a rudimentary burl. Many of these will die because the growth rate of sprouts from the topkilled trees is much greater than that of the sprouted seedlings. With heavy disturbance over larger areas, like that from a crown fire, the primary reproduction mode is sprouting from the top-killed trees. These root-crown sprouts grow vigorously and deny site resources to the seedlings that originated from rudimentary burls.

From the standpoint of reproduction, fire can be a blessing for black oak, tanoak, and Pacific madrone. It creates the necessary growing space and site resources by killing competing conifers, shrubs, and other vegetation. Capability to sprout and sprout vigor are valuable attributes in this regard.

Although disturbance is necessary for the establishment of reproduction, hardwood stands generally are resistant to further disturbance, particularly from fire. The green leaves of hardwoods do not burn readily, and crown fires have been noted again and again to drop to the ground beneath hardwood canopies. Characteristically dense shade and low humidity then keep the fire on the ground. Even ground fires are of low intensity in California black oak stands, because the leaves decompose rapidly and little debris is present to carry fire.

Animals also are more of a blessing than a curse for young hardwoods, although at times browsing and seed consumption can be severe. The two reproductive modes (sprouts and seeds) of California black oak, tanoak, and Pacific madrone serve the species well. Sprouts keep the species in place; seeds, through the action of disseminators, allow the species to expand to new areas. Birds, bears, rodents, deer, and a host of other animals both consume and distribute the acorns and berries of these hardwoods. Grinnell (1936) noted “It is not extravagance, but good investment for the oaks to provide subsistence for a continuing population of animal associates.”

Insects and diseases, although almost always present, rarely have a major impact on the seedlings and sprouts of these hardwoods. For example, total defoliation of black oaks in northern California by the fruit-tree leaf roller occurred in April to May 1968, but evidence of the attack could scarcely be found by mid-July (McDonald 1969). Shoestring root disease (*Armillaria* spp.) is endemic on the roots of California black oak trees, but kills them only when they are old or weak. The length of root-crown sprouts of California black oak did not differ significantly among trees with or without heartrot (Garrison and others 2000). However, an unknown species of *Phytophthora* termed “sudden oak death phytophthora” has recently been killing mature, healthy trees in six coastal counties in northern California (Kliejunas 2000). To date, the species affected are tanoak, California black oak, and coast live oak (*Quercus agrifolia* Neé).

Seeds

In this part of the paper, we present information not only on the traditional categories of seed production, storage, and germination, but also on direct seeding and, more specifically, on the fate of acorns and berries and the effect of acorn position on germination and number of surviving seedlings. The seedlings that result from direct seeding are discussed in terms of early survival and cause of mortality. Growth and subsequent survival are presented in the section on artificial regeneration.

Seed Production

California black oak and tanoak acorns mature the second year (*figs. 3, 4*); Pacific madrone, berries mature at the end of a single growing season (*fig. 5*). Acorns are borne singly, or in clusters of two to four, rarely five or more. Madrone berries are borne on racemes having up to 60 berries on each.

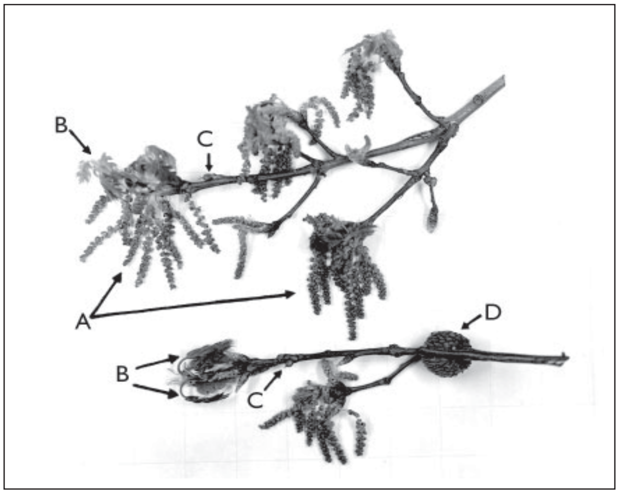

Figure 3—Reproductive anatomy of California black oak in early spring (A) pollen flowers, (B) young leaves, (C) small 1-year-old acorns, and (D) cup of mature acorn that fell a few months earlier.

Figure 4—Branches of tanoak showing leaves, cups, and mature acorns.

Figure 5—Twig of Pacific madrone showing leaves and cluster of berries.

The size of seed crops and the factors governing seed production are not well understood. Site quality, tree size and vigor, position in the stand, abortion, and weather, all play a role. In general, the better the site quality, the more resources will be available for tree functions, including the production of seed. Concomitantly, larger and more vigorous trees will have more branches, more loci on which acorns and berries can be produced, and more energy to commit to reproductive material. The position of the tree in the stand and the exposure of the crown to light have also been observed to affect the amount of reproductive material. Several observers have noted that weather at the time of flowering is important, probably because of its effect on pollinators. Warm, dry weather encourages pollinators and eventually the production of acorns and berries, and cold, wet weather discourages them.

Abortion of tiny black oak and tanoak acorns the first year is a common observation, and has been noted as being more severe during drought years than in years of plentiful moisture—suggesting that balancing the trees' resources with the acorn crop is probably necessary. Obviously, fewer fully developed acorns are better than many substandard acorns. For Pacific madrone, the number of racemes and the number of berries per raceme have been noted to vary, but the variables and processes that govern development, and ultimately the number of mature berries, are unknown.

Age at the onset of seed production for California black oak and tanoak has been reported as early as 5 years on vigorous root-crown sprouts in clearcuttings. However, acorn production is generally lacking until age 30 or 40 (Tappeiner and others 1990). After age 40, acorn production for tanoak increases rapidly, but it is not until age 80 to 100 that acorns are produced in large quantities on California black oaks (McDonald 1990). The age at which Pacific madrone first produces berries is reported as 3 to 5 years (Roy 1974). Sixty-two berries were counted on a vigorous 4-year-old root-crown sprout on a productive site (McDonald 1978). Number of seed per madrone berry ranged from 2 to 37, averaging 20 in one test (McDonald 1978) and from 7 to 44 in another test (Harrington and others 1998). The production of seeds is highly variable for all three species. Some trees produce seeds almost every year, although others of similar size and crown nearby rarely produce any. Genetics obviously is a factor that governs the periodicity and magnitude of acorn and berry crops. In general, large, vigorous trees of all three species, 100 to 200 years old, with well developed crowns, consistently produce the most acorns and berries.

The periodicity of seed crops is quite variable and depends more on local conditions than on regional ones. For example, one study reported that abundant seed crops of California black oak were produced at 2- to 3-year intervals (Roy 1962). At the 2,500-foot elevation on the Challenge Experimental Forest in the northern Sierra Nevada, medium to heavy black oak seed crops were produced in 4 of 20 years. At the 2,800-foot elevation in south-central Shasta County, medium to heavy seed crops were borne on large trees in 4 of 8 years. At the 560-foot elevation in Shasta County, black oaks yielded sound acorns in 6 of 7 years. Of these, two each rated as heavy, medium, and light (McDonald 1990). In central-coastal California above the 2,500 foot elevation, Koenig and Knops (1995) recorded five above-average acorn crops for California black oak during the 1980-1994 period.

Guides for estimating acorn crops by visual surveys are available (Garrison and others 1998b, Graves 1980, Koenig and others 1994). A general age-tree size-acorn yield relationship for a medium seed crop of California black oak on an above-average site is available (*table 1*) (McDonald 1969, U.S. Forest Service 1973).

Tanoak on the Challenge Experimental Forest in northern California, produced four medium-heavy and nine light to very light seed crops from 1958-1981. During the same period, Pacific madrone yielded 2 medium-heavy

Table 1—*Seed production of California black oak by age and size of tree for a medium seed crop on a high-quality site, northern California.*

Age	Breast-height diameter	Crown diameter	Acorn yield
yrs	inches	ft	lbs
30	5	15	0
50	9	20	5
80	13	26	20
100	17	32	60
150	24	41	100
200	32	52	140

and 10 light to very light seed crops (McDonald 1992). The fecundity of the hardwood species, as indicated by individual trees, is amazing. In Trinity County, California, Roy (1957) recorded the number of tanoak acorns under 18- to 24-inch diameter (dbh) tanoak trees during a good seed year. More than 78,000 to almost 83,000 acorns per acre were produced; 49 percent were sound. A 16-inch dbh tanoak tree on the Challenge Experimental Forest had 1.1 million acorns per acre beneath it in a bumper seed year. The acorns were 79 percent sound (McDonald 1978). On the same site in a light seed year, a 15.7-inch d.b.h. Pacific madrone tree produced 107,640 berries or about 2.1 million seeds (McDonald 1978).

Storage and Germination

When gathering acorns for future propagation, it is important that they be ripe and sound. Mature acorns of both black oak and tanoak vary from dark tan to a rich chocolate brown. Warm, dry weather, usually with a north wind and low relative humidity, stimulates acorn fall. Under such conditions and a bumper crop, the forest fairly rains with fully ripe acorns. This is the time that they should be gathered, not before. Acorns that fall early tend to be unsound because of insects, immaturity, or internal problems, chiefly with the embryo. Insects, especially the filberworm (*Melissopus latiferreanus*) and the filbert weevil (*Curculio uniformis*) are particularly destructive. Relatively new evidence on an old technique may lessen their depredations. Many Native-American tribes "frequently burned under the black oaks to decrease this pest" (weevils) (Anderson 1992). Skinner (1981) noted that a prescribed burn in northern California in March resulted in a bumper crop of sound California black oak acorns while trees on unburned ground nearby bore only unsound acorns. Apparently, destructive insects in the duff and soil were reduced greatly by the burn.

Fully ripe acorns should be gathered from shady locations soon after they fall. Because moisture content is critical to acorn viability and they may have dried too much before they fell, rinsing or soaking acorns in water soon after gathering is recommended. Exposure often is deadly to acorns on the ground, and only a few hours of sunlight slanting beneath a tree crown can overheat and kill the embryos. Once the moisture content of acorns falls below 25 to 30 percent, the cotyledons, which comprise the bulk of the acorn and provide energy for the embryo, no longer are crisp, firm, and cream-colored. Instead, they become limp and dull with a tan-colored tinge. Later, the embryo becomes hard and the cotyledons spongy with a brownish hue. In one study, cotyledons of exposed California black oak acorns had withered to about one-half normal size nine days after falling (McDonald 1978). Freezing also kills the embryos in acorns that are not covered by leaves or other organic material. McDonald (1978) found that the cotyledons of frozen tanoak acorns were gray-black in the center with bright yellow, dry, and hard embryos. Although leaves often shield the acorn from freezing, they can create an environment where mold becomes a problem. A blue-gray mold often forms in the circular scar of the absent cup, penetrates the acorn, and destroys its contents. Jaeger (1920) reported that Native-Americans would gather only newly fallen acorns to avoid the mold.

Determining the soundness of newly-fallen black oak and tanoak acorns at the time of gathering is fairly easy. Because both species produce large, heavy acorns, and damaged and unsound acorns are much lighter, the latter can be discarded on the basis of weight. Interestingly, acorn weight and exit holes were the best indicators of insect damage to Native-Americans (Anderson 1992). An alternative technique for determining soundness is to place the acorns in a vat filled with water and discard those that float. Both tests eliminate most of the unsound acorns, but not all.

At least nine short-term storage trials (3 to 4 months) with acorns of black oak and tanoak in northern California produced variable results; some were fatal (McDonald 1978). Another trial in southern California attempted to store about 3,000 California black oak and canyon live oak acorns for about 6 months (Anonymous 1980). They were stored first in a cool shed and then in a refrigerator. Upon removal, the cotyledons were found to be severely dehydated, and all were discarded. Storage was more successful for both black oak and tanoak acorns if they were immediately placed in bags in a temperature-controlled refrigerator at 34 to 38˚F.

Low temperatures and moderate moisture contents are best for acorn storage and near-perfect for stratification. The breaking of dormancy, or after-ripening as it often is called, is not really necessary for the two species because some acorns will germinate without it. However, most propagators prefer to retard germination until spring and to compress it into as short a timespan as possible. Thus, in practice, both storage and stratification take place simultaneously.

Although some acorns of the red-oak subgenus, which includes California black oak, retain viability for 5 years in storage, storage for not longer than 2 to 3 years is recommended (Bonner and Vozzo 1987). The best storage method is one that maintains acorn moisture content above 30 percent, allows some gas exchange with the atmosphere, and keeps the temperature just above freezing. Because moisture content is critical, it should be monitored and a damp tissue or sponge placed in the bag if needed. Long-term storage trials for California black oak and tanoak are not known.

Probably the most reliable short-term storage and stratification technique for California black oak and tanoak acorns is burial on-site. After gathering, California black oak and tanoak acorns are put in wire baskets or similar containers and placed in shallow holes in the ground near the outplanting site. The containers are then covered with a layer of soil and 2 to 3 inches of duff and leaves and allowed to overwinter in the natural environment. They can easily be opened in early spring and the acorns checked for soundness. This is accomplished by observing the opening of the acorn at the pointed end and the presence of the radicle (tiny white root). This radicle, if allowed to extend beyond 1 inch, makes outplanting difficult; thus, acorns should be sown before this happens. These acorns, which have essentially germinated, almost always lead to seedlings and result in high stocking levels after planting.

Gathering madrone berries from the ground is rarely feasible. Most berries never reach the ground because they are consumed in the tree, or once on the ground, soon are devoured by a host of animals and insects. Colorful accounts of gorging by birds abound. Smith (1968) tells of a band-tailed pigeon (*Columba fasciata*) that ingested 111 berries—so many that it could not fly. Peattie (1953) noticed band-tailed pigeons devouring Pacific madrone berries, and remarked "... the madrone groves ring with the shots of their persecutors." Consequently, berries are collected from the tree either by knocking bunches off it with a long pole, pruning branches, or by falling the tree.

Several investigators have shown that the seed of Pacific madrone must be separated from the berry to facilitate storage and eventual germination (McDonald, 1978, Roy 1974). The berry can inhibit germination of the seed within, retard the emergence of the seedling, and aid the colonization of damping-off fungi. However, the berry may indirectly facilitate storage and germination of the seed. After passing through the digestive system of birds and other animals, the now-naked seed is in a better position to eventually produce a seedling. Harrington and others (1998) found that storing seed dried to 5.6 percent moisture content for 3 years in a sealed polypropylene jar at 3 to 5°C did not appreciably decrease seed germination. Longer-term storage has not been documented.

Seed of Pacific madrone need stratification in order to germinate. Early investigators (Emery 1964, Mirov and Kraebel 1937) recommended stratification in cool, moist conditions for 3 months. An extensive trial—involving four treatments: cool-moist, acid and cool-moist, heat and cool-moist, and heat, acid, and cool-moist stratification for 30, 60, 90, and 120 days—showed that a short time period was desirable for both completeness and timing (McDonald 1978). Should the plant propagator desire at least 90 percent of seed to germinate, cool-moist stratification for only 40 days is recommended.

Once the stratification requirement has been met, germination is prompt. Most seed germinate in a few days; most within a week if placed in a warm, moist environment (Harrington and others 1998).

Direct Seeding

Trials with directly seeded California black oak acorns took place on the Challenge Experimental Forest in northern California in 1966 and 1969. In both instances, the acorns were placed in conventional plantations characterized by full sunlight, bare mineral soil, and freedom from almost all understory plants, especially shrubs. The exposure was south on gently sloping ground. Acorns, sorted for soundness, were seeded in the fall, buried 1 to 2 inches deep in soil loosened by hand tools, and protected by wire-mesh screens.

Emergence began April 8 for the 146 seed spots in the 1966 trial and extended through July 8. Seventy-nine percent of acorns produced a seedling. Some were recorded as dead from drought by the end of summer, but most remained alive belowground and sprouted in the spring, usually with one stem. Survival in spring 1967 was 70 percent. A hard freeze in mid-April 1968 damaged recently emerged leaves and terminal buds, and killed some seedlings back to the root crown. These also sprouted, generally with one stem.

Emergence began April 18 in the 1969 trial, and involved 996 seed spots in eight blocks. It continued through October 9. Early emergers were frozen to groundline by heavy frosts on April 20 and April 30, but most subsequently sprouted with one stem. The long (174 days) emergence period was atypical. It was caused by severe winter storms that buried some acorns up to 4 inches deep and formed a hard crust on the soil surface. Thus, some seedlings emerged in the spring, some broke through in the summer, some finally emerged after the fall rains had softened the crust, and some held-over until the following spring. The hold-over "seedlings" were examined closely. In many, a small, irregular, knobby protrusion formed just below the soil crust and the seedling overwintered in this form. Most emerged by mid-May 1970. The hold-over seedlings were visually weaker and had skinny stems and small leaves. They also did not have the robust taproot development of their first-spring counterparts. Many died from drought. Peak stocking (number of spots having a living seedling) was 72 percent in summer 1970 and 67 percent at the end of the growing season.

For the early trials with direct-seeded tanoak acorns on the Challenge Experimental Forest, acorn position was of interest. From a monitoring and economic viewpoint, the ideal plantation is one where all outplanted spots have a seedling, and the time it takes for all the seedlings to emerge is as short as possible. The factor that governs this best is acorn position. An early definitive study on this subject was conducted by Molotkovskii (1955) in Russia. He found that reversing polarity resulted in higher germinative capacity (more seedlings per number sown), greater germinative energy (shorter time to peak germination), a decrease in time between planting and germination, increased seedling vigor, and straighter seedling stems. Reversing polarity is where the pointed end of the acorn is oriented pointed up, instead of down. Thus, the emerging radicle has to grow up and then curve downward. Molotkovskii speculated that the point-up position increased certain chemicals in the acorn that stimulated and speeded germination to overcome this obstacle.

The various positions serve to lengthen the germination period. In nature, acorns reside in all positions: some orient point up, some point down, but most rest on their sides or at a slight angle. This increases the odds that weather will be favorable and that consumers will be absent or miss some acorns during this period. To test the effect of acorn position on germination capacity and speed, 255 stratified black oak acorns were divided into equal lots of 85 and placed point-up, point-down, and on their sides (McDonald 1978). They were buried 0.5 inch in moist peat moss in deep flats in a controlled environment (water and temperature) in a greenhouse. Although total germination was rather poor, trends could be ascertained:

Variable	**Point up**	**Side**	**Point down**
Germinative capacity (percent by peak day)	95	46	62
Germinative energy (days)	34	34	47

On the basis of these results, a much larger test was performed. It involved 844 tanoak acorns seeded point up and 772 placed point down in a field test in northern California. Seeding took place from January 6 through February 11. New seedlings were recorded at 2-week intervals after emergence, which was first observed on April 17. A sharp freeze with a temperature minimum of 21°F occurred on April 20 followed by four successive days of below-freezing temperatures. All seedling with stems and leaves aboveground during this period turned black and died. Because no seedlings from point-down acorns had emerged, these were all from point-up acorns. Of those blackened, about 70 percent eventually sprouted from belowground with two to four stems. Acorns seeded point up germinated much faster than those placed point down. By April 29, 316 seedlings from point-up acorns were present before the first seedlings from point-down acorns began to emerge from the soil. Maximum germination was achieved by July 18 for acorns placed point up, but not until September 18 for those placed point down. Almost three times as many seedlings originated from acorns placed point up (McDonald 1978). Exhuming plantless seed spots where acorns had been placed point down revealed acorn after acorn to have germinated and put forth a short radicle that died before the epicotyl (tiny new shoot) reached the surface. Late germination almost always resulted in death from drought. By fall 1971 or after two growing seasons, seedlings from point-up acorns numbered 275 (31 percent); from point-down acorns, 65 seedlings (8 percent).

In an extensive study in southwestern Oregon, Tappeiner and others (1986) found that second-year survival of tanoak seedlings from sown and protected acorns in exposed clearcuttings and in young and old conifer stands ranged from 58 to 70 percent, and after 4 years to between 44 and 49 percent. Rodents were the primary cause of mortality followed by drought and root disease.

The only direct seeding trial with Pacific madrone that we could find took place in southwestern Oregon (Tappeiner and others 1986). It was an extensive trial involving 43,200 seeds, 90 percent sound, sown in lots of 200 seeds in exposed clearcuttings and in young and old conifer stands. Mortality began immediately after emergence, and on most plots was 100 percent after 1 year. Average survival at the end of the first summer was significantly lower ($p = 0.05$) in old stands (5 to 14 percent) and young stands (8 to 12 percent) than in clearcuttings (32 to 34 percent). At the end of the second year, survival ranged from less than 1 to 3 percent in the young and old stands, and in the clearcuttings after 2 and 3 years, it ranged from 5 to 12 percent. First-year survival in clearcuttings increased significantly if microsites were shaded. In all stands, mortality in order of significance was caused by drought, litterfall, damping-off fungi, invertebrates, and frost.

Whether in the bright sunlight of conventional plantations or as outplantings in partially shaded openings, acorns are at risk from consumers. Even acorns protected by pinned-down wire screens (*fig. 6*) are vulnerable to rodents. In a trial with black oak acorns on the Tahoe National Forest in northern California, Duer (1989) lost 287 seedlings out of 300 to western gray squirrels (*Scirus grisius*). He excavated the dead seedlings and found that the squirrels had dug under the seedlings, clipped the acorns, and consumed them. Obviously, the acorn still had some food value to the squirrels, even though a seedling had been produced. Clipping the acorns apparently deprived the seedlings of needed energy, and they died soon after. McDonald (1978) noticed that western gray squirrels would dig under wire screens to extract germinating tanoak acorns. Unsound acorns or those that germinated later were not touched. Apparently, a germinating acorn can be sensed by the squirrels. In four clearcuttings in southwestern Oregon, Tappeiner and others (1986) found that 99 percent of sown, but unprotected, tanoak acorns were lost to predation in three annual sowings.

Germinated acorns of California black oak and tanoak should be buried at least 2 inches deep to avoid consumption by herbivores, to avoid embryo death, and to give the radicle time to elongate before the epicotyl emerges aboveground. But even buried acorns need protection. Screens usually are cone- or pyramid-shaped and of 1/4-inch-mesh hardware cloth. They should extend into the soil at least 4 inches, more if pocket gophers (*Thomomys bottae*) are present, and be of equal height aboveground.

Figure 6—A typical wire screen and pin used to protect buried acorns.

Reproduction

Natural seedlings are those that originate directly from seed and have not died back and sprouted. Seedling-sprouts are defined as seedlings whose tops have died back and sprouted at least once. They are defined in this paper as originating from seedlings that are less than 2 inches in diameter at ground line when top-killed. Root-crown sprouts arise from stumps or trees larger than 2 inches in diameter at ground line whose tops have been killed. All three types of reproduction are often collectively termed "advance reproduction" in the literature. Because the three reproductive types have different silvical requirements and growth trajectories, they are considered to be unique and presented separately in this paper.

Natural Regeneration

The amount of energy available to seedlings from the seeds of black oak, tanoak, and Pacific madrone is a study in contrast. The large energy-rich acorn is sufficient to produce a seedling with a thick stem and well developed root system, whereas the tiny seed of Pacific madrone can produce only a small, tender-stemmed seedling with a much weaker root system.

The seed/seedling ratio of California black oak, tanoak, and Pacific madrone is best described as "many acorns and berries, but few seedlings." The proportion of seedlings to sound seed almost always is less than 1 percent. For example, the number of tanoak seedlings beneath five seed trees in Trinity County California averaged 264 per acre with an average acorn/seedling efficiency of 0.64 percent (Roy 1957). In southwest Oregon, only one tanoak seedling resulted from 156 sound acorns present after the Douglas-fir overstory had been removed (Tappeiner and others 1986). In central-coastal California, only one Pacific madrone seedling out of 100 was alive after 4 months (Pelton 1962).

Germination of California black oak acorns in the field is best described as being highly variable, scanty (Sudworth 1908), and high (95 percent) (Mirov and Kraebel 1937). The radicle, which is the first structure to emerge from the acorn, grows downward for 10 to 20 days before the epicotyl emerges from the soil. This strategy benefits the seedling in getting to and staying in available soil moisture and in minimizing transpirational loss. It also temporarily avoids damage or death from above-ground herbivores. During the first growing season, seedlings only 2- to 6-inches tall, may extend their taproots as deep as 30 inches (McDonald 1969). On the Sierra National Forest, the most vigorous of black oak seedlings had a taproot of 36 inches, many lateral roots (but none longer than 1 inch), and a shoot of about 12 inches after one growing season (Anonymous 1909). For tanoak, root length after one growing season is conservatively estimated to be several times that of shoot length (McDonald and Tappeiner 1987). Two-month-old Pacific madrone seedlings in a shaded, bare soil environment on a good site in northern California had a 1-inch shoot and a 2-inch root.[1]

A comprehensive study on the fate of emerging Pacific madrone seedlings in the Santa Cruz Mountains of central coastal California involved 276 seedlings in a shade environment and an equal number in a sun environment (Pelton 1962). Plots in the shade environment were described as densely shaded with heavy litter and moist mineral soil; sun plots were characterized as moderately open with thin litter, if any, and dry soil. By August 2, no seedlings in shade plots survived, and only 2 percent were alive in sun plots. Invertebrates, chiefly slugs, accounted for 29 percent of mortality. Drought associated with drying of the root tip while trying to penetrate the deep litter layer was 10 percent. Fungi, especially post-emergence damping-off and root decay types, accounted for 28

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[1] Unpublished data on file, Pacific Southwest Research Station, Redding, Calif.

percent of mortality and was more important in sun than in shade plots. Combinations of factors (root decay plus drought, for example) killed 23 percent. Rodents and litterfall constituted the remaining 9 percent of mortality.

Natural regeneration of California black oak and tanoak occurs most often and in larger numbers beneath the crowns of parent trees, with only scattered individuals found elsewhere. The typically deep litter and organic material found beneath large trees is not an impediment to the new seedling root, and the moisture held in the organic matter probably is an asset. For Pacific madrone, bare mineral soil in shade, and the almost complete absence of organic matter, is the preferred seedbed for seedling establishment. In northern California and to a lesser degree in southwestern Oregon, most natural seedlings of Pacific madrone are found in recently disturbed areas along road cuts or on bare mineral soil at the base of uprooted trees. Occasionally, they become established beneath woody shrubs or small trees in clearcuttings where shade is plentiful (McDonald and Tappeiner 1990). Partially cut areas that have been burned or bulldozed often provide the necessary shade and loose bare soil needed by Pacific madrone seedlings. Black oak and tanoak seedlings become established in this environment as well. In general, seedlings of all three species tend to have a clumpy distribution over the landscape resulting from gaps brought about by disturbance.

On the Challenge Experimental Forest in northern California, natural regeneration of hardwoods was evaluated from 1958 to 1968 in 15 compartments that were cut to shelterwood, seed-tree, and single-tree selection standards. Compartment size ranged from 6 to 38 acres. Soil disturbance, created by site preparation, ranged from heavy to slight. Although conifers predominated, 3 to 17 relatively small trees (less than 12 inches in breast-height diameter) of each hardwood species on each acre, were present. Seeds from these hardwoods, plus that disseminated by birds and rodents from other hardwood trees, comprised the seed source. The number of new California black oak seedlings ranged from 0 to 700 per acre per year during the 11-year period. In many cutting methods and for several years, seedlings were not found. Survival after 4 years ranged from 15 to 44 percent with the highest occurring in the single-tree selection compartments and the lowest in the seed-tree compartments (McDonald 1978). In these same blocks and for the same time span, the number of new tanoak seedlings ranged from 4 to 347 per acre each year in every cutting method. Survival after 4 years did not differ among cutting methods and averaged about 50 percent.

For Pacific madrone, new seedlings in these compartments and for roughly the same time span, except for 1961, numbered 0 to 550 per acre per year with many absences in years and cutting methods. Only a few seedlings became established. One huge seed crop in 1960 resulted in 4,083 new seedlings per acre in the shelterwood compartments, 3,917 per acre in the seed-tree areas, and 866 per acre in the single-tree selection compartments in 1961. Survival after 4 years ranged from 41 percent in the seed-tree and shelterwood cuttings to 3 percent in the single-tree selection compartments.

To augment these results, natural regeneration of the three hardwood species in this study was evaluated in a pure hardwood stand on the Challenge Experimental Forest. The stand was characterized by being undisturbed, having 3 to 4 inches of organic matter on the forest floor, and containing a good seed source for each species. The number of California black oak seedlings numbered 40 per acre; tanoak, 4,600; and Pacific madrone, 0 seedlings per acre (McDonald 1978).

Height growth of natural seedlings of all three species is slow. Except where deep shade forces a long skinny stem, shoot growth probably does not begin to accelerate until root capacity is extensive enough to obtain adequate moisture. This may take 6 or 7 years or longer. After initial shoot growth (2 to 6 inches for black oak, 2 to 8 inches for tanoak, and 1 to 2 inches for madrone), seedling growth is variable, but seldom exceeds 8 inches per year. Partial shade is the environment most conducive to growth. Growth of some seedlings, particularly those stressed by competition, never accelerates and these seedlings eventually die.

Seedling-sprouts

The strategy of becoming a seedling-sprout is to keep the species present until a better environment for growth occurs. An individual seedling may die back several times and produce one to seven new stems with the largest stem being the oldest. On the basis of scores of samples, Tappeiner and McDonald (1984) found no reliable relationship between the age and size of the above-ground stem and the total age of tanoak seedling-sprouts. However, the total age of seedling-sprouts can be ascertained quite accurately by counting the xylem rings in the stem below the burl.

Seedling-sprouts may persist for scores of years until fire or logging removes the overstory—freeing them to grow. California black oak, tanoak, and Pacific madrone all have seedling-sprout capability, but the use of this ability differs among species and between sun and shade environments. In order to sprout, dormant buds must be present, and to be present, a structure is necessary. This structure is the burl, which takes the form of a thickened rootstock in young seedling-sprouts, and becomes present just below groundline at a young age. In tanoak for example, seedlings that had emerged only 7 days before a heavy frost died back to groundline and sprouted with three to seven members per seedling (McDonald 1978). Two months later, 80 percent of frozen seedlings had become seedling-sprouts. None sprouted with a single stem. The conversion from seedlings to seedling-sprouts generally is a slow, steady process except when a fire or climatic event causes a pulse of them to occur. The build-up of seedling-sprouts, usually in the shade of the overstory, is the classic seedling-bank reproductive strategy (Grime 1979).

Because at least some food reserves are stored in the burl, seedling-sprouts have a better-than-average chance of outgrowing competing vegetation. They also can become saplings and eventually trees. In western Oregon, Fried and others (1988) studied the density and growth of bigleaf maple (*Acer macrophyllum* Pursh) seedlings in a range of ages and overstory canopy classes. The seedlings of this maple are similar to those of tanoak, which are found in aggregations, and form seedling banks. A major finding was that the maple seedlings eventually became trees, especially when the canopy was more open.

Of the three forest zone hardwoods in this paper, California black oak is intermediate in terms of frequency of becoming a seedling-sprout. A rudimentary burl develops on young seedlings, but precisely at what age is unknown. Observation suggests that it forms earlier and more frequently on poor sites and in shady environments. It is not nearly as likely to become a seedling-sprout in a sun environment as in a shade environment. In either environment, however, when it sprouts or resprouts, it almost always is with only one stem. In the shade environment, growth is very slow (*fig. 7*), and 30- to 50-year-old seedling-sprouts may be only 2 to 12 inches tall. Their tenacity for life, however, is strong. Repeated regeneration surveys on permanent plots with marked seedlings showed that a few black oak seedling-sprouts in deep shade would die back to the root crown; put forth a shoot in some years, but not in others; and still be alive after 10 years of examination. As early as 1912, Lyons described the seedlings as being "persistent," (p. 2), especially after burning.

California black oak seedling-sprouts in the three conifer cutting methods on the Challenge Experimental Forest ranged from 342 to 910 per acre and

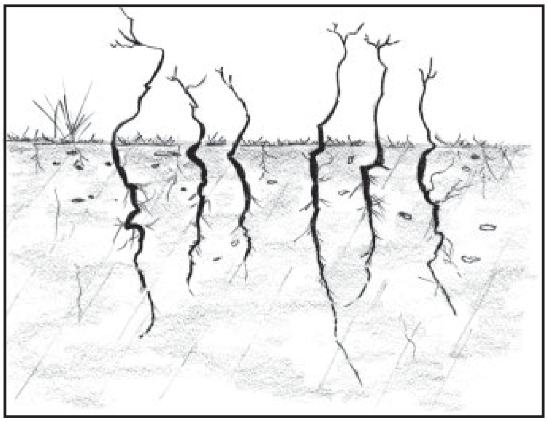

Figure 7—Above- and below-ground development of California black oak seedling-sprouts in deep shade. Height of tallest seedling-sprout is about 1 foot.

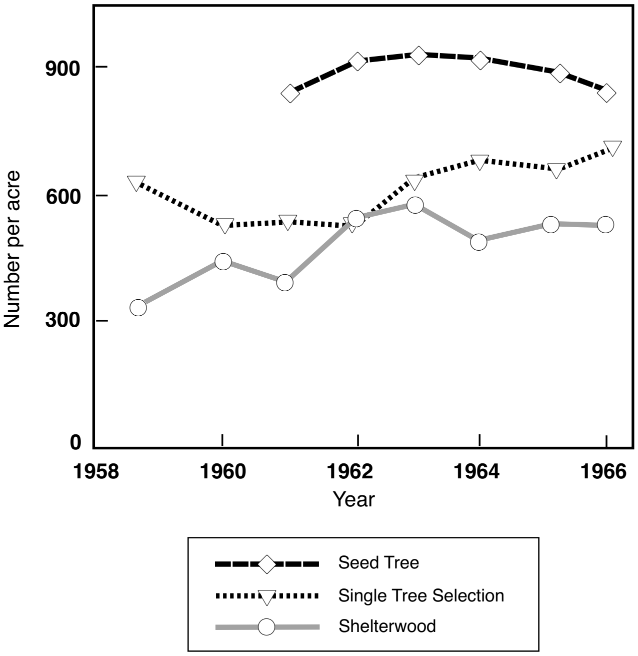

Figure 8—Increase and decline of California black oak seedling-sprouts in three silvicultural regeneration cutting methods, Challenge Experimental Forest, 1959-1966.

Figure 9—Density and development of California black oak seedling-sprouts in a small opening with partial shade, Challenge Experimental Forest, California.

indicated a pattern of both mortality and recruitment (*fig. 8*) (McDonald 1978). These data and observations elsewhere suggest that a slow but steady buildup of seedling-sprouts takes place. Height growth and form tend to be best in small openings in partial shade, particularly if density is high and the seedling-sprouts have to grow straight and tall to keep their tops in sunlight (*fig. 9*). The

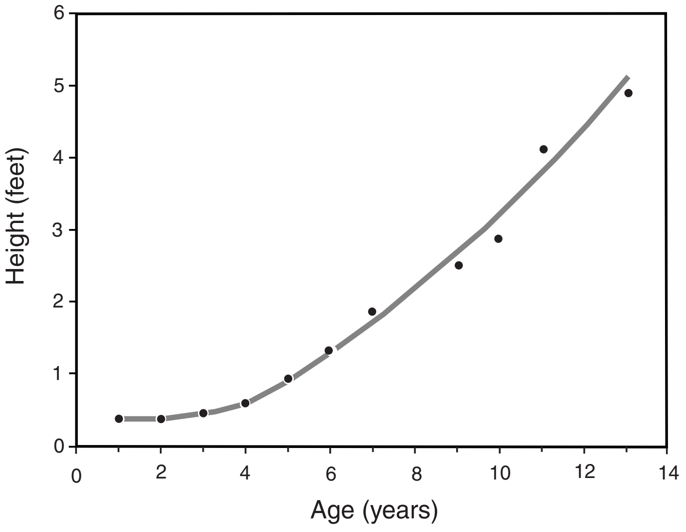

Figure 10—Average height development of California black oak seedling-sprouts in small openings in a shelterwood, Challenge Experimental Forest, California.

average height of black oak seedling-sprouts in openings among shelterwood trees was 5 feet in 13 years (*fig. 10*).

As noted earlier, the distribution of California black oak seedlings often is dense beneath the crown of large trees and widely scattered elsewhere. Consequently, when the large trees die, the typical distribution is clumpy with most of the seedlings and seedling-sprouts present in small openings. If the trees are numerous and good acorn producers, the number of seedlings can be large over a much larger area. The number of seedling-sprouts can be large as well, particularly if a disturbance impacts the area. This happened in Placer County, California, on about 52 acres of a productive site covered with large California black oaks and ponderosa pines (Garrison and others 1998a). The pines were harvested and the slash scattered and broadcast burned in 1985. This combination killed the black oak seedlings to groundline and provided a partial-shade environment. In 1994 to 1995, the number of seedling-sprouts numbered 23,769 per acre (Garrison and others 1998a). In 1999, they were 1.5 to 6.0 feet tall (Garrison 1999). The new stand is not stagnating, and some stems are beginning to dominate. Although atypical in size of area and density of seedling-sprouts, these data show the potential reproductive capability of black oak seedling-sprouts under ideal conditions. In nearby compartments of equal size, black oak seedling-sprouts ranged from 4,506 to 5,828 per acre. Angress (1985) noted that more than 70 percent of black oak seedlings in an underburn in Yosemite National Park had resprouted 5 months later.

Of the three forest-zone hardwoods in this paper, tanoak has the greatest tendency to become a seedling-sprout. The burl on tanoak seedlings develops slowly and is strongly related to age and site quality (Tappeiner and McDonald 1984). It is just as likely to produce sprouts in a sun environment as in a shade environment; however, the number of stems tends to be less in shade (*fig. 11*). Barring injury, each natural tanoak seedling consists of a single stem for the first 5 to 12 years. After that, dieback occurs not only for the obvious reasons of frost, drought, or browsing, but also for unknown reasons. Perhaps, the need for shade is a factor, and the outer stems of clumps provide shade to the inner stems and leaves. At any rate, the stems die back to the burl at least three to five times by age 60. Growth is slow and tanoak seedling-sprouts may be only 2.7 to 5.3 feet tall after 50 years.

In southwest Oregon, tanoak seedling-sprouts were studied beneath old (135-250 years) and young (50-75 years) conifer and hardwood stands, and the density-age-height relationship determined (Tappeiner and McDonald 1984). Together, these data portray the density and growth dynamics of young tanoaks over time in the understory (*fig. 12*).

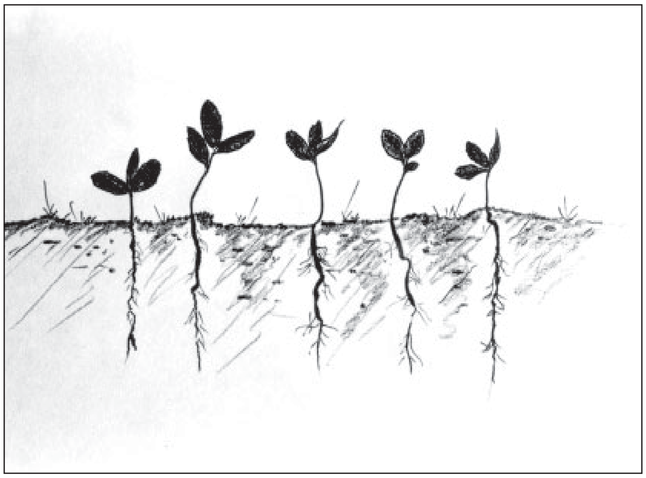

Figure 11—Root-shoot development of young tanoak seedling-sprouts in deep shade. Height of tallest seedling-sprout is about 4 inches.

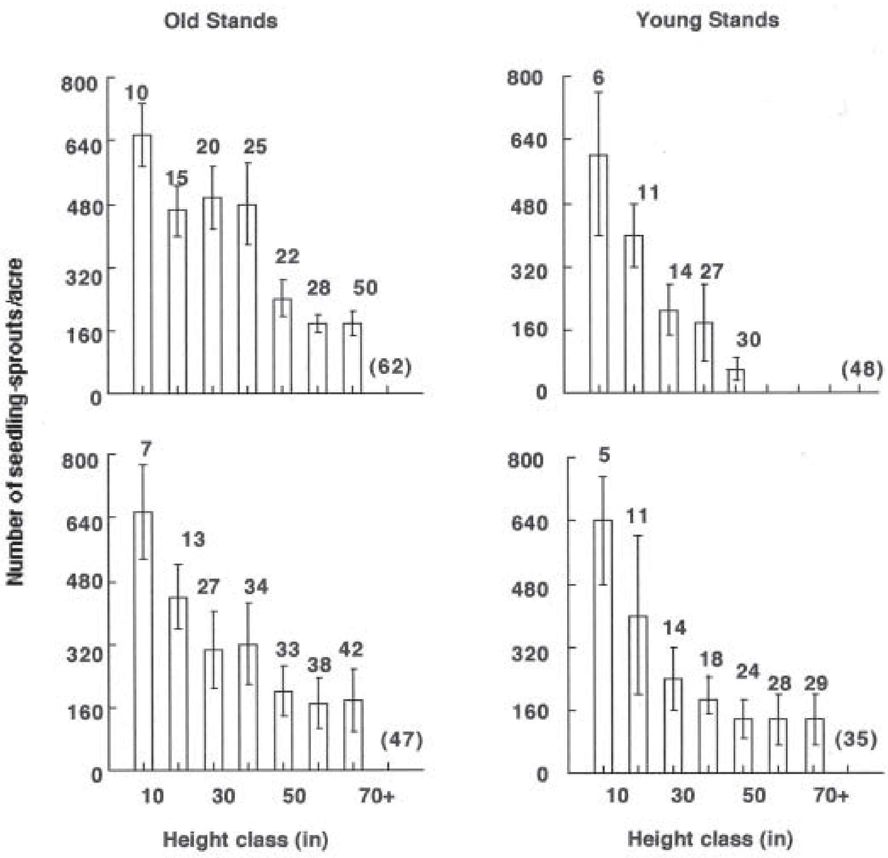

Figure 12—Density-age-height relationships of tanoak seedling-sprouts in two representative old and two representative young stands in southwest Oregon. Vertical bars are standard errors; numbers above bars are the average ages in each height class; numbers in parentheses are the ages of the oldest small tanoak.

Under ideal conditions, the number of seedling-sprouts can be enormous. One almost pure tanoak stand on the Challenge Experimental Forest was thinned from 231 ft^2 per acre to 153 ft^2 per acre in 1972, and the trees responded by producing acorns almost every year. This led to new seedlings being produced almost every year as well. In spite of the thinning, the environment was still shady with 3 to 4 inches of organic matter on the soil surface. Annual observations showed that the seedlings would become seedling-sprouts sometime in the next 4 years for no apparent reason. By spring 1989, young tanoaks averaged 95,000 per acre, most of which were seedling-sprouts. The tallest was 30 inches and most had two stems per clump.

Tanoak seedling-sprouts in the three conifer cutting methods on the Challenge Experimental Forest ranged from 267 to 822 per acre with both mortality and recruitment taking place (*fig. 13*) (McDonald 1978). In the pure, but dense and shady hardwood stand, tanoaks numbered 5,680 per acre. Overall, their pattern was one of increasing numbers. Height growth and form were best in small openings under tree crowns having flecks of sunlight. An average seedling-sprout at age 10 would have a 0.5-inch diameter burl, four sprouts, and a height of 20 inches. By age 40, the burl will have at least doubled in size, the number of sprouts will be slightly larger or the same, and their height will have doubled.

Compared to California black oak and tanoak, Pacific madrone ranks last in terms of tendency to become a seedling-sprout. A burl develops on young seedlings, but precisely at what age is unknown. Madrone rarely becomes a seedling-sprout in a shade environment, but if it does, only one stem usually results (*fig. 14*). In a sun environment, multiple stems are common. Injury is usually the only reason for sprouting in the shade environment, but injury, drought, too much sunlight, and other reasons can result in dieback and sprouting in sunny locations. Growth of the few seedling-sprouts in the shade environment is unknown, but probably better than that of the seedlings. Growth of madrone seedling-sprouts in the sun environment is variable and depends on intra-clump shading and the amount of dieback.

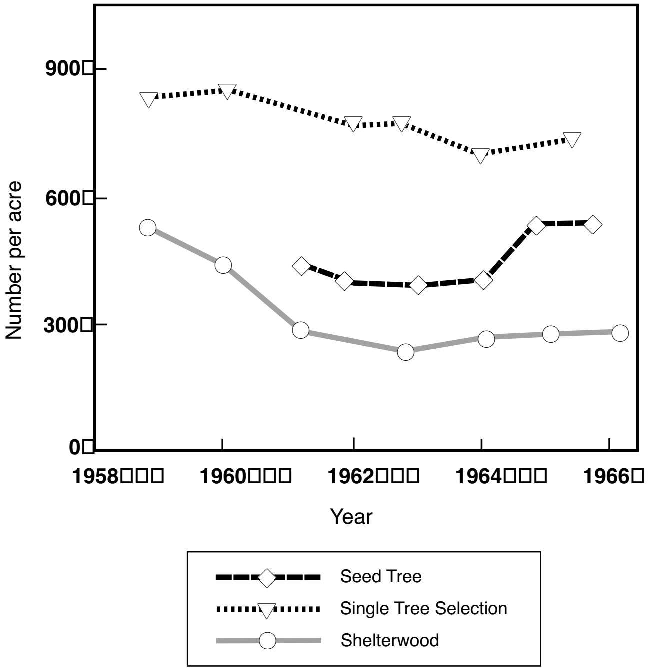

Figure 13—Pattern of tanoak seedling-sprout accumulation by cutting method, Challenge Experimental Forest, 1959-1966.

Figure 14—Root-shoot development of young Pacific madrone seedling-sprouts in deep shade. Height of tallest seedling-sprout is about 4 inches.

The largest number of madrone seedling-sprouts in the conifer cutting methods on the Challenge Experimental Forest were found in those that were the most disturbed—seed-tree and shelterwood (*fig. 15*) (McDonald 1978). Slightly more madrones were present in the seed-tree method but fewer died in the shelterwood. In the pure hardwood stand on the Forest, about 80 seedling-sprouts per acre were present. These relationships reflect the mineral soil and partial shade requirements of the species.

Artificial Regeneration

In this paper, seedlings from two artificial regeneration techniques are reported: direct seeding and the outplanting of containerized seedlings. Both techniques were applied on the Challenge Experimental Forest and elsewhere. Specific information on the plantation site, germination, emergence, and early survival (first 2 years) for California black oak, tanoak, and Pacific madrone were presented in the section on direct seeding. Material in this section covers the response of the hardwood seedlings to the plantation environment, generally through ages 3 to 10.

For the direct seeding trial in the 1966 black oak plantation on the Challenge Experimental Forest, seedling survival after one growing season was 70 percent. Another hard freeze in 1968, deer browsing in 1970, drought in 1971, pocket gophers in 1973, and drought again in 1974 either damaged or killed seedlings. After the tenth growing season in 1975, survival was 54

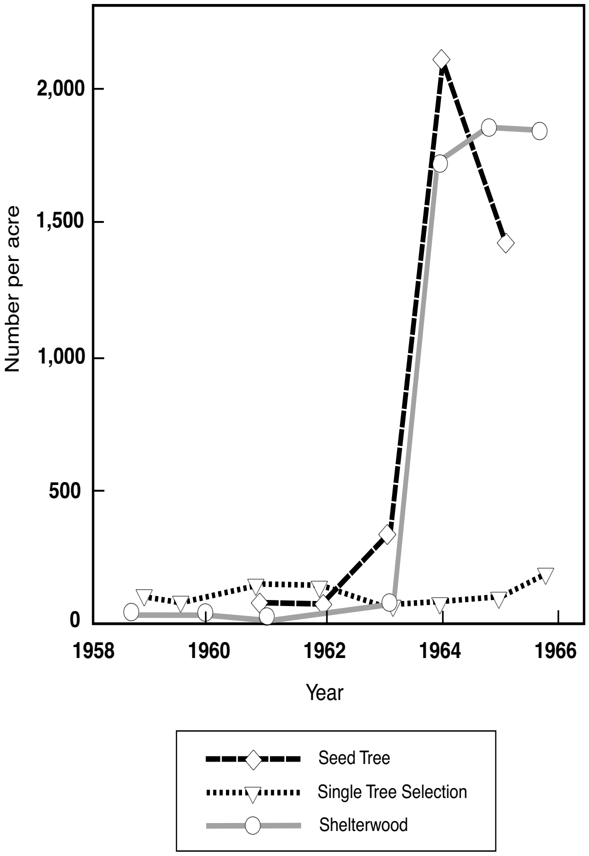

Figure 15—Cumulative density of Pacific madrone seedling-sprouts by cutting method, Challenge Experimental Forest, 1959-1966.

percent. Average height was 1.1 feet with a standard deviation of 1.0 foot and a range of 0.1 to 7.0 feet (McDonald 1978). Technically, many seedlings had become seedling-sprouts.

For the 1969 black oak plantation, survival after two growing seasons was 67 percent. Interplanting of acorns in unstocked spots took place in 1971 and increased total stocking to 82 percent at years end. By 1975, stocking had fallen to 64 percent; 44 percent in 1976. Drought and pocket gophers were the primary causes of mortality. In 1978 or after 10 growing seasons, stocking was 41 percent. Average height after 3 growing seasons was 0.4 foot; after 7 seasons, 0.7 foot; and after 10 seasons, 3.8 feet (*fig. 16*).

Because seedling height growth was slow, a fertilizer trial with 16-20-0 (16 percent nitrogen, 9 percent phosphorous, 0 percent potassium) was installed in February 1970 with 100 seed spots in two blocks of the plantation. Every other row was fertilized and compared to counterparts in alternate rows. A handful of fertilizer was placed about 4 inches above each seedling with the intent that rainfall would put it in the rooting zone when growth began.

Fertilizer stimulated height growth of California black oak seedlings from the beginning (*fig. 17*). After five growing seasons, fertilized seedlings were more than three times taller than unfertilized seedlings. Stems of fertilized seedlings were more robust and thick, leaves were more numerous and larger, and leaf color was darker than for unfertilized plants. The amount of minerals

Figure 16—At 1.2 feet, this 3-year-old, artificially seeded California black oak seedling is three times taller than average, Challenge Experimental Forest, California.

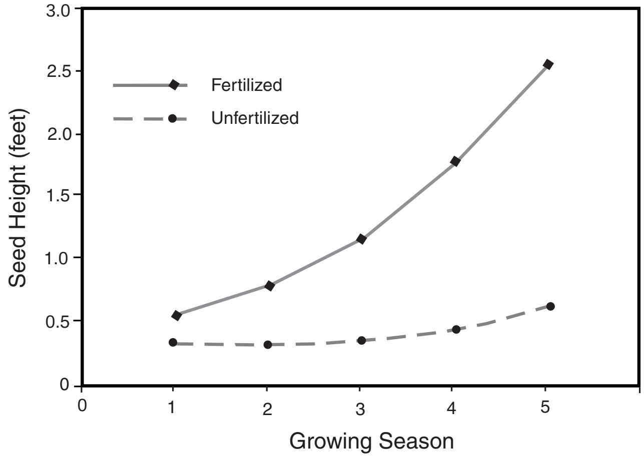

Figure 17—Height development of artificially seeded California black oak seedlings with and without fertilizer, Challenge Experimental Forest, California.

in the leaves of fertilized and unfertilized seedlings was determined by foliar analysis in the laboratory in late June 1970. Analysis of variance indicated that nitrogen and phosphorous were significantly higher ($p = 0.05$) in fertilized seedlings (*table 2*).

Because both foliar analysis and actual stem measurements indicated significant gains, fertilizer was applied to each spot in the entire plantation from 1976 through 1978, using the same fertilizer, amount, and technique of the first trial. The 10th-year survey in 1978 provided a perplexing observation: only 50 percent of black oak seedlings had responded to fertilization.

Internal moisture stress (xylem sap tension) of black oak seedlings was evaluated to help explain the poor growth rates noted earlier. Twigs from five typical seedlings were placed in a pressure chamber using the technique prescribed by Scholander and others (1965). The sampling date was a clear, hot day in early September 1975. At this time of year, the seedlings were under maximum physiological stress because of high moisture deficits. For fertilized seedlings, the mean predawn xylem sap tension was -0.7 MPa (megapascals) (range of -0.45 to -0.8 MPa); for unfertilized seedlings it was much higher (mean of -1.l MPa, range of -0.6 to -1.8 MPa) (McDonald 1978). This relationship indicated that fertilized seedlings had a lower level of internal moisture stress and that the root system of fertilized seedlings probably was better developed and hence better able to capture scarce soil moisture.

In the large field trial of tanoak at the Challenge Experimental Forest with point-up and point-down acorns, seedling survival after two growing seasons (1971) was 21 percent (McDonald 1978). Because this was unsatisfactory, all blank spots were again seeded in early 1972. The soil was loosened and the acorns placed point up and point down as before, and just as before, the early emergers were killed to groundline by frost and sprouted with multiple stems. Seedlings from this interplanting did not survive much better than earlier counterparts. However, they did increase the stocking of the tanoak plantation to 66 percent. In subsequent summers, drought and dieback were rampant. Seedlings would repeatedly die back and resprout and eventually die. After six growing seasons (1975), stocking was 33 percent. Mean height of tanoak seedlings was 1.1 feet in the range of 0.2 to 10.2 feet. After another interplanting in spring 1976, overall survival at the end of the study in 1979 was 41 percent. Many, but not all, seedlings had multiple stems, and average height had scarcely changed from the 1975 values.

Because tanoak survival and height growth were poor, fertilizer and water were applied in each of 4 years (1972 to 1975) in an effort to increase establishment (McDonald 1978). The same fertilizer (16-20-0) and application technique as in the black oak plantation was used. A generous handful of fertilizer was placed just above selected seedlings in February of each year.

Table 2—*Mean foliar nutrient concentrations of fertilized and unfertilized California black oak seedlings, Challenge Experimental Forest, 1970.*

Nutrient	Fertilizer	No fertilizer
	------ percent of foliar dry weight -------	
Nitrogen	2.59 a[1]	2.26 b
Phosphorous	0.20 a	0.14 b
Potassium	0.46 a	0.58 a
Calcium	0.53 a	0.58 a
Magnesium	0.18 a	0.18

[1] For each nutrient, dry weight percentages in each row followed by the same letter do not differstatistically at the 0.05 level.

Table 3—*Average tanoak seedling height with and without fertilizer and water, Challenge Experimental Forest, 1970.*

Year	Fertilizer and water	Water	Fertilizer	Control
	---------- ft ----------			
1972	0.49 a[1]	0.43 a	0.43 a	0.34 a
1974	1.15 a	0.78 ab	0.90 ab	0.65 b
1975	1.68 a	1.05 b	0.93 b	0.75 c

[1] For each year, mean height in each row followed by the same letter does not differ statistically at the 0.05 level.

Irrigation amounted to about one-half gallon of water per spot from a hose. It collected in a shallow earthen basin constructed around each seedling. Irrigation began about mid-June each year and took place at about 2-week intervals. Sampling intensity was 808 randomly selected seed spots, with approximately equal representation of original and interplanted seedlings and plants from point-up and point-down acorns.

The effect of fertilizer and water on tanoak seedling height first showed up in 1974 and was more pronounced in 1975. Analysis of variance and a Tukey test showed significantly better height growth for each treatment relative to the control, and especially from fertilizer and water combined (*table 3*). Water apparently was an aid in getting the fertilizer into solution and making it available to tanoak seedling roots. The amount of minerals in the leaves of seedlings in the various treatments was determined by foliar analysis in the laboratory in late June 1975. The higher amounts of nitrogen and phosphorous in the leaves of watered and fertilized plants conformed with the height relationships of the measured seedlings.

Internal moisture stress (xylem sap tension) of tanoak seedlings was evaluated to help explain the poor survival and growth rates noted earlier. As for California black oak, twigs from five typical seedlings were placed in a pressure chamber (Scholander and others 1965) on a clear, hot day in early September 1975. Seedlings had not received any water for 15 days and the soil around them was as dry as that elsewhere.

Average predawn minimum moisture stress of the tanoak seedlings by treatment was:

Treatment	Stress (MPa)
Fertilizer and water	-0.50
Water	-0.49
Fertilizer	-0.68
Control	-0.62

This relationship showed that the tanoak seedlings were able to recharge their systems over night and that internal moisture stress was less in seedlings that had been receiving water for three consecutive summers (implying a better developed root system). In a complementary study, moisture stress of two 6-year-old seedlings was monitored continuously for 24 hours to determine the diurnal trend in moisture stress. Average values during the day were:

Pacific Standard Time	**MPa**
4 a.m.	-0.4
6 a.m.	-0.8
8 a.m.	-1.5
10 a.m.	-1.8
1 p.m.	-2.3
4 p.m.	-2.2
6 p.m.	-1.3

Internal moisture stress in one of the seedlings reached -0.2 MPa at midnight. This value is similar to that of trees with roots in running water and again shows tanoak's capability to recharge its system. These data also show that internal moisture stress increased rapidly after first light in the morning, leveled off about 8 a.m., peaked at 1 p.m., and then rapidly declined.

Additional moisture stress values were determined for six very young (6-month-old) seedlings in the plantation area. These were so small that they had no branches (twigs) and the entire seedling had to be inserted in the pressure chamber. Two seedlings reached -2.0 MPa at first light in the morning, but before sunrise. An obviously stressed seedling in full sunlight with dead and partially dead leaves had a value of -3.4 MPa at 11:40 in the morning. Another robust-looking seeding in full sunlight endured a stress of -3.5 MPa in late afternoon. Two other seedlings that had been in full sunlight most of the day but were in shade at 6:10 p.m. indicated a stress of -2.2 MPa.

Together, the internal moisture stress data suggest the reason for the death and dieback of the tanoak seedlings. At the first hint of light in the morning, the stomates in the leaves open widely and transpiration rapidly drains moisture from the plant's system. Transpiration apparently exceeds the daylight recharge capability and the plant eventually dies. Efficient recharge ability at night only prolongs the process.

Because too much light, too much heat, and too much transpiration could be mitigated by shade, 175 tanoak acorns with newly-emerged radicles were seeded point up in early March in another trial on the Challenge Experimental Forest (McDonald 1978). Some seedlings also were irrigated and fertilized as in earlier trials. Large wooden shingles were placed southwest of each seedling shortly after emergence. Although first-season mortality was slightly lower than for unshaded seedlings nearby, second-season survival was no better, and the trial was abandoned. Time and again, the tanoak seedlings would grow tall and skinny behind the shingle, lean away from it out into the sunlight, promptly die back, and eventually die.

In the extensive direct seeding study with tanoak and Pacific madrone in southwestern Oregon (Tappeiner and others 1986), the height of tanoak seedlings ranged from 2 to 5 inches and for madrone from 1 to 2 inches after three growing seasons.

Some seedlings were raised in containers in the greenhouse and then outplanted in prepared areas on the Challenge Experimental Forest (McDonald 1978). For all three species, the plantation environment was essentially bare mineral soil in full sunlight.

One-hundred California black oak seedlings were grown in 6-inch deep containers filled with potting soil in a greenhouse, transferred to a lathhouse to harden off, and outplanted on the Challenge Experimental Forest in mid-March. Seedlings had been watered and fertilized and were robust with short, thick stems and root systems that extended beyond the containers. The roots were pruned just before outplanting. The soil at each planting spot had been loosened to about 12 inches with hand tools. Survival after one growing season was 66 percent. However, subsequent surveys indicated that survival was no better than that from direct-seeded acorns, and the effort was discontinued.

The growing and outplanting procedures for tanoak were similar to those used for black oak, except that the containers were 8-inch deep, half-gallon milk cartons. The bottom of each carton was removed just before outplanting. And similar to black oak, the root:shoot ratio after pruning was 2 to 1. After one growing season, survival was 81 percent, but after two seasons survival had fallen to 46 percent. Height growth after outplanting was essentially nil. Examination of dead tanoaks showed that the seedling roots had grown through the loosened soil, but no farther. Root elongation was inadequate and the seedlings died from drought.

One-year-old Pacific madrone seedlings in 13 half-gallon milk cartons were outplanted as plugs (bottom of carton removed), one to a spot. After three growing seasons, only 6 of the 13 spots had a living madrone seedling. Dieback, sprouting, poor form, and death were common. Plainly, the environment was too bright and too hot. After six growing seasons, five spots contained seedlings. Average height was 4.5 feet, and stems were crooked and forked.

Additional trials of containerized hardwood seedlings, other than on the Challenge Experimental Forest, took place in California and Washington. Some trials were with stock grown in commercial nurseries and some took place in small greenhouses on National Forest land. Most involved starting the seedlings in the nursery and then transplanting them to the field as container seedlings or plugs.

An intensive trial with California black oak seedlings took place in 1989 in Yosemite National Park, California, under an open overstory of mature trees. Five-hundred 2-year-old seedlings, grown from local acorns, were transplanted into D-pots (4 x 4 x 12 inches) and then into pre-drilled holes (Fritzke 1997). The holes were lined with steel mesh bottomless cylinders to protect the roots from rodents. Solid and open-mesh tree shelters were installed to protect seedlings from browsing. A time-release fertilizer tablet was dropped into half of the holes. After seven growing seasons, survival was 22 percent with mortality from drought and other causes. Average survival and height of fertilized seedlings was somewhat better than unfertilized seedlings, but not significantly. Average height of seedlings in solid plastic tree shelters (23 inches) was significantly better than for those in open mesh shelters (15 inches); however, an average difference of only 8 inches may not be practicably important.

McCreary (2001) also grew black oak seedlings in tree shelters at the Sierra Field Station in Yuba County, California, and found that they did not promote accelerated height growth. Furthermore, he noted: “it is unclear why this oak species seems to initially grow so slowly, both with and without treeshelters” (p. 49).

Several regeneration trials with California black oak from both commercial and USDA Forest Service stock have been installed in southern California National Forests. Various combinations of germinated and nongerminated acorns, 12- to 18-inch open bottom pots, irrigation, fertilizer, and screens made of various materials were evaluated (Anonymous 1980, Blankenbaker 1986, Roberts and Smith 1982). The screens extended about 12 inches belowground and up to 36 inches aboveground. Values of 59 and 82 percent survival after 1 year, and 40 percent after 9 years were recorded. Pocket gophers, drought, and browsing were the principal causes of mortality. The 9-year old seedlings averaged 3 to 4 feet in height.

Artificial regeneration of Pacific madrone is difficult because the seeds are so small and the fate of the seedlings so uncertain, that scores, if not hundreds of seeds, are often used per container. Excess seedlings, if present, need to be removed. To lessen this burden, a trial with germinated seeds was performed in the laboratory. The goal was to have one virtually assured seedling per container. Stratified seeds were placed on a moist medium in petri dishes and, after a tiny white radicle was visible, were carefully placed in containers at a depth of 1/8 inch. Damping-off fungi ruined the experiment, but the technique showed promise.[1]

In the Puget Sound area of coastal western Washington, Gonzalez (1999) grew 250 to 400 containerized Pacific madrone seedlings by using "standardized nursery practices." He stressed the importance of placing the seedlings into containers at a very young age so that further transplanting maintained the fine root system. Winters and Hummel (1999) noted that nurseries did not grow many madrone seedlings because of "transplant failure." To combat this lack, they transplanted madrone seedlings into three successively larger containers in the nursery, provided optimum levels of moisture and nutrients, and then transplanted them into the landscape. After one growing season, survival was high and some trees were about 3-feet tall. Unfortunately, a hard December freeze killed almost all the seedlings and terminated the study. Shoffner (1999) grew 168 madrone seedlings with seed from a single tree and outplanted them in sun and partial shade environments. After 1 year, he found that plants grown in full sunlight with weekly irrigation accumulated the most biomass and maintained the highest rate of photosynthesis despite moderate water stress.

Provenance Trial

Because early emergence was critical for California black oak seedling survival and point-up acorns resulted in early emergence, this technique seemed promising. However, late spring frosts consistently damaged seedlings. If seedlings could be found that withstood frost damage either directly or indirectly by emerging later, but with more rapid early height growth, the problem could be circumvented. Consequently, seed from eight sources that ranged from 3,200 to 5,625 feet were tested. Two of these locations were not only higher but drier, and the possibility existed that such seedlings would be more drought resistant than seedlings from the Challenge Experimental Forest.

Acorns from each location were gathered, stored, and outplanted on prepared ground free of competing vegetation on the Challenge Experimental Forest as in previous studies (McDonald 1978). Survival, height and diameter growth, leaf-flush, and leaf-fall data were sampled both annually and periodically for seven growing seasons. Leaf-flush data were evaluated in five categories and leaf-fall data were differentiated by six different colors. The results were disappointing. Little difference among provenances and high variation within each provenance characterized all measured variables. However, some worthwhile adjunct information was gathered during the eighth growing season. About 82 percent of all seedlings began to elongate in height on April 26 with diameter growth beginning 7 to 21 days later. Diameter and height growth ceased after 43 days. Taller seedlings grew for a longer time span than shorter seedlings, but did not grow as fast. Thus, average height was the same at the end of the season.

Root-crown Sprouts

The three forest-zone hardwoods in this paper produce both sprouts and seed. Obviously, species that have both reproductive modes have an advantage over those that have only one. When the above-ground portion of the tree is killed by fire or the tree is cut in logging, these species sprout from the burl, or root crown as it often is called. The root-crown sprouts are often thought of as being "instant reproduction" because of their abundance and rapid growth. Continuous vegetative reproduction may have a long-term disadvantage—the species may eventually become out-of-tune with the ever-changing environment and decline. Reproduction with seedlings, via the sexual process, helps the species adapt to the environment.

Dormant buds are almost always present on the root crown of the tree, which is located at or just below groundline. When the top of the tree is alive, they are kept dormant by hormones produced in buds in the uppermost whorls. After the top is cut or killed, the hormones disappear, and the dormant buds become free to produce sprouts. Not all buds sprout in a given disturbance, however, and many are kept in reserve. Each sprouting bud has a direct vascular connection to a piece of the parent tree root system and a vast amount of resources are available to the sprout. A few quickly dominate and rapid growth is the result. Then, like the parent tree, hormones develop in the top of the dominant sprouts and inhibit the sprouting of dormant buds on the burl. This inhibition is effective for California black oak and Pacific madrone and sprouting occurs only in the first year after cutting. The inhibition is not as restrictive for tanoak, and new sprouts are formed for up to 3 years after the tree is killed aboveground.

Root-crown sprouts are the primary reproductive mode of the forest-zone hardwoods in this paper. The attributes of being both numerous and fast-growing allows them to outgrow most competing species and, if the disturbed area is small, to be in position to receive sunlight before the canopy closes.

After cutting, burning, or other damage, sprouting is assured except for very old, moribund trees whose buds are occluded by thick bark. In fact, it is almost impossible to keep stumps of these hardwood species from sprouting. After the tree is killed aboveground, the number of sprouts in the initial flush varies tremendously, ranging from as high as 1,400 on one large tanoak stump (Tappeiner and others 1990) to more than 300 on one 10-inch Pacific madrone stump (McDonald and Tappeiner 1990). Other sprouts originate from the top of the stump or on the vertical part of the stump between the top and the ground. These are called stool sprouts and are undesirable for several reasons. They are weakly attached to the stump, are peeled off by wind and snow, and are prone to heart rot at an early age. Leaving a low stump less than 8 inches tall promotes numerous, healthy, rot-free sprouts.

The size and vigor of the parent tree largely determines the number of sprouts and their height and crown spread (McDonald 1978, Roy 1955, Tappeiner and others 1990). In general, stumps from larger trees produce a larger number of sprouts and more vigorous ones. This proved true in both the northern Sierra Nevada and in southwest Oregon. In a clearcutting in the northern Sierra Nevada, number of California black oak sprouts and the width of their crowns were statistically correlated to stump diameter at sprout ages 4 and 10 (McDonald 1978). For tanoak and Pacific madrone in southwest Oregon, sprout height, clump width, clump area, leaf area, total aboveground biomass, and number of stems per clump 1 to 16 years after cutting, were statistically correlated with parent tree diameter at breast height before cutting or burning (Harrington and others 1984, 1991, 1992, Tappeiner and others 1984). For example, tanoak and Pacific madrone trees whose parent stems were 8.7 inches in diameter were predicted to have sprout clumps 217 inches wide and 236 inches tall 16 years after cutting; trees with 4-inch parent diameters would produce clumps about 158 inches wide and 177 inches tall over the same period (Harrington and others 1992). Thus, sprout clump size and total cover of sprout clumps can be predicted on a per-acre basis and used to estimate competition, biomass, and other useful determinations.

Season of cutting and amount of shade can also affect the number of root-crown sprouts. In southeastern Mendocino County, in the inner Coast Range of California, Longhurst (1956) cut five black oaks each month from December through November. For those cut in the December through May period, 92 percent sprouted; for those cut in the June through November period, only 45 percent sprouted. In a similar environment in Trinity County California, Wilkinson and others (1997) noted that sprouts from tanoak clumps in deep shade were about one-fourth as tall as those reported for a sunlit environment in southwest Oregon and northern California. Furthermore, sprouting in deep shade was delayed for several months after cutting of the parent tree, probably because the hormonal and metabolic processes in the stump were not sufficiently stimulated to produce sprouts. Light, of course, is a strong stimulant. Many sprouts were negatively impacted by mold and browsing by deer. In shade, the sprouts grow more slowly and have greener, more palatable leaves longer than counterparts in the sun. Mold rarely, if ever, occurs on sun sprouts, but is fairly common on those in the shade. Both factors decrease sprout height.

Smith (1962) noted that "vegetative reproduction obtained after clearcutting is usually superior to that resulting from partial cutting." In a study on the Challenge Experimental Forest with California black oak, tanoak, and Pacific madrone, sprout clump dynamics were quantified in both a clearcutting and in a hardwood shelterwood where 50 percent of the stand basal area was removed (McDonald 1978). Diameters ranged from 6 to 17 inches at breast height. For all three species, more sprouts per stump were found in the clearcutting (*table 4*). Even shade-tolerant tanoak grew best in the clearcutting, probably because no roots of parent trees were utilizing site resources, particularly water. After 10 years, sprout clumps of California black oak and tanoak in the clearcutting averaged 20 feet tall and about 10 feet wide (*table 5*). Clumps of Pacific madrone

Table 4—*Number of sprouts per stump at various years after cutting for California black oak, tanoak, and Pacific madrone, Challenge Experimental Forest, California.*

Year	**California black oak**		**Tanoak**		**Pacific madrone**	
	clearcut	shelterwood	clearcut	shelterwood	clearcut	shelterwood
	(29)[1]	(20)	—[2]	(7)	(6)	(5)
0	63	28	—	28	100	60
2	50	23	—	31	85	30
4	35	17	—	34	50	18
6	23	15	—	33	30	12
8	18	13	—	26	18	8
10	15	12	—	24	15	7

[1] Number of stumps.

[2] Too many and too difficult to count.

Table 5—*Average height and crown width of California black oak, tanoak, and Pacific madrone sprouts at various ages after cutting, Challenge Experimental Forest, California.*

	California black oak		Tanoak		Pacific madrone	
Age	clearcut	shelterwood	clearcut	shelterwood	clearcut	shelterwood
			Height			
			ft			
4	8	4	8	4	8	5
6	12	5	12	5	15	7
8	16	6	15	7	19	8
10	20	7	19	8	22	9
			Crown width			
			ft			
4	6	3	8	3	5	4
6	8	4	8	3	7	4
8	9	5	9	5	9	5
10	10	7	10	7	10	7

were slightly taller (22 feet) after 10 years, but they also were 10 feet wide. The black oak sprouts in the shelterwood averaged as much in width as in height (7 feet). This was caused in part by a cynipid gall wasp (*Callirhytis perdens* Kinsey) that damaged the terminal shoots of the black oak sprouts in the shelterwood (*fig. 18*), but not of those in the clearcutting. The more shady environment typical of the shelterwood apparently was more favorable to the wasp than that of the clearcutting.

Harrington and others (1994) found that 6-year-old tanaok sprouts in southwest Oregon were better able to minimize the effect of water stress than Pacific madrone sprouts or planted Douglas-fir seedlings. Predawn plant water potential throughout the year never fell below about -0.5 MPa (megapascals) for tanoak, but it reached -1.2 MPa for Pacific madrone and nearly -2.0 for Douglas-fir. Madrone was able to photosynthesize longer than the other species when deficits in soil and atmospheric water were high. Both tanoak and Pacific madrone were able to photosynthesize in the spring and fall when soil moisture was available and the air temperature was warm. They were even able to photosynthesize during periods of mild winter temperatures.

Internal plant moisture stress of 7-year-old root-crown sprouts on the Challenge Experimental Forest was determined by pressure chamber for the three species, following the sampling procedures described earlier for the seedlings (McDonald 1978). Likewise, the date was a clear, hot day early in September. Predawn minimum stress varied from -0.5 to -0.8 MPa, and peak stress, which took place about 10 a.m., ranged from -2.3 MPa in Pacific madrone to -3.0 MPa in tanoak. Immediate ill effects from this stress were not observed.

In addition, Hanson (1977) studied internal moisture stress of young tanoaks—at least 5-years-old—in both a sun and a shade environment on the Challenge Experimental Forest. Full grown leaves in the sun were about half as long and wide as those in the shade. They averaged almost 346,000 stomata per whole leaf in the sun and almost 821,000 stomata in the shade. Having less evaporative surface with more stomata per unit area, and fewer total stomata than shade leaves could increase heat loss with less evaporative loss and enhance survival potential in the sun. This factor and possibly others caused a

Figure 18—Typical damage to shoots of California black oak in partial shade by a cynipid gall wasp, northern California.

peak and decline relationship of internal moisture stress during the season for plants in both the sun and shade environments, and internal moisture stress was actually less during the season in sun plants than for those in shade. One would expect internal stress to increase steadily throughout the summer and to be greater in sun plants than in shade plants. Apparently, the fail-safe mechanism operates seasonally as well as diurinally, and the use of soil moisture by roots of overstory trees in the shade increases internal moisture stress of seedlings more than does evaporative demand for those in the sun.

Other investigators have quantified the growth of tanoak and Pacific madrone sprouts. In Trinity County California, Roy (1955) measured 50 clumps of each species and after the third growing season noted:

Species	**Average height of tallest sprout**	**Average clump diameter**	**Sprouts per clump**
	ft	ft	number
Tanoak	6.8	7.0	12
Madrone	0.1	7.6	13

Minore (1986) found similar relationships for 4- through 7-year-old hardwood clumps in the western Siskiyou Mountains of southwestern Oregon:

Species	**Average height of tallest sprout**	**Average clump diameter**
	ft	ft
Tanoak	5.1	11.5
Madrone	7.4	15.1

Additional data on the development of Pacific madrone root-crown sprouts was provided by Hughes and others (1990) in the Cascade Mountains of southwestern Oregon. Seven years after cutting and burning, dense clumps of madrone, spaced 9 feet apart, were about 10 feet tall and had a basal area of 96 ft^2 per acre, 84 percent cover, and an aboveground biomass of 22,500 pounds per acre. Clumps at the 18-foot spacing were about the same height with 40 percent cover, 57 ft^2 of basal area, and 14,800 pounds of biomass per acre. There were three to four times more cover of shrubs, forbs, and grasses at the 18-foot spacing than at the 9-foot spacing.

Given that the number of sprouts per clump are numerous and that natural thinning is rapid, artificial thinning at an early age seemed a likely technique to stimulate growth of selected stems. This was done on the Challenge Experimental Forest for California black oak, tanoak, and Pacific madrone, always leaving three or four sprouts well distributed around the stump. Thinning was performed at ages 1 and 4. Thinning at age 1 was difficult and ineffective, and many selected stems were inadvertently removed. Thinning at age 4 was much easier because sprouts were more firmly attached, and dominant individuals could be identified and saved (McDonald 1978). These were quantified for the next 6 years and compared to sprouts in unthinned clumps. An advantage in average height, crown width, or crown volume of thinned over unthinned sprouts was not found for any species.

Many observers over scores of years have noted the remarkable lack of mortality of clumps of root-crown sprouts from all three hardwood species discussed here. Individual stems may die, but the clump lives. For instance, mortality was recorded on 1,200 tanoak clumps in southwestern Oregon and none had died after 6 years (McDonald and Tappeiner 1987).

Only one example of the whole clump dying was found. On the Challenge Experimental Forest, McDonald and others (1988) sampled 19 tanoak sprout clumps that were characterized by chlorotic leaf color, an abnormally large number of sprouts, a vastly different height-width relationship than healthy sprout clumps nearby, and a peculiar flat top with no exhibition of dominance by any sprout. All clumps were from at least two generations of sprouting. No pathogens or viruses that could account for the abnormal development were found in field or laboratory, and the reason for the decline and eventual death is unknown.

Summary and Recommendations

Because native hardwoods like California black oak, tanoak, and Pacific madrone need to be replaced in many locales in the California landscape, and because some managers would like those seedlings and sprouts that are already present to grow faster, the need for knowledge on reproductive mechanisms and growth potentials is obvious and pressing. The many habitats where these hardwoods are present need to be sustained. To be sustained, they need to be managed, and to be managed, they need to be propagated. More specifically, all three reproductive modes need to be maintained and enhanced. Although much remains to be learned, the following recommendations summarize what is known about propagating California black oak, tanoak, and Pacific madrone in the forest zone of California and southwest Oregon.

- Because reliable techniques for multiple-year storage of acorns have not been determined, short-term, on-site storage in buried wire baskets is suggested. This type of storage avoids predation, is in-tune with the local environment, ensures a high degree of acorn soundness, and results in full or nearly full early stocking of the plantation with seedlings.
- The typically long, hot, dry summers in California and southwestern Oregon make soil moisture the limiting environmental factor for the establishment of California black oak, tanoak, and Pacific madrone. This has caused them to develop various strategies to enhance early seedling development. For example, California black oak and tanoak concentrate energy from the acorn into a long, slender, deep-thrusting taproot with very little lateral root development. They also tend to delay emergence

of the epicotyl aboveground until the taproot is extended, and to limit first-year shoot growth.

- Deep, moist duff and litter are ideal for germination and downward penetration by the relatively stout taproots of new California black oak and tanoak seedlings. Loose mineral soil is equally advantageous. However, almost any amount of organic matter on the forest floor is deadly to tender madrone stems and roots, and sunlight and frost are undesirable, at least in California and southwestern Oregon. Hard, compacted soil is anathema for establishment of black oak, tanoak, and Pacific madrone seedlings.
- Natural regeneration of all three species tends to be clumpy and to occur in gaps of various sizes brought about by disturbance. For California black oak and tanoak, disturbance is not necessary for seedling establishment, but is necessary for growth; for Pacific madrone, disturbance is necessary for both establishment and growth. The environment beneath seed trees is ideal for seedling establishment from acorns, but not for seedlings from tiny Pacific madrone seed. Consequently, animal disseminators that carry seeds to disturbed mineral soil environments are critical for madrone, but less so for the other species. Partial cutting and site preparation (broadcast burning, bulldozing) that provide mineral soil and shade enhance establishment and growth of black oak, tanoak, and madrone.
- Natural regeneration of California black oak, tanoak, and Pacific madrone in an undisturbed setting is characterized more by a slow, steady accumulation of seedlings, than by large pulses of them.
- California black oak, tanoak, and Pacific madrone all have capability to convert from seedlings to seedling-sprouts. Shoot dieback is the seedling’s way of alleviating environmental stress. Sprouting compensates for it. However, even on the best of sites, shoot growth is slow and does not increase until root biomass is large enough to capture adequate soil moisture. Consequently, the recurrent dieback and sprouting of seedling-sprouts probably is an adaptive strategy for becoming established in the Mediterranean climate of California. The tendency to become a seedling-sprout differs among species and between sun and shade environments. Unless damaged, black oak rarely becomes a seedling-sprout in the sun and Pacific madrone rarely becomes a seedling-sprout in the shade. On the basis of our data and observations in California and Oregon, the relationship is:

Species	**Environment**	**Number of stems**
California black oak	Sun	1
	Shade	1
Tanoak	Sun	3-7
	Shade	1-3
Pacific madrone	Sun	3-5
	Shade	1

- Seedling-sprouts, which occur irregularly over the landscape, usually form small aggregations of high density that are long-lasting and often regarded as seedling banks. They are worthy of future management. Being established, with root systems in place, is a big advantage. Their low growth rate is a drawback, but it probably can be increased through thinning and overstory manipulation.

- Because seedling-sprouts die back repeatedly and their age may exceed 50 years before they reach breast height, total age is difficult to determine. Conclusions about age-class distribution need to be made cautiously.
- Similar to conifers, hardwood seedlings in plantations need to be from local seed sources, particularly at similar elevations, and to be maintained weed-free or nearly so until established.
- Artificial regeneration of California black oak, tanoak, and Pacific madrone is characterized by many trials, but few successes. Almost all trials have been installed in conventional sunlit plantations with seed from local sources and good control of competing vegetation. The trend is for high initial seedling stocking, early mortality, seedling dieback, poor overall growth, increasing seedling death, and a failed plantation. Few saplings usually result from many seedlings. Consequently, silviculturists do not know how to achieve a reliable and consistent seedling growth rate, even when fertilizer and water are provided during the first few years.
- Trials with fertilizer and water and concomitant foliar analysis and determination of internal moisture stress suggest that inadequate internal moisture is the primary reason for the poor growth of California black oak and tanoak seedlings. Although fertilizer provided significantly better seedling growth than not fertilizing, the magnitude of the increase was not enough to enhance the overall growth rate of the planted seedlings. Virtually all seedlings of these species are stressed for moisture in sunlit plantations. Those that were the most stressed apparently could not respond to fertilizer, and those that were less stressed could not respond adequately.

One possibility for enhancing the early growth rate of oak seedlings in plantations involves seedling root mass and morphology. It is based on northern red oak (*Quercus rubra* L.), which grows in the northern and central United States. On prepared ground free of competing vegetation in a moderate shelterwood, 2-0 seedlings with clipped roots and tops and at least a 1/4-inch diameter stem measured 1 inch above the root collar developed well (Johnson and others 1986). The tops were clipped 8 inches above the root collar and the taproot and laterals were trimmed 10 inches below it. This prescription produced a thick-stemmed seedling with a dense, fibrous root system that apparently absorbed enough soil moisture for rapid growth. The shelterwood was removed after three growing seasons.

- Manipulating root-crown sprouts is the principal regeneration method currently available to silviculturists, and until artificial regeneration techniques are perfected, vegetative propagation is the most reliable means for renewing hardwood stands and for attaining an acceptable growth rate.
- Root-crown sprouts of Pacific madrone grow faster than tanoak and black oak counterparts and occupy more space. However, clump density has a major effect on the height/width ratio of individual clumps. If close together, clump height exceeds clump width, but with increasing space between clumps, width exceeds height. Growth differs with local conditions but in general is rapid for the first 10 years.
- Thinning of root-crown sprouts is impractical through age 10, but after age 10 it should stimulate growth of remaining sprouts. Retaining three to four of the most healthy sprouts evenly spaced around the circumference of the stump is necessary to maintain clump health.

- By assigning comparative ratings to seed production, regeneration, and growth, future researchers can more accurately compare the potential of the various modes of natural regeneration and artificial regeneration for California black oak, tanoak, and Pacific madrone (*table 6*).

More specific knowledge for enhancing the establishment and growth of black oak, tanoak, and Pacific madrone in each of their three reproductive modes needs to be developed. For seedlings and seedling-sprouts, information on optimum spacing, degree of shading, and amount of soil moisture and nutrients are needed. For root-crown sprouts, the number of sprouts per stump and the number of sprouting stumps per acre at a given age needs to be determined to maximize growth.

For artificial regeneration of all three species, the plantation environment has not been fitted to the seedling, or the seedling fitted to the plantation environment. The environment where the seedlings of these species will establish consistently and grow reliably is yet to be determined. Much work on overstory manipulation with monitoring of light, internal moisture, and nutrients is needed. Because soil moisture is the limiting environmental factor in the Mediterranean climate of California, the key to successful artificial regeneration could be to develop a seedling that captures more soil moisture.

Table 6—*Comparative rating of California black oak, tanoak, and Pacific madrone seed production, regeneration, and growth both quantitatively (many, some, few) and qualitatively (good, fair, poor).*

Variable	California black oak	Tanoak	Pacific madrone
Biennial seed production	Poor	Fair	Good
Dissemination	Good	Good	Good
Natural Seedlings			
Number	Few	Some	Few
Survival	Fair	Fair	Poor
Growth	Poor	Poor	Poor
Seedling-sprouts			
Number	Few	Many	Few
Survival	Fair	Good	Poor
Growth	Poor	Poor	Fair
Root-crown sprouts			
Number	Many	Many	Many
Survival	Good	Good	Good
Growth	Good	Good	Good
Artificial Regeneration			
Survival	Fair	Poor	Poor
Growth	Fair	Fair	Fair

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