

AN ABSTRACT OF THE THESIS OF

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Title: Silviculture-Ecology of three native California hardwoods on
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Abstract approved _____

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Alan B. Berg

Pacific madrone, tanoak, and California black oak are the most economically promising native California hardwoods. Volume and value data indicate upward trends in growing stock levels and prices received for their products. These trends are likely to continue. They suggest research is particularly needed for: (1) seed fall and regeneration, (2) sprout growth and development, (3) stand growth and yield, and (4) species adaptation and strategy. Much new material in these categories is presented here.

The ability to produce copious amounts of seed at frequent intervals is a hallmark of Pacific madrone and tanoak, and only slightly less so for California black oak. Few of these seeds result in trees, but enough do so to insure continuous environmental tuning of the species.

For Pacific madrone a seedbed free of an organic layer, which harbors invertebrates (slugs) and post-emergence fungi, is best for regeneration. A partially shaded environment is best for natural development of the oaks. Reversing polarity of tanoak and California black oak acorns speeds up germination and enhances seedling survival and growth.

Fertilization with nitrogen and phosphorous significantly boosted California black oak seedling height growth, but was less effective for tanoak. In spite of irrigation, fertilization, shading, and use of containers, survival of tanoak seedlings in a plantation was only 33 percent after 4-6 years. Dieback and deformation were rampant. Tanoak apparently cannot be established in conventional plantations. Survival of California black oak was 64 percent after 7 years and establishment in standard plantations is recommended.

In clearcuttings, sprouts of these hardwood species initially number up to 150 per clump, but after 10 growing seasons decrease to less than 35. Height and crown width after 10 years is about 20 and 10 feet, respectively, with only minor differences among species. For the same timespan, sprouts in a shelterwood are about half as tall and three-fourths as wide.

Based on new volume tables, cubic volume growth of thinned stands ranged from 48 to 93 cubic feet per acre per year with indications that thinning to 100-125 square feet of basal area per acre was best.

Ecologically, Pacific madrone, tanoak, and California black oak possess a host of adaptations that serve them well in severe environments. Huge numbers of seeds and sprouts insure that the species both remain in place and capture new area. Other adaptive phenomena discussed are the means taken to discourage competition beneath tree crowns, epicormic branching, the role of seed disseminators, competitiveness of sprouts, the stretched-out germination period, root-shoot ratios, thickened rootstocks, need for multiple stems per clump, and ability to withstand high moisture stress.

Silviculture-Ecology of Three Native
California Hardwoods on High Sites
in North Central California

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Philip Michael McDonald

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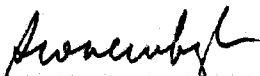
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I. INTRODUCTION

California black oak (Quercus kelloggii Newb.) and tanoak (Lithocarpus densiflorus [Hook. & Arn.] Rehd.) are the two most potentially manageable hardwoods in California (Roy 1962). Pacific madrone (Arbutus menziesii Pursh) also has high promise on high sites. The potential worth of these species was recognized long ago.

"The wood should be of more economic value in a region so lacking in hardwoods," said Sudworth of Pacific madrone in 1908. When speaking of tanoak, Sudworth also noted the "promise it gives of furnishing good commercial timber in a region particularly lacking in hardwoods."

Peattie (1953) called tanoak "a tree with a magnificent bole and fine hard wood." In 1882 Albert Kellogg stated that, after seasoning, the wood of California black oak "makes excellent axles for truck wagons, buffer for cars, and for a vast number of useful purposes." These statements suggest the future of these native California hardwood species.

Today, questions about these hardwoods are being asked by landowners and specialists in many natural resource fields. Landowners ask: Are my hardwood stands worth keeping? Will it pay to manage them, and if so, what growth and yield can I expect? Foresters are

looking at hardwoods from this viewpoint and from that of being competitors to conifers as well. They are particularly interested in the competitive potential of hardwood seedlings and sprouts.

Ecologists note that these hardwoods are arborescent members of the broad sclerophyll group. They are aware of these species ability to adapt and persist in a wide range of environments, and would like to know more about how this is accomplished.

Wildlife biologists are concerned with quantifying the seed potential of the three species as they are prime sources of food for deer and upland game. The amount of browse produced by California black oak also needs to be quantified. Landscape architects like the diversity and contrast hardwoods provide to travelers along scenic highways. To properly blend species, life forms, sizes, colors, and age classes, they need to know growth characteristics such as seedling and sprout growth rates and rates of crown expansion.

The foregoing questions and expressions of interest point out the need for a silvicultural-ecological program on native California hardwoods. So little biological information presently is available that basic research must accompany operational studies for the program to be effective.

The silvicultural and ecological studies that follow are described in five chapters. After the introductory chapter (I), which is mostly utilization, these are (II) seed, regeneration, and early seedling growth, (III) development and growth of a sprout stand, (IV) stand growth and yield, and (V) species adaptation and strategy.

Several specific studies are included in each chapter and in each Pacific madrone, tanoak, and California black oak are presented separately. Each chapter contains both basic and applied results, and where necessary background information from the available literature.

Chapter II through IV are mostly silvical, chapter V is ecological. In it, some of the results from the preceeding chapters are presented and discussed from the point of view of the individual species. These species or "crafty green strategists" are shown to possess numerous collective and specific adaptations that result in unique survival mechanisms. These mechanisms serve the species well and once established, allow them to almost continuously occupy an area as well as capture new area.

The research need is great. An overwhelming majority of the hardwood stands throughout Oregon and California are not being managed. They either are being exploited for low yield products or produce no products at all. Altogether, their potential for wood products, fiber, and energy is enormous. Proper management could lead to major new industries. The logical species to study initially are those with the most economic promise. These are tanoak, California black oak, and Pacific madrone.

UTILIZATION OF PACIFIC MADRONE, TANOAK, AND CALIFORNIA BLACK OAK

Today, future utilization of native California hardwoods is brightening. This is critical. Some degree of utilization or its potential must be recognized. It is the first step toward management of heretofore unmanaged species. A number of factors dealing with supply, demand, wood technology, and rising prices account for this brightening.

Before a species can be utilized economically it must be extensive enough in area and abundant enough in supply to justify at least one processing plant for several years. California black oak, tanoak, and Pacific madrone fulfill this requirement.

California black oak ranges from central Oregon to near the Mexican border. East to west in California it spans the state (McDonald 1969). The species is particularly abundant and reaches its best form in the Pacific Ponderosa Pine and California Black Oak forest types (Society of American Foresters 1954). Sawtimber volumes are 1.95 billion board feet in California (U.S. Forest Service 1954) and 1.2 billion board feet in Oregon (Overholser 1968). Of paramount importance is that 69 percent of the merchantable volume is in trees over 20.9 inches in diameter (U.S. Forest Service 1954):

<u>Diameter class</u> <u>(inches)</u>	<u>Supply</u> <u>(MMbf)</u>	<u>Percent</u>
11 - 20.9	600	31
21 - 30.9	829	43
31 - 40.9	452	23
41+	65	3

Tanoak grows best and is most abundant in northwestern California and southwestern Oregon, and specifically in Del Norte, Humboldt, Mendocino, Curry, and Josephine Counties. The species extends southward in the California Coast Ranges to Santa Barbara County. In the central Sierra Nevada, tanoak grows particularly well and is abundant in Butte and Yuba Counties. Tanoak sawtimber volumes are 2.04 billion board feet in California (U.S. Forest Service 1954) and 1.52 billion board feet in Oregon (Overholser 1968). About 58 percent of this volume is in trees larger than 20.9 inches in breast-height diameter (U.S. Forest Service 1954).

In California, Pacific madrone is found in about the same general range as tanoak. It extends northward throughout coastal Oregon and Washington and into British Columbia and Vancouver Island. Estimated sawtimber volume on commercial forest land in Oregon is 1.5 billion board feet (Overholser 1968). In California, the approximate sawtimber volume of this species is about 0.8 billion board feet (Smith 1956).

Distribution of all three species is best described as being scattered. Trees consistently are found as individuals, in clumps and groves, or occasionally clothing entire hillsides. All three species can form extensive stands, particularly when disturbance by fire or heavy cutting has been severe.

Growing stock volumes are large and increasing. In California, hardwood growing stock volumes (U.S. Forest Service 1954) are:

	<u>Million cubic feet</u>
California black oak	831
Tanoak	836
Pacific madrone	500

Past logging practices and wild fires have promoted hardwood stands (Fig. 1). In many instances hardwoods have replaced conifers (Horton 1960; Jenson 1939). Many stands have become merchantable and are augmenting the sawtimber supply. And large numbers of hardwood seedlings and sprouts are adding to growing stock volumes and will continue to do so (McDonald 1973).

In the northern California counties of Shasta, Trinity, Siskiyou, Lassen, and Modoc, forest inventory statistics for 1970 have been reported by Bolsinger (1976). He noted that net growing stock volumes were 261 million cubic feet for California black oak, 95 million feet for tanoak, and 126 million cubic feet for Pacific madrone.

These data are for a region not particularly supportive of hardwoods. Their magnitude suggests that hardwood growing stock volumes for California as a whole have increased significantly since the 1954 survey.

Net annual growth on hardwood sawtimber and growing stock on commercial forest land in California was about 45 million cubic feet (U.S. Forest Service 1954) and currently is probably much higher.

The trend of hardwood timber products output and annual cut is characterized by strong ups and downs (U.S. Forest Service 1954; Muerle and Hornibrook 1965; Barrette et al. 1968; Barrette 1971). These fluctuations are caused, in part, by fluctuations in the amount of hardwood pulpwood utilized in a given year. For example, in



Figure 1.--A typical scene in California. At least six California black oak advance seedlings have replaced the ponderosa pine.

California in 1952, 340,000 board feet were cut for pulp (U.S. Forest Service 1954), but in 1962, 19.7 million board feet were produced (Muerle and Hornibrook 1965). Another example is the output of fuelwood which was 188,000 board feet in 1952 and 2.3 million board feet in 1962.

Annual output of all hardwood timber products in California was:

	<u>Million board feet</u>
1952	20
1962	26
1968	13
1971	15 ^{1/}
1975	20 ^{1/}

Prices paid for California black oak logs delivered at the mill have increased steadily during the last 10 years (Dost and Bemis 1966; Barrette 1971; Allen 1975^{2/}):

	<u>Dollars per thousand board feet</u>
1966	38
1971	65
1975	85

^{1/} Estimated. Based on personal communication with forest industries in Shasta and Butte Counties, California. Output from these two counties was well over 16 million board feet. An estimated yield of 4 million board feet from all other California counties is considered conservative.

^{2/} Allen, Dick. Cal-Oak Lumber Company, Oroville, California. December 10, 1975. Personal communication.

The total annual harvest of hardwoods has increased in Oregon since the late 1940's (Overholser 1968):

	<u>Million board feet</u>
1949	2
1960	28

In California about 95 percent of the hardwood utilized as fuelwood is oak. The value of this resource after delivery to the buyers yard^{3/} is upward:

	<u>Dollars per cord</u>
1957	18
1958	20
1959	15
1966	27
1971	35
1975	50

Before 1965, oak stumpage charges for fuelwood were minimal. Since then, stumpage costs^{4/} have increased dramatically:

	<u>Dollars per cord</u>
1965	2.50
1967	4.00
1973	6.00
1974	7.50
1975	14.00

Indeed, a record price of \$24.40 per cord for a reasonably accessible lot of California black oak on the Shasta National Forest was recorded in December 1975.

^{3/} Various sources including California Agricultural Extension publications entitled "Markets for woodland products in California" and classified ads in Redding and Oroville, California newspapers.

^{4/} U.S. Forest Service. Timber Management Staff, Plumas and Shasta-Trinity National Forests.

The demand for hardwood forest products is increasing in California. Several factors account for this, not the least of which are a rapidly increasing population and a steady loss of commercial forest land to nonforestry uses. For example, from 1965 to 1980 the amount of commercial forest land will decline in California by 25,000 acres annually (Oswald 1970). Another cause of increasing demand is the rapidly dwindling supply of large, high-quality sawlogs from traditional eastern sources. For example, less than one-fifth of United States hardwood sawtimber is 15 inches d.b.h. or larger and of grades 1 and 2 (Siegel and Row 1965). Rail transportation costs from the southeast and Appalachia to California also are becoming prohibitive. But western producers have an advantage over other regions in the United States because freight rates are favorable to them west of a line extending from Arizona through North Dakota. West of this line lies a potential market (in 1964) of 110 million board feet. The hardwood forests of this region probably could supply all of this western market (Bloch 1964).

Nationwide, shortages for quality hardwoods are becoming more prevalent. A Northern Hardwood Association spokesman (Anonymous 1972a) noted that shortages exist in hard maple (Acer spp.), red oak (Quercus spp.), basswood (Tilia spp.), ash (Fraxinus spp.), butternut (Juglans cinerea L.), and cherry (Prunus spp.) in the high grades. Three months later this same spokesman emphasized that "shortages exist in all species and all grades of hardwoods." Consequently, furniture factories were beginning to reduce their standards concerning both

lumber species and grade specifications to broaden their range of available hardwood lumber (Anonymous 1972b). To cause the "hidebound" furniture factories to change their specifications signals a meaningful shortage indeed. "Mills are finding it hard to meet the demand from the export, furniture, flooring, box, and pallet markets." Increased demand in the furniture and bowling alley export markets have caused a shortage of dry kiln capacity" (Anonymous 1972b). These shortages mean that California hardwoods should receive more attention and stepped-up utilization.

The primary reason for increased demand of California hardwoods is that local managers and industries realize the potential of the native species and are penetrating wood product markets. Research on wood technology has helped.

After extensive research in wood technology and marketing, Forest Products Specialist William Dost (Anonymous 1963a) noted that California's little known hardwood lumber industry has real potential which can be unlocked by a combination of research and market development. Two years later such research resulted in the marketing of 2 billion board feet of tanoak in the north coast area for rail car decking.

To be economically marketable, products from a species must have certain sensory and workability characteristics. Product suitability is based mainly on appearance, and physical, mechanical, and machineable properties.

An extensive literature exists on the wood technology of California black oak (McDonald and Sundahl 1967), Pacific madrone (McDonald and Sundahl 1966), and tanoak (McDonald 1977). Seasoning has been a major problem for these three species and much research has been directed to its solution. Much of the past seasoning difficulty has been the result of using kiln drying equipment and short time-high temperature softwood schedules. At least 18 references pertain to seasoning California black oak and 14 each to tanoak and Pacific madrone. Methodology for piling as well as schedules for air and kiln drying have been worked out. A comparatively recent study noted that "careful drying under close control, employing recently developed techniques and treatments, make it possible to produce quality hardwood lumber of uniform moisture content with a minimum of degrade" (U.S. Dep. of Commerce 1968).

In Oregon, strength properties for California black oak, tanoak, and Pacific madrone were summarized by Overholser (1968) as are details of appearance, gluability, machinability, bending, seasoning, and treatability. The suitability of these species has been tested in Oregon for pulp and paper, veneer, and pallets. In addition, California black oak and Pacific madrone are compared to closely related, heavily-utilized eastern counterparts--northern red oak (Quercus rubra L.) and black cherry (Prunus serotina Ehrh.), respectively. Tanoak has no specific counterpart, but was compared to nine valuable eastern hardwood species. In terms of bending, shock, end-wise compression, hardness, breaking strength, specific gravity, and

weight, the three native California species compare favorably to valuable eastern species (Paul et al. 1955; Pfeiffer 1960).

In California, characteristics of appearance as well as physical, mechanical, machining, and seasoning properties are presented in great detail (U.S. Dep. of Commerce 1968). In the same study, marketing research identified 47 hardwood products that were recommended for manufacture from California black oak, tanoak, and Pacific madrone. These have been assembled into product groups by species.

California black oak

Lumber, flooring, furniture, paneling, boat parts, heavy beams and timbers, pallets, crossties, charcoal.

(Anonymous 1972c; U.S. Dep. of Commerce 1968; Dickinson 1958; Malcolm 1962; Smith 1952)

Tanoak

Flooring, paneling, veneer, plywood, pallets, boat parts, pulp, crossties, decking, mine timbers, baseball bats.

(Anonymous 1966, 1969a, 1969b; U.S. Dep. of Commerce 1968; Mast 1968; Pfeiffer 1957; Sander 1958).

Pacific madrone

Veneer, furniture, paneling, flooring, interior trim, bobbins and shuttles, novelties, tobacco pipes, stirrups, charcoal, pulp, and odor-free food storage units.

(Balls 1962; Dieter 1975; U.S. Dep. of Commerce 1968, May 1957, 1958; Robinson 1948; Ross and Hayes 1950).

An important new market began to develop in 1973. This was the Japanese market for "dirty" chips. Such chips are manufactured in the woods from whole trees and thus include wood, bark, leaves, branches and twigs. Tanoak and Pacific madrone were the preferred species, but California black oak was accepted in the expanded market. In 1974, the world-wide recession hit and curtailed the market. However, the market is expected to recover soon^{5/}.

Altogether, the combination of a large supply of large-size logs and increasing volumes of sawtimber, growing stock, and net growth, plus shortages of raw materials from traditional eastern sources indicate an extensive-enough supply to justify increased manufacturing capability. Trends of an increasing demand and higher unit prices should augment the profitability of such ventures utilizing tanoak, California black oak, and Pacific madrone.

That much of the hardwood volume is located on small acreages owned by nonindustrial private landowners is important. An example is provided by Bolsinger (1976) who found that in five northern counties of California, 45 percent of the total California black oak resource existed in small private holdings. In California (and the Nation) it is land owned by farmers and private nonindustrial owners that needs forest management and the employment of sound silvicultural and ecological practices most (Anderson 1973; Jones and Lord 1970;

^{5/} Personal communication with Soper-Wheeler Company, Strawberry Valley, California. December 8, 1975.

Worrell 1969). Increased volumes of forest products are needed from these acres if the nation is to produce necessary additional forest products (Wheeler 1970).

THE STUDY AREA

The silvicultural and ecological research program on selected native California hardwoods is needed now. Questions are being asked. Answers must be provided soon. Thus the research program must be located where the biological response to manipulation is fastest. This mandates high sites. Later, the research program can be extended to lesser sites.

The principal study site is the Challenge Experimental Forest, Yuba County, California. Characteristics of site quality, species, and stands are representative of about 1.5 million acres of high-site forest land in California.

This Experimental Forest's outstanding attribute is its high site quality. Soils are often over 100 feet deep, the mean annual temperature is 55° F., and annual precipitation averages over 68 inches. This combination of environmental conditions insures that vegetation becomes established quickly and is abundant in all successional stages. And with adequate resources it is fast growing. The tree form usually predominates.

The present timber stands are young-growth and mixed conifer-hardwood. The overstory is evenaged, largely because of earlier

harvesting. Logging first began about 1862 when heavy demand by the gold mining industry necessitated a relatively large sawmill at Challenge. This mill was located within the present boundary of the Experimental Forest and became the center of logging for the area until the early 1890's. Most of the virgin timber on the Forest was either harvested or burned by 1870. Consequently, the present conifer overstory is about 105 years old.

The dominant species presently is ponderosa pine (Pinus ponderosa Laws.). Other tree species are Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco), sugar pine (Pinus lambertiana Dougl.), white fir (Abies concolor [Gord. & Glend.] Lindl.), and incense-cedar (Libocedrus decurrens Torr.). Hardwoods, are primarily California black oak, tanoak, and Pacific madrone.

A stand table with the principal tree species arrayed in 4-inch diameter classes presents not only stand structure and species composition, but also insight into the successional status of the stand (Table 1). High numbers of hardwoods in the small diameter classes indicate more a persistent pioneer seral stage than a climax community. Imprisoned by a shorter life form than the taller conifers, these hardwoods are eventually relegated to the codominant, intermediate, and suppressed crown classes. If present, it is here that the species often are found.

Table 1.--Stand table for undisturbed young-growth forest. Challenge Experimental Forest, California

Species	Diameter class (inches)						Total
	3.5-8.0	8.1-12.0	12.1-16.0	16.1-20.0	20.1-30.0	30.1+	
	----- Trees per acre -----						
Conifers:							
Douglas-fir	27	13	7	3	4	2	56
Ponderosa pine	2	4	7	7	17	6	43
Sugar pine	1	0	1	0	1	1	4
White fir	6	2	1	1	1	0	11
Incense-cedar	47	12	4	1	1	0	65
Total	83	31	20	12	24	9	179
Hardwoods:							
California black oak	11	3	2	1	1	1	19
Tanoak	13	5	2	1	0	0	21
Pacific madrone	22	6	1	0	0	0	29
Total	46	14	5	2	1	1	69
Total	129	45	25	14	25	10	248

II. SEED, REGENERATION, AND EARLY SEEDLING GROWTH

Once seed forms, it is often subjected to a precarious existence in terms of climate, consumers, and human seed collectors. Seed that survives often does so because it is fortunate: falling into a protected place having an advantageous environment, or being placed in one by the collector. Knowing the most advantageous environment and creating or maintaining it to the benefit of a species is one of the most pressing needs in forestry today.

This portion of the study identifies specific silvical attributes of Pacific madrone, tanoak, and California black oak that are poorly known, and after intensive study, adds to our knowledge for regenerating and growing each.

INTERNAL SEED CHARACTERISTICS

After fertilization, the tiny one-celled embryo in the seed is the starting point of the next plant generation. Often the embryo is surrounded by the endosperm, which furnishes nourishment to it. In many seeds, the endosperm has been absorbed completely by the embryo by the time the seed matures. Acorns are good examples of seeds having no endosperm when mature. Seed of Pacific madrone possess this organ at seed maturity.

With time, the embryo enlarges and four important structures are formed: the young bud (plumule), stem (hypocotyl), root (radicle),

and in many species, one or two cotyledons (seed leaves). The cotyledons serve as food storage organs, as did the endosperm, and in acorns are the principal source of energy both for germination and growth of the young seedling.

Some seed, like that of Pacific madrone, contains both endosperm and cotyledons, which together with the true leaves, function much as a 3-phase system. The first phase, the endosperm, fuels embryonic development and provides the energy for germination and early seedling growth. The cotyledons, by virtue of their chlorophyll, serve as the second stage, manufacturing nourishment for the tiny seedling. The true leaves of the third stage then take over and synthesize food.

Once the seed is filled, it is thought of as being mature. At later stages of maturity, growth-promoting hormones decrease markedly, seed enlargement ceases, the various internal structures lose moisture, and the seed become dormant. In this state, it can withstand incredibly adverse conditions. Dormancy can be of five different types: (1) seed coats impermeable to gases and water, (2) mechanically hard seed coats, (3) physiologically immature embryos, (4) dormant embryos, and (5) rudimentary embryos (Amen 1963; Bonner and Varner 1965; Hatano and Asakawa 1964). Types 1 and 2 can generally be classified as physical dormancy, surmounted by physical treatment of the seed coat. Types 3 and 4 can be thought of as physiological dormancy, which can be overcome only through the mediation of certain physiological processes (Hatano and Asakawa 1964). In many instances,

however, two or more of these types cause actual seed dormancy.

Regardless of type of dormancy, a common regulatory mechanism apparently exists. Dormancy onset, prolongation, control, and termination are regulated by a balance between growth inhibitors and promoters. At the onset of dormancy, this balance is shifted in favor of the inhibitor component and internal seed development is held in check, sometimes for years. At this point a paradox exists: growth has ceased, yet the potential for resuming growth without loss of biologic integrity must be preserved, and at the same time death must be circumvented.

Eventually, increased light or temperature can serve as germinative stimuli, reduce the effect of the inhibitors, and increase the gibberellin level in the seed. In turn, the increased gibberellin might then overcome the inhibitors, and promote enzymatic digestion of reserved foodstuffs. Germination then could occur (Galston and Davies 1969).

Dormant embryos are the prime cause of dormancy in Pacific madrone and California black oak. Overcoming this form of dormancy is often practiced by subjecting the seeds to a period of prechilling or cold stratification. This process is thought to after-ripen such seeds and enhance germination.

PACIFIC MADRONE

Although many reproductive and regenerative aspects of this species were studied, particular emphasis was placed on seed characteristics, stratification, germination, effect of mold and invertebrates, seedling survival, and natural regeneration.

Physical Characteristics of Seed

Flowers of Pacific madrone appear as showy, white clusters in March and April at lower elevations in the north central Sierra Nevada. In early fall, each transforms into a brilliant red fruit (berry) with a thin, rough, granular skin. The generic name derives from "arboise," a Celtic word for rough fruit (Schopmeyer 1974). The fruit is quite mealy and contains about 20 hard seeds, ranging from 2 to 37 per berry. Berry color when fully ripe is bright red or bright reddish-orange. Yellowish-orange or yellowish-green berries also may occur along with red berries in the same cluster at the same time (Peattie 1953). October to December is the best time to gather berries for future propagation.

Bumper seed crops have been produced at Challenge for 2 of 18 years (1958-1975), with 7 light crops borne in intervening years. Some seed is produced every year. In a bumper year, fresh red berries gathered in November numbered about 1,130 per pound. Dried fruits are reported to number about 2,000 per pound (Mirov & Kraebel 1939). The yield of clean seed from red berries ranged from 1.59 to 1.93

pounds per bushel of fruit, or 3.60 to 4.35 pounds per 100 pounds of fruit. Seed numbered about 324,000 to the pound.

Yellowish-orange and yellowish-green berries from the same trees, at the same location, collected at the same time, were separated from the red berries and formed a different population. Both populations are discussed in the tests that follow.

Fresh yellowish-green and yellowish-orange berries numbered about 1,170 per pound, and contained about 237,000 seed. The seed were observed to be slightly larger in both length and width than seed from red berries. They also were lighter in color and more of them were small and hollow.

The age at which Pacific madrone first produces fruit is not recorded in the literature. On the Experimental Forest, initial flower production occurred at age four on a vigorous sprout; 62 berries resulted. On another sprout clump, the tallest and most vigorous sprout produced 11 racemes at age 8. Only a few berries resulted however.

The number of berries per tree also is not recorded. Consequently, three trees, judged representative of seed production for their diameter and height, were sampled for seed production. Tripod-mounted 6 X 30 binoculars were used for dividing the tree crown into easily-seen segments, and to aid in counting clusters and berries. Results are representative of a seed year rated as light. But even then, each tree that bore seed did so throughout most of its living

crown. Amount of living crown relates materially to berry production (Table 2).

These results give insight to the tremendous regenerative potential of the species and the amount of energy directed to reproductive material.

Seed Handling Practices

Berries of both colors were collected from fallen trees in November and taken to the laboratory. There they were gently crushed and allowed to ferment in water for 3 to 4 weeks. This process aided separation of the seed from the tightly adhering pulp. After drying at room temperature, all pulp except that which was similar in size and shape to the seed, was screened out. About 90 percent of the pulp was removed. Further cleaning with static electricity (Sundahl 1974) proved ineffective.

For red berries, sound seed was noticeably darker in color and slightly rounder at the pointed end than unsound seed. Proof of basing soundness on these characteristics was exemplified by a germination and cutting test of 6,400 thought-to-be sound seed. Of these, 96.7 percent proved sound.

Detecting soundness of seed from yellowish berries was more difficult. Seed color was not diagnostic. Small size proved to be the only useful criterion for separating sound from unsound seed. Henceforth, only seed sorted for soundness was used in this study.

Table 2.--Relationship between Pacific madrone tree characteristics
and berry production

<u>D.b.h.</u> <u>(in)</u>	<u>Height</u> <u>(ft)</u>	<u>Crown</u> <u>Ratio</u> <u>(pct)</u>	<u>Number</u> <u>of</u> <u>Clusters</u>	<u>Number of</u> <u>Berries per</u> <u>Cluster</u>	<u>Number of</u> <u>Berries per</u> <u>Tree</u>
9.1	59	.33	360	37	13,320
14.2	60	.25	924	28	25,872
15.7	51	.75	2760	39	107,640

Storage consisted of placing the dry, cleaned, and sorted seed in plastic bags and keeping them in a dry dark place at room temperature for 8 to 10 months.

Stratification

Seed and berries of Pacific madrone have been observed lying exposed to below freezing temperatures for weeks. Seed and berries also have been noted exposed in the snow in December. In contrast, Pacific madrone is an ericaceous species as is manzanita (Arctostaphylos spp.). whose seed are reported to give a variable response to heat, acid and stratification (Emery 1964).

In the literature, studies on stratification and germination of Pacific madrone are sketchy both in number and duration. Mirov and Kraebel (1939) attained 55 percent germination after 3 months stratification at 35- to 40-degrees F. Emery (1964) also recommended 3 months stratification, as did Chan.^{6/} It also is known that cold moist stratification can counter the light requirement for germination of some species.

Thus to be conclusive, stratification tests should include treatments of cold, light, heat, acid, and stratification.

^{6/} Chan, Frank. May 28, 1968. Personal communication.

Test With Cool Temperatures

Preliminary tests with cold treatments were attempted first. About 80 sorted Pacific madrone seed were carefully placed on moist blotters in each of five covered petri dishes. Each dish was then randomly assigned one of the following treatments:

Stratify 24 days at 36 ± 2 degrees F. No water added (dry stratification).

Stratify 24 days at 36 ± 2 degrees F. 11 milliliters (mls) of water added.

Stratify 24 days at 36 ± 2 degrees F. 25 mls of water added (seeds floating).

Stratify 24 days at 3 ± 10 degrees F. No water added.

Stratify 24 days at 3 ± 10 degrees F. 11 mls water added.

The seed, still on moist blotters in the petri dishes, were then removed from stratification and allowed to germinate. Each seed was considered to have broken dormancy when the radicle protruded $1/16$ inch beyond the seed coat. Temperature was maintained at 74 ± 4 degrees F. Light was not controlled and alternated in normal day-night pattern. During the day, light was both from overhead fluorescent lamps and that coming through windows and doors.

Germination results 30 days after removal from stratification indicated that freezing temperatures destroyed germinative ability. This is true whether the seed is dry or moist. Likewise, stratification above freezing yielded germination results of 43 percent for both 11 and 25 milliliters of water. Amount of water apparently has

little effect on stratification, providing it is plentiful. Mold threatened in all treatments and promised to be troublesome at longer stratification and germination periods.

Test In Darkness

Seeds of some species exhibit a requirement for light of a specific quantity and quality. During stratification in darkness, however, processes which substitute for a photochemical requirement may take place. For example, Bonner (1967) found that cold moist stratification essentially removes the light requirements for germination of sweetgum (Liquidambar styraciflua L.) seed.

Sorted seed from mixed red and orange berries was placed in covered petri dishes filled with fine, screened (2 mm) sand. Sand received preference over moist blotters because previous tests indicated the moistened blotters and seed dried out when the moisture collected on the underside of the petri dish covers.

In this study, enough sand filled each dish to touch the dish cover at several locations. Each dish received 11 milliliters of water.

Five dishes, four plus a control, of 100 seeds each, were sealed in a light-proof container and placed in the refrigerator. Stratification was at 36 ± 2 degrees F. for 35 days. After removal from the refrigerator, the container remained sealed for 15 days at 74 ± 4 degrees F. The seal then was broken and the germinated seeds counted.

The control also was removed at the same time; temperature was 74 ± 4 degrees F. and light was both natural and artificial as in the test with cool temperatures.

Results showed 44 percent germination in darkness, 53 percent germination in light. Mold was prolific in the test, and although present, not as bad in the control. Because of the mold problem, differences between test and control are not regarded as meaningful. Test seedlings had white hypocotyls and pale-yellow cotyledons. Generally, seedlings were long and spindly. It appears that light is not a necessary factor for germination of Pacific madrone seed.

Seed From Red Berries--Effect of Heat, Acid, and Stratification

In 1968, sound seed from red berries was used to test four stratification treatments for time periods of 0, 30, 60, 90, and 120 days. Each treatment for each period was replicated four times. Treatments were: (1) Immediately set out 1 replicate without stratification, stratify others for four time periods; (2) Place in concentrated sulphuric acid for 1 minute, set out one replicate without stratification, stratify others for four time periods; (3) Place in muffle furnace 1 hour at 203 degrees F., set out one replicate, stratify others for four time periods; and (4) Place in concentrated sulphuric acid 1 minute, in muffle furnace 1 hour at 203 degrees F., set out one replicate, stratify others for four time periods.

Testing to determine the optimum period of immersion in acid was necessary. After several trials, a 1-minute interval proved best. Longer intervals pitted the seed coat or exposed the endosperm; shorter intervals left the seed coat glossy and not dissolved enough. After treatment, stirring and washing with copious amounts of running water removed any remaining acid.

Each replicate was a standard petri dish and cover with a disk of moistened blotting paper at the bottom. One hundred sound seeds were carefully distributed about the disk, with no berry pulp or foreign material permitted. The stratification temperature was maintained at 36 ± 2 degrees F. in the specially equipped refrigerator. Each dish was checked at 2-day intervals and the blotting paper kept moist by adding water.

Preliminary work had indicated potentially severe problems with mold. Thus to reduce susceptibility of infection, the petri dishes remained covered throughout the study, except for brief moments when adding water or removing germinated seedlings. Also, a weak solution of fungicide (Captan) was initially added to each dish.

Upon reaching the end of the designated stratification period, the petri dishes with blotters were taken from the refrigerator and placed on tables in the laboratory for germination. Temperature was controlled at 74 ± 4 degrees F., and light alternated between daylight and darkness as described earlier. Added water kept the seed and blotters continually moist.

Germination counts were taken every other day for 80 days. At the end of the germination period, ungerminated seed with fully

developed embryos were considered sound. Some seed became moldy. These were checked, always found sound, and added to the number of sound seed.

Evaluation of the various stratification treatments was by germinative capacity (completeness), germinative energy (speed), and amount of germination at peak day and initial 10-day intervals. Results for germinative capacity are presented in terms of percent sound seed, germinative energy in days, and peak and 10-day germination in percent of viable (germinated) seed.

Analysis of variance and Tukey's Multiple Comparison Test were utilized to statistically portray significant differences among the four stratification treatments and five stratification periods mentioned earlier. Only germinative capacity was subjected to these tests. These data were transformed previously by arc sine to produce an approximately homogeneous variance (Dixon and Massey 1957).

Germinative capacity readily portrays the total and sometimes long-term effect of the treatments applied. In this study of various stratification times and techniques, major differences occurred (Table 3). Analysis of variance indicated differences among treatments and stratification periods ($p = .01$). Differences among replications were not significant, hence composite values from all replications were formed and analyzed further by Tukey's test. Results of this test proved stratification alone, and acid and stratification, to significantly better germination ($p = .05$) over those treatments

Table 3.--Germinative capacity of Pacific madrone seed after four stratification treatments
and five time periods. Challenge Experimental Forest, California

Stratification period (days)	Treatment			
	Stratification	Acid & stratification	Heat & stratification	Heat, acid, & stratification
	----- Percent of sound seed -----			
0	—	1	1	0
30	85	77	19	24
60	94	96	65	64
90	94	94	62	60
120	96	96	2	67

employing heat. No stratification caused germination to be significantly poorer ($p = .05$) than any other treatment.

Over the four stratification time periods, germination as influenced by treatment, was:

<u>Treatment</u>	<u>Germination (percent)</u>
stratify	92.0
acid and stratify	90.8
heat and stratify	36.8
heat, acid, and stratify	54.0

Mold was a constant problem in spite of the fungicide and covered petri dishes. In general, it became worse with length of stratification period, and with treatments involving heat. In the 30-day stratification period, mold reduced germination by 5.6 and 7.7 percent for stratification alone and stratification after acid, respectively. The percentage of seed that became moldy was much higher in the two treatments employing heat. It is not correct, however, to assume that low germination in these treatments was the result of mold. Most seeds in the heat treatments would not have germinated anyway.

The heat-treated seeds exhibited not only an erratic germination pattern but incomplete germination. They would imbibe water, perhaps too much, quite rapidly and burst open at the pointed end. In fact, several instances were noted where the entire seed contents were expelled from the seed coat. The tiny radicle also would swell and develop an easily-seen, dark-colored tip. In some seed, the radicle

would eventually elongate, in others, radicle elongation progressed no farther. Mold eventually engulfed most of the nonelongating seed.

Stratification was the key to germination. In a separate test, 400 seed, taken directly from dry storage and placed on moist blotters for germination at room temperature, were monitored for 142 days. Only 1 seed germinated. Seed subjected to heat and acid or both, but not stratified, exhibited a similar trend (Table 3). Of 1,200 seed, only six germinated in 142 days.

Germinative speed is presented only for the four treatments involving stratification, and only for the 30- and 60-day stratification periods. Nonstratified seed germinated too poorly to determine any other relationships. Seed stratified longer than 60 days germinated in the refrigerator. In fact, 50 days is about as long as Pacific madrone seed can be kept ungerminated at 36 degrees F.

Two days after removal from stratification, germination exploded. Germinative energy of all treatments was 2 to 6 days for seed stratified 30 and 60 days (Table 4). Of particular note was the percentage of seed that germinated on the peak day. This ranged from 79 percent for just-stratified seed to 33 percent for seed subjected to acid, heat, and stratification (Table 4).

A further illustration of the rapidity of germination is demonstrated by the percentage of seed that germinated after 10 days. Stratification alone and stratification and acid conditioned the seed best for rapid and complete germination (Table 5).

Table 4.--Germinative energy of Pacific madrone and percent of viable seed
germinating on peak day

Time period days	Treatment							
	Stratification		Acid & stratification		Heat & stratification		Heat, acid, & stratification	
	days	percent	days	percent	days	percent	days	percent
30	2	79	4	50	6	35	4	33
60	2	71	2	62	2	34	4	35

Table 5.--Amount of viable seed germinating after 10 days

Time period (days)	Treatment			
	Stratification (percent)	Acid & stratification (percent)	Heat & stratification (percent)	Heat, acid, & stratification (percent)
30	99	94	78	88
60	100	99	90	89

For the stratification time period of 90 days, germination for stratified but untreated seed was 99 percent completed in the refrigerator. From 68 to 85 percent of the viable seed in the other treatments for the same time period germinated in the refrigerator. Over 98 percent of the viable seed kept in the refrigerator for 120 days germinated in it.

Close scrutiny of the three tables and the statistical analysis indicates a distinct difference between nonstratified and stratified seed. Plainly, stratification is necessary for reliable germination. Another strong and easily seen difference is between stratified seed or acid-dipped and stratified seed, and those treatments involving heat. In the heat treatments, dormancy in the embryo apparently was partially and imperfectly broken. Low germinative capacity, slightly slower germinative energy, lower peak-day germination, and lower 10-day germination all support this thought. Another supportive point is that several seed reverse germinated--that is, the cotyledons emerged and turned green. Normally the radicle is the first to emerge from the seed coat.

The 30-day stratification period conditioned the seed to the point that 85 percent of the seed germinated, and 99 percent of those that did germinate, did so in 10 days. The 60-day stratification period indicated a germinative capacity of 94 percent, germinative energy of 2 days, and 100 percent germination of viable seed in 10 days. Should the plant propagator desire a germinative capacity of at least 90 percent, a stratification period of about 40 days is

recommended. Germination and mold while undergoing stratification should not be a problem for the 40-day period.

Seed from Yellow Berries

Seed from yellowish berries was stored in a cool, dark, dry room for 10 months in sealed plastic bags. Four replications, each of 100 seed, were then stratified in the refrigerator at 36 ± 2 degrees F. for 30 days. At no time did the blotter paper or seed become dry. No fungicide was used.

Based on germination and cutting tests, over 99 percent of the seed proved sound. Germinative capacity was 93 percent. Germinative energy was manifest at 2 days, with 57 percent of the seed germinating on the peak day. Over 99 percent of the viable seed germinated in 10 days. Mold continued to be a problem, decreasing germination by 5.3 percent.

Another test with yellowish berries contrasted the effect of stratification. Four replications of 100 seed each, were taken from storage, moistened, and allowed to germinate without stratification. Less than 6 percent of the seed germinated. The remainder were rotten in 28 days.

Seed from Red and Yellow Berries--Little Difference

Contrasting physical seed characteristics and germinative behavior for seed from red and yellow berries was revealing. Physically, seed from yellowish berries were larger and lighter in color, but had a higher percentage of small and hollow seed. These atypical seed were removed when sorting for soundness. For this reason and because of larger size, seed from yellowish berries numbered less per pound than seed from red berries.

After 30 days of stratification, germinative capacity, germinative energy, percent germination at 10 days, and amount lost to mold, were remarkably similar for seeds from the two colors of berries. Slight differences in percent germination the peak day and the amount of seed which germinated without stratification probably are not meaningful.

Thus, the propagative implications of this contrast are that seed from berries of both colors can be effectively sorted to promote soundness. Once sorted, both have a high and equal reproductive potential if properly stratified.

Germination from Berries--Laboratory

To evaluate the germinative effect of leaving seed in the berry, 51 stored berries were placed in moist peat moss at marked locations and then in the refrigerator for stratifying. The stratification

temperature was 36 ± 2 degrees F., and the interval was 45 days. The peat moss received water as needed and never was allowed to dry out. After stratification, each berry was carefully buried 1/2 inch in a sterilized vermiculite bed. The bed was then subjected to the same conditions of temperature and light as the previously-discussed seed.

Eleven berries showed evidence of germinating seed within. Two berries were boosted above ground by the burgeoning radicles. One of these berries yielded five radicles and seven cotyledons; two cotyledons being trapped in the berry. Five seedlings resulted and all became free of the berry. The other above-ground berry yielded seven radicles and one cotyledon. Within 35 days, cotyledons of both berries developed a grayish cast, bent over at the middle, and died. Mortality symptoms strongly indicated post emergence damping-off by Pythium and Phytophthora fungi.

The other nine berries remained below ground, and only emergent cotyledons were reported. One set of cotyledons, about one-inch tall, never escaped the inner seed coat and soon died. Only ten living seedlings remained after 55 days. Again symptoms indicated high mortality from damping-off fungi.

Germination of Pacific madrone is epigeous. The cotyledons begin to photosynthesize soon after emergence from the seed coat, and continue to do so for several months.

While a small sample, this test indicated the best propagation practice is to separate the seed from the berry. Evidence from berries indicated poor and intermittent germination, problems by

seedlings in getting disengaged from the berry and seed coat, and heavy mortality from fungi. Although care was taken, fungal problems may have been magnified by the laboratory environment. These same problems, however, also may occur in nature.

To better assess the problem of fungi, several hundred germinating seed were carefully placed in loam-filled half-gallon milk cartons in a heated greenhouse. Several seed occupied a carton, each 1/8- to 1/4-inch deep. No fungicide was used. Tiny seedlings resulted, but perished by the hundreds. One day they would be green and robust and erect; the next day, bent over and shrivelling. Entire cartons of seedlings would succumb overnight. Eleven months later, only 13 cartons contained one or more seedlings.

Germination from Berries--Field

Because fungi were rampant in the laboratory, a germination study with red berries was conducted in bare mineral soil on the Experimental Forest. Test variables were full sunlight vs. partial shade, berries on surface vs. 1/4-inch deep, and screened (protected) vs. not screened. Berries were set out in February and allowed to stratify in situ.

Problems arose almost immediately. Some berries disappeared, and depredation by mice and birds was common. Because these problems can plague Pacific madrone regeneration specialists elsewhere, they are discussed more fully in the section that follows.

Pacific madrone berries, seed, and seedlings lead a precarious existence in nature. Birds and rodents are voracious eaters of seed and berries. At Challenge, mousetraps baited with a single red berry were more effective at catching the white-footed deer mouse (Peromyscus maniculatus) than traps baited with peanut butter and wheaties. Mice even dug under screens to devour Pacific madrone berries. Birds also were observed eating unprotected berries.

Depredation by birds is well referenced in the literature. Van Dersal (1938) noted five species of birds, including the band-tailed pigeon (Columba fasciata) and dove (probably Zenaidura macroura) eating Pacific madrone berries. Martin et al. (1961) listed the band-tailed pigeon, long-tailed chat (Icteria virens auricollis), and varied thrush (Ixoreus naevius) as berry eaters. Smith (1968) found that 17.3 percent of the band-tailed pigeons' November diet and 11.4 percent of its December ingestion were Pacific madrone berries. In fact, 111 berries were found in one pigeon--so many that it was incapable of flight. Peattie (1953) noticed band-tailed pigeons devouring Pacific madrone berries, and remarked "... the madrone groves ring with the shots of their persecutors."

In addition to mice and birds, a wood rat (Neotoma fuscipes) also eats the berries of Pacific madrone. So do deer (Odocoileus hemionus hemionus, Odocoileus hemionus columbianus) (Taylor 1956; Sampson and Jespersen 1963).

If the berries and seed survive long enough to germinate, damping-off fungi kill many. In the Santa Cruz Mountains of central

coastal California, Pelton (1962) found fungus to cause 28 percent of total seedling mortality. Death was from constriction of the hypocotyl, decay of the radicle, or both.

Losses on the Experimental Forest were severe. Not only did the berries or tiny seedlings die from birds, rodents, and damping-off, but also from unknown causes. Some berries and seedlings simply disappeared, even though protected by buried, pinned-down screens. Soil-dwelling invertebrates were suspected. Pelton (1962) observed slugs (Order Pulmonata) feeding on cotyledons in early morning although most damage was nocturnal.

Because of these losses, germinative speed and completion could not be ascertained. Only the following trend was reportable: berries that were covered and protected, in a partial-shade environment, yielded more seedlings, which survived better.

Seedling Survival and Growth

Berries of Pacific madrone are heavy. They either fall directly beneath the tree into organic material of mostly tough leathery leaves, or are more widely disseminated by birds and possibly rodents. Both mechanisms cause most seedlings to begin development in heavy organic litter in shade. Such an environment leads to high fungal mortality, succulent tissues vulnerable to drought, and because of impedance by the organic matter to downward-thrusting seedling roots, heavy mortality from drought.

Interactions also operate. Heavy concentrations of organic material in shade favor root-tip killing fungi. After attack, root growth slows down and seedling height growth is stunted. Small tender seedlings with poorly developed root systems become even more susceptible to slugs and drought.

Those seedlings which began life in forest openings or clear-cuttings are subjected to searing soil surface temperatures, high ambient temperatures, and prolonged drought. Thus both shade and sun environments ultimately are harsh. Early mortality of Pacific madrone seedlings is correspondingly high. For example, Pelton (1962) found that by July 29 no Arbutus seedlings were alive in shade plots and only 2 percent were alive on sun plots. His original population numbered 829 seedlings.

Other authors have noted the difficulty of establishing Pacific madrone regeneration from seed. Van Dersal (1938) stated that a yield of about 1,000 usable plants per pound of seed could be obtained, presumably in near-ideal nursery conditions. Sudworth (1908) observed Pacific madrone seed to germinate best when it was well covered by moist soil. In drier places, germination was poor and seedlings scarce. Cooper (1922) recorded no Pacific madrone in the Quercus-Arbutus-Aesculus forest on Jasper Ridge in the Santa Cruz Mountains. Tarrant (1958) was more direct and stated that seedlings generally are not abundant. Sprouts form the principal mode of reproduction.

Artificial Regeneration

Thirteen half-gallon milk cartons, each containing 1 to 5 year-old Pacific madrone seedlings, were outplanted in a 5-acre clear-cutting on the Experimental Forest. The soil was scarified by a bulldozer-mounted toothed blade, and was free of competing vegetation. Aspect was northeast.

Six cartons contained living seedlings after three growing seasons. Seedling height averaged 2.7 feet, ranging from 1.8 to 4.0 feet. After six growing seasons, five spots remained stocked, and seedling height averaged 4.5 feet. Thus mortality of nursery-grown, containerized seedlings on bare mineral soil free of competing vegetation, was 62 percent in 6 years.

Natural Regeneration in a Mixed Conifer-Hardwood Stand

Pacific madrone seedling frequency, density, and mortality were evaluated in contrasting environments created by different conifer regeneration cutting methods. These were seed tree, shelterwood, and single-tree selection. Results also were compared to composite values from three uncut control compartments that ranged from 13 to 30 acres. Seed-tree compartments numbered eight and ranged in size from 10 to 38 acres; shelterwood, four compartments of six acres each; and single-tree selection, three compartments each of six acres. Regeneration data were recorded for at least 6 years in

in each cutting method:

	<u>Year Cut</u>	<u>Years of Record</u>
Shelterwood	1958	1958-1966
Single-tree selection	1958	1958-1966
Seed tree	1960	1961-1966
Seed tree	1962	1963-1968

In all cutting methods, a combination slash disposal-site preparation treatment was applied. This consisted of dozer piling and winter burning slash on two-thirds of the area in each method, and top-logging and scattering slash on the remaining one-third. Of course where dozing took place, much mineral soil was created, but where tops were merely lopped, mineral soil resulted only from logging. The two thirds-one third proportion was consistent in each cutting method, but the amount of mineral soil created decreased as the intensity of cutting method decreased from seed tree to single-tree selection.

Eight conifer seed trees per acre served as the seed source in the seed-tree method. These ranged from 20 to 50 inches in diameter at breast height. Twelve trees per acre in this diameter range remained as the shelterwood. In both methods, seed and shelterwood trees were present for the entire study period.

In the seed-tree and shelterwood methods, conifers 12 to 20 inches d.b.h. were harvested, and hardwoods over 12 inches d.b.h. were poisoned. Many trees 3.5 to 12 inches in diameter were removed in the piling site preparation treatment, but individual trees and

clumps of hardwoods and conifers in this diameter class remained. These averaged about 57 per acre in each method.

In the selection cut, after logging, many more trees of all species remained:

<u>Diameter class</u> <u>(inches)</u>	<u>Number</u> <u>(per acre)</u>
3.5-12	94
12.1-20	25
20.1+	29

In general, the more intensive the cutting method, the more intensive the site preparation treatment and the fewer the number of residual hardwood trees. Also, the more intensive the cut, the greater the loss of the organic layer on the forest floor. The amount of shade was reduced as well. Thus the intensive seed-tree method removed most of the seed source but provided much bare mineral soil. In contrast, the single-tree selection method provided a larger potential seed source for Pacific madrone but a poorer regeneration medium.

After logging, Pacific madrone trees 3.5 to 12 inches d.b.h. numbered 7 per acre in the seed-tree method, 10 per acre in the shelterwood, and 9 per acre in the selection cutting. Seed from these few small trees, plus that carried into the cutting areas by birds, constituted the Pacific madrone seed source. About 28 trees per acre in this diameter class and 1 per acre in the 13- to 16-inch class were present in the control.

Sampling for regeneration was by circular milacre plots which followed a random-start systematic design. Sampling intensity for the three cutting systems generally was proportional to size and number of compartments. For seed tree sampling intensity was 348, shelterwood 120, and single-tree selection 90 plots. Over 100 plots were present in the control. New seedlings were examined initially when about 2-months-old and annually thereafter. All were marked to expedite growth and survival trends. Seedlings 4 years and older, and less than 4.5 feet tall before logging, were recorded as advance reproduction. In this study, frequency denotes how well the seedlings are distributed throughout the sampling area. High values indicate good distribution; low values indicate either few seedlings or a clumpy distribution.

Seed production of Pacific madrone in 1960 was high and rated as a bumper crop. This was the only bumper crop in this 11-year study, although light crops were produced frequently. They resulted in new seedlings in each cutting method almost every year (Fig. 2). Regeneration from a light and bumper crop is presented to portray seedling survival for the different cutting methods. Seedlings from each crop were evaluated as a specific crop for at least 3 years, after which they were aggregated as advance reproduction along with that already present.

At this point, one should remember that Pacific madrone was an unwanted and partially eliminated species. Therefore these data do not illustrate the regeneration potential of the species. Seedling

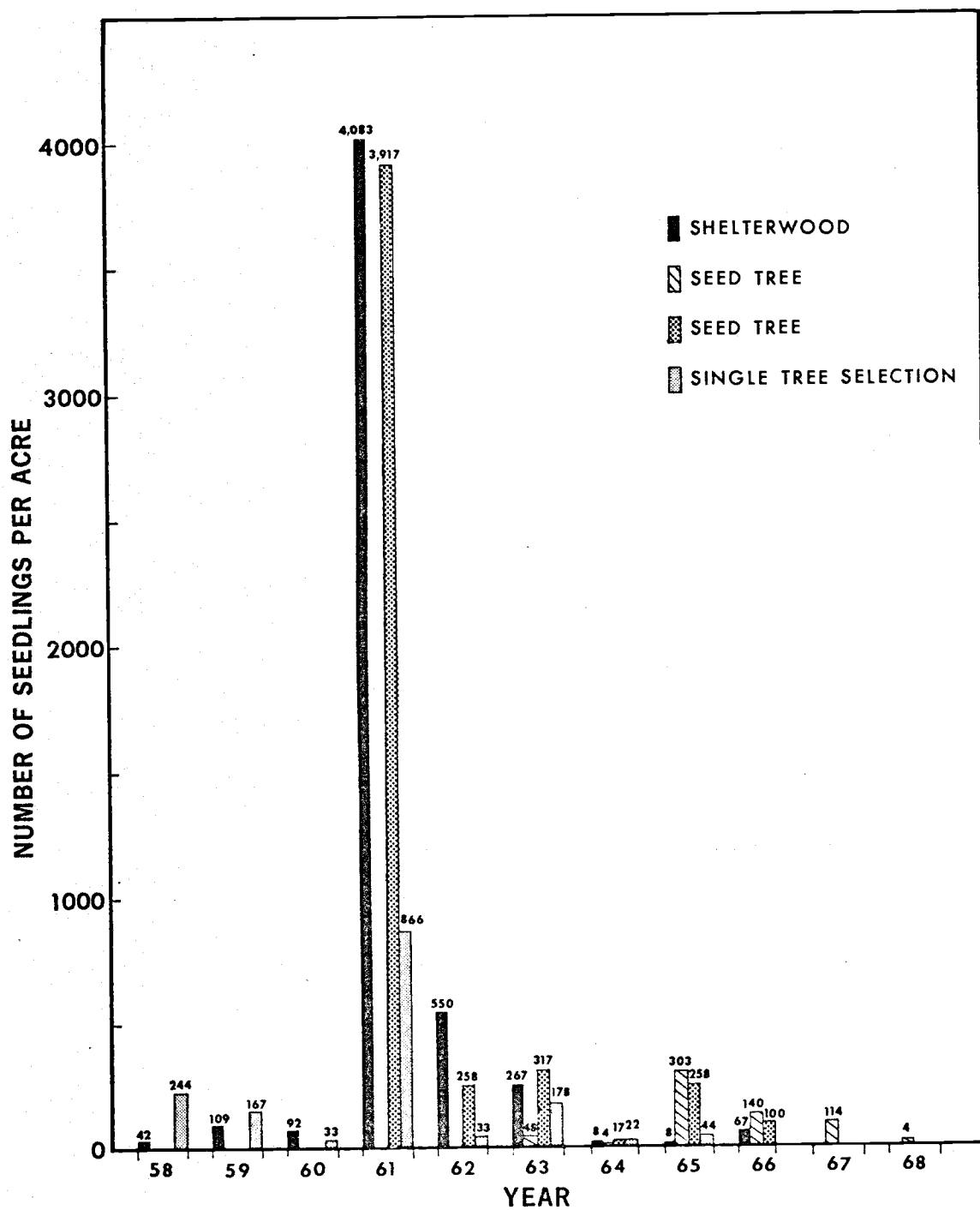


Figure 2.--Eleven-year record of new Pacific madrone seedlings.

survival trends, however, are meaningful.

"Poor" best describes first-year seedling survival from the 1960 seed crop for the three cutting methods (Fig. 3). After 4 years, 43 percent of the seedlings in the seed-tree cut, 40 percent of those in the shelterwood, and only 3 percent in the single-tree selection method remained. Such declines reflect high within-plot mortality. When Pacific madrone seedlings numbered 20 or more per milacre, they often suffered from intensive competition which reduced their numbers drastically. Corresponding frequency values quantify a generally poor seedling distribution: seed tree, a decrease to 30 percent; shelterwood, to 30 percent; and selection, to only 3 percent. Mortality probably was caused by a number of agencies. Many seedlings succumbed to drought as evidenced by dead dry seedlings; others simply had disappeared by the next survey.

Seedlings from the lighter seed crops were much fewer. First year density values were under 550 seedlings per acre, and frequencies under 14 percent. As before, a lower proportion of seedlings died in the seed-tree environment than in that of the other cutting methods. These trends were true of the other light seed crops as well. Although mortality was high, a few seedlings from most seed crops survived and became advance reproduction.

Seedlings which survive long enough to become advance reproduction represent the reproductive payoff of the species. They are the most robust and vigorous seedlings, occupy the most favorable microsites, and have a much lower risk of mortality. Should fire, storms,

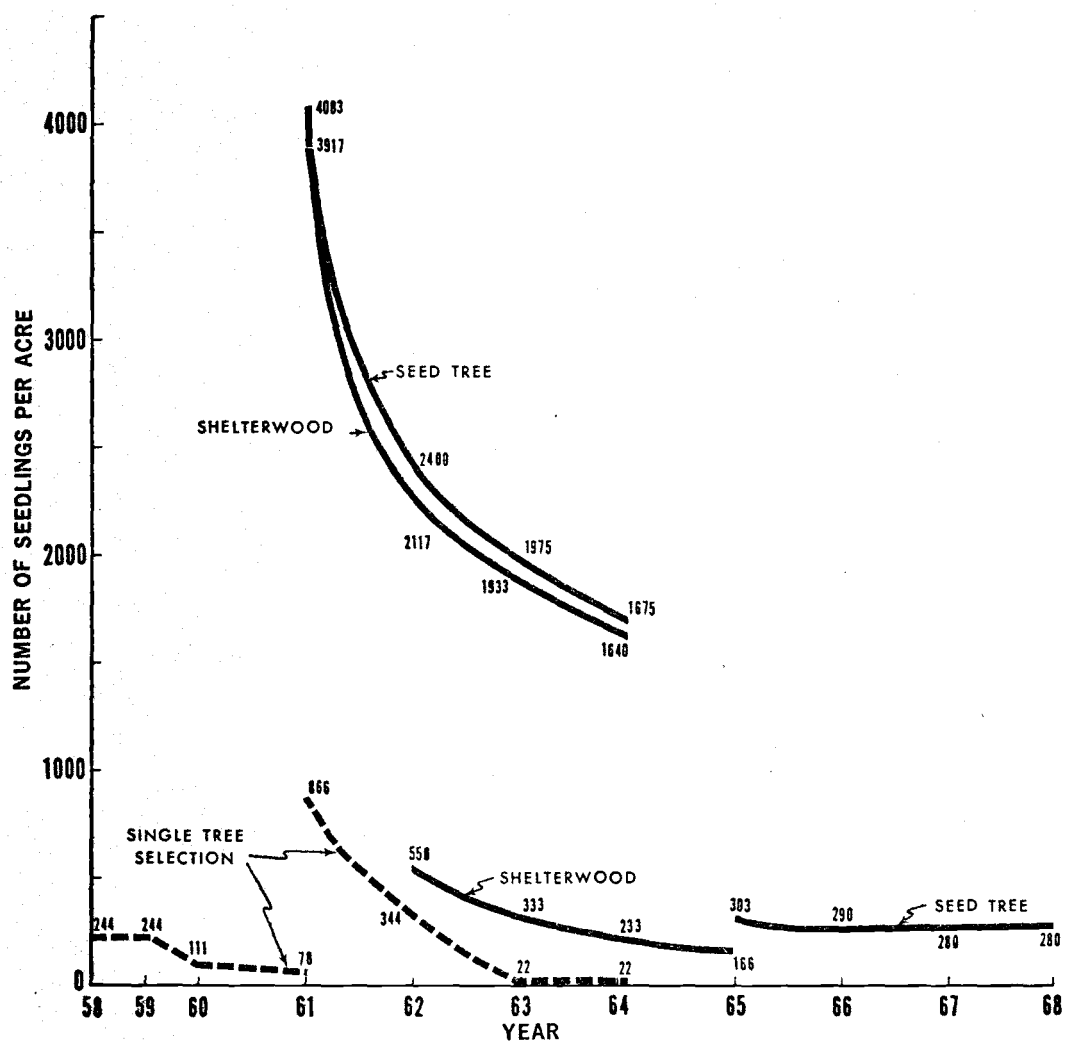


Figure 3.--Seedling survival patterns of Pacific madrone by several cutting methods and years of origin.

or logging take place, most have enough energy to become sprouts. Sprouting, of course, gives Pacific madrone a major competitive advantage over nonsprouting species.

By 1966, the accumulative density of Pacific madrone advance reproduction for the 1958 through 1966 period, excluding that initially present, was 1417 seedlings for seed tree, 1833 seedlings for shelterwood, and 178 seedlings per acre for single-tree selection (Fig. 4). The contribution of the bumper seed crop is well illustrated. Lighter seed crops, falling on similarly prepared ground resulted in many-times fewer seedlings. A good example of this is the 285 advance seedlings from the 1964 seed crop in the seed-tree area of 1962 (Fig. 4). Corresponding frequency distribution of advance reproduction by cutting method was: seed tree 33 percent, shelterwood 40 percent, and selection 16 percent.

Compared to the "background" density of 19 advance seedlings per acre and a frequency of 2 percent in the control, cutting enhanced Pacific madrone regeneration. This enhancement was caused by stimulation of the smaller trees to produce more seed, and the presence of bare mineral soil. Pacific madrone trees in the seed-tree and shelterwood methods were observed to be heavily laden with berries, while those in the selection cutting yielded few. In 1971 and 1974, trees of similar size in thinned hardwood growth plots produced prodigious amounts of seed; trees in the uncut control bore none.

Drought, acting alone and through interaction with fungi and invertebrates, appeared to be worse where mineral soil was absent.

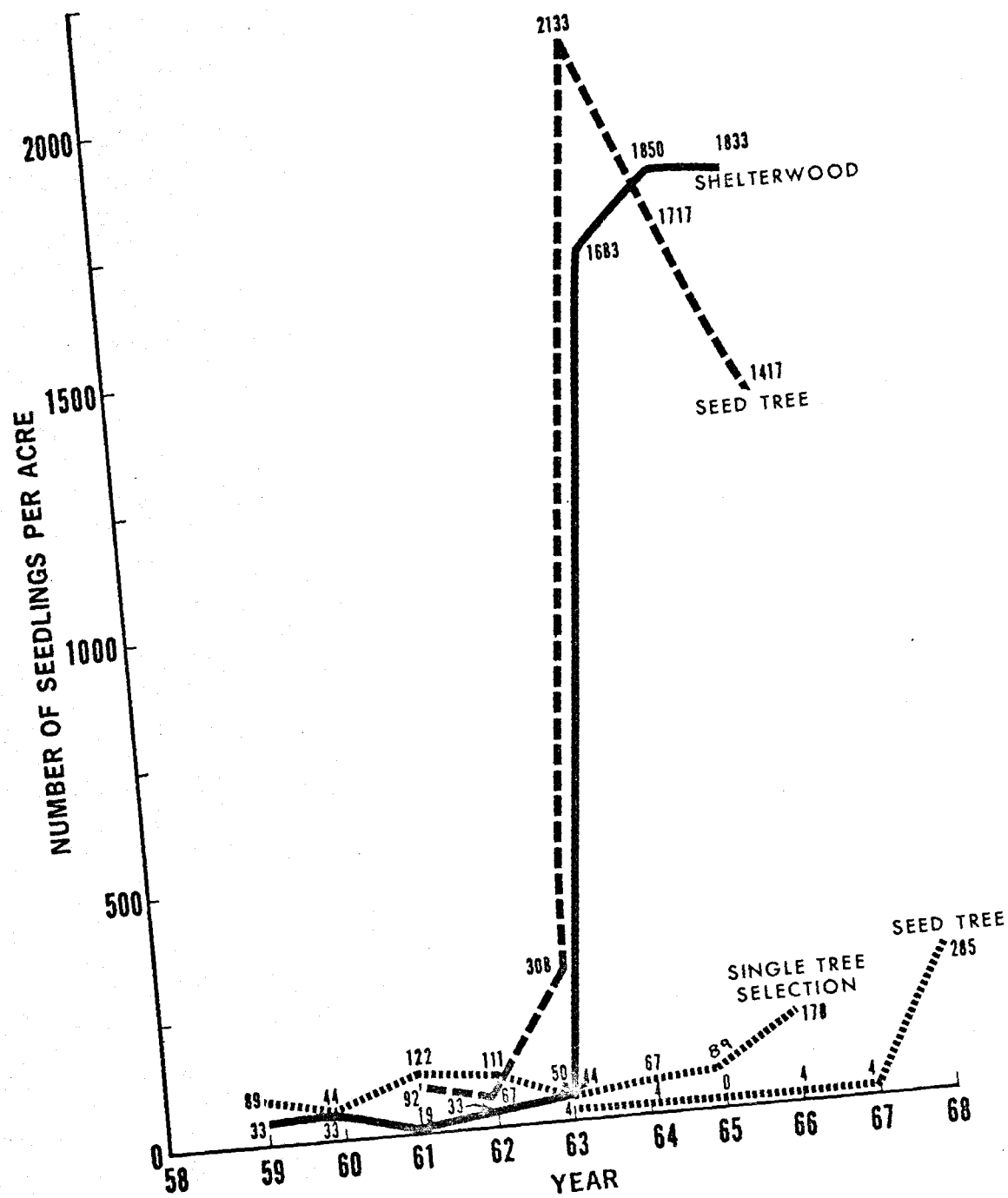


Figure 4.--Cumulative density of Pacific madrone advance reproduction.

Lack of mineral soil best explains the demise of nearly all seedlings from the 1960 seed crop in the single-tree selection method, and perhaps the many-times smaller amount of advance reproduction associated with it. It is inescapable that not one new seedling in 11 years was found in the cool shady control compartments having a heavy accumulation of organic material on the forest floor. Yet about 4,000 seedlings per acre began life in the heavily disturbed mineral soil seedbed beneath seed trees and shelterwood.

The shelterwood environment probably is best. High mortality for advance reproduction beneath seed trees as compared to the virtual lack of mortality in the shelterwood (Fig. 4) suggest that this environment is more advantageous for continued prosperity of Pacific madrone advance reproduction.

Seedling height growth was rather slow. Two-year-old seedlings on the Experimental Forest were 3.5 inches tall. After 10 years, advance reproduction in the single-tree selection cutting averaged 2.6 feet tall with a range of 0.4 to 10.0 feet. Pelton (1962) also found seedling height growth to be slow. After one year, undamaged seedlings on bare mineral soil in full sunlight were 1.9 inches tall. Root length was 4.0 inches.

In the seed-tree and shelterwood areas, advance reproduction densities of 1,417 and 1,833 seedlings per acre could constitute formidable competition to softwood seedlings. But Pacific madrone seedling height growth is slow and seedling distribution is clumpy. Thus competition from Pacific madrone seed is not likely to be severe except

possibly in small areas where density is high.

In the future, Pacific madrone trees, from seed, will be present in all cutting areas, mostly as individual trees or occasionally as small groves. Most will be relegated to intermediate and understory strata. But they will flower and bear seed. Their contribution to the evolutionary potential of the species is large. Because of the sexual process, the genetic constitution of the species is constantly given new information and kept adaptable to the ever-changing environment. This is most important in a species like Pacific madrone whose most effective reproductive mode is via a vegetative process--sprouting.

Natural Regeneration in a Pure Hardwood Stand

This trial augments the study of natural regeneration. Fifty temporary 1/2-acre plots at 50-foot intervals were sampled throughout a 60-year-old pure hardwood stand. The stand was predominately tanoak but contained a good mixture of California black oak and Pacific madrone. It was undisturbed and quite dense (200 square feet of basal area per acre). Reproduction thus was a function of a good seed source, deep shade, 3 to 4 inches of organic material on the forest floor, and a pure hardwood environment in general.

Regeneration results for Pacific madrone showed no seedlings and about 80 advance seedlings per acre. Frequency values need to be

converted to the milacre standard. The conversion formula (Grant 1951) is:

$$S_B = 100 \left[1 - \left(1 - \frac{S_A}{100} \right)^{\frac{B}{A}} \right]$$

where S = stocking percentage
A & B = respective plot sizes.

About 4 percent of the plots (milacre basis) contained one or more Pacific madrone advance seedlings.

SUMMARY

Pacific madrone is a species with tremendous reproductive capability. Bumper seed crops are produced every 5 or 6 years and light crops are borne at least every other year. Rare is the year when no seed is produced. Usually a few trees are out of phase and bear seed when the majority of trees do not. Even then, seed production of individual trees is high. Amount of crown is important. On a high site, a 14.2 inch diameter tree with a crown ratio of 25 percent yielded nearly 26,000 berries. A tree that was 9 feet shorter in height but with a crown ratio of 75 percent produced over four times more berries.

Young stump sprouts produce flowers and berries as early as age 4. At this age, the dominant sprout usually is the sole producer in the clump, and in one instance produced 62 berries.

After the seed is gathered, it should be crushed and allowed to ferment in water for three or four weeks. Fermentation weakens the

bond between pulp and seed. It facilitates seed removal. After drying, all pulp except that which is similar in size and shape to the seed, can be removed by screening.

Even late in the fall, Pacific madrone berries are both reddish- and yellowish-colored. Seed from these different-colored berries is slightly different in size and color. That from reddish berries is usually smaller and darker. Sound seed from berries of both colors can be sorted successfully from unsound seed on the basis of size, color, and shape. After careful sorting, seed is at least 96 percent sound.

Storage of Pacific madrone seed is accomplished easily by placing clean dry seed in plastic bags and storing in a dry, dark place at room temperature.

Detailed stratification tests involving subfreezing temperatures, darkness, heat, acid, and stratification indicated that dormancy in this species primarily is embryonic. Most seed imbibed water quite rapidly regardless of previous treatment.

Heat, cold, dry cool stratification, or lack of stratification either prevented or strongly inhibited germination. Stratification following a brief immersion of seed in concentrated sulphuric acid proved satisfactory, but not significantly better than stratification alone. Stratification for 30 days at 36 degrees F. in an atmosphere high in moisture yielded a germinative capacity of 85 percent, germinative energy of 2 days, 79 percent germination of viable seed the

peak day, and 99 percent germination of viable seed in 10 days. Stratification for 60 days gave a germinative capacity of 94 percent and comparable values for germinative energy, peak-day, and 10-day germination percentages. A 40-day stratification period is recommended if a germinative capacity of at least 90 percent is desired.

Cool-moist stratification apparently cancels any need for light. Seed germinated almost as well in darkness as with combined natural and artificial light.

Stratification periods of 60, 90, and 120 days also were tested. They are not recommended--30 to 40 days is adequate to fully after-ripen seed of Pacific madrone. After 50 days, the seed germinates while stratifying in the refrigerator. And seed mortality from mold also increases with time.

Germination of seed in berries both in laboratory and field, proved to be poor and erratic. Seedlings had difficulty disengaging from the berry and seed coat, and suffered heavy mortality from fungi. Damping-off fungi, however, were rampant both in field and laboratory, and to cleaned seed or seed in berries. Fungi appear to be a major problem in natural and artificial regeneration of this species. In general, propagation in nursery and field is best with seed, not berries.

In the field, berries, seed, and seedlings, are devoured with gusto by many birds, animals, rodents, and invertebrates. Birds are a principal disseminator of Pacific madrone seed. That which is not devoured falls directly below the trees. Here the environment is

characterized by deep shade, a thick organic layer of duff and litter, lower temperatures, and higher relative humidity.

In this environment, germination of Pacific madrone is probably high. But seedling survival is abysmal. The heavy organic layer inhibits the downward-thrusting radicle, and provides an environment conducive to both damping-off and root-tip rotting fungi. Physically impeding the moisture-seeking root, or damaging it by fungi, result in an increased risk of mortality from drought. And cool, moist, environments high in organic material are optimal for invertebrates, chiefly slugs. Thus fungi, drought, and slugs, often in concert, cause high mortality to newly germinated seedlings.

In mixed conifer-hardwood stands, different silvicultural cutting methods result in differential Pacific madrone seedling abundance and survival. Intensive conifer cutting methods like seed tree and shelterwood, together with a site preparation treatment that bares much mineral soil, give best results. This is because residual Pacific madrone trees are stimulated into producing more seed. Increased levels of moisture, nutrients, and light facilitate stimulation. Bare mineral soil, or rather lack of a thick organic layer, also is conducive to seedling survival. The importance of stimulation and mineral soil is illustrated by initial seedling densities from shelterwood (4,083 seedlings per acre), seed tree (3,917 seedlings), and single-tree selection (866 per acre). Corresponding frequencies, based on milacre plots, were 53, 31, and 1.7 percent. After 5 years, densities had

decreased to 1,640, 1,675, and 22 seedlings per acre for the respective cutting methods. Frequency data indicated a rather clumpy distribution.

Survival of these seedlings and those from other light seed crops resulted in various amounts of accumulated advance reproduction: shelterwood 1,833 seedlings per acre, seed tree 1,417 seedlings, and single-tree selection 178 per acre.

Natural regeneration of Pacific madrone in an undisturbed pure hardwood stand was practically nil.

Together, these results indicate a strong trend: survival is keyed to disturbance. Although disturbance generally creates a hot, dry, environment, it is markedly better than that of shade and a heavy organic layer.

Even on high sites, seedling height growth is slow. One-year-old seedlings in the Santa Cruz Mountains were 1.9 inches tall. Two-year-old seedlings on the Experimental Forest averaged 3.5 inches in height, and after 10 years under a single-tree selection cut were 2.6 feet tall.

Because of slow height growth and a clumpy distribution, Pacific madrone from seed is not likely to furnish strong competition to softwood regeneration. Trees, from seed, will be present in all cutting areas in the future, however, and serve to furnish new genetic information to the species.

TANOAK

Detailed study of this species was applied to seed yield, acorn fate, storage, acorn position, germination, effect of irrigation and fertilization, and natural regeneration.

Physical Characteristics of Seed

Tanoak produces flowers in the spring and irregularly during autumn. Most flowers arise from the axils of new leaves, occasionally from buds at the base of year-old leaves. April, May, and June are the months of heaviest flowering. Female flowers form at the base of the catkins, below the spike of the staminate flowers (Peattie 1953). These flowers are 3- to 4-inches long, and form crowded clusters in such profusion as to conceal the foliage. Initially, their color is white, eventually turning to yellow.

Acorns mature at the end of the second season. They are borne singly or in clusters of two, three, and occasionally four. Ripening takes place in the tree in September, and as it progresses, the acorns change color from light green to yellowish to brown. Concomitant decreases in moisture content take place in the acorn and acorn-cup. Eventually the acorn separates from the cup and falls to the ground.

Detailed records of tanoak acorn production, timing, and magnitude on the Experimental Forest are available from 1958 through 1975. Three bumper seed crops and seven light crops were produced in this period. Rare is the year that no tanoak seed falls. A few, but

different, trees always produce seed.

When this species produces a bumper crop, the forest fairly rains with acorns. Indeed, no oak on the Pacific Coast produces a heavier crop of acorns (Schopmeyer 1974).

Sampling by temporary milacre plots during the bumper seed year of 1974 indicated sound tanoak acorns to average between 89,000 and 168,000 per acre. A single milacre plot beneath a 16-inch diameter, free-to-grow tree indicated 1,118,000 acorns per acre, 79 percent of which were sound. This should be considered about the maximum acorn density possible from this size of tree on this site. A regeneration survey the following year showed no seedlings present on the milacre plot. Sampling beneath an open-grown clump of trees 10-, 13-, 14-, and 14-inches in diameter, about 75 feet tall, yielded an average of 482,000 acorns per acre and 73 percent soundness. On a poorer site at the same elevation Roy (1957a) reported tanoak acorn yields of 78,000 to 83,000 acorns per acre. Soundness, however, was only 49 percent--extensive damage being done by several coleopterous and lepidopterous insect larvae.

Although sprouts have been reported to bear acorns when 5 years old (Roy 1957b), the first acorns produced on sprouts at Challenge occurred at age 9. A representative 9-year-old open-grown sprout clump was 15 feet tall with a crown spread of 12 feet. Over 190 greenish-yellow acorns were counted on the clump late in September of a poor seed year. Cutting tests revealed most to be sound on that date.

Typical timing and fate of tanoak acorns at Challenge is as follows: By September 15, a few wormy and aborted acorns begin to fall. If days are warm and sunny with a dry north wind, acorn drop accelerates dramatically. By September 25, acorns are falling in profusion. A much higher percentage of them are sound. Unsound acorns generally are developed fully externally, but contain only a wisp of tissue internally. Most acorns fall by November 7.

Surveys in December and early January showed a steady decline in the number of viable acorns on the ground. Birds, squirrels, and deer are known to utilize this food source (Martin et al. 1961), and did so here. Birds were particularly noticeable. Among them were the band-tailed pigeon, varied thrush, stellar jay (Cyanocitta stelleri), California woodpecker (Balanosphyra formicivora), white-breasted nuthatch (Sitta carolinensis), red-shafted flicker (Colaptes cafer), California horned lark (Eremophila alpestris), valley quail (Lophortyx californica), plain titmouse (Parus inornatus), and rufous-sided towhee (Pipilo maculatus). The California gray squirrel (Sciurus griseus) and Douglas chickaree (Tamiasciurus douglasii) devoured many acorns as did deer. Wood rats and a black bear (Euarctos americanus) probably consumed acorns also. Those acorns that fell into exposed openings succumbed to overheating and dessication. By January 20, only those under trees or brush in cool and protected habitats remained viable.

A check of sheltered and hidden acorns on February 1 revealed their cotyledons to be full, crisp, and creamy white. Normally, most of these acorns would germinate in early March and contribute to the

pool of seedlings on the forest floor. However, as commonly happens, the temperature plunged nightly to 22 degrees F. for 6 days. When subjected to such low temperatures, the cotyledons turned grayish-black in the center and were no longer viable. By February 25, only those acorns buried by squirrels or covered by leaves were living. Most of these had split at the pointed end. Tiny radicles were visible, although not yet protruding beyond the acorn shell. On March 6, seedling radicles on 50 percent of the acorns were about 1/2-inch long. Nearly all viable acorns had produced elongated radicles by March 15. It was not until mid-April, however, that the hypocotyl and tiny leaves appeared above ground. Radicle elongation and emergence of above-ground plant parts often are conditioned by warm temperatures. Maximum temperatures on the Experimental Forest may exceed 75 degrees F. in late March and be above 65 degrees F. for a 10-day period in mid-April. Should the warm period be absent and April be continuously cold and wet, with freezing temperatures and even snow flurries, plant parts may not appear above ground until May 15.

Seed Handling Practices

Acorns should be gathered at or shortly after the time of maximum seed fall. The first acorns to fall usually are unsound. And those that land in an exposed environment quickly overheat and dry out. Consequently, it is best to gather acorns from shady, sheltered locations.

Sound acorns differ markedly in weight from unsound acorns. After a little practice, one can quickly and accurately recognize sound acorns by their heavier weight. Some acorns have tiny insect-engineered holes in the shell. These should be rejected as they consistently prove to be unsound. Likewise, light-colored acorns generally are unfilled and also should not be collected.

Storage

A test of various storage techniques indicated that tanoak acorns are sensitive to temperature and moisture. Carefully selected acorns were gathered on November 14 and immediately subjected to five treatments.

Acorns were stored in burlap sacks in a dry shaded shed. Temperatures ranged from 29 to 58 degrees F. and fluctuated diurnally. Cutting tests revealed acorns to be somewhat flaccid but viable on January 18, and ruined by February 15. Cotyledons of ruined acorns were almost full sized but yellowish-tan outside, gray-black in the center, and flaccid; the embryo was bright yellow, dry, and hard.

A closely related test involved placement of acorn-filled burlap sacks under a periodically heated trailer, where the environment was dry and partially shaded. Cutting a few acorns after 45 days revealed the cotyledons to be somewhat shrunken internally but viable. After 90 days, acorns still were viable. They were not ruined by freezing

temperatures as the acorns in the first trial apparently were. Of note is that a few acorns germinated in the sacks after 75 days.

Immediately after gathering, acorns were placed in thin polyethylene bags in a temperature-controlled refrigerator at 34- to 38-degrees F. Periodic cutting tests indicated full-sized cotyledons. Acorns were seeded 96 days after gathering. Subsequent germination and seedling establishment were high--indicating the success of this storage technique.

The immediate placement of acorns in prepared seed spots was the fourth storage test. Acorns were buried 2 inches and protected by pinned-down cone-shaped wire screens. Periodic unearthing and cutting tests showed this to be a worthwhile storage technique.

The fifth test was the most efficient. Acorns, selected for soundness, were enclosed in shallow rectangular wire screens, buried about 2 inches, and covered with dead leaves. Storage locations generally were close to the seeding site, and under a dense canopy of overhanging branches. Acorns remained in storage until early March when most possessed elongated radicles. Only those with healthy radicles were seeded. A big advantage was that acorns were near the seeding location and in tune with the local environment.

Long-term storage was not attempted. The fact that at least a few acorns are available each year and that the species can be vegetatively propagated from branch tips (Mirov and Kraebel 1939) precluded this work. Storage for at least 16 months may be desirable, however, at other locations where seed crops are not common. And implications

for long-term storage are present from these storage trials: temperatures should be just above freezing and fluctuate little. Moisture content should be high and probably no lower than 40- to 50-percent of fresh weight. Even then, some sprouting in storage probably will take place and should be allowed for.

Storage should be in polyethylene bags. Wang (1974) stated that the loss of germinability in acorns in storage is caused by dehydration or inhibited respiration due to an inadequate oxygen supply under anaerobic conditions. Thus, the polyethylene bags should be porous enough to permit gaseous exchange and yet restrict excessive moisture loss.

Stratification

Acorns of this species possess the ability to germinate without after-ripening treatment (Emery 1964; Schopmeyer 1974). However, to retard germination until spring, most plant propagators keep tanoak acorns at a temperature just above freezing (Schopmeyer 1974). With this treatment, after-ripening inadvertently takes place.

Germination in Laboratory

A limited number of trials show tanoak germinative capacity to be 78 percent (Mirov and Kraebel 1939). Seedlings appear about 3 weeks after seeding. Tanoak germination is hypogeous.

In this study, acorns selected for soundness were gathered late in October and stored in a refrigerator at 35- to 38-degrees F. for 114 days. One hundred of them were placed in moist peat moss, pointed end up, and then in a greenhouse. Here, temperature was 70 ± 5 degrees F. with automatic watering (mist) for 20 minutes every fourth day.

Germinative capacity (completeness) was 97 percent in 20 days, germinative energy (speed) was 6 days, and the amount of germination after 6 days was 43 percent of the viable seed.

These values substantially exceed those in the literature. This could be from higher selectivity when gathering acorns, or to placing them point up. This latter procedure, in effect, reverses normal polarity and places the growing point of the hypocotyl downward and that of the radicle upward.

Working with red oak (Quercus rubra L.) acorns and Persian (Juglans regia L.) walnuts, Molotkovskii (1955) found that reversing polarity resulted in higher germinative capacity, greater germinative energy, a decrease in time between planting and germination, increased seedling vigor, and straighter seedling stems.

Germination in Field

Several extensive trials tested germination and seedling survival from acorns placed in normal and reversed position. These trials involved establishing seed spots in a plantation of about three acres

of cleared (bulldozed) ground (Fig. 5). This carefully selected location was as homogeneous as possible with uniform site quality, slope (10 percent), and aspect (south). Newshrub plants and sprouting hardwoods were removed annually as well. Thus the ground was bare and competition from other plant species was minimal. Altogether, 808 seed spots comprised the sample. At each spot, the ground was loosened with a pulaski, and the soil shaped to form a shallow basin around it. Acorns were buried 1 1/2 to 2 inches and covered with loose soil. Pinned-down, cone- and mound-shaped wire screens protected the acorns from rodents (Fig. 6).

Acorns, gathered from nearby compartments, were seeded January 6 through February 11, 1970 as weather permitted. Two acorns per spot was the seeding rate. Over 840 acorns were positioned point up; 772 acorns point down in alternate rows. Germination first was observed April 17 when the hypocotyl and tiny upright leaves cleaved the soil surface. A sharp freeze with a temperature minimum of 21 degrees F. occurred on April 20 followed by 4 successive days of below-freezing temperatures. All seedling stems and leaves above ground turned black and died. These seedlings were marked with plastic sticks to separate them from subsequent seedlings. Because only acorns placed point up had germinated at this date, damage occurred only to them, not to acorns positioned point down. Of those blackened, about 70 percent eventually sprouted from below ground, putting forth 2 to 4 stems. But it was not until July 2 that the last frozen plant sprouted.



Figure 5.--A portion of the tanoak plantation test area. Challenge
Experimental Forest, 1970.



Figure 6.--Cone-shaped wire screens protect acorns at each seed spot.

These seedlings are 1-year old.

Differences in timing and magnitude of germination for the two acorn positions differed so markedly that no statistical analysis was necessary. Differences obviously were highly significant. Acorns having reversed polarity (point up) demonstrated a germinative capacity of 53 percent in 140 days, germinative energy of 12 days, and 71 percent germination of viable seed after 12 days. Acorns placed normally (point down) indicated a germinative capacity of 21 percent in 140 days, germinative energy of 41 days, and only 5 percent germination of viable acorns after 12 days.

Low germinative capacity was at least partly caused by an unusually cold, dry, windy spring. Precipitation from April through July was 54 percent below the Challenge normal. An examination of the soil on May 28 indicated extreme drying.

Minor losses also took place when a California gray squirrel ravaged about 50 seed spots of point-up and point-down acorns. The squirrel would dig under the wire screens (Fig. 7) and scoop out the acorns. Only germinating acorns were taken. Sound but ungerminated acorns remained untouched. Germinating acorns apparently emit a beckoning odor to squirrels.

Germinative capacity for point-down acorns was pitiful. Exhuming plantless seed spots revealed acorn after acorn to have germinated and put forth a short radicle that died before the hypocotyl reached the surface. Another drawback of point-down acorns was difficulty or failure to break through the soil crust. The blunt end of the acorn



Figure 7.--The two acorns beneath the round-shaped screen were robbed by a California gray squirrel. Although not shown, two wire pins held the screen firmly in place.

would remain over the emerging plant parts. As they elongated, they would push the acorn up to the soil crust, but progress no farther.

The net result of low germinative energy and late germination, plus difficulty in getting the hypocotyl above ground, is that seedling roots could not keep pace with the retreating zone of adequate soil moisture. Drought then took its toll.

Because germinative capacity was unsatisfactory, all blank spots again were seeded in early 1972. To verify previous results, the soil again was loosened and acorns placed point up and point down as before.

When acorns were placed point up, germinative capacity was 66 percent in 160 days, germinative energy was 8 days and 50 percent of the viable acorns germinated after 8 days. Point-down acorns yielded a germinative capacity of 47 percent in 160 days, germinative energy of 42 days and only 3 percent germination of viable acorns after 8 days.

Germination of point-up acorns began in early April and after 7 days a hard freeze with a minimum of 25 degrees F. occurred. As before, all just-emerged tender little seedlings froze back to ground line. Two months later, 80 percent of these had recovered--not with a single stem, but with multiple stems. Weatherwise, this was a more-typical growing season, although precipitation from April through July was 17 percent below average.

Substantial differences between the 1970 and 1972 trials are minimal. Those differences that did occur could have been caused by the greater amount of precipitation in April and May of 1972. This

precipitation could account for the longer germination period of the second trial and the improved germinative capacity of the point-down acorns.

Seedling Survival and Growth

Effect of Acorn Position--1970 Seeding

When establishing a plantation, it is desirable to have a minimum of blank spots and a high stocking percentage (number of spots stocked with at least one tanoak seedling). After three growing seasons, stocking of point-up acorns decreased from 53 to 33 percent; point-down acorns from 21 to 10 percent. Number of seedlings followed a similar trend (Fig. 8).

Because frozen seedlings continued to sprout until July 2, it is this date that mortality from freezing is assigned. Most seedlings probably were killed outright, but others could have died between the time of freezing and July 2.

This date also is when mortality from drought first was observed. Dating seedling mortality from drought was a difficult task. Seedlings often would die back to the root crown. Some would perish quickly; others would remain alive and sprout that fall, the following spring or even in early summer.

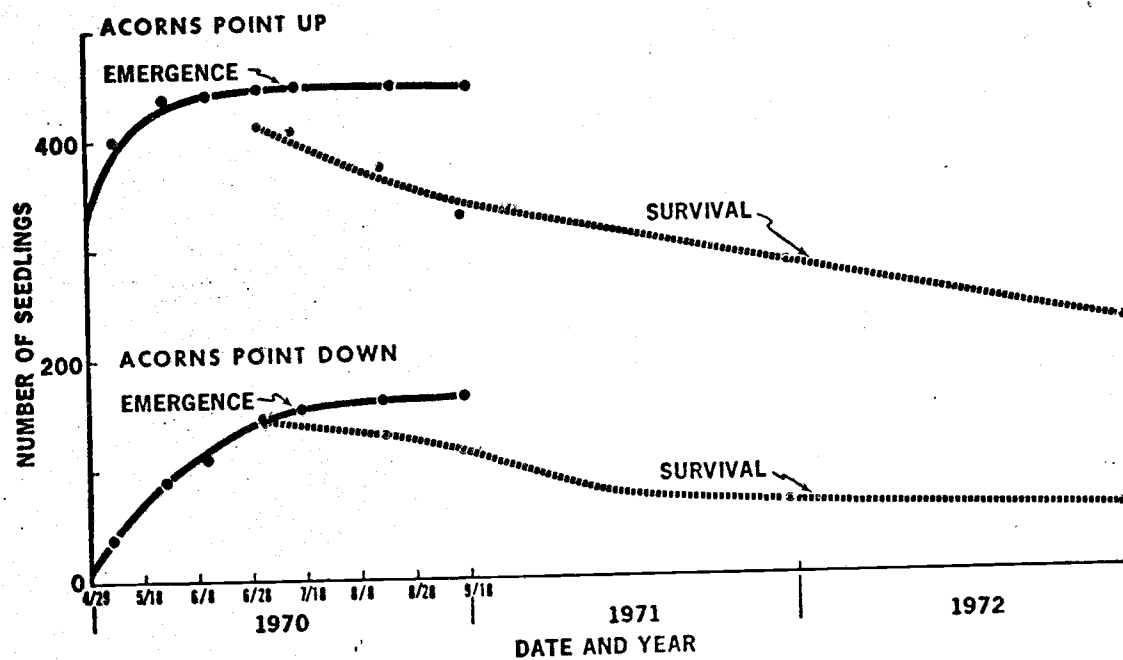


Figure 8.--Magnitude and timing of tanoak seedling emergence and survival when acorns are placed point up and point down.

Effect of Acorn Position--1972 Seeding

For tanoak seedlings from the 1972 seeding, mortality from drought first was noted on July 7. It steadily worsened until the first rain of late September. At the end of the first growing season, the number of seedlings from point-up acorns had decreased by 30 percent; point-down acorns by 36 percent. Stocking of 1972 seedlings also was poor. After one growing season, stocking from point-up acorns amounted to 57 percent of the available (interplanted) spots and from point-down acorns, 40 percent of the available spots. Again, drought was the cause of seedling mortality.

Effect of Water and Fertilizer

In an effort to increase the magnitude and certainty of tanoak regeneration, irrigation and fertilization trials were begun in 1972. Irrigation amounted to about 1/2 gallon of water per spot from a hose. It collected in the shallow basin around each plant. Irrigation usually began about mid-June each year and took place at about 2-week intervals.

Fertilization consisted of applying a generous handful of commercial pelleted fertilizer that consisted of 16 percent nitrogen as ammonium sulphate and 20 percent phosphorous as P_2O_5 per spot. The application date was late in February of each year. Rainfall in February and March seemed about the right amount to transport the

fertilizer to the rooting zone by the time that seedling growth began. Selected seed spots were fertilized each year regardless of whether or not a seedling was visible.

Sampling intensity for the various treatments and treatment combinations was:

<u>Treatment</u>	<u>Number of Seed Spots</u>
Fertilizer & water	151
Water only	295
Fertilizer only	131
Untreated control	231
Total	808

Average seedling height of all surviving seedlings, including those from both the 1970 and 1972 seedlings, was relatively constant among treatments in 1972, variable in 1974, and showed a definite trend in 1975 (Table 6). A Tukey test (Hamilton 1965) of the 1975 data showed water and fertilizer combined to have a positive effect on seedling height growth. This variable differed from the others most significantly ($p = .01$). Water alone and fertilizer alone did not differ from each other, but did significantly differ from the average height of the untreated control ($p = .05$).

At the end of the 1972 growing season, virtually no visual or phenological effects of fertilization were observed on fertilized-only plants. Time of bud burst and leaf elongation, total height, survival, and time of leaf fall all coincided with control plants. The only visual effect of fertilization was that leaf color tended to be darker.

**Table 6.--Tanoak seedling height as affected by fertilizer and
irrigation. 1972-1975**

Year	Treatment			
	Fertilizer and Water	Water	Fertilizer	Control
	height (feet)			
1972	.49	.43	.43	.34
1974	1.15	.78	.90	.65
1975	1.68	1.05	.93	.75

Water alone, and water and fertilizer combined, both resulted in a more healthy appearance of more seedlings.

By 1974, visual differences among treatments were recognized easily. In the control, seedling leaves turned brown earlier in the season. Dieback was more frequent and more pronounced. Fertilized-only seedlings fared little better. Some seedlings died outright, others died back to just above ground level, and others appeared healthy and vigorous. A common trait of fertilized-only and control plants was a tendency to produce tufts of unusually small leaves. These were dark bluish-green where fertilized, and were of slightly lighter color in the control. Irrigated plants also suffered death and dieback. Indeed, several 3-foot-tall seedlings died back to within a foot of the ground. In general, only the watered and fertilized seedlings looked healthy. Leaves were larger and of good color. Shoot growth also was good. Some of these seedlings, however, also remained small, with little height growth.

At the end of the 1975 growing season, it was visually apparent that water was having a beneficial effect. In conjunction with fertilizer, the seedling root system apparently was developing not only more mass, but also more feeder roots. In turn, more moisture became available, which furthered plant nutrition. Stocking in the fall of 1975, however, did not fully reflect these observations:

<u>Treatment</u>	<u>Stocking in 1975</u> (percent)
Fertilizer and water	41
Water only	39
Fertilizer only	35
Control	23

Because quantitative physiological data from tests of plant moisture stress and foliar nutrient concentrations would better explain irrigation and fertilization effects on tanoak seedling survival and growth, they were performed.

Plant moisture stress.--This term or its analogue, xylem sap tension, results from the "balancing pressure" measured in twigs or needle bundles by the pressure chamber first described by Scholander et al. in 1965. This apparatus can estimate moisture stress in trees regardless of rooting depth, and has many other advantages over soil moisture values. It may not be closely related, however, to leaf water potentials in northern red and white oaks as measured by thermocouple psychrometer (Kaufmann 1968). If Kaufmann's findings relate to the hardwood species tested in this study, then my pressure chamber readings may exaggerate leaf water potentials, particularly at high values. Apparently the discrepancy between psychrometer and chamber values occurs in the chamber as backward-forced water fills voids in the xylem vessels of hardwoods or pith of shrubs--voids that existed before the twig was removed from the plant.

Nevertheless, the pressure chamber has been used to measure xylem sap tension in three woodland oaks in California (Griffin 1973), birch-leaf mountain-mahogany in Arizona (Campbell and Pase 1972), and a white oak in Missouri (Hinckley et al. 1975). The pressure chamber yields perfectly good relative xylem sap tension data, and relates these data to soil moisture availability.

In this study, the pressure chamber was used to determine: (1) predawn minimum moisture stress of irrigated and fertilized seedlings, (2) diurnal fluctuation of large and small 6-year-old seedlings, and (3) moisture stress in 4-month-old seedlings. A number of instruments defined the physical environment about the seedlings.

The portable pressure chamber and peripheral equipment, including lights, were set up within 100 feet of the tanoak area. Representative seedlings were flagged before sampling began. The sampling date was September 4 and 5, 1975. Also installed were instruments for measuring illumination near the ground, for determining soil surface and sub-surface temperatures, and for recording ambient temperatures and relative humidity.

Five packets of light sensitive papers manufactured by the Ozalid Company were placed randomly throughout the sampled area on June 23, 1976, one day after the summer solstice. These papers are coated with diazo compounds, part of which are bleached by light, and part are colored by ammonia vapor (Friend 1961). In general, light and length of exposure determine the bleaching and penetration of light through the different numbers of papers in each packet. This method works

well for relating illumination to vegetation (herbs, shrubs, and small trees) near the ground. A light meter furnished data for calibration of the Ozalid papers.

Quantification of soil surface temperatures was by use of pellets having calibrated melting points. They begin to liquify at the contact line when the surface upon which they rest reaches the temperature rating of the pellet used. Thus partially buried pellets will become etched at ground line if the soil surface heats to the calibrated temperature for only an instant. The method has been reported to be cheap, easy to install, and accurate (Silen 1956). Three clusters of partly buried pellets, ranging in melting points from 125- to 163-degrees F., were randomly located in the sampling area on the sampling date.

A soil thermograph with leads at 7.9- and 19.7-inch depths indicated subsurface soil temperatures. Although located about one mile from the tanoak plantation, soil, slope, aspect, and condition of soil surface were nearly similar. A standard weather bureau shelter at this location provided data on ambient air temperatures and relative humidity. Data from these instruments on the sampling date are considered representative of the tanoak area.

For determination of xylem sap tension, the sampling procedure and collection technique were standardized to minimize sample-to-sample variation. Cut twigs comprised the sample. Each twig supported a full complement of uninjured fully mature leaves of the current season, taken from the top one-third of the plant on the

southwest side. After cutting, each sample was placed immediately in a plastic bag, rapidly carried to the pressure chamber, and placed in it for testing. Elapsed time between cutting and testing never exceeded two minutes. Most twigs were double-tested in the chamber, particularly if readings seemed too high or too low.

At the time of sampling, seedlings had received no irrigation water for 15 days. The surface soil was dry and dusty. Prior surveys had shown increasing mortality of tanoak seedlings, particularly if not watered. In addition, many seedlings indicated severe moisture stress in terms of dead or partially dead leaves and twigs.

Weatherwise, the date of sampling was typical of late summer at Challenge; temperatures ranged from a low of 47 degrees F. at 7:45 a.m. PST to a high of 99 degrees at 2:40 p.m. Relative humidity ranged from 58 to 92 percent. The day was cloudless with a light breeze from 7:35 to 10:00 a.m.

Partially-buried calibrated pellets indicated that soil surface temperatures in the tanoak sampling area just reached 138 degrees F. Temperatures have reached 163 degrees F. in a 12-acre clearcutting on a south-facing slope on the Experimental Forest.^{1/}

The soil thermographs showed that temperatures at the 7.9-inch depth varied diurnally from 70 degrees F. at 11:00 a.m. PST to 78

^{1/} Data by W. E. Sundahl, 1969, on file at the Pacific Southwest Forest and Range Exp. Stn., Redding, Calif.

degrees F. at 7:00 p.m. At the 19.7-inch depth, temperature was constant at 70 degrees F.

Calibration of the Ozalid papers by the light meter involved linear regression, the coefficient of determination (R^2) from which was 0.99. Illumination of the tanoak area on June 22 was about 58 percent of full sunlight or 40,500 foot-candle-hours. Of course, it would have been somewhat less on the September sampling date.

Of particular interest was the average predawn minimum moisture stress of five representative seedlings in each treatment:

<u>Treatment</u>	<u>Stress</u> (atmospheres)
Fertilizer and water	4.95
Water	4.90
Fertilizer	6.80
Control	6.20

Moisture stress of two seedlings from the 1970 seeding was monitored continuously for 24 hours to determine diurnal fluctuation. One of these seedlings was small and described as: 1 foot tall, 1 foot average crown spread, 8 upright stems, 1/2 inch in diameter at the root crown. The other seedling was larger: 10.2 feet tall, 3.5 feet average crown spread, 1 upright stem, 2 inches in diameter at the root crown.

Diurnal fluctuation of the two seedlings was quite similar (Fig. 9). Moisture stress began to increase with first light in the morning (about 5:20 a.m. PST). It increased even faster after 7:10 a.m. when

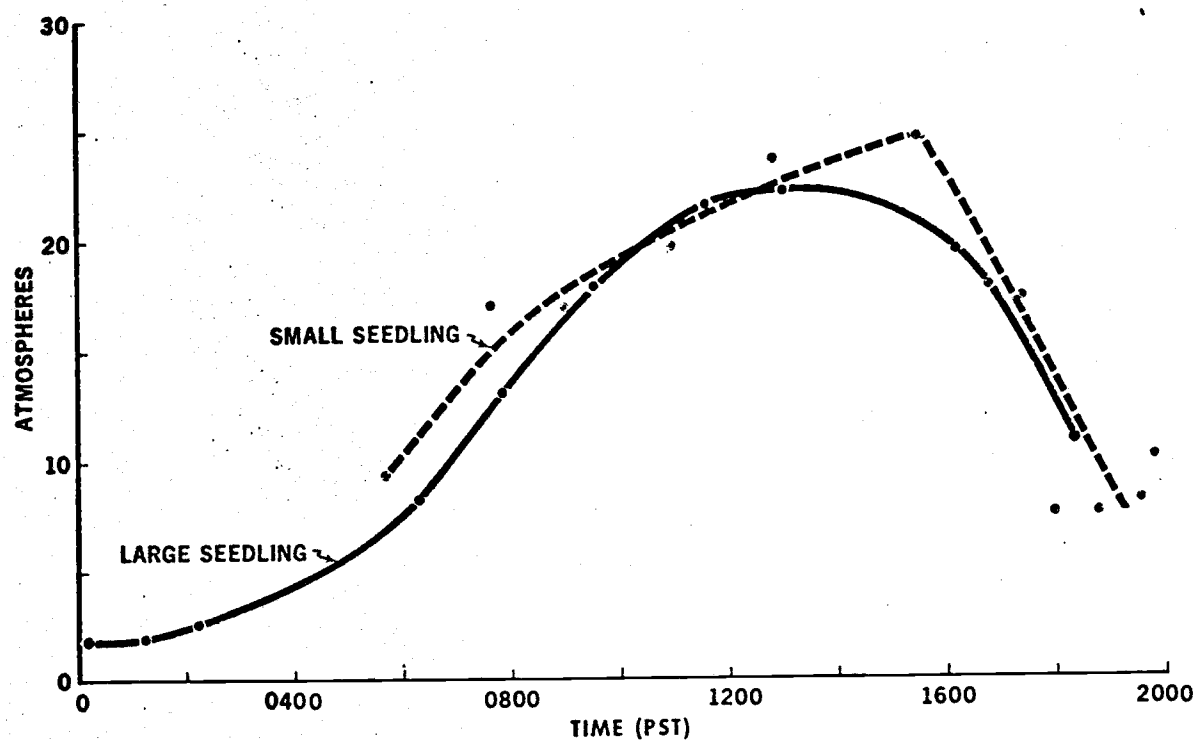


Figure 9.--Diurnal fluctuation of xylem sap tension in a large and small tanoak seedling, September 4-5, 1975.

sunlight first reached the area. The first sunlight directly on the leaves was in the form of sunflecks. These reached the larger seedling at 9:35 a.m. and the smaller shortly after. At this time, moisture stress of both plants was about 18 atmospheres. Plant moisture stress peaked at 22 to 24 atmospheres around 3:00 p.m. and decreased rapidly thereafter. Plants were in shade by 5:45 p.m.

Xylem sap tension of the larger seedling continued to decrease, reaching 2 atmospheres at midnight. This value was noted by Waring (1969) to be the lowest predawn tension of any tree in the Siskiyou Mountains. It also is near the 1.7 atmosphere value of a white alder actually growing in running water (Griffin 1973). Thus, this low tension value, and those noted for seedlings in the fertilizer and irrigation trials, indicate that the tanoak seedling root system is efficient in providing water to the plant.

Destructive sampling of six 4-month-old tanoak seedlings in the plantation was particularly revealing. At first light in the morning, but before sunrise, plant moisture stress of two seedlings reached 20 atmospheres. Moisture stress of a seedling in full sunlight at 11:40 a.m. was 34 atmospheres. This seedling had been undergoing severe moisture stress; most of its leaves were dead or partially dead. Stress in a robust-looking seedling in late afternoon in full sunlight reached 35 atmospheres. Two seedlings that had been in full sunlight during most of the day, but were in shade at 4:10 p.m., indicated a stress of 22 atmospheres.

The air-soilsurface-subsoil temperature gradient, amount of light, and range in relative humidity did not indicate any abnormal, or unusually severe environmental forces acting on the tanoak seedlings.

The reason for death and dieback of tanoak seedlings must be lack of stomatal control and transpiration of water beyond the point of rehydration. The seedling moisture stress data suggest that the stomates of these seedlings respond quickly to light. More and more stomates either open or open more fully as the amount and intensity of sunlight increases throughout the day. At a point in late afternoon, however, an apparent "fail-safe" mechanism is triggered at a xylem sap tension of about 25 atmospheres in 6-year-old seedlings. From then on moisture stress declines as stomates apparently close and transpiration lessens. Four-month-old seedlings could lack this mechanism--moisture stress reached at least 35 atmospheres in seedlings whose leaves were dying from drought.

Foliar analysis.-- This method is becoming well established for assisting in the diagnosis of mineral requirements of vegetation in agriculture and forestry (van den Driessche 1974). It is particularly useful for identifying the cause of pronounced nutrient deficiency in forest stands. It is not yet sufficiently perfected to predict potential stand growth (Tamm 1964), especially when foliar nutrient concentrations are above critical levels (Heilman and Gessel 1963). Under these circumstances, more precise interpretation of foliar nutrient concentrations is needed to predict the response to stand fertilization.

Nevertheless, foliar nutrient concentrations provide an excellent relative measure of a species response to different fertilization treatments.

Foliar samples were taken in late June 1975 at the time of maximum seedling growth. This was desirable as it is the time of maximum nutrient stress, and the best time to quantify nutrient deficits. The youngest fully matured leaves of the current season from the upper one-third of each seedling comprised the sample. Enough leaves were taken from each seedling to yield about 200 milligrams of material when oven dried. Ten seedlings were sampled individually in each treatment.

After leaves were carefully gathered and placed in labeled bags, they were put in a refrigerator to minimize respiratory losses and hence stabilize their weight. Samples then were oven dried at 75 degrees F. for 3 days, ground in a Wiley mill to pass through a 40 mesh screen, and stored in tightly-stoppered plastic vials. Each sample of ten then was composited to form three replicates.

For nitrogen determination, about 125 milligrams from each replicate were digested in concentrated sulphuric acid and mercuric oxide using a standard micro-kjeldahl procedure. Quantitative nutrient determination for phosphate phosphorous, potassium, calcium, and magnesium was by a perchloric-nitrate acid treatment. For phosphorous, the Klett-Summerson photoelectric colorimeter method then was used (Johnson and Ulrich 1959). The remaining cations were diluted as necessary, screened from quantitative interference by aluminum, iron,

and phosphates by addition of lanthanum, and analyzed by a Perkin and Elmer atomic absorption spectrophotometer.

Mean foliar nutrient concentrations indicate the response of tanoak seedlings to the water and fertilizer treatments (Table 7). Standard errors ranged from $1/8$ to $1/16$ of the mean for nitrogen, $1/3$ to $1/5$ for phosphorous, $1/5$ to $1/7$ for calcium, and $1/10$ to $1/20$ for potassium and magnesium.

Analysis of variance indicated nitrogen in the tanoak leaves to differ most significantly among treatments ($p = .01$). Phosphorous levels differed significantly among treatments as well ($p = .05$). For the other macronutrients, the foliar concentration of each was about the same in all treatments and no significant differences were detected ($p = .05$).

Fertilization obviously enhanced the nutrient capital available to the tanoak seedlings. Relative to the unfertilized control, nitrogen and phosphorous were being taken into the plant and translocated to the leaves. And more fertilizer reached the leaves if the seedlings were irrigated. Fertilizer alone contributed to plant nutrition, but to a lesser extent. Water alone also resulted in higher nutrient concentrations in the seedlings, probably by facilitating mineral uptake.

Of particular interest is the close relationship of nutrient levels in the control to "poverty" or deficiency levels in the seedlings.

Table 7.--Mean foliar nutrient concentrations of tanoak seedlings
with and without irrigation and fertilization

<u>Nutrient</u>	<u>Fertilizer and water</u>	<u>Water</u>	<u>Fertilizer</u>	<u>Control</u>
	- - - - percent of foliar dry weight - - - - -			
Nitrogen	1.530	1.164	1.267	1.092
Phosphorous	.164	.109	.097	.088
Potassium	.471	.444	.514	.508
Calcium	.282	.470	.264	.273
Magnesium	.152	.169	.136	.151

<u>Nutrient:</u>	<u>Percent of foliar dry weight</u>	
	<u>Poverty level^{8/}</u>	<u>Control</u>
Nitrogen	1.00	1.092
Phosphorous	.09	.088
Potassium	.50	.508
Calcium	.20	.273
Magnesium	.08	.151

Obviously, control seedlings at the time of maximum nutrient usage, are close to the poverty level for four of the five macronutrients tested, magnesium being the exception.

Overall Stocking of Plantation

Stocking of the tanoak plantation as a whole steadily declined from 1973 through 1975 for seedlings from both point-up and point-down acorns:

<u>Date</u>	<u>Point up</u> <u>(percent)</u>	<u>Point down</u> <u>(percent)</u>
1973	62	44
1974	50	32
1975	41	25

At the end of the 1975 growing season only one-third of the plantation was stocked with 4- to 6-year-old seedlings. Mean seedling height was 1.1 feet and ranged from 0.2 to 10.2 feet.

^{8/} Powers, Robert F. 1974. Evaluating fertilizer programs using soil analysis, foliar analysis, and bioassay methods. In: Servicewide silvicultural work conference proceedings. U.S. Dep. Agric. Forest Serv. Sacramento, Calif. Oct. 21-25. p. 138.

Scarcely a seedling remained that consisted of a single stem--nearly all had multiple stems. Most of the seedlings had died back to some degree at least once. Some seedlings had died back all the way to the root crown; others back only a few inches. Some seedling heights receded the first year from drought, frost, or unknown causes. Others diminished in later years, and still others regressed nearly every year. And this, in spite of over half the seed spots being irrigated and one-third of them being fertilized for 4 years.

Container-grown Seedlings

Low initial stocking and subsequent high seedling mortality mandated that a better, more certain regeneration technique be found. Container-grown seedlings seemed the answer.

In 1973 about 85 tanoak seedlings were grown from point-up acorns in a greenhouse and hardened off during winter months in a lathhouse. The container was an 8-inch milk carton filled with potting soil. At the time of outplanting early in March, the seedlings were one-year-old and visually robust and vigorous. Root-shoot ratios were 2:1 in favor of the roots. The soil at each planting spot was loosened to a 12-inch depth. The bottom of the container was removed just before planting, although the sides remained. The object was to discourage lateral root growth and force root development downward. As previously noted, water and fertilizer were applied.

After one growing season, survival was 81 percent and after two growing seasons had fallen to 46 percent. Height growth after out-planting was essentially nil. Examination of dead plants showed that plant roots either remained in the potting soil or grew downward only through the loosened soil. Here a few short lateral roots formed. In both instances, root elongation was inadequate and the seedlings died from drought. Container-grown seedlings were not the answer.

Shaded Seedlings

Visual observations indicated a possible seedling response to shade. For example, when two seedlings per spot resulted, mortality was slightly less than if only one seedling was present. Seedling survival also was better if shade from bracken (Pteridium aquilinum L.), bull thistle (Cirsium vulgare [Savil] Ten.), or other herbaceous vegetation was present. Stem dieback, however, was visually independent of herbaceous vegetation.

About 175 acorns with just-emerged radicles were seeded point up in early March. As before, about one-third received fertilizer shortly after seeding. The spring was cold and wet and seedlings did not emerge above ground until mid-May. Shingles were placed southwest of each seedling shortly after. About half the seedlings were given subsistence irrigation every 2 weeks as in previous tests. Because treatments were similar, comparison to unshaded seedlings from point-up acorns in previous trials was performed.

After one growing season, mortality of shaded seedlings was 19 percent as compared to 25 percent mortality from unshaded seedlings in 1970 and 30 percent mortality from unshaded seedlings in 1972. However, the cold wet weather atypically affected seedling survival. For example, seedling emergence was about 30 days later than in previous trials. Thus, first-year results from shading were inconclusive, although seemingly beneficial.

Results after a second year of shading also were inconclusive. Plainly, factors other than shade were influencing tanoak seedling survival and early height growth.

Natural Regeneration in a Mixed Conifer-Hardwood Stand

Tanoak seedling frequency, density, and mortality also were evaluated in contrasting environments created by different conifer regeneration methods and site preparation-slash disposal techniques. These, the composite control, poisoning of hardwoods over 12 inches d.b.h., and specifics of sampling for seedlings and advance reproduction, are the same as for Pacific madrone.

After logging, tanoak trees 3.5 to 12 inches in diameter numbered 17 per acre in the seed-tree method and 3 per acre in both the shelter-wood and selection cuttings. However, nearly 65 percent of the tanoaks in the seed-tree cutting were smaller than 8 inches in diameter. Seed from these trees, plus that disseminated in the cutting areas by birds and squirrels, constituted the tanoak seed source. About 35 trees per

acre in this diameter class, plus 5 trees in the 13- to 20-inch class were present in the control.

Although tanoak produced three bumper seed crops during the 18 years of record on the Experimental Forest, none were produced during this 11-year study. Rather, acorn production and resultant regeneration is best described by its consistency--4 to 400 new seedlings in every cutting method every year that data were taken (Fig. 10). Corresponding frequency values ranged from 1 to 14 percent.

Stimulation of acorn production from cutting probably takes place to some degree. Although watched for, it was not observed.

Seedlings from each seed crop were averaged for successive growing seasons. Survival after 3 years ranged from 49 to 61 percent and was independent of intensity of cutting method. After 4 years, projected seedling survival in all cutting methods is expected to average about 56 seedlings per acre with a frequency of 4 percent. That density and survival of tanoak seedlings is similar in the various cutting methods is not surprising. Acorns remain viable and germinate, and seedlings become established and survive only in those specific micro-environments that are free of strong moisture stress.

Density, frequency, and survival were higher in the composite control. For all seed crops, survival after 3 years was 79 percent. After 4 years, projected survival is expected to average about 140 seedlings per acre with a frequency of 12 percent.

Of prime importance when evaluating tanoak regeneration is the density and distribution of tanoak advance reproduction. Often beneath

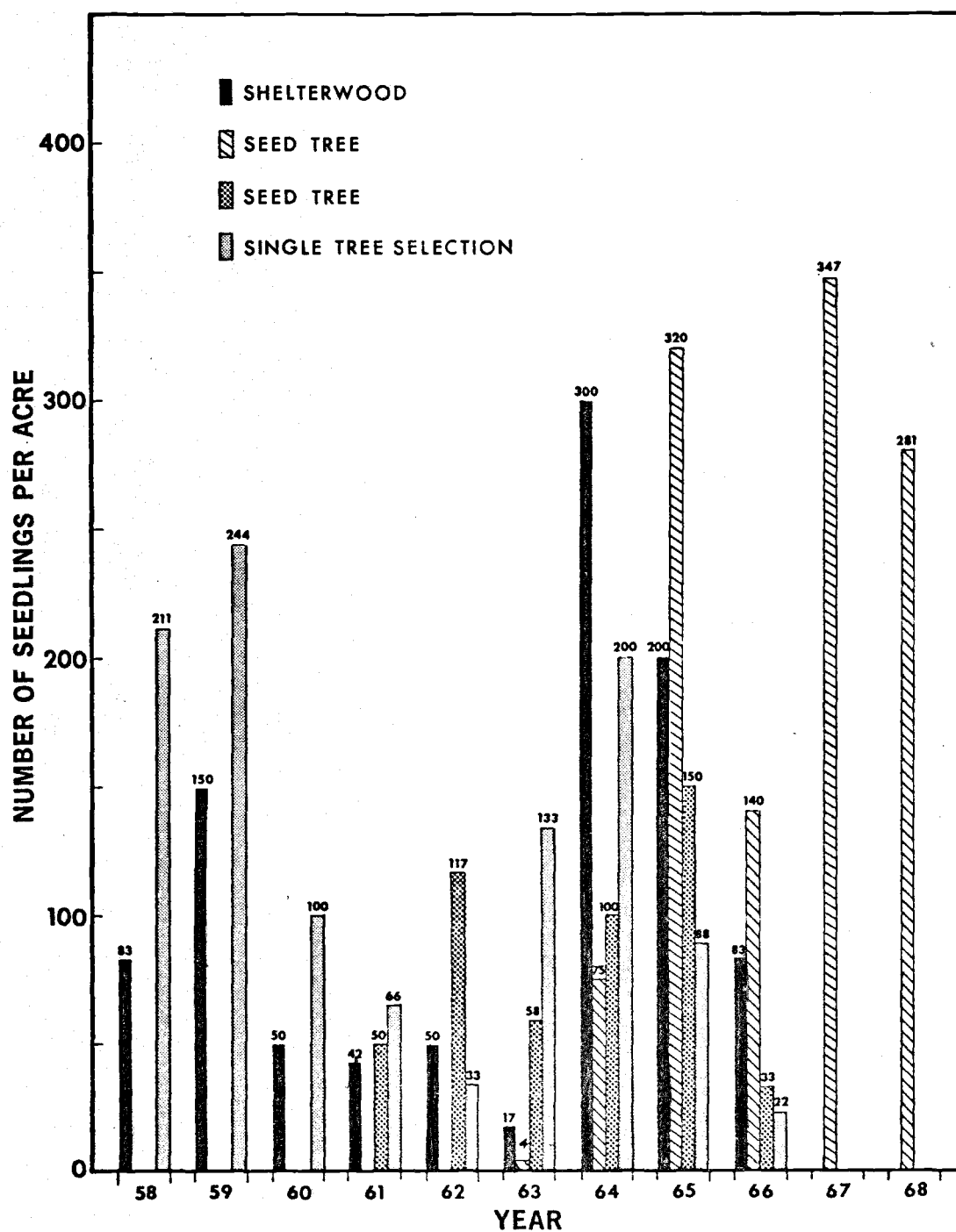


Figure 10.--Eleven-year record of new tanoak seedlings.

individual tanoak trees or groves, small tanoaks literally carpet the ground (Fig. 11).

In the undisturbed forest, the abundance of tanoak advance reproduction is more the result of a slow, steady buildup, rather than a large "catch" from one seed crop. In the uncut control compartments, density of tanoak advance reproduction in 1961 averaged over 2100 seedlings per acre and by 1966 had increased to about 2700 seedlings per acre. Frequency increased from 59 to 66 percent. Obviously tanoak advance reproduction, although already high, was still in the buildup phase.

Little is known about these seedlings. Most exhibit virtually no annual height growth, little lateral growth, and strong persistence. Apparently they exist in a minimal-growth state for years, possibly channeling sparse food reserves to the development of the root system or to storage in root burls. When the overstory is cut, these plants do not respond very much. A few die back to the root crown and resprout with one or two shoots. Those that do not die back to the root crown remain quiescent. Some of them eventually respond to release but when and with what magnitude is unknown.

By 1966 the cumulative density of tanoak advance reproduction for the 1958 through 1966 period, excluding that initially present, was 458 seedlings per acre for seed tree, 267 seedlings for shelterwood, and 733 seedlings per acre for single-tree selection (Fig. 12). In the seed-tree cutting of 1962, 1084 advance seedlings per acre had accumulated by 1968. Frequency distribution by cutting method was; seed



Figure 11.--A thick carpet of tanoak seedlings beneath a dense grove of trees. Sun flecks are the only source of light.

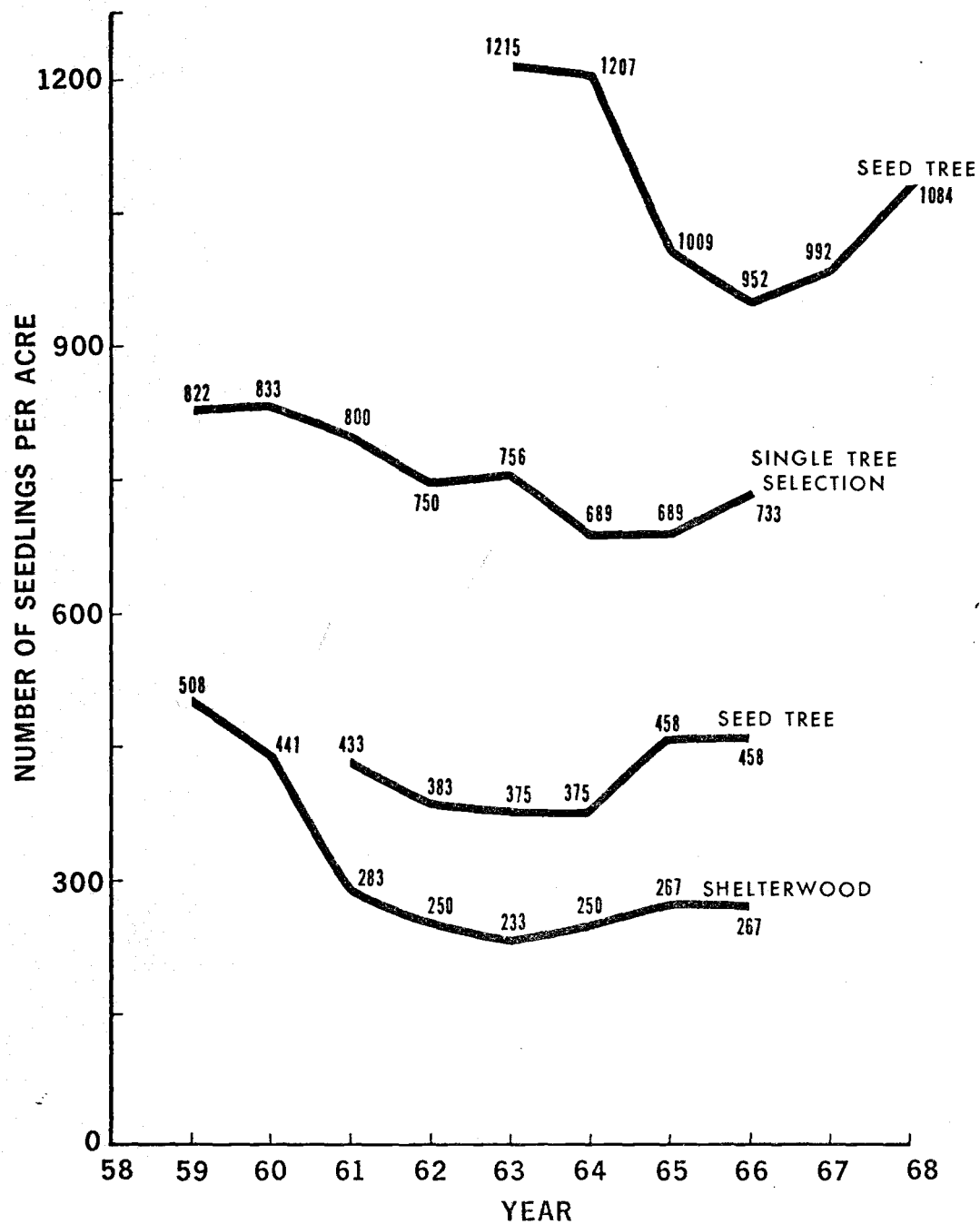


Figure 12.--Cumulative density of tanoak advance reproduction.

tree (28 percent), shelterwood (18 percent), single tree selection (36 percent), and seed-tree cutting of 1962 (35 percent). If seedling levels were fairly high, as in the shelterwood and seed-tree cutting of 1962, mortality continued at high rates for at least 2 more years. Sudden exposure to unaccustomed light and heat as manifested in severe moisture stress undoubtedly contributed to seedling mortality.

Of particular note is that 5 to 8 years after logging, tanoak advance reproduction in all cutting methods is far below the precutting levels of 2100 advance seedlings per acre and frequency of 60 percent. The effects of the slash disposal-site preparation techniques that were applied are inescapable.

Tanoak seedlings characteristically devote most of their energy to root development. On good sites seedlings about 65-days old in mid-July averaged 5.2 inches above ground and about 24 inches below (Roy 1957a). The environment consisted of partial shade and fairly loose soil following logging. Total first-year growth could have been more as the growing season was not yet complete.

On the Challenge Experimental Forest, first-year height growth is variable but generally best if in a shady environment. Here tanoak seedlings will average 6 inches in height at year end. Individual seedlings on sunny slopes also will reach 6 inches in height, but most will not. After the first year, height growth tends to be slow in all environments for the next 3 to 4 years. Height development seems to pause, apparently while the root system develops further. Growth then resumes upward. It is best if in partial shade (Roy 1957b), and poor

in both excessively shady and sunny situations. After 10 years, advance reproduction in the single-tree selection cutting averaged 3.5 feet tall with a range of 0.2 to 12.0 feet. Dieback of seedlings in the seed-tree method rendered height growth data meaningless, although in general, they were similar to that of the selection cutting.

Competition to conifer regeneration from advance reproduction could be serious, but only in small areas where density is high or where a favorable microsite allows for greater individual tanoak height growth.

In the future, tanoak trees from seed will be present in all cutting areas, especially in single-tree selection, the seed tree area of 1962, and anywhere else that site preparation did not eliminate most of the tanoak rootstocks. With height growth of tanoak advance reproduction being slow and distribution fairly clumpy, these trees most likely will become part of the intermediate and understory strata in the mixed conifer-hardwood forest. Like Pacific madrone, trees from seed also enhance the evolutionary potential of this species whose most effective reproductive mode is by sprouting.

Natural Regeneration in a Pure Hardwood Stand

Tanoak regeneration in this trial was sampled by fifty 1/2-milacre plots on transects founded on a random start-systematic procedure. The hardwood stand was the same as that reported for Pacific madrone: 60 years old, undisturbed, quite dense, and predominately tanoak.

Tanoak seedling density was 4600 per acre and advance reproduction was 5680 per acre. The converted frequency value for seedlings was 79 percent (milacre basis) and for advance reproduction, 95 percent. Such high density and frequency values demonstrate the efficacy of this environment to tanoak seedling establishment and the buildup of advance reproduction.

SUMMARY

The reproductive ability of tanoak on high sites is tremendous. Some seed is produced every year and bumper seed crops are produced every 5 or 6 years. When a bumper crop is produced, the forest fairly rains with acorns. In opportune locations beneath productive trees, acorns may number over a million per acre and be nearly 80 percent sound. More average values are near one-half million per acre and 73 percent soundness beneath open-grown clumps. Even young stump sprouts produce acorns as early as age 5, and by age 9 yield about 190 acorns per clump.

After acorns survive depredation by several coleopterous and lepidopterous insects and fall to the ground, their number decreases rapidly. Those in exposed positions are devoured by a host of consumers, and overheating and dessication render most inviable. Freezing temperatures also take their toll. Those acorns that survive to germinate are generally those that fall in cool, shady, protected places or are covered with leaves and soil. Covering is the best

protection of all. Fresh loose soil in a small opening is the best environment for acorn survival and germination, as well as for seedling survival and growth.

Sound acorns are easily identified, being heavier in weight and darker in color than unfilled or insect-infested acorns. But overheated and dessicated acorns also can be dark and heavy. Thus the acorn collector as a general rule, should gather acorns soon after they fall and only from cool, shady locations.

Storage of tanoak acorns in sacks at various temperature and moisture regimes proved risky. Storage is more certain if acorns simply are placed in plastic bags immediately after gathering, and then in a refrigerator at 34 to 38 degrees F. Briefly soaking the acorns, or sprinkling a little water on them before storage in plastic bags also helps. Probably the most efficient method is in situ storage near the seeding site. Acorns, selected for soundness, are stored in shallow wire-screen containers, buried about 2 inches, and covered with leaves and soil. At seeding time, only acorns with just-emerged radicles are used. This method has the advantage of insuring that acorns are "in tune" with the environment of the intended site, and that only viable acorns are seeded.

Germination in the laboratory resulted in a germinative capacity of 97 percent in 20 days, germinative energy of 6 days, and 43 percent germination after 6 days.

Germination in the field took place on a gently sloping, 4-acre clearcut having prepared (bulldozed) ground. It involved extensive testing of acorn position.

Reversing polarity of the acorns (placing them pointed end up) proved highly beneficial. Acorns so positioned had higher germinative capacity, higher germinative energy and higher germination of viable seed in a shorter timespan. Seedlings from point-up acorns also were more abundant, tended to have lower mortality rates, and in general, resulted in taller seedlings. But because the point-up acorns germinated earlier than those placed normally (point down), they also were subjected to freezing. About 75 percent of those frozen when 7-days old eventually sprouted from the root crown--indicating the young age at which tanoak seedlings possess sprout ability. When these seedlings did sprout, however, it was with multiple stems.

Placing acorns point down significantly lowered germinative energy. When they finally did germinate, the soil often was too dry and many tiny seedlings perished before breaking through the soil crust. Others died shortly after. Some also had difficulty extracting themselves from the acorn shell. This delayed germination and jeopardized their survival.

Extensive irrigation and fertilization trials showed water and fertilizer combined to have a positive effect on seedling survival and height growth. Water alone and fertilizer alone had less beneficial effects, but both were better than nothing. Watered and fertilized seedlings, 4- and 6-years old, were over twice as tall as their

counterparts in the untreated control and bettered them in stocking by 41 versus 23 percent.

To better understand results from the irrigation and fertilization trials, plant moisture stress, foliar nutrient concentrations, and other environmental data (subsurface soil temperature, soil surface temperature, light, air temperature, relative humidity) were gathered.

Trends in xylem sap tension showed the tanoak seedling root system to be efficient in acquiring water even on a hot day in early fall. Indeed, the predawn moisture stress of a large 6-year-old seedling was only 2 atmospheres--a value close to that of a tree with roots in running water. This same seedling, however, underwent a stress of 22 atmospheres in midafternoon. Four-month-old seedlings fared much worse--reaching a xylem sap tension of 35 atmospheres.

Foliar nutrient concentrations in tanoak seedlings, as determined by micro-kjeldahl, colorimeter, and atomic absorption spectrophotometer, quantified the amount of macronutrients in tanoak seedlings on the Experimental Forest. At time of maximum growth and nutrient stress in late June, seedlings were near the poverty level for nitrogen, phosphorous, potassium, and calcium. Fertilization with nitrogen and phosphorous increased mineral availability as did irrigation. But fertilization and irrigation combined, resulted in the highest concentrations of these elements in tanoak seedling leaves--substantiating the trends in seedling height growth and stocking noted earlier.

In spite of the utmost in care as manifested in initial site preparation, yearly removal of new shrubs, loosened ground at

every seed spot, careful seeding, use of acorns known to be viable when seeded, rodent protection, fertilization, and irrigation, seedling survival was poor. Seedlings died back to some degree or died outright at the slightest provocation. Heat, cold, and drought all resulted in death or dieback. High internal plant moisture stress resulting from poor stomatal control and excessive transpiration undoubtedly was the primary cause. Survival of 4- and 6-year-old tanoak seedlings in 1975 was less than 34 percent. Mean seedling height was about 12 inches. And many plants had multiple stems from dieback and sprouting.

Because of this poor showing, container-grown seedlings were outplanted early in the spring. Robust in size, vigorous of health, and physiologically of good balance with 2:1 root-shoot ratios, these seedlings survived only a little better than their seeded brethren. Survival after two growing seasons was 46 percent. Seedling roots tended to remain in the potting soil or that loosened when outplanted. This lack of downward root extension resulted in death from drought.

Seedlings also were shaded with wooden shingles placed southwest of them. This proved modestly beneficial, but did not greatly improve survival.

In mixed conifer-hardwood stands, different conifer regeneration cutting methods resulted in differential tanoak seedling abundance and survival. These cutting methods were designed to enhance conifer regeneration, not hardwoods. Hardwoods were mostly unwanted and partially eliminated.

In terms of environment, an intensive cutting method like seed tree closely resembles that of clearcutting while the less intensive single-tree selection method more closely resembles the uncut forest. Combination site preparation-slash disposal treatments, like dozer piling and lop and scattering, further disturb both environments.

Tanoak seedling and advance reproduction density and frequency seemed to be independent of cutting method. While large differences resulted, no meaningful trends were apparent. Success of tanoak natural regeneration is keyed more to advantageous micro-environments than to the overall environment created by cutting. This is seen by the 11-year record of new seedlings in the different cutting areas: every year in every method, from 4 to 400 new tanoak seedlings per acre were present, regardless of method.

Density and frequency of tanoak advance reproduction were 2100 seedlings per acre and 60 percent in the uncut mixed conifer-hardwood control. Six to eight years after cutting, tanoak advance reproduction ranged from one-eighth to one-half of this density in the various cutting methods. Obviously, the cutting and site preparation techniques applied were effective in reducing competition from tanoak advance reproduction both in magnitude and time.

Natural regeneration of tanoak in an undisturbed pure hardwood stand was high: 4600 seedlings and 5680 advance seedlings per acre with good distribution. Deep shade and lack of disturbance benefited tanoak regeneration.

Early height growth of tanoak is best in shade but slows down in all environments for the next 3 to 4 years. When it resumes, it is best in partial shade and poor in excessively sunny or shady situations. Advance reproduction in the single-tree selection method was 3.5 feet tall after 10 years.

Altogether, these trials lead to an inescapable conclusion--artificial regeneration of tanoak is exceedingly difficult in an exposed environment. Thus the probability of artificially establishing tanoak by planting or seeding in large open plantations is low indeed. Natural regeneration from seed in small openings is better, providing one accepts a rather clumpy distribution and a long timespan for the advance seedling population to build up.

In the future, tanoak trees from seed will be part of the intermediate and understory strata of the forest. The species is likely to be more abundant where disturbance from logging and slash disposal are less severe. This means that uneven-aged cutting methods like single-tree and group selection are more likely to favor tanoak than evenaged methods such as shelterwood, seed tree, and clearcutting.

CALIFORNIA BLACK OAK

Research emphasis for this species was placed on acorn yield, consumers, storage, germination, enemies of new seedlings, effect of fertilization, a provenance trial, and natural regeneration in various environments created by cutting.

Physical Characteristics of Seed

Flowering in California black oak takes place from mid-March to mid-May depending on physiography and local climate. Staminate flowers form long hairy aments that emerge from buds in the leaf axils of the previous years growth. Pistillate flowers are borne singly, or 2 to 7 on a short stalk that originates from leaf axils of the current years growth.

Acorns mature the second year. They occur either singly or in clusters of two or three. Acorn shape and size vary tremendously from tree to tree and from grove to grove.

Seed production of California black oak on the Experimental Forest for years 1958 through 1975 was: 2 bumper crops, one medium crop, and several very light crops. A few trees bear at least some acorns every year and exceptional numbers during a bumper seed year. Other trees of similar diameter and crown characteristics never produce an acorn. Apparently, the ability of a given tree to produce many or few acorns is an inherent characteristic.

Age, diameter of bole, and crown spread influence acorn yield. Young trees of this species characteristically produce seed between ages 30 and 75, but seldom large quantities before 80 to 100 years. A general relationship for a medium seed crop on a high site (McDonald 1969, U.S. Forest Service 1973) is:

Age (years)	Bole diameter (inches)	Crown diameter (feet)	Acorn yield (pounds)
30	5	15	0
50	9	20	5
80	13	26	20
100	17	32	60
150	24	41	100
200	32	52	140

Crown widths and bole diameters are based on a sample of 19 representative forest-grown trees ranging in diameter from 6 to 42 inches. At least three and usually four crown radii were measured for each tree depending on crown configuration. The crown width-bole diameter relationship is expressed by: $Y = 3.9 + 0.7x$ and r of .85, where

Y = average crown radius in feet, and

x = bole diameter at d.b.h. in inches

Crowns of forest-grown California black oaks characteristically are narrow. Free-to-grow trees in fields or large openings could have much wider crowns.

Acorns begin to ripen on the tree in late August and early September. As ripening progresses, acorn color changes from green to

yellowish to brown. The first acorns that fall usually are not sound. These are the aborted and insected acorns.

Ovule abortion in Quercus is commonplace and can take the form of zygote or embryo failure, lack of an embryo sac, an empty embryo sac, or most commonly, development of a normal embryo sac and contents, but lack of fertilization (Mogensen 1975).

Insects destroy many acorns, primarily in the development stage. Immature acorns are attacked by both lepidopterous and coleopterous species. They can destroy up to 95 percent of an acorn crop (Keen 1958). Heavy damage commonly occurs to a seed crop that immediately follows a bumper crop. A good example of this took place at low elevations in Shasta County in 1975. California black oak trees were heavily laden with acorns in 1974. A high percentage of them were free of insects. Some acorns even had scars on the kernal but no evidence of insect damage to the contents. Young acorns were abundant in mid-summer 1975, and promised a bountiful crop. When they fell, however, all but a handful were ravaged by insects--not with just one larva as is most common, but with 3 or 4. Acorn contents were devoured completely.

Some acorns fall when not yet fully mature. These germinate and store poorly. If the pointed end is brown and the acorn separates readily from the cup, the acorn is mature. The bulk of sound acorns fall from late September through mid-November in the north central Sierra Nevada.

After falling, acorns are susceptible to consumption and the microclimate near the ground. Acorns are eaten by at least 14 species of song and game birds, especially the steller jay, band-tailed pigeon, California woodpecker, and valley quail (Martin et al. 1961).

In the fall, the migratory band-tailed pigeon often can be seen clinging precariously to small oak branches while obtaining acorns. Acorns also are gathered from the forest floor. When searching for them, leaves and debris are flipped aside by rapid horizontal movement of the beak. California black oak acorns formed 3.2 percent of this pigeon's diet in September and 7.7 percent in November (Smith 1968).

Squirrels, deer, wood rats, bears, and other rodents also consume California black oak acorns.

The California gray squirrel is particularly important as a disseminator of acorns. It does not hibernate in the fall and thus is busy burying acorns until winter (California Fish and Game 1961). It does not bury food in caches but carries one acorn at a time and buries it in the ground singly (Ingles 1947). This practice contributes materially to reforestation. And it moves resultant seedlings out from under parent trees into a more favorable environment. In the process it spreads the oak into new areas where normally it would not reach for many years.

Acorns are a significant food for the California gray squirrel during a large part of the year. In Trinity County seasonal use ranged from 2 percent (July-September) to 31 percent (October-December). In Tehama County acorn use peaked in February (37 percent) and comprised

11 percent of the yearly total (Stienecker and Browning 1970).

Deer eat prodigious numbers of acorns. In a hardwood timber sale, several large trees were fallen on September 22 and sawed into logs. Large numbers of acorns were hidden and buried in the leaves and branches of their shattered tops. By October 1, numerous piles of fresh deer pellets and extensive pawed-out spots indicated both the preferred status of acorns and the dedication of the deer in getting them. Branch tips also had been browsed.

Deer consume acorns other than just after they fall. Many are eaten in autumn and winter when does, bucks, and fawns avidly root about in the leaves and snow for them. Moist, matted leaves also are relished, and form a valuable addition to the winter diet (Robinson 1937). In January, acorns and leaves of California black oak formed the chief diet of deer in Yosemite National Park (Dixon 1934). Even in the spring, acorns were vigorously searched for, particularly where melting snowbanks might reveal them.

On the Tehama winter deer range, leafage and acorns of California black oak constituted 28 percent of the total monthly diet of mule deer in October and 21 percent in May (Leach and Hiehle 1957). On the winter range of the Jawbone deer herd in Tuolumne County, California black oak acorns, twigs, and leaves constituted 13 percent of the winter diet (Leopold et al. 1951).

On another timber sale, acorns again were gathered from fallen trees on a high site during a poor seed year. Only a few of the largest, tallest trees on the ridge produced acorns and only in the

topmost portions of them. After the trees had been felled, a dense tangle of branches and leaves resulted. Acorns had jarred off the branches and had been scattered in every direction. Seven days later acorns were collected. Those that remained were beneath the densest tangles. Accessible acorns had been consumed. Range cattle either stood by or continued to search for acorns, California gray squirrels scampered along the ground and steller jays flitted from trees to ground and back again. Never have I seen so dense a population of squirrels and jays in one area at one time. Cattle obviously had been present in the area in large numbers for some time as well.

If acorns are exposed for only a few days, the typically hot autumn weather can cause severe drying. Mature acorns lying in light litter were found to have full-sized cotyledons 2 days after falling. Two days later, cotyledons remained full sized. But after 9 days, they had withered to about one-half normal size. If acorns were buried in leaves and branches or shaded by logs, cotyledons remained full-sized after 20 days.

Acorns are sensitive to small decrements of contained water. They cannot tolerate drying, and a moisture content below 30 percent probably is critical. After the critical point is reached, cotyledons no longer are crisp, firm, and cream colored. They become limp and dull with a tan-colored tinge. With time the embryo becomes hard and the cotyledons spongy, with a brownish hue.

Mold can be a problem. Forming in the circular scar of the absent cup, a blue-gray mold often penetrates into the acorn and destroys its

contents. Acorns that were moldy had been covered by newly fallen leaves for about two months. Rainfall had been proficient and leaves and acorns were saturated. For other acorns in this same environment cutting tests revealed cotyledons to be full sized. Examination of acorns from other crops, after overwintering in saturated leaves and partially decomposed organic material, indicated no mold. Nevertheless, Jaeger (1920) reported that Indians would gather only newly fallen acorns to avoid the mold.

Seed Handling Practices

The acorn collector should gather acorns at the time of maximum seed fall. By then, most of the insected, aborted, and immature acorns have fallen. Exposed acorns are poor risks. They might be large and healthy looking but they probably have become too dry. Collections should be gathered from shady, protected locations. Sound California black oak acorns can be determined by weight and color. Acorns that are lighter colored and low in weight should be rejected. So should acorns with cracks, holes, or mold.

Storage

Because of the need to stockpile against poor seed years, it is necessary to store acorns. But storage of California black oak acorns is difficult. The classical storage criteria of just-below-freezing

temperatures and a low moisture content is fatal. A high moisture content is necessary as is an above-freezing temperature. Under these conditions, the acorns germinate.

Mirov and Kraebel (1939) recommended storing acorns in sacks in a cool room for 1 to 2 months if not allowed to overheat or dry out. This was good advice. Large, fresh, sound acorns were gathered in Shasta County from mid-September to mid-November and stored there in a large paper sack in a room at 40 to 75 degrees F. All acorns were ruined by mid-December. Cotyledons had shriveled to about $2/3$ normal size and changed from a crisp to flaccid state. The embryo altered color to a dark yellow and cotyledons no longer were cream colored, but a dull tan.

Later trials were more successful. Over 825 acorns were gathered in late November, 1965, and retained if of proper color and weight. Cutting tests showed cotyledons to be full sized at the time of acorn fall. Each acorn averaged 0.18 ounces in weight. Acorns were then soaked for about one hour in cold water and placed in a sealed polyethylene bag in a refrigerator at 34 to 38 degrees F. Here they remained for 66 days. Although moisture collected on the inside of the bag, cotyledons were about $2/3$ normal size after storage. Cotyledons and embryos, however, were the proper color and apparently were viable. But some acorns were ruined by mold penetrating the cup end. Eventually, acorns were spot-seeded in a plantation on the Experimental Forest.

In a 1968 trial about 2500 acorns were collected, spread out on a concrete floor, and all cups were removed. The clean, sound-appearing acorns then were placed in a refrigerator where temperature was maintained at 34 to 38 degrees F. and relative humidity at 30 to 80 percent. Both were monitored by instruments. Acorns were not soaked in water, but placed in shallow, open, plastic trays.

After 46 days, cutting tests revealed cotyledons to be of good color, but flaccid. So acorns were soaked in water for 8 hours and placed in a sealed polyethylene bag. Nine days later, cotyledons were crisp and full. No mold was noticed. They were spot-seeded in a plantation soon after.

A third storage trial involved about 1200 sound-appearing acorns collected in 1970. Light-colored and insected acorns again were discarded. Acorns were rinsed in water and placed in a sealed polyethylene bag in the refrigerator at 34 to 38 degrees F. Cutting tests every 2 weeks evaluated cotyledon size and appearance. Color always was good; cotyledons consistently were slightly flaccid. In mid-January, acorns were taken out of storage and placed in containers for outplanting on the Forest.

Tentative methodology for long-term storage (1 to 2 years) is indicated. Because cotyledons consistently were somewhat flaccid during storage, it appears they can tolerate or even store better at a lower moisture content. Acorns probably should not be soaked before storage unless precautions are taken against mold.

Thus storage should be in sealed polyethylene bags of a thickness suitable to inhibit moisture loss but freely emit respiration by-products. The storage temperature should be low enough to inhibit respiration and be just above freezing. Moisture content during storage probably should be about 30 to 40 percent of fresh weight.

Stratification

Dormancy in California black oak is caused primarily by dormant embryos (Chan 1971; Schopmeyer 1974). But the short-term storage criteria of low temperature and a high moisture content serve perfectly as stratification criteria. Thus stratification commonly takes place in storage.

Germination in Laboratory

Germination trials of this species are limited. Mirov and Kraebel (1939) show the best germinative capacity obtained to be 95 percent, apparently from a single trial (Schopmeyer 1974). Under optimal conditions, seedlings appear above ground 15 days after seeding. Germination is hypogeous.

In this study acorn position was tested for speed and completeness of germination. Three lots of about 85 acorns each were placed point up, point down, and on their sides. After storage in the refrigerator for over 3 months, acorns were buried 1/2 inch in moist peat moss in

deep flats in a greenhouse. The temperature was maintained at 70 ± 5 degrees F. and the acorns received water as mist for 20 minutes every fourth day.

Germination was rather poor, although trends in germinative energy and capacity by acorn position could be ascertained:

	<u>point up</u>	<u>point down</u>	<u>side</u>
Germinative energy (days)	34	47	34
Germinative capacity (percent)	24	21	16
Germinative capacity (percent) by peak day	95	62	46

Number of days between sowing and germination, by acorn position, was: point up (22), point down (44), and side (27).

Germinative energy was similar for acorns placed point up and on side, but total number of acorns that germinated and germinative capacity by the peak day was much better for acorns positioned point up.

In a second laboratory germination trial, about 300 acorns were taken from cold-moist storage after 104 days and placed point up in small containers. The soil mix was mostly sandy loam with increments of sand and peat moss added. Greenhouse temperature and watering was as before. Acorns were examined periodically for germination. After 21 days most acorns had split open at the pointed end. A few radicles had extended. Several acorns were opened and the cotyledons examined. All looked good, crisp and full. Two days later a hypocotyl cleaved

the surface. The duration between seeding of stratified acorns and germination was 23 days.

Germinative energy for this trial was 34 days. Germinative capacity was 63 percent in 118 days, and germinative capacity by the peak day was 58 percent of the viable acorns.

Germination in Field

In nature, stratification takes place while the acorns overwinter in covered, shady and protected places. The germination period in the spring can be several weeks. Germinative capacity is extremely variable--changing with microclimate, depth acorns are buried, amount of mold, degree of insect damage, and other factors.

When germinating, the radicle is first to emerge, and grows downward for 10 to 20 days before the hypocotyl appears above ground. This is an advantageous adaptation to a dry climate and aids the seedling in getting to and staying in a zone of adequate soil moisture. Of course, no transpirational losses occur until stem and leaves are above ground. Thus critical moisture losses are minimal while the energy stored in the large cotyledons fuels root development downward.

Two extensive trials portray field germination of California black oak. Seeding dates were 1966 and 1969. The first was applied to a 1-acre plantation and the second to about 3 acres of land bulldozed free of all shrub competitors (Fig. 13). The plantations were as homogeneous as possible with uniform high site quality, aspect (south), and slope



Figure 13.--A portion of a California black oak plantation.

Challenge Experimental Forest, 1971.

(10 to 15 percent). Shrub species and unwanted hardwood sprouts were removed periodically as well.

Altogether, 146 and 996 seed spots comprised the population of the two plantations. At each spot, the ground was loosened with a pulaski and the soil shaped to form a shallow depression. Acorns were buried 1 to 2 inches and covered with loose soil and leaves. Most spots received two acorns, up to five if acorns were small. Pinned-down, mound-shaped wire screens protected the acorns from rodents.

Every seed spot received a careful check at weekly intervals in the spring, biweekly in the summer, and once per month in the fall. Newly germinated seedlings of each survey were marked so that mortality could be keyed to emergence date.

In the first trial, seeding took place November 29. An examination February 15 showed no hypocotyl elongation. Another survey on March 10 indicated a few just-emerged hypocotyls. The first broke through the soil surface on April 8. Germination continued through July 8.

Germinative energy of sound acorns was 34 days and germinative capacity 31 percent in 91 days. Germinative capacity of viable acorns after 34 days was 79 percent.

In the second field germination trial, seeding took place December 4. An examination March 28 showed a few radicles just emerging from acorns. More had emerged by April 18, when a few had extended radicles downward about 6 inches. The first hypocotyl broke through

the soil surface on May 9. The germination period continued through October 9.

Germinative capacity was 38 percent in 153 days. Germinative energy was not clear, being bimodal at 5 and 54 days. The long germination period and bimodal germinative energy values were caused by the seeding technique.

Extensive rainfall and resultant erosion filled in many of the shallow basins constructed around each seed spot, and in some instances completely covered the wire screens. Instead of being 1-inch deep, some acorns were buried up to 4 inches. Moreover, a distinct crust formed at the eroded-residual soil interface. Most of the screens were pried up and set aside. This resulted in the burst of seedlings the 54th day. New seedlings grew through the soil crust where the edge of the wire screen had been.

Acorn germination and seedling growth were followed closely throughout the summer. Both were delayed and erratic. Some acorns tarried too long and their tiny hypocotyls turned black from drought. Others, however, put forth a little whitish hypocotyl that grew up to the soil crust and progressed no farther. Small knobby protrusions formed there. These became quite hard and of a light tannish color. Most overwintered in this state and appeared above ground the following spring.

A few hypocotyls found their way to the soil surface in August and September and were counted as germinated seedlings. Many of these

late emergers put forth multiple stems while those that germinated earlier consisted of single stems.

Seedling Survival and Growth

1966 Seeding

Seedlings are subjected to depredation from the time of germination onward. A detailed record of depredation and mortality by causal agency was planned. This proved fruitless, however, as it became impossible to determine if a seedling was dead or alive. Many seedlings were, in fact, dead above ground by the end of the first growing season. Many of them sprouted from the root crown the next spring.

Three weeks after the first seedlings appeared above ground, several were damaged by insects. An unidentified leaf miner, a caterpillar (Hemerocampa vetusta), and tiny ants accounted for most of the damage. A nocturnal rodent also nipped off many seedlings 1 to 2 inches above ground.

As the season progressed, mold took its toll. As noted earlier, some acorns were soaked in water before storage. Mold developed in storage and ruined some of them. These were discarded. Other acorns with just a little mold were seeded. Some of these acorns germinated and a skinny little seedling resulted. Presumably a large part of the cotyledons was consumed by mold and the germinated embryo lacked

sufficient energy for normal development. When the soil became dry in mid-June, these seedlings perished.

Later in the summer, grasshoppers became particularly fierce, and scores of seedlings were reduced to mere stems. A few seedlings simply disappeared and a few were pulled up by deer seeking the germinated acorn. Drought was the primary killer.

A regeneration survey in the spring of 1967 showed survival to be 70 percent. Each subsequent year a few seedlings died. Drought was the primary cause but other, often interacting, causes contributed. Bracken and bull thistle vigorously competed for soil moisture. Grasshoppers and other insects defoliated seedlings in the fall, and rodents nipped off a few seedlings just above ground.

Just-emerged leaves and terminal buds were damaged by hard freezes on April 17, 1968 and April 20, 1970. But little pink buds formed by May 8 and new leaves appeared by mid-May. Many seedlings, however, had frozen back to the root crown. These sprouted, generally with only one stem. Dieback during summer occurred in 1971 and 1974. Drought was suspected. Deer browsed the tops out of seedlings in 1970 and pocket gophers (Thomomys bottae) killed four seedlings in 1973 and eight seedlings in 1974.

In 1975, survival after 10 years was 54 percent. Average seedling height was 1.1 feet with a standard deviation of 1.0 feet and range of 0.1 to 7.0 feet.

1969 Seeding

Seedlings that emerged first generally were taller and more vigorous than late emergers. A few early seedlings even put forth a second set of leaves the first growing season. Late emergers tended to have small leaves. Mortality from drought first appeared in mid-June and was worse if the seedlings were in dense bracken, poison oak (Rhus diversiloba T. & G.), or western raspberry (Rubus glaucifolius Kell.).

By early September, twelve seedlings possessed only one green leaf--other leaves were brown and dead from drought. An October survey noted much damage from grasshoppers and a first season mortality of 3 percent. The number of spots stocked with at least one California black oak seedlings was 51 percent. A survey the following spring indicated winter mortality to be 4 percent, primarily from eroded material smothering seedlings.

In 1970, seedlings began flushing about mid-April in response to maximum temperatures in the mid 70's. The hard freeze of April 20 killed tender, just-emerged leaves, first turning them grayish-green and then black. Seedlings that flushed after April 20 were frozen April 30 when freezing temperatures again prevailed. Subsequent surveys indicated nearly all sprouted from the root crown with a single stem. Similar weather April 13, 1972, when seedling leaves were one-fourth developed, resulted in the seedlings needing new foliage once again.

Those hypocotyls that held-over a full growing season beneath the eroded material emerged in 1970. Because all other seedlings were marked, the emergence and fate of these seedlings could readily be ascertained. A few appeared above ground on April 30, and two weeks later 295 were present (Fig. 14). Altogether, 420 hold-over seedlings resulted. They increased stocking in the California black oak plantation from 51 to 72 percent at peak, and total number of seedlings to 1184. Physiologically, these were weaker seedlings than their predecessors. By seasons end 22 percent of them had perished, mostly from drought.

Other than for hold-over seedlings, second year mortality in the plantation was low. Pocket gophers killed three seedlings in June. Grasshoppers and various insects chewed leaves, and some stems were nipped off at ground line by rodents. No browse damage was observed, although California black oak sprouts in an uncut stand nearby received heavy browsing.

Seedling height averaged 0.2 feet after one growing season and 0.3 feet after two seasons. After three growing seasons, seedlings averaged 0.4 feet and after seven were 0.7 feet tall with a range of 0.4 to 4.0 feet.

In 1971 acorns were interplanted in unstocked spots. Although these did not prosper, they boosted stocking to 82 percent. By 1975 stocking had fallen to 64 percent. Drought was the prime cause; pocket gophers were second. Twelve seedlings were killed by these rodents in 1971 and eight in 1972. More were killed in 1973 and 1974

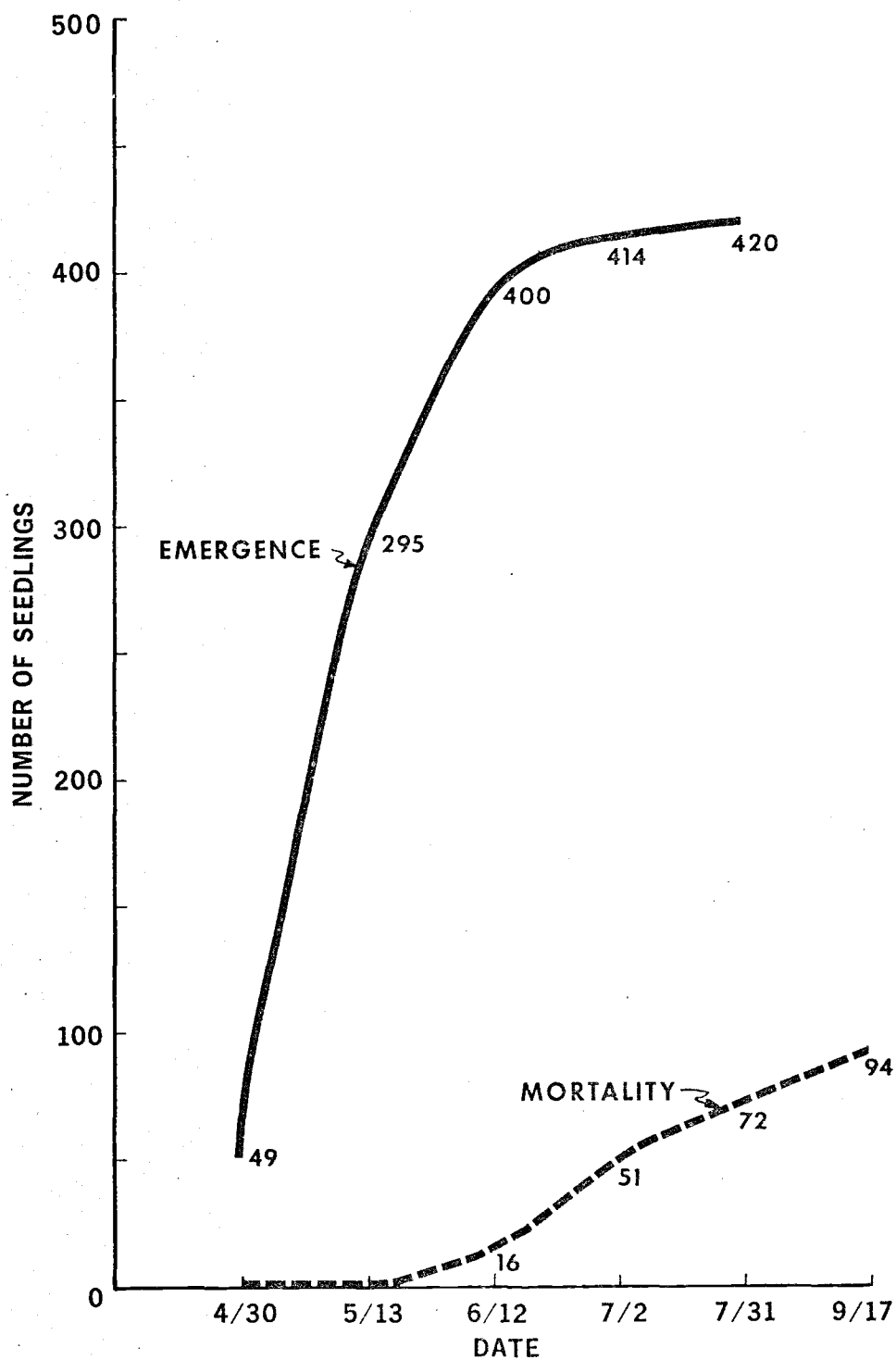


Figure 14.--Magnitude and timing of California black oak hold-over seedling emergence and mortality. 1969 seeding.

when pocket gopher depredation expanded dramatically. In nearly every instance, seedling roots were almost completely devoured, and only a nub remained below ground. Minor grasshopper and browse damage also was noted. No dieback of stems occurred.

Provenance Trial

California black oak is a most adaptable species. It is found on sites that range in quality from the very best to the very worst, and even on ultrabasic soils and physiographic badlands where conifers rarely grow. The elevational range of the species is from about 200 to 8000 feet and its natural range spans the state from border to border (McDonald 1969). The evident adaptability of the species might endow trees from some other geographical race to burst buds later and have more rapid, early height growth than that of local stock.

A limited provenance study seemed advantageous to possibly circumvent the problems of spring frosts and poor early height growth. Eight seed sources from elevations higher than that of the Experimental Forest were tested. These ranged from 3200 to 5625 feet. Being of higher elevation, these seedlings should flush later and avoid freezing. Two sources were from mid elevations on the Inyo National Forest--provenances that should be highly adapted to drought and cold. Would drought-adapted ecotypes exhibit strong early height growth in an environment more moist and warm than normal? The Challenge provenance was represented by seedlings in the 3-acre plantation of 1969.

Acorns were stored in the refrigerator at 34 to 38 degrees F. for several months, and then outplanted in early spring in a plantation free of competing vegetation. Number of seed spots per provenance ranged from 26 to 110.

Survival, height growth, leaf flush, and leaf fall data were gathered both annually and periodically. Leaf flush data were categorized further as: swollen buds, flushing, partly open and pinkish colored, open but not mature, and mature. Leaf fall data were differentiated primarily on the basis of color: leaves green, greenish-yellow, yellowish-brown, brown, reddish-brown, and absent.

As a whole, survival, growth, and phenological data yielded indefinite results. After seven growing seasons, stocking of provenances ranged from 26 to 52 percent which is lower than the Challenge provenance. Height growth of provenances ranged from 0.7 to 1.2 feet. These values are close to those of the Challenge provenance at comparable age. Leaf flush data revealed no meaningful differences relative to original elevation of provenance. Variation within a provenance was extensive. For example, midway through the leaf development period, different seedlings within a given provenance had leaves in all five developmental stages. And as many as three stages would be represented on a given seedling. Plainly, leaf flush data were poor descriptors of provenance phenology. Leaf fall data also were poor.

Consequently, height and diameter growth were measured relative to a pin placed in the stem below the last node. Periodic height growth was the distance between the pin and the tip of the terminal

bud. Measurements were at weekly intervals to the nearest hundredth of an inch. Growth began when 5 percent of total seasonal growth had been completed and ended when 95 percent had taken place (Fowells 1941). Weather the eighth season was abnormally dry and windy. January-through-May precipitation was 32 percent of the long-term Challenge average for these months.

Little differences among provenances and high variation within each provenance characterized California black oak seedling height and diameter growth. About 82 percent of all seedlings began height elongation on April 26. Diameter growth began 7 to 21 days later. All seedlings ceased to extend in height and diameter after 43 days. Seedling height and diameter at the beginning of the season were poor indicators of subsequent seasonal growth at least for this dry spring. No trend of larger seedlings growing most was discernible even though it appeared that taller seedlings grew for a longer timespan than short seedlings.

Mean seedling height growth was 1.52 inches and ranged from 0.4 to 11.3 inches. Standard error of the mean was .46 inches. Diameter growth averaged .05 inches in the range of .004 to .16. Standard error of mean diameter was .01 inches.

Containerized Seedlings

Because initial stocking levels were inadequate and survival unstable, a more certain regeneration technique was needed. Containerized seedlings held promise.

The container was open bottomed, felt paper, two and 3/4 inches square by 6 inches deep, placed in wooden flats. Seedlings germinated in the spring and were grown in a greenhouse until November 1. Then they were transferred to a lathhouse and allowed to harden off before outplanting on the Experimental Forest in mid-March. As a whole, seedlings were robust with thick short stems (0.3 feet) and had well developed root systems that grew laterally along the bottom of the wooden flats. These roots were pruned when outplanted, an operation that removed about two-thirds of each seedling root system.

First-year seedling survival was 66 percent in spite of an abnormally dry spring. Subsequent surveys indicated survival of containerized seedlings to be no better than that of seedlings from acorns. Drought was the prime cause of mortality. Much deeper containers should be tested for propagating California black oak.

Effect of Fertilizer

The tendency for poor early height growth in California black oak seedlings makes them susceptible to overtopping by other vegetation and browsing by deer. Height growth in terms of wood production also

is lost. Would fertilizer stimulate height growth?

Fertilization trials were begun in February 1970 when about 100 seed spots each received a handful of 16-20-0 fertilizer. An equal number of spots in alternate rows were not fertilized and served as the comparison to fertilized. Both were located in open plantations on prepared ground free of slash and competing vegetation. Date of application was in February of each year.

Fertilizer stimulated height growth of California black oak seedlings from the beginning (Fig. 15). After five growing seasons, fertilized seedlings were over three times taller than unfertilized seedlings. Fertilized seedling stems were robust and thick, leaves were more numerous and much larger, and leaf color was darker than unfertilized plants.

Foliar analysis.--Analysis of minerals in the leaves of California black oak seedlings, as in tanoak, quantified the nutrients present (Table 8). Standard errors ranged from 1/9 to 1/11 of the mean for nitrogen, 1/3 to 1/4 for phosphorous, 1/5 to 1/8 for potassium and calcium, and 1/12 to 1/18 for magnesium. Analysis of variance indicated both nitrogen and phosphorous in the leaves of this oak to be significantly higher ($p = .05$) when fertilized. Comparison of nutrient levels in unfertilized seedlings and poverty levels indicated all nutrients except potassium to be adequate at the time of maximum nutrient stress.

Plant moisture stress.--These same seedlings were sampled by the same standardized sampling procedure and twig collection technique as

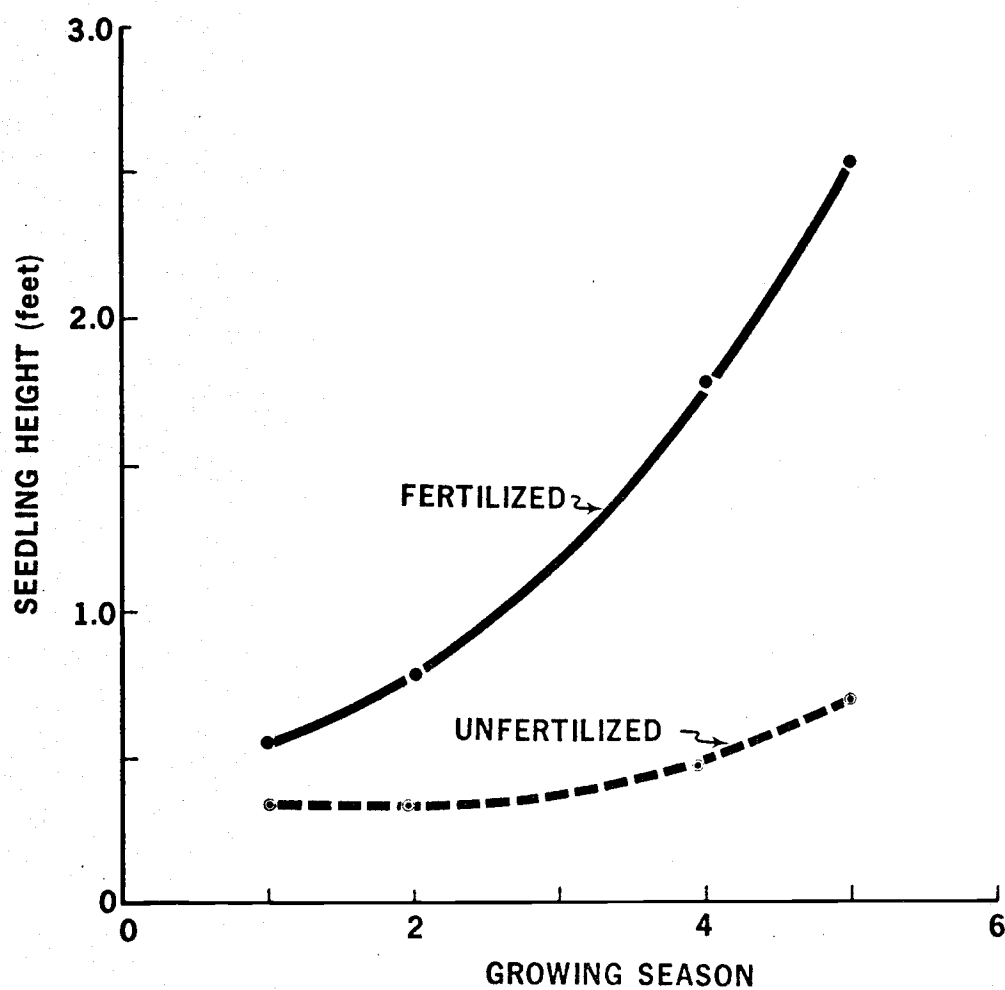


Figure 15.--Effect of fertilizer on height growth of California black oak seedlings.

Table 8.--Mean foliar nutrient concentrations of fertilized and unfertilized California black oak seedlings

<u>Nutrient</u>	<u>Fertilizer</u> percent of foliar dry weight	<u>No fertilizer</u> percent of foliar dry weight
Nitrogen	2.591	2.262
Phosphorous	.199	.135
Potassium	.457	.580
Calcium	.527	.579
Magnesium	.185	.185

tanoak. The sampling date in early September also was similar. For fertilized seedlings, the mean predawn xylem sap tension was 7.0 atmospheres in the range of 4.5 to 8.0; for unfertilized seedlings, 11.1 in the range of 6.0 to 18.0 atmospheres. This difference suggests that the root system of fertilized seedlings probably was better developed and hence better able to glean scarce moisture from the soil.

Some browsing of fertilized seedlings by deer was noticed each year. Damage tended to be minimal and was confined mostly to lateral shoots. Only in 1974 were unfertilized plants browsed.

Natural Regeneration in a Mixed Conifer-Hardwood Stand

Contrasting environments created by different conifer regeneration methods (seed tree, shelterwood, single-tree selection), and an uncut control served as an ideal base for evaluating California black oak seedling frequency, density, and mortality. Combined site preparation-slash disposal techniques such as dozer-pile and burn, and top lop and scatter also were applied in each method. In the dozer-piled portions of each compartment, not only was the slash piled, but many unmerchantable conifers and hardwoods were uprooted and piled also. In the process, mineral soil was created. Its amount was in direct proportion to the intensity of the cutting method--most in seed tree, some in shelterwood, and little in single-tree selection. An additional treatment was to poison hardwoods over 12 inches in diameter at breast height.

After logging, California black oak trees 3.5 to 12 inches in diameter numbered 4 per acre in the seed-tree method, 3 in the shelterwood, and 6 per acre in the selection cutting. Seed from these few small trees plus that disseminated in the cutting areas by birds and squirrels constituted the black oak seed source. Nine trees per acre in this diameter class plus 2 trees per acre in the 13- to 37-inch class were present in the control.

California black oak seed production was sporadic. A bumper seed crop was produced in 1958 with a medium crop in 1967. These and several very light crops constitute seed production of this species for the 1958-1968 period.

For California black oak, "bumper" means many times fewer seed per tree than for a bumper crop from tanoak trees. This is to be expected. Most of the California black oak trees were less than 65-years old during the study. At that age they rarely produce heavy crops. Stimulation of seed production from cutting was not observed.

Even the bumper seed crop of 1958 did not result in many new seedlings except in the shelterwood. New seedlings ranged from 4 to 700 per acre (Fig. 16) and frequency between 1 and 20 percent for all cutting methods and seed crops. Seedling survival trends were calculated by averaging year-by-year density values for each seed crop and each cutting method. Seedling survival after 3 years was:

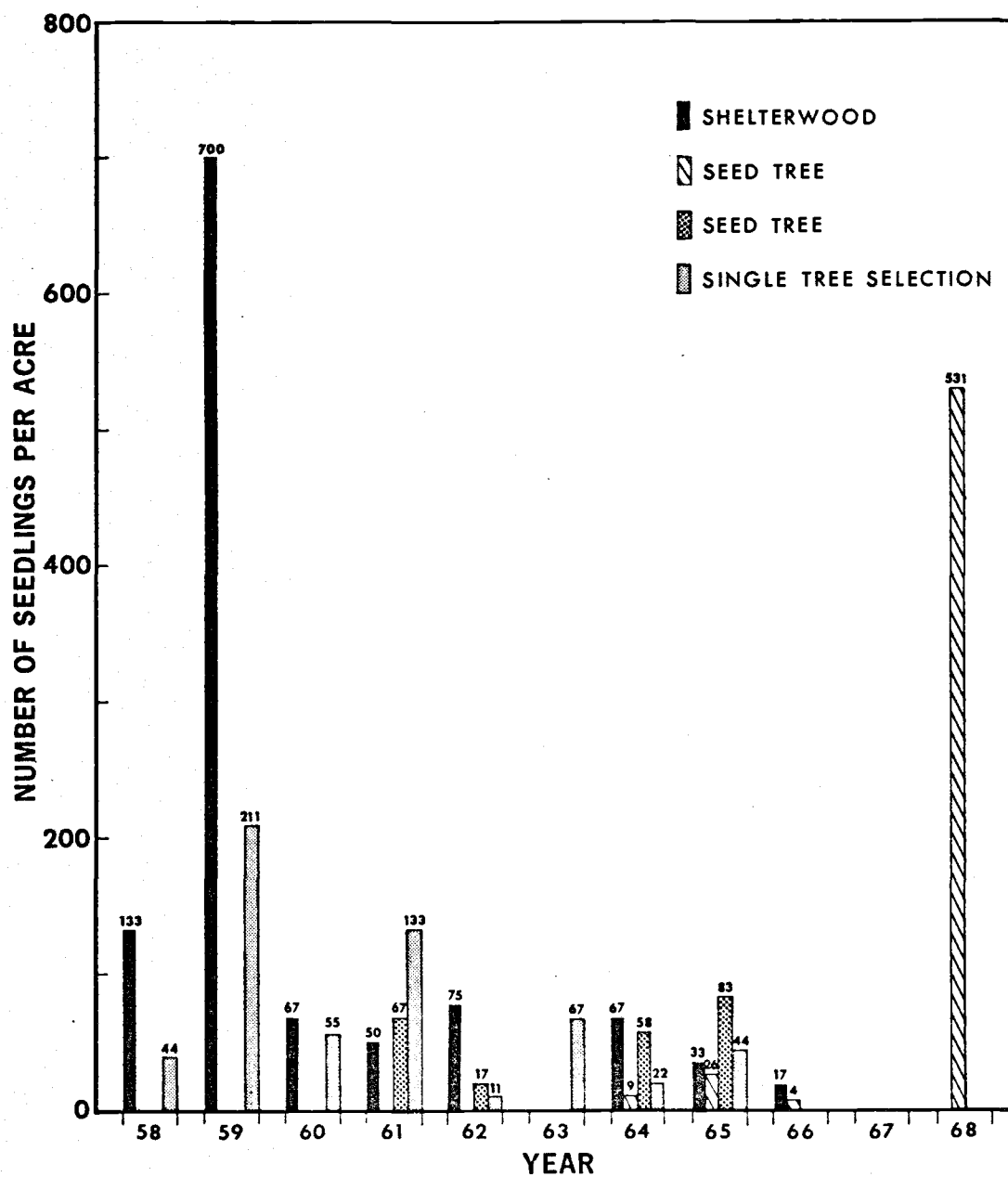


Figure 16.--Eleven-year record of new California black oak seedlings.

<u>Cutting Method</u>	<u>Percent</u>
Seed tree (combined 1960 and 1962 cuttings)	60
Shelterwood	37
Single-tree selection	58

Survival trends are somewhat confounded by density: high survival often is associated with low initial seedling density and vice versa. This was the case in the seed-tree cuttings. The fourth-year projection of seedling survival by cutting method was:

	<u>Density</u> (seedlings per acre)	<u>Frequency</u> (percent)
Seed tree	15	2
Shelterwood	25	3
Single-tree selection	44	4

These trends suggest that a cool, shady environment is best for establishment and survival of California black oak seedlings.

They are verified by survival in the control. Here density was 112 seedlings per acre and frequency, 9 percent. After 3 years, these values had not changed--no mortality had occurred.

In undisturbed stands on the Experimental Forest, advance reproduction of California black oak tends to be scattered throughout each compartment. Aggregation of seedlings is low and one or two seedlings per milacre plot is commonplace.

In the uncut control, density of California black oak advance reproduction in 1961 averaged 317 seedlings per acre with a frequency of 17 percent. By 1966 it had steadily increased to 392 seedlings per

acre and a frequency of 24 percent. Thus California black oak advance reproduction was increasing slowly.

These advance seedlings are an enigma to the ecologist because so little is known about them. They are shade tolerant and persistent. Height growth rates are virtually nil and often less than 1/2 inch per year. Sometimes the length of living stem actually decreases. And sometimes, if in continuous shade, the entire plant will die back to ground line and resprout with one stem the following year. Repeated regeneration surveys on permanent plots with marked seedlings showed a few California black oak advance seedlings in deep shade to die back to the root crown one year, not extend above ground the next, and put forth a small shoot the third. Seedlings in sunny environments also exhibit dieback, but to a lesser extent.

The root collar of advance seedlings contains dormant buds which give the species an early ability to sprout. Injury from logging or fire often causes sprouting. After sudden release from a dense overstory, spindly little advance seedlings also may die back from sunscald and sprout. Those of more robust size do not die back, but grow very little for several years.

By 1966, the cumulative density of California black oak advance reproduction for the 1958 through 1966 period, excluding that initially present, was 792 advance seedlings per acre for seed tree, 516 for shelterwood, and 711 per acre for single-tree selection (Fig. 17). In the seed-tree cutting of 1962 only 228 advance seedlings per acre had accumulated by 1968. Corresponding frequency values by cutting method

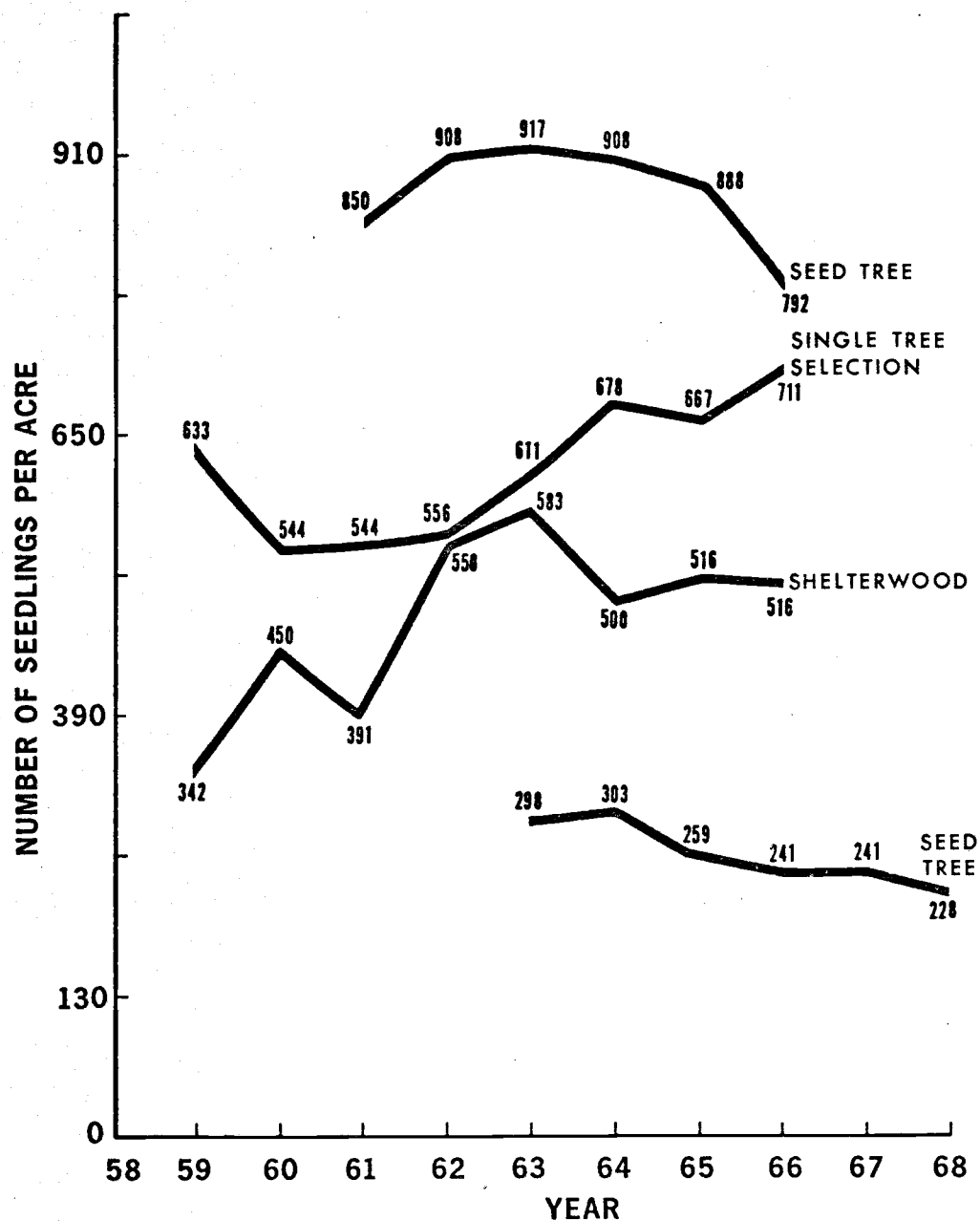


Figure 17.--Cumulative density of California black oak advance reproduction.

were seed tree (35 percent), shelterwood (27 percent), single-tree selection (47 percent), and seed-tree cutting of 1962 (16 percent).

The overall trend in the selection and shelterwood cuttings was a gradual buildup of California black oak advance reproduction. The two seed-tree cuttings both indicated downtrends that probably resulted from mortality exceeding the combination of no or poor seed crops, seedling mortality, and low numbers of seedlings becoming advance reproduction.

Relative to the before-logging density of 317 advance seedlings per acre and frequency of 17 percent, it is clear that cutting and site preparation, in general, enhanced the buildup of the California black oak advance seedling population. And, like the seedlings, California black oak advance reproduction survives, becomes established, and is better distributed in the cool, shady environment of selection cutting.

Survival and establishment are only part of regeneration success. The other part is height growth. As noted earlier, dieback is associated with California black oak advance seedlings in deep shade, and to a lesser extent in strong sunlight. Height growth of seedlings is best in partial shade.

In a shelterwood-like cutting in a nearby compartment, with only top light available, California black oak advance seedling height growth was slow for the first few years and increased thereafter (Fig. 18). These small plants were of unknown age and had died back to the root crown after overstory removal. All sprouted with a single

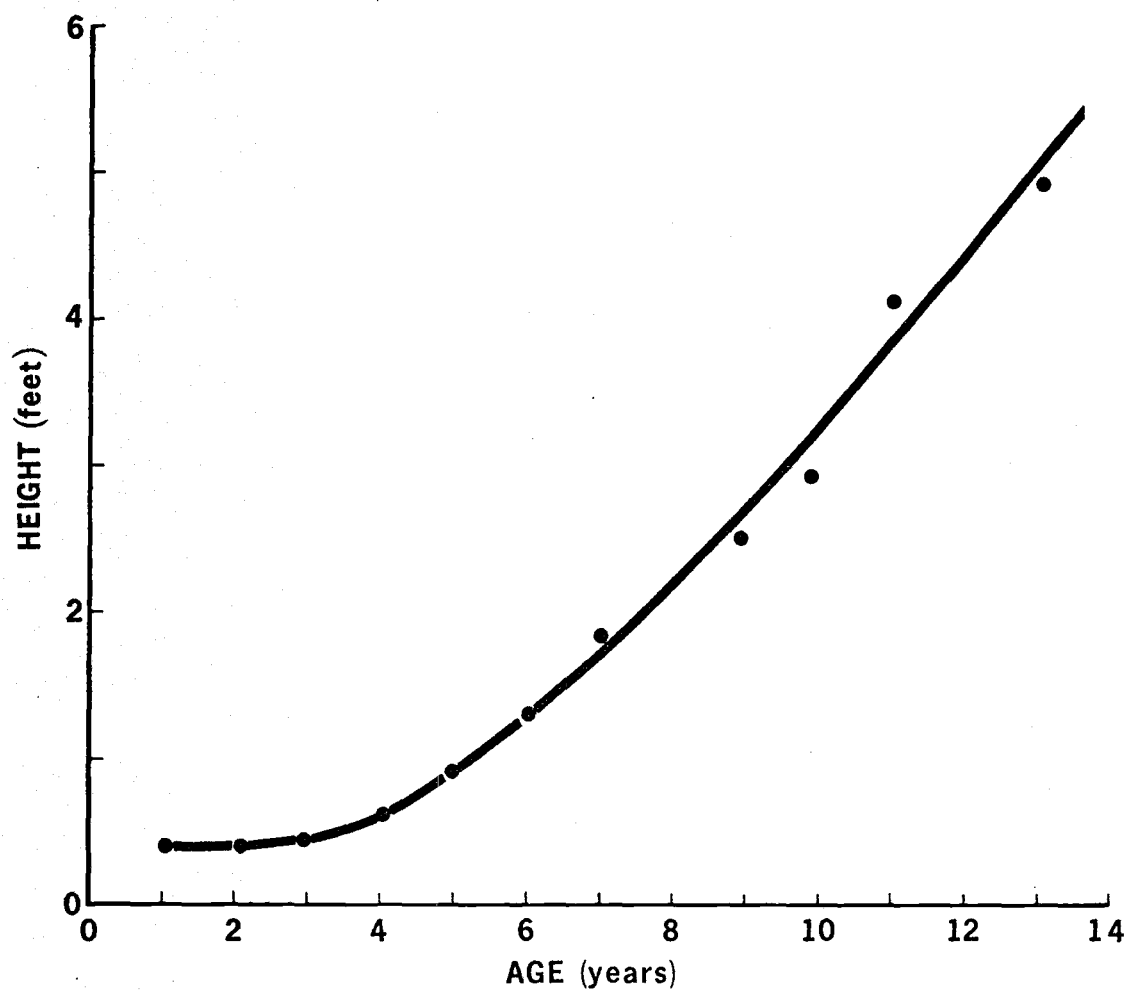


Figure 18.--Height development pattern of California black oak advance reproduction in a shelterwood environment.

stem. Their height growth remained quite variable. At age 13, seedling height ranged from 2.3 to 7.4 with a standard deviation of 1.7 feet. Lateral development was sparse. Thirteen years after sprouting, crown spread was 1.7 with a standard deviation of 0.4 feet.

In the single-tree selection cutting method, California black oak advance seedling height was 2.9 feet, ranged from 0.4 to 8.6, and indicated a standard deviation of 2.4 feet. Some of these plants were present when the study began and were of unknown age. Others began as seedlings and were accumulated as advance reproduction at age four. The bulk of the seedlings, however, were at least 10-years old. All were single stems, gave no indication of dieback, and had not sprouted.

As noted earlier, California black oak seedlings in full sunlight in the plantation averaged 1.1 feet tall with a range of 0.1 to 7.0 feet (Fig. 19) and standard deviation of 1.0 feet after 10 growing seasons.

Comparison of the three environments indicated that seedlings in the 4- to 20-year age class develop best in partial shade, with full shade being next best, and full sunlight poorest.

The competitive potential of California black oak advance reproduction to conifer seedlings is low. This oak's height growth is slow and the distribution of advance seedlings more scattered. Small groves of trees will be formed, however, and here competition could be severe.

In the future, California black oak trees, from seed, will be present in all cutting areas, and especially in those portions where



Figure 19.--This California black oak seedling is growing rapidly in the sunlit environment.

moderate to fairly large amounts of light reach the forest floor. Presence of this species (from seed) will be mostly by individual trees or occasionally in small groves. As California black oak becomes notably intolerant in the sapling and small pole stage (McDonald 1969), those trees that survive will be found in the upper strata of the forest in dominant and codominant positions.

Trees from seed enhance the evolutionary potential of the species. They also give it good form. Handicapped by slow initial growth, and forced to stay in sunlight to survive, these trees typically grow slender, straight, and tall. They often are the best-formed trees in the stand.

Natural Regeneration in a Pure Hardwood Stand

Sampling layout, plot size, and intensity are the same as for tanoak and Pacific madrone. The forest floor beneath a dense, pure stand of hardwoods typically consists of a deep organic layer of mostly amorphous material with a thin layer of unincorporated leaves, bark, twigs, and branches on the surface. Acorns falling into this medium seldom move less than one foot after falling. Thus they accumulate beneath acorn-producing trees and not elsewhere unless carried away by consumers. Consequently, California black oak seedlings tend to be aggregated beneath parent trees which were distributed throughout the predominately tanoak stand.

California black oak regeneration was 40 seedlings per acre and advance reproduction, 720 seedlings per acre. The converted frequency value for seedlings was 4 percent (milacre basis) and 36 percent for advance reproduction.

These data show this environment not to be conducive to establishment of new California black oak seedlings, although those started earlier are persisting. Barring disturbance, none of these plants will survive long enough to become trees.

SUMMARY

The reproductive ability of young-growth, narrow-crowned California black oak is only moderate. Good seed crops occur every five or six years. The tendency is for either a good seed crop or none at all. Nevertheless, a few large trees bear seed out of phase with crop years. Acorn yield is related to tree age, crown diameter, and bole diameter. For example, on a good site, a 100-year-old forest-grown California black oak with a 17-inch bole diameter and a crown diameter of 32 feet will produce 60 pounds of acorns during a medium seed year.

Immature acorns are susceptible to several acorn-devouring insects, particularly after a bumper seed crop when insect populations are high. After falling, acorns are avidly eaten by such consumers as birds, squirrels, deer, wood rats, bears, and cattle. Squirrels are particularly useful as they carry acorns away from parent trees and bury them. These germinate and extend the species into new locations.

If not consumed, acorns overheat and dry out quickly. After 9 days in an exposed condition, cotyledons were badly shriveled and the acorns nonviable. Mold also can be a problem under certain conditions. Consequently, collections of black oak acorns should be from cool, shady, protected places. Light colored acorns and those with holes or mold should be discarded.

California black oak acorns were stored successfully for 3 1/2 months. The best storage method is to seal them in relatively thin polyethylene bags, in a refrigerator at 34 to 38 degrees F. Mold can be a problem if acorns are soaked in water before storage. In general, cotyledons tend to become somewhat flaccid during storage, although this apparently does not affect germination.

Stratification is necessary to break dormancy of the embryo. But as storage criteria and stratification criteria are similar, stratification commonly occurs while acorns are being stored.

Placing acorns point up speeds germination and increases germinative capacity. The point-up position should become a standardized regeneration procedure.

In the laboratory the duration between sowing and germination was about 23 days. Germinative capacity was 63 percent in 118 days, germinative energy was 34 days, and 58 percent germination of viable acorns took place after 34 days.

Germination in the field involved two large-scale tests on prepared ground free of slash and woody competition. Radicles elongated for about 30 days before hypocotyls appeared above ground. Germinative

energy was 34 days and germinative capacity varied between 31 and 38 percent. In one trial, acorns became buried about 4 inches beneath crusted eroded material. Nearly all of these acorns germinated, however, and sent radicles downward. Many died from drought. Others put forth a hypocotyl that grew up to the crusted material and formed little swollen knobs that resembled root burls. These "seedlings" held over in this state and appeared above ground the following spring. Physiologically, they were weaker seedlings than their predecessors. About 22 percent perished from drought the first growing season.

Some seedlings contracted mold in storage. It worsened after sowing and consumed all or most of the acorn contents. If the embryo remained, but most of the cotyledons were ruined, a weak little seedling resulted. These perished quickly when soil moisture became deficient.

A major goal was to evaluate damage and mortality of California black oak seedlings. This proved difficult as below-ground portions of seedlings would live, while above-ground parts would die. Early spring frosts, grasshoppers, nocturnal rodents, deer, and summer die-back killed seedlings above ground. Most sprouted from the root crown the following spring--nearly always with only a single stem.

Drought was the primary cause of mortality and was notably severe where bull thistle, bracken, poison oak, and western raspberry were dense and vigorous. Deer pulled up a few seedlings while consuming the attached acorns. Pocket gophers moved into the plantations the second and fourth growing seasons and multiplied. Mortality from these

rodents has increased ever since and could become a serious threat to satisfactory stocking of the plantations.

Overall stocking in the small plantation was 54 percent after 10 years; in the larger, 64 percent after 7 years. But the latter figure included seeding of acorns in unstocked spots after 3 years. Seedling height growth generally was poor. Although some seedlings consistently averaged 0.6 feet of height growth per year, others scarcely grew. Average height growth after 7 years was 0.7 feet and after 10 years was 1.1 feet.

The decline in stocking mandated investigation of a better regeneration method. Although relatively large open-bottomed containers (2 3/4 x 2 3/4 x 6 inches) were used, they could not contain the vigorous taproot of this species. Thus, about two-thirds of the taproot was removed when seedlings were outplanted. Seedling survival was no better than seedlings from acorns. Unless longer containers are used, much of the taproot is lost--weakening the seedling and increasing the chance of its demise.

Poor early height growth and the danger of overtopping and browsing indicated need for developing faster growing seedlings. Fertilization with a handful of 16-20-0 at each spot every year did just that. After five growing seasons, fertilized seedlings were over 3 times taller than their unfertilized counterparts. Quantitative foliar analysis of seedling leaves indicated adequate macronutrients present during the period of high nutrient stress. Fertilization significantly augmented nitrogen and phosphorous levels over those in unfertilized

seedlings. And robust seedling stems, more numerous and larger leaves, and undoubtedly better developed root systems as determined by low pre-dawn xylem sap tension, mean that the stimulatory effect of the fertilizer will increase in the future. Increased browsing by deer was a potential threat, but to date has been minimal. Fertilization is a recommended procedure when regenerating and growing California black oak.

Because of repeated damage from spring frosts, a small provenance trial was installed. Acorns from eight locations, which were higher in elevation and more arid than the Experimental Forest, were spot-seeded at Challenge. Seedling survival, height growth, leaf flush, and leaf fall provided comparison to the Challenge provenance. Survival of seedlings from the eight provenances was poorer and height growth about equal to that of the Challenge provenance after 7 years. Leaf flush and leaf fall data were poor phenological indicators because of high within-tree and within-provenance variation.

Terminal shoot elongation the eighth year quantified phenological differences among provenances. In general however, timing of bud swelling and magnitude of elongation were similar among all provenances. Again, substantial variation within provenances was indicated.

Survival and height growth of California black oak regeneration was studied in contrasting environments created by different conifer regeneration cutting methods. These were single-tree selection, seed tree, and shelterwood. A cool shady environment like that of the single-tree selection cutting was best for establishment and survival

of California black oak seedlings. Seedling frequency, density, and survival were even better in the uncut control.

Advance reproduction of California black oak averaged 317 seedlings per acre and a frequency of 17 percent in the control. Both values slowly increased during the study. Corresponding cumulative density and frequency values by cutting method were single-tree selection (711 per acre and 47 percent), shelterwood (516 per acre and 27 percent), and seed tree (792 per acre and 35 percent). A later seed-tree cutting indicated advance seedling density to be 228 per acre and frequency 16 percent. An increasing buildup trend in density and frequency took place in the selection and shelterwood methods. Downtrends were indicated in both seed-tree cuts although this effect may be temporary.

Natural regeneration in an undisturbed pure hardwood stand consisted of 40 seedlings and 720 advance seedlings per acre with corresponding frequencies of 4 and 36 percent. In this environment California black oak seedlings can best be described as "persisting." None will survive to become trees.

Relative to the control, cutting and site preparation enhanced the buildup of California black oak advance reproduction. And, as for seedlings, the selection method proved best for establishment of advance reproduction.

But seedling height growth also is important. Dieback of advance reproduction was noted in deep shade and to a lesser extent in full sunlight. In partial shade, 10-year height growth of California

black oak averaged 3.3 feet as opposed to a height of 2.9 feet in selection cutting, and 1.1 feet in the clearcut plantation. In terms of development, form was ideal in partial shade. After 13 years, stems were straight and tall; crown width was about one-third of height. Because California black oaks become increasingly intolerant in the sapling and small pole stages, those in the selection cutting will suffer a decreased height growth rate. Those in the clearcut plantations have yet to demonstrate vigorous height growth. Plainly, a partially shaded environment is best for natural development of this species.

When the demand for hardwoods reaches the point that plantations are installed, California black oak should be considered. With fertilization and possibly pocket gopher control, satisfactory plantations can be established from seed.

In the future, California black oak trees from seed will be present in the forest. They will be scattered individually throughout or occasionally reside in groves. Barring future disturbance, the species will be found in upper stand strata, mostly in codominant crown position.

Trees from seed contribute to the evolutionary potential of the species, not only because of their adaptability to environment, but also because of their good form. Such trees often are the best-formed trees in the stand.

III. DEVELOPMENT AND GROWTH OF A SPROUT STAND

This portion of the study qualifies and quantifies the interrelationships of sprout stands in partially-cut and completely-cut environments for 10 years. To more fully understand moisture stress patterns in these hardwoods, its evaluation was extended to sprouts. Together, these research categories provide knowledge on hardwood sprout dynamics, which in turn aids in evaluating where and how Pacific madrone, tanoak, and California black oak grow as they do.

THE MECHANISM OF SPROUTING

Most investigators of sprouting in eastern oaks agree that the sprout buds which form after the initial cutting are from dormant buds. These form at or above the root collar, never from the roots (Roth and Hepting 1943; Woods and Cassady 1961).

The dormant buds connect with the primary xylem and move outward to the extent that the tree grows in radius each year. Some of the bud traces divide as they progress outward and thus the number of subsurface buds increase as the tree grows. In large old trees, the buds eventually become buried, however, and few or no sprouts result.

The dormant buds are held latent by the downward flow of auxins from terminal shoots. When the source of auxins is removed by cutting, or their flow is interrupted by loss of leaves, elevated bark temperature, etc., the dormant buds burst forth.

If sprouts from the dormant buds are killed and the bark and inner tissue of the tree injured, callus tissue forms at the terminating point of the radial trace. This callus tissue then serves as the source of many new buds. These buds, however, are adventitious buds as they lack connection to the primary xylem. In either case, the number of buds, and hence potential sprouts, is tremendous. As many as 1,400 buds have been observed on a large tanoak stump (Roy 1957), and about 300 on a 10-inch diameter Pacific madrone stump.

The tendency to sprout from the root collar differs among species. A ranking of the three species studied here in terms of propensity for sprouting is: 1-tanoak, 2-Pacific madrone, and 3-California black oak. Tanoak trees with no visible injury sometimes sprout; but California black oaks must be damaged extensively before sprouts from the root collar appear.

SPROUT DEVELOPMENT

After logging, fire, or other gross disturbance, stump sprouts of Pacific madrone, tanoak, and California black oak soon become abundant. This abundance, combined with vigorous height growth, makes stump sprouting the primary reproductive mode for these species (McDonald 1969; Roy 1957; Tarrant 1958).

An oncoming trend in the Sierra Nevada and the east-facing slopes of the Coast Range is harvesting by even-aged methods like clearcutting and shelterwood (Bolsinger 1976). As the conifers are harvested, so

are the hardwoods. If hardwoods are present, the stump sprouts soon become a major component of the young stand. In the California black oak forest type, the Pacific mixed evergreen type, at the lower elevational fringe of the Pacific ponderosa pine type, and in other types where the topography consists of physiographic badlands or edaphic islands, the relative importance of sprouts often is magnified by the scarcity of other desirable regeneration. Here, and wherever the native California hardwoods are cut, multiple-stemmed stands of sprout origin result.

Multiple-stemmed clumps persist for years, particularly if of Pacific madrone or tanoak. For California black oak, however, multiple-stemmed clumps become less common as tree age increases. The number of stems per clump decreases to about 2 at age 50 on high and medium sites (McDonald 1969). Thus in older California black oak stands, the number of stems per clump usually is one or two:

<u>Breast height age (Years)</u>	<u>Number of sprouts per clump</u>
20	4
30	3
50	2
120	1

Nevertheless, for the hardwood species studied, the predominant biological and cultural unit is a clump of interacting stems. Likewise, the major cultural group is a number of closely interactive clumps. Present knowledge for the culture and management of such a coppice is scant indeed.

Roy (1955) evaluated Pacific madrone and tanoak sprout growth in northwestern California for 3 years. The stand had been severely burned and thus resembled a clearcutting. Only single stumps were studied and the range of stump diameters ranged from 3 to 20 inches.

After 3 growing seasons, unthinned Pacific madrone sprout clumps were 10.1 feet tall, 7.6 feet wide, and had 13 sprouts per clump. Tanoak sprout clumps averaged 6.8 feet tall, 7.0 feet wide, and indicated 12 living sprouts per clump.

Also in northwestern California, Estes and Blakeman (1970) found that tanoak sprouts in their third growing season were 1 to 5 feet tall.

Two contiguous areas on the Experimental Forest comprised the setting for the sprout study. Criteria for selecting the two areas was that they must support pure hardwoods (no conifers), be typically dense (over 500 stems larger than 3.5 inches in breast height diameter and 160 square feet of basal area per acre), and have a good representation of the three hardwood species studied. Both areas were clothed with stands ranging in age from 42 to 65 years. In late 1963, one area was clearcut by woodcutters who removed all material larger than 2 inches in diameter. Stumps were no higher than 8 inches above mean ground line, and all stems were cut. Slash was hand piled in part of the area and scattered in another part. Both parts were burned in the fall.

The second area was partially cut in 1967. It received a crown thinning that removed about 50 percent of the basal area and 65 percent

of the stems larger than 3.5 inches d.b.h. After cutting, this area resembled a dense shelterwood. The cutting and slash disposal rules were similar to those in the clearcutting.

Low-cut stump heights, and in some instances burned stumps, insured that sprouts of all three species would be root crown- rather than stool-sprouts. Stool sprouts are those that grow at the top edge of the stump. Thus, the material that follows pertains only to root-crown sprouts, the majority of which originated from dormant buds.

One year after clearcutting, all but 1 to 4 of the best-formed sprouts were thinned in an attempt to ascertain if thinning was practical when the sprouts were small. It proved impractical as: (1) there were too many sprouts, (2) no real expression of dominance was discernible, (3) sprouts were weakly attached to the root collar, and (4) sunscald to remaining sprouts was likely. For these reasons sprouts should not be thinned at least until age 3 or 4 when dominance is better expressed, some have died, they are more firmly attached to the stump, and the danger of sunscald has lessened.

No detailed study on the number or percentage of stumps that sprouted was performed. Nearly all stumps sprouted. A few, with debris piled against them, sprouted only on the debris-free side; and a few, again with debris, sprouted only from the stump surface. Occasionally sprouts would grow through the debris, but inevitably have poor form.

Yearly measurements included sprout density, crown width, and average height of the three dominant stems in each clump. Crown width

was determined by measuring each clump in two directions, 90 degrees apart, with a graduated pole. Placement of the pole always was at mid-height. In all instances, crown width was a tight crown width--that which would cast a solid shadow. Thus, "leggy" branches were "brought in" and sparse upper branches, in effect, became fuller. Crown volume, then, was treated as a cylinder and calculated as crown width times average dominant height.

These data were analyzed by use of graphical and regression techniques where applicable.

Pacific Madrone

In late 1967, when the sprouts in the clearcutting were 4-years-old, eleven sprout clumps from single stumps were designated for repeated measurement. As expected, most initial Pacific madrone clumps were multiple-stemmed. Delineating the number of sprouts per stump, as well as defining crown width, soon would have become impossible. For these reasons, multiple-stemmed clumps were rejected for sprout study; only individual stumps were acceptable. These ranged from 6 to 15 inches in diameter, and were well distributed throughout the clear-cutting.

Stumps were paired by diameter size as closely as possible; then one of each pair was randomly chosen for sprout thinning. Five stumps were thinned and six remained untouched. Residual stems numbered 1 to

3. A small hand saw was used, and care taken not to injure "leave" stems.

Because the stand was typically dense before logging, sprout clumps were quite close together. Intraclonal factors probably influenced sprout height, width, and form the first few years, with interclonal influence increasing as the sprout clumps began to compete.

The five sprout clumps in the shelterwood were not thinned. Their environment was such that intraclonal competition continued for a longer timespan than for sprouts in the clearcutting. For some sprout clumps, little or no interclonal competition took place the first 10 years after cutting. Overall, sprout growth undoubtedly was influenced by the overstory trees.

Thinning Pacific madrone sprouts at age 4 proved quick and easy. The previous problems of thinning year-old sprouts had largely disappeared. A few additional sprouts were noted but those died after a year or two. Thinned sprouts were examined for incipient rot. Not a single incidence was found. A few stool sprouts in a nearby area also were examined. Two indicated heart rot present. Apparently rot is much less frequent in root collar sprouts than in stool sprouts.

After one growing season, the number of sprouts per stump numbered 60 or more in the shelterwood and clearcutting. Heavy mortality took place, especially in the shelterwood, and intraclonal sprout density decreased rapidly at first and less so with increased time since cutting (Fig. 20). By age 4, mortality in the clearcutting was still fairly heavy as dominant sprouts accelerated in height over their

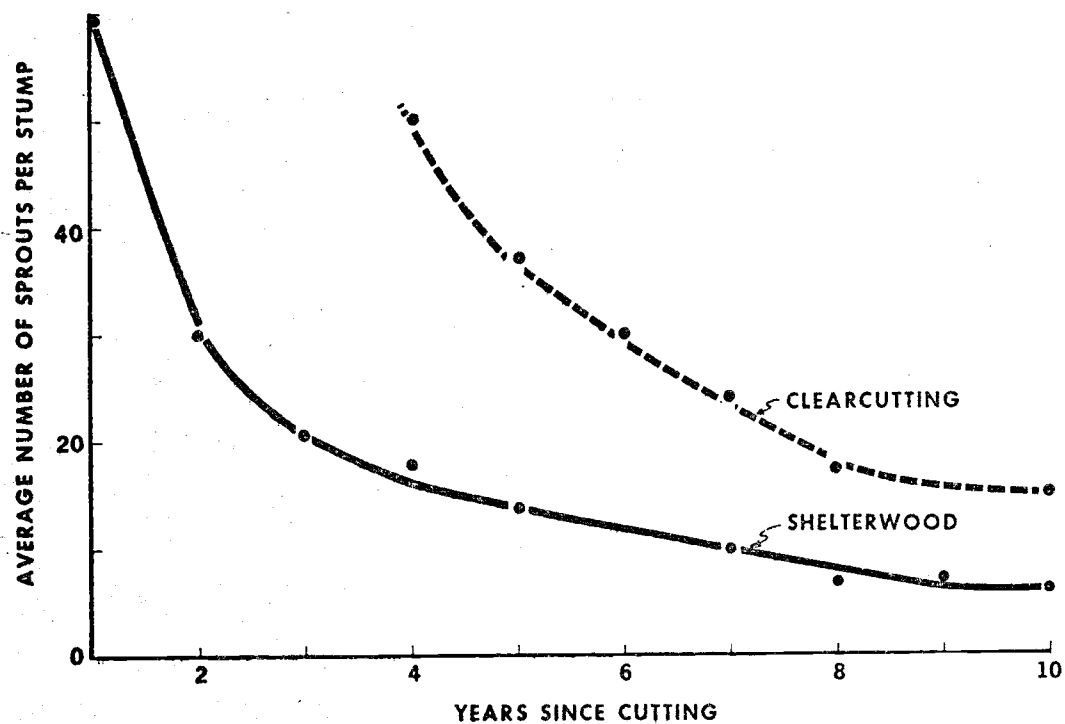


Figure 20.--Annual decline of Pacific madrone sprouts 10 years after cutting.

struggling brethren (Fig. 21). After 10 years, the average number of sprouts per stump numbered 15 in the clearcutting and 7 in the shelterwood. Analysis indicated that stump diameter related weakly to the number of sprouts per stump surviving after the first and tenth year in both the clearcutting and shelterwood.

Average dominant height of thinned and unthinned clumps in the clearcutting was not meaningfully related to stump diameter at ages 4 and 10. This also was true of sprouts in the shelterwood at age 10. In nearly all clumps, one or more sprouts expressed dominance by age 4. Dominance of a given sprout at an early age could not be predetermined visually from above-ground phenomena. Outer and inner sprouts appeared to have equal chance of dominating. Proximity to other hardwood clumps or competing vegetation likewise was indeterminate. Dominance probably was a function of how fast and how much of the parent-tree root system became available to the sprout. Grafting of roots of one sprout to those of another also was likely. In any case, once a sprout became dominant, it tended to stay dominant, at least during the study period.

In the clearcutting, average dominant height increased curvilinearly with time since cutting. Differences in average dominant height between thinned and unthinned sprout clumps were small (Fig. 22). After 10 years, dominant stems from unthinned clumps averaged about 1.6 feet taller than dominant stems from thinned clumps (22.2 vs. 20.6 feet). This difference is even less meaningful when one considers that a Pacific madrone clump, thinned to one stem, became sunscalded in 1968



Figure 21.--A 4-year-old Pacific madrone sprout clump in the clearcutting.

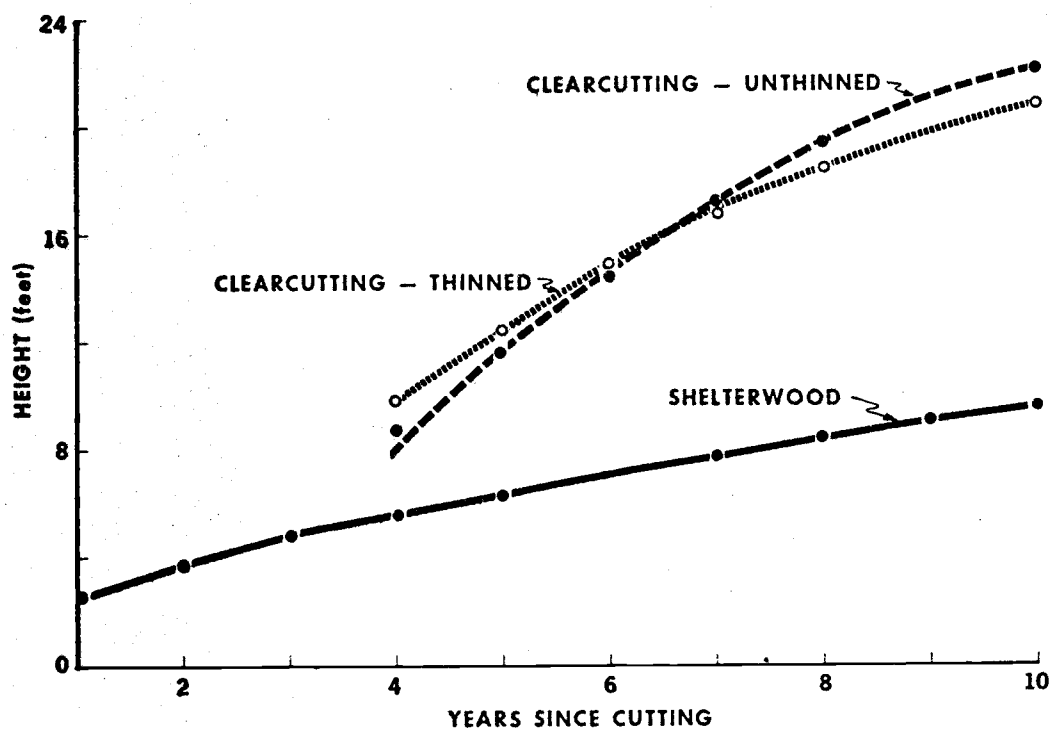


Figure 22.--Average height of dominant Pacific madrone sprouts for 10-year period after cutting.

(Fig. 23). Height growth of this stem lagged behind the others, lowering the thinned-sprout average.

In the shelterwood, fewer stems per clump were present. These grew rapidly the first year or two (Fig. 24), but then slowed down. At age 10, average dominant height of shelterwood sprouts was 9.7 feet, or about 44 percent of that for dominant unthinned sprouts in the clearcutting.

Crown width of thinned and unthinned sprout clumps in the clearcutting increased linearly with time since cutting (Fig. 25). Natural sprout clumps averaged 5.5 feet wide at age 4 and 10.2 feet at age 10. Crowns of thinned sprout clumps were 2 feet less wide than unthinned clumps at age 4, and nearly 4 feet less at age 10. In the shelterwood, crowns expanded rapidly, then slowed, and again expanded. After 10 years, the average Pacific madrone sprout crown was about 7 feet wide.

The widening gap between sprout clumps in the clearcutting and shelterwood, in terms of sprout density, height, and crown width, is expressed strongly in cubic volume. The average volume of an unthinned clump in the clearcutting at age 10 was 1840 cubic feet, or about three times that of a natural clump in the shelterwood (Fig. 26). Thinned clumps in the clearcutting had about half the volume of their unthinned counterparts at age 10.



Figure 23.--A thinned Pacific madrone sprout clump one year after thinning. Note wrinkled dead bark on stem, and three new sprouts at base.



Figure 24.--Although not a study clump, height and shape of crown are typical of Pacific madrone sprouts in deep shade. Extended portion of rule is 8 inches.

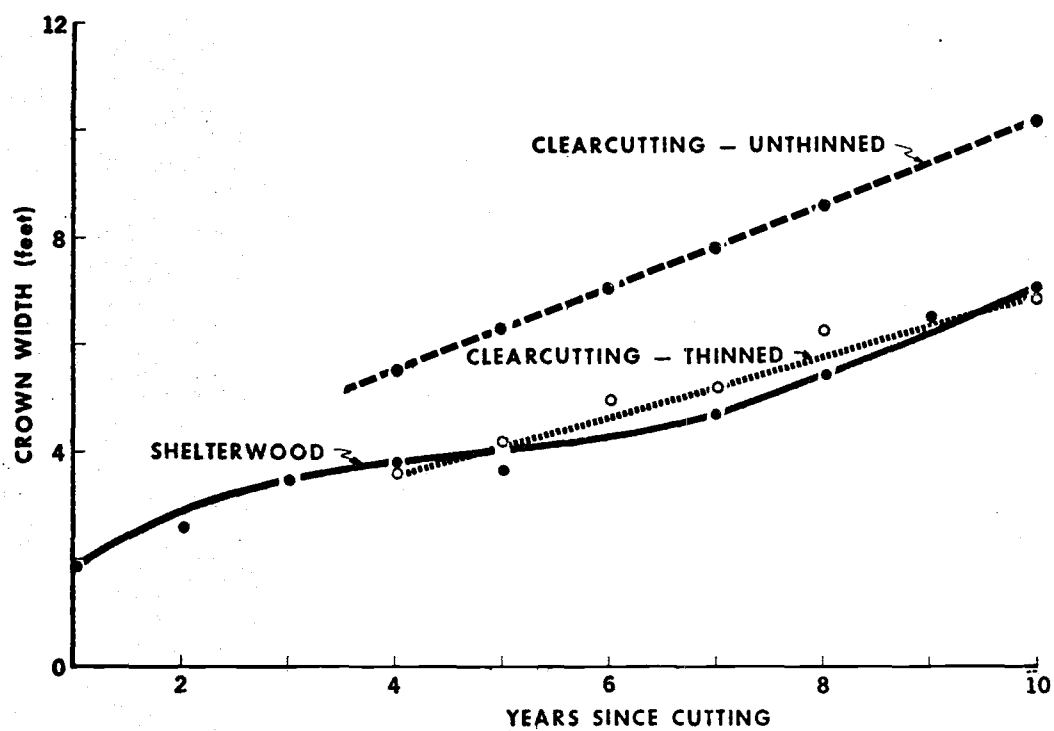


Figure 25.--Average annual width of Pacific madrone sprout clumps 10 years after cutting.

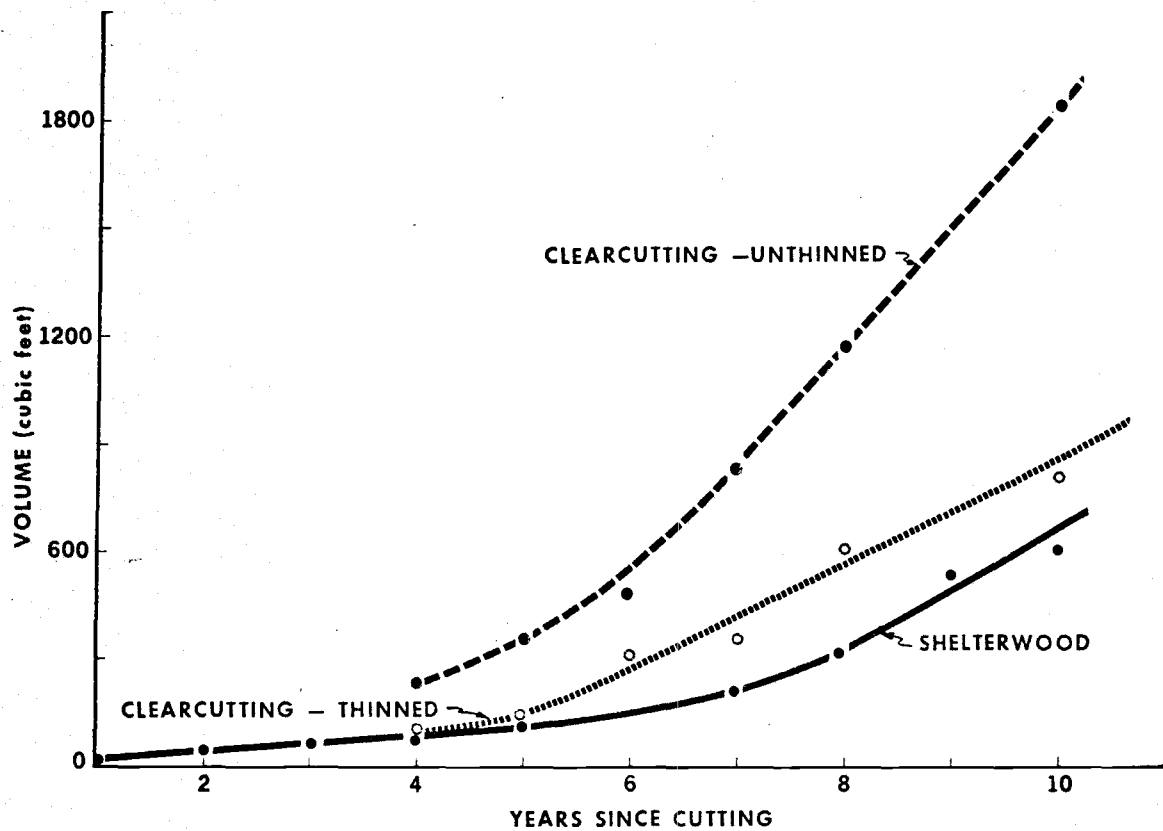


Figure 26.--Average annual volume of Pacific madrone sprout clumps 10 years after cutting.

Tanoak

After cutting, tanoak stumps sprout prolifically (Fig. 27). Number of sprouts per stump almost was impossible to ascertain. Likewise, thinning tanoak sprouts was impractical until well after age 10, if at all. A good example of sprout fecundity took place in the clearcutting. One tanoak clump of three stumps, each 6 to 10 inches in diameter, was thinned in 1964. Three dominant, well-formed sprouts were left and all others were removed with a small hatchet.

New sprouts, from both dormant and adventitious buds, burst forth. These were removed each fall:

<u>Year</u>	<u>Number removed</u>
1964	well over 100
1965	well over 100
1966	well over 100
1967	100
1968	91
1969	40
1970	55
1971	29
1972	30

In 1976, or 13 years after cutting, 23 sprouts remained in addition to the three selected sprouts. Apparently the parent-tree root system continued to be more vigorous than the three selected sprouts for at least 10 years. These sprouts did prosper, however, and height growth and crown spread for "thinned" sprouts were evaluated from this one clump. Although not definitive, they are indicative of tanoak sprout growth from thinned clumps on high sites.



Figure 27.--A typical tanoak sprout clump from a single stump.

Sprouts are 4 years old.

Because evaluating number of sprouts was so difficult, it was done only in the shelterwood. As for Pacific madrone, sprouts from single stumps were sampled, and single stumps were relatively scarce. Hence, sample size was small--seven stumps--with a range of 7 to over 11 inches in diameter.

In the shelterwood, no trend between number of sprouts per stump and stump diameter was found. Number of sprouts amounted to about 30 after one growing season, and was slightly higher after four seasons (Fig. 28). A few sprouts died each successive season. By age 10, the number of sprouts per stump declined to 24. The chief cause of mortality for tanoak sprouts was from intraclonal competition; interclonal effects for this species are small the first 10 years.

In the clearcutting, 10 tanoak sprout clumps comprised the sample for determining average dominant height and crown width in the unthinned condition. These were not measured until age 5, however. Height growth of thinned and unthinned sprouts did not differ meaningfully. After 10 years, average dominant height of tanoak sprouts was about 19 feet (Fig. 29).

In the shelterwood, no relationship between sprout height and stump diameter was shown. Here, height growth of unthinned sprouts was rather slow. After 10 growing seasons, the average height of dominant sprouts was about 8 feet or 42 percent of that in the clearcutting. Part of the difference could be that dominance was not as well expressed by sprouts in the shelterwood as those in the clearcutting at a comparable age (Fig. 30).

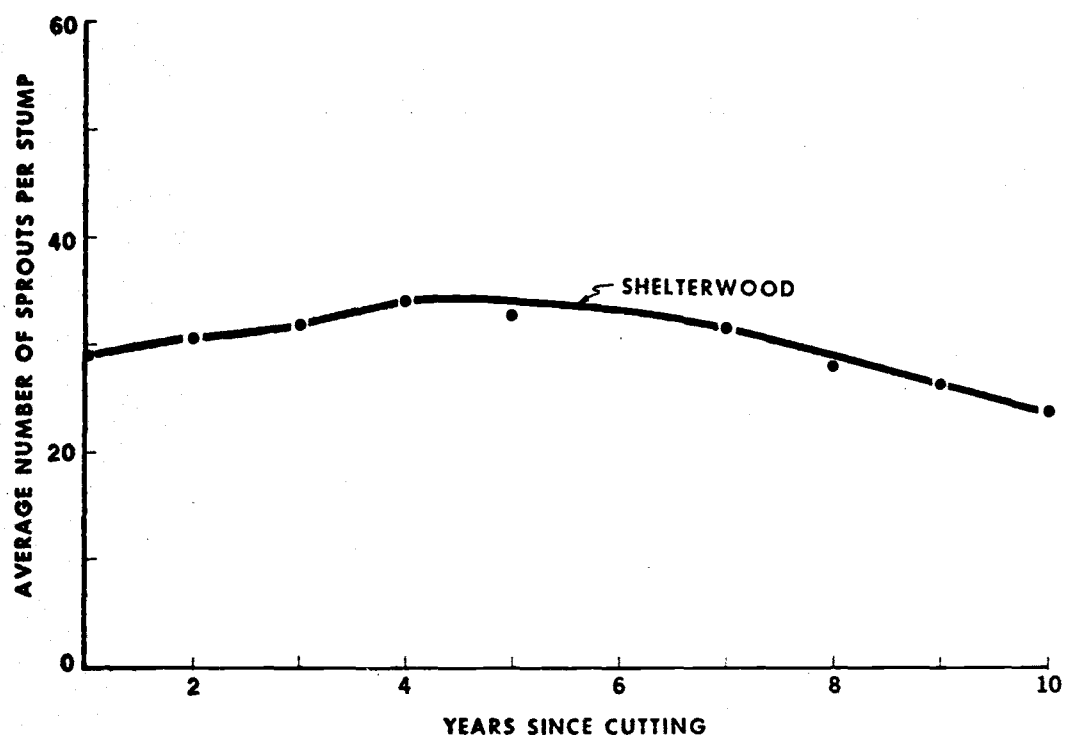


Figure 28.--Buildup and decline of tanoak sprouts in the shelterwood.

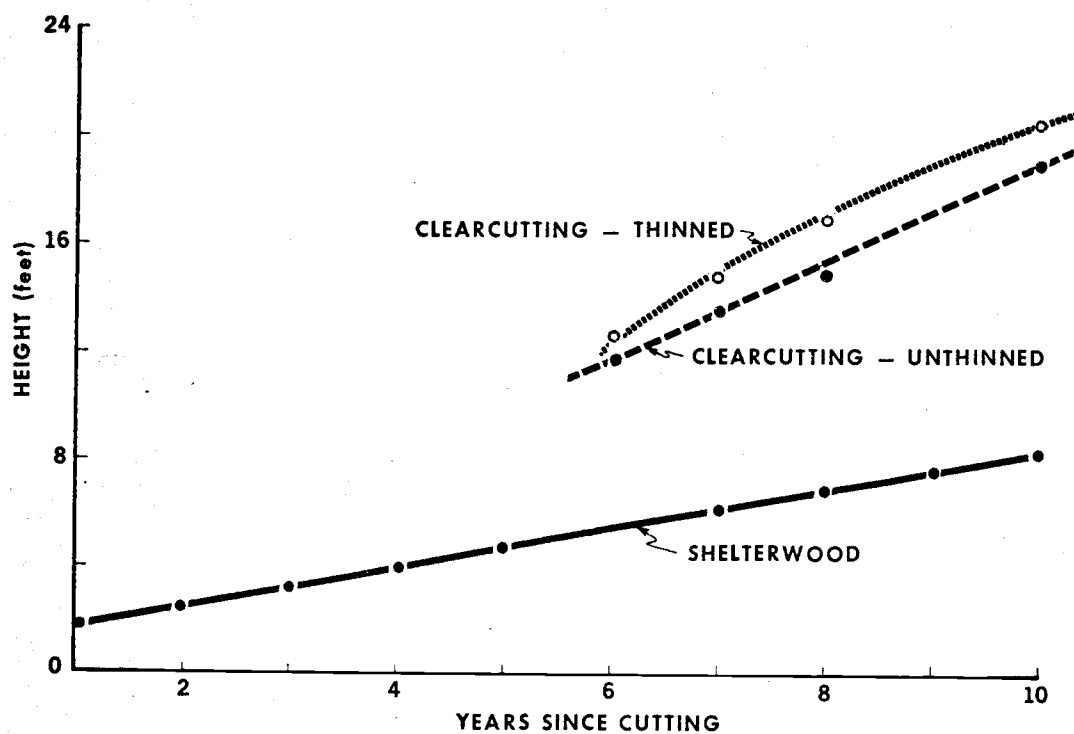


Figure 29.--Average height of dominant tanoak sprouts for 10-year period after cutting.



Figure 30.--Little expression of dominance is shown by sprouts in
a 4-year-old tanoak clump at the edge of the shelterwood.

Crown width of thinned and unthinned sprouts in the clearcutting increased curvilinearly with time (Fig. 31). After 10 growing seasons, unthinned sprout clumps were over 10 feet wide; thinned clumps were about 8 feet wide.

Crown expansion of tanoak sprout clumps in the shelterwood was fairly rapid through age 3, slowed at ages 5 and 6, and expanded more rapidly after that. Through age 10, the average crown width of a tanoak clump was 7 feet.

Average volume of an unthinned sprout clump in the clearcutting at age 10 was 1509 cubic feet or almost three times that of a natural clump in the shelterwood (Fig. 32). Thinned clumps in the clearcutting had over 1000 cubic feet of volume or about 70 percent of their unthinned brethren.

California Black Oak

At a stand age of 50 years or so, many California black oak clumps have become single stems. And as sprouts from single stumps were desired, the sample size of California black oak sprout clumps was highest of the three species studied.

In the clearcutting, sample size of unthinned clumps was 29, of thinned clumps, 20. Anticipated variance, particularly in crown width, was judged greater for unthinned sprouts, hence the larger sample. In both categories the range of stump sizes, from which sprouts were studied, spanned 6 to 17 inches.

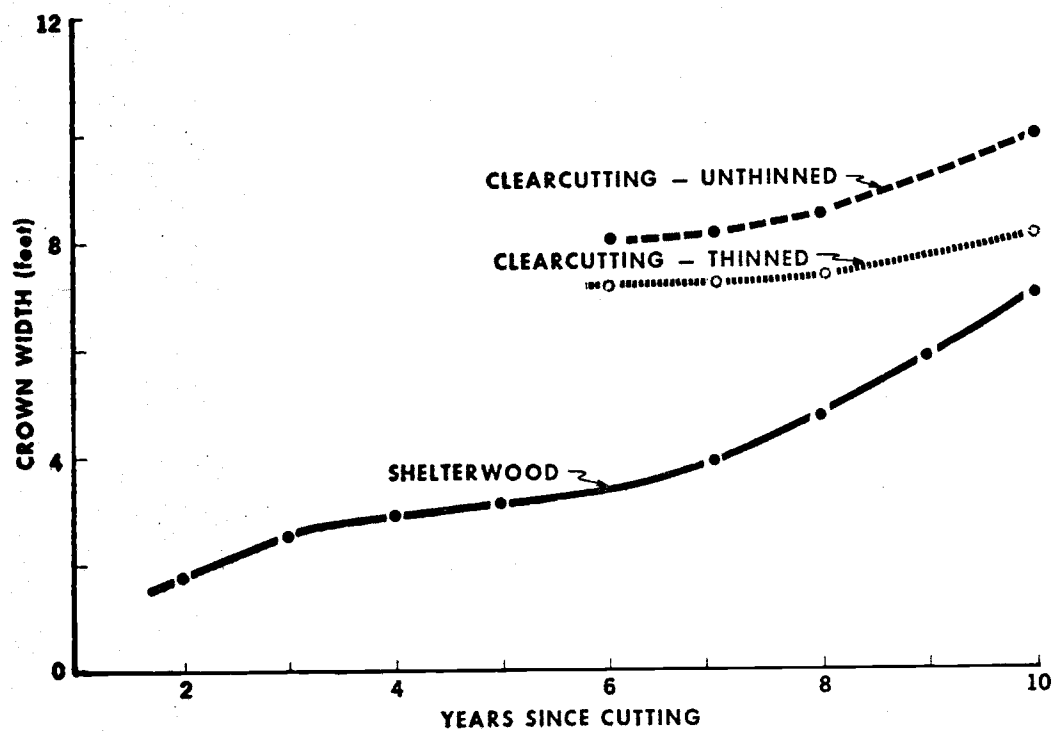


Figure 31.--Average annual width of tanoak sprout clumps 10 years after cutting.

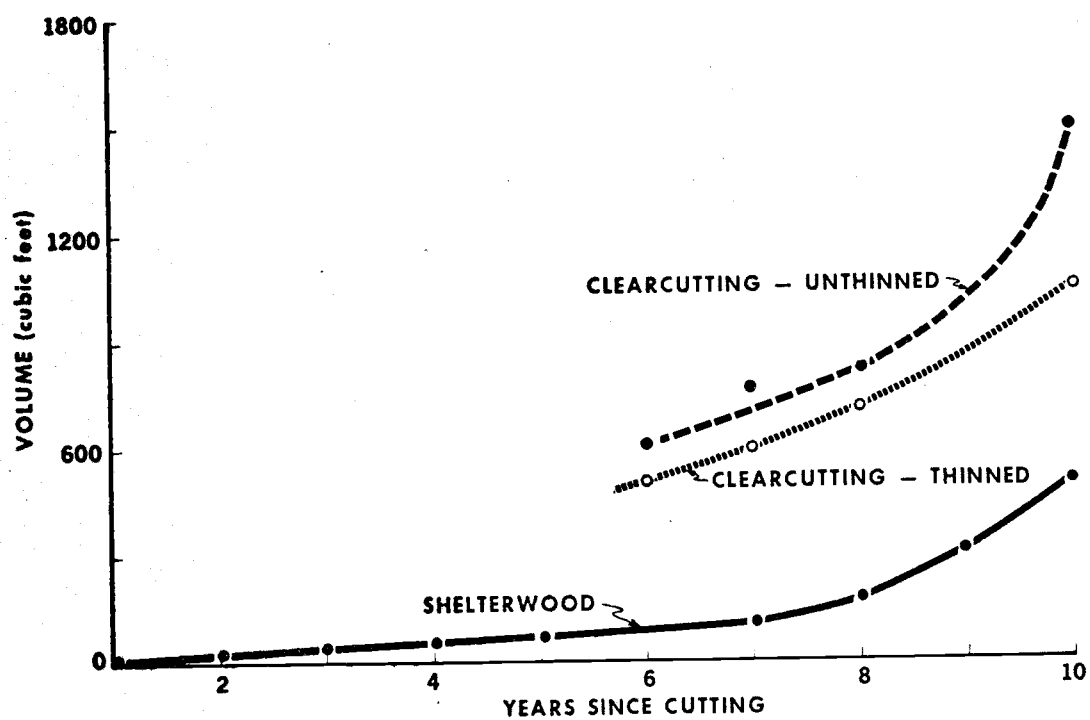


Figure 32.--Average annual volume of tanoak sprout clumps 10 years after cutting.

As for the other species, California black oak was thinned after one growing season. The bond between sprouts and root collar was quite fragile, and only slight side pressure inadvertently removed desirable sprouts. This was the main reason for not thinning sprouts of this oak at an early age.

In the clearcutting, all stumps sprouted. By age 4, each sprout clump was well developed (Fig. 33). Dominance of several sprouts was apparent and intracolonial competition raged unabated. Thinning of sprouts at this age proved efficient with small pruning shears. In each sprout clump 3 or 4 of the best formed, dominant sprouts were retained. Cut sprouts were examined carefully for incipient heart rot. None was found. Callus tissue then formed around the cutting scar and adventitious buds developed. These promptly sprouted. This second crop of sprouts averaged 19 per clump the first year, and 8 per clump the third year. They remained small, however, and by the fourth year, most were moribund. None added to the residual sprouts. At age 4 apparently, the remainder of the root system of the parent tree (stump) was nearly in balance with 3 or 4 of the most robust, thrifty sprouts.

In the shelterwood, sample size was dependent on anticipated variation in sprout response. Although unknown, it could have been high because California black oak would be at least somewhat intolerant of the shady shelterwood environment. Consequently, sample size was 20 stumps with a diameter range of 7 to 16 inches.



Figure 33.--A 4-year-old California black oak sprout clump in the clearcutting.

The number of sprouts per stump was far more numerous in the clear-cutting than in the shelterwood. By age 4, sprout density was 35 per clump in the clearcutting, 17 per clump in the shelterwood (Fig. 34). Mortality, however, was greater in the clearcutting, so that by age 10, the gap had narrowed to 3 sprouts per clump (15 per clump in the clear-cutting, 12 in the shelterwood). Apparently, the clearcut environment, with its large number of interacting clumps, and the shelterwood environment with its overstory, were tending toward similarity at least in terms of sprout density after 10 years.

Differences in sprout response between the clearcutting and shelterwood are expressed most vividly in terms of height growth (Fig. 35). At age 4, sprouts in the clearcutting were twice as tall as those in the shelterwood (8 versus 4 feet), and by age 10 were 3.3 times taller (20 versus 6 feet). For both environments, the relationship of sprout height to time since cutting was linear.

Unthinned sprouts were slightly taller than thinned sprouts, but no real difference was expressed. A few thinned sprouts suffered from sunscald and the overall form of thinned sprouts was poorer than if unthinned. Tendency to fork was more noticeable if thinning had lessened intraclonal sprout density. Density of vegetation, whether inter- or intraclonal, or from trees or brush, seemed to strongly affect sprout form (Fig. 36). In general, the more dense the vegetation, the better the form.

Crown width of unthinned and thinned sprout clumps in the clear-cutting averaged 9.4 and 8.6 feet respectively after 10 growing seasons

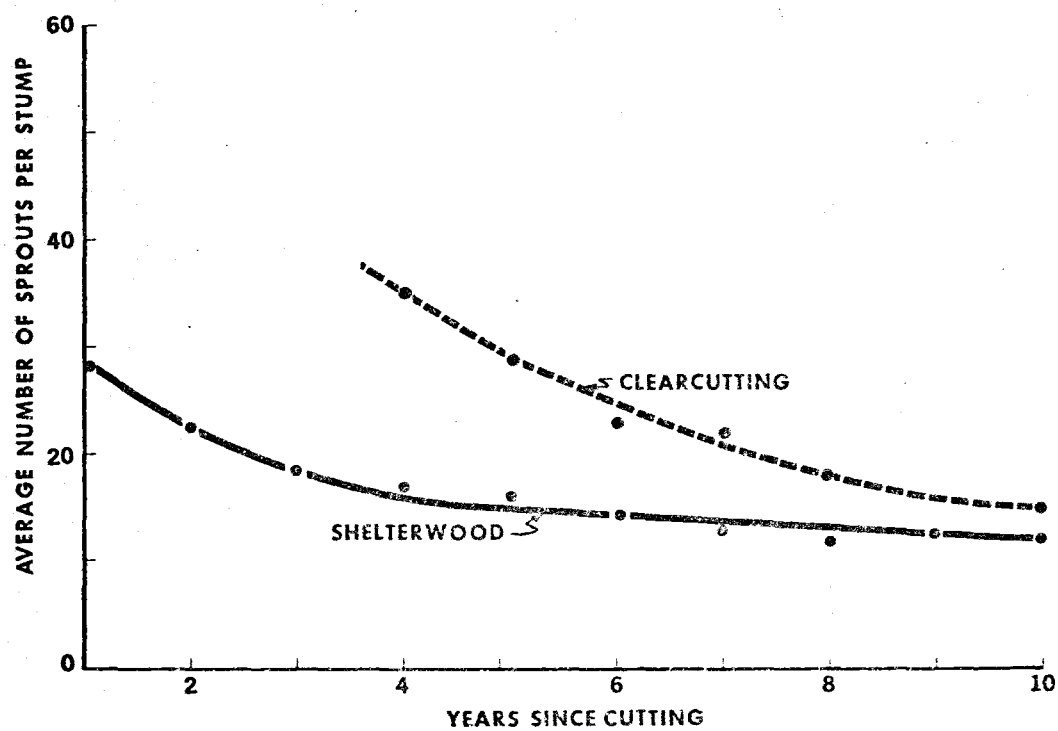


Figure 34.--Annual decline of California black oak sprouts 10 years after cutting.

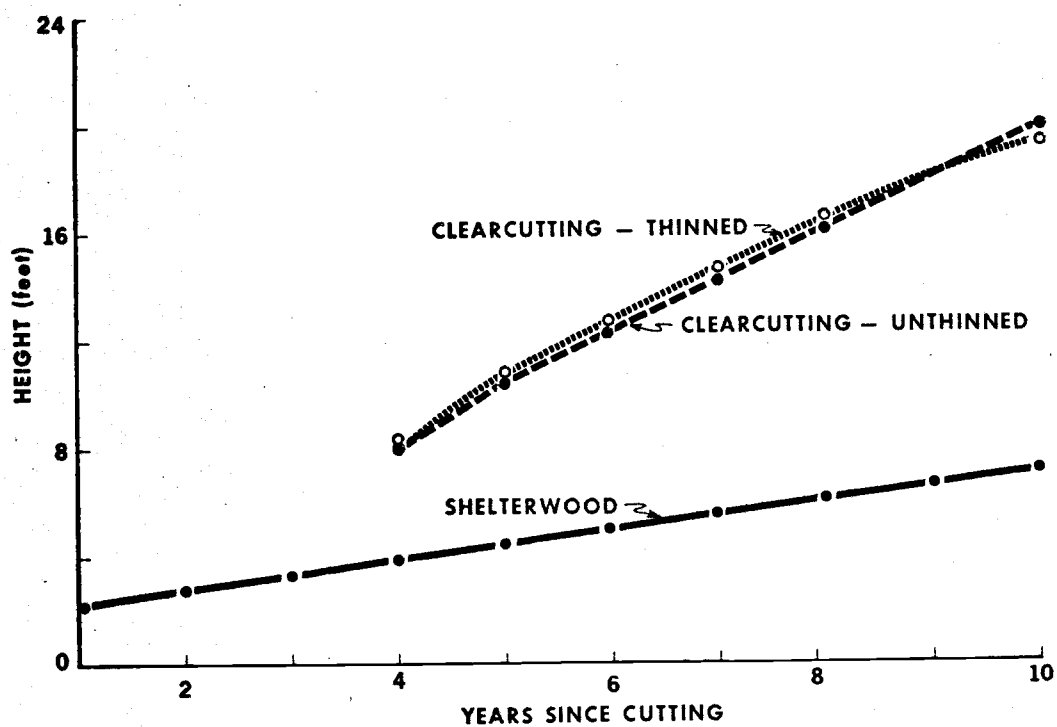


Figure 35.--Average height of dominant California black oak sprouts for 10-year period after cutting.



Figure 36.--Typical form of unthinned California black oak sprouts surrounded by dense vegetation.

(Fig. 37). The overall trend in crown width was that sprouts from thinned clumps were catching up to those from unthinned clumps. Crowns of sprouts in the shelterwood widened at an early age, slowed down, and then expanded again. After 10 years, the average crown width of sprout clumps in the shelterwood was 7.2 feet.

Volume of an average unthinned California black oak sprout clump after 10 years was 1446 cubic feet (Fig. 38). In the shelterwood, natural volume for a similar timespan was 430 cubic feet. Thinned sprout clumps in the clearcutting averaged 1173 cubic feet or 81 percent of their unthinned counterparts.

Good crown expansion, but poor height extension of sprouts in the shelterwood is contrary to that expected from an intolerant species. Part of this phenomenon is explainable by damage to sprout terminals by the cynipid gall wasp (Callirhytis perdens Kinsey). Apparently the female wasp injects eggs into tender new tissue along with a chemical which interrupts normal cell development and causes a proliferation of undifferentiated tissue. This tissue forms a series of swellings on the twig. In each swelling a cavity is formed, which houses a hard, creamish, flattened, seed-like cell containing the larva. The California gray squirrel often clips the swollen twigs, strips away the outer material, and eats the seed-like cells (Fig. 39). When this happens browsing often is recorded erroneously as the causal event.

Sprouts in the shelterwood received not only much heavier damage than their counterparts in the clearcutting, but also damage was much

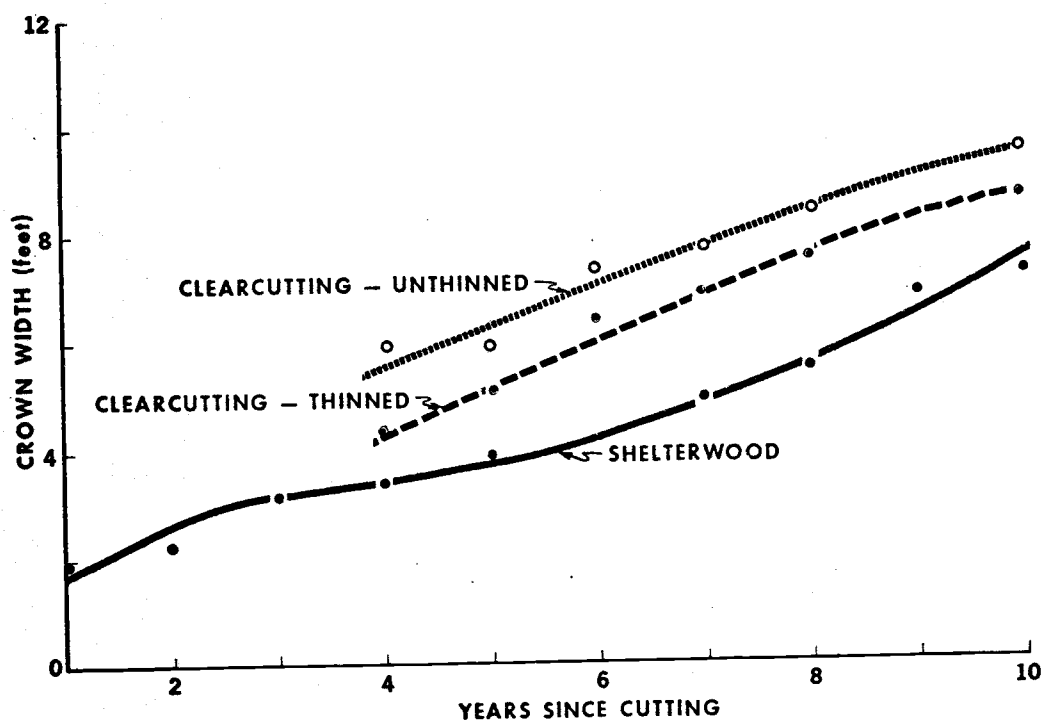


Figure 37.--Average annual width of California black oak sprout clumps 10 years after cutting.

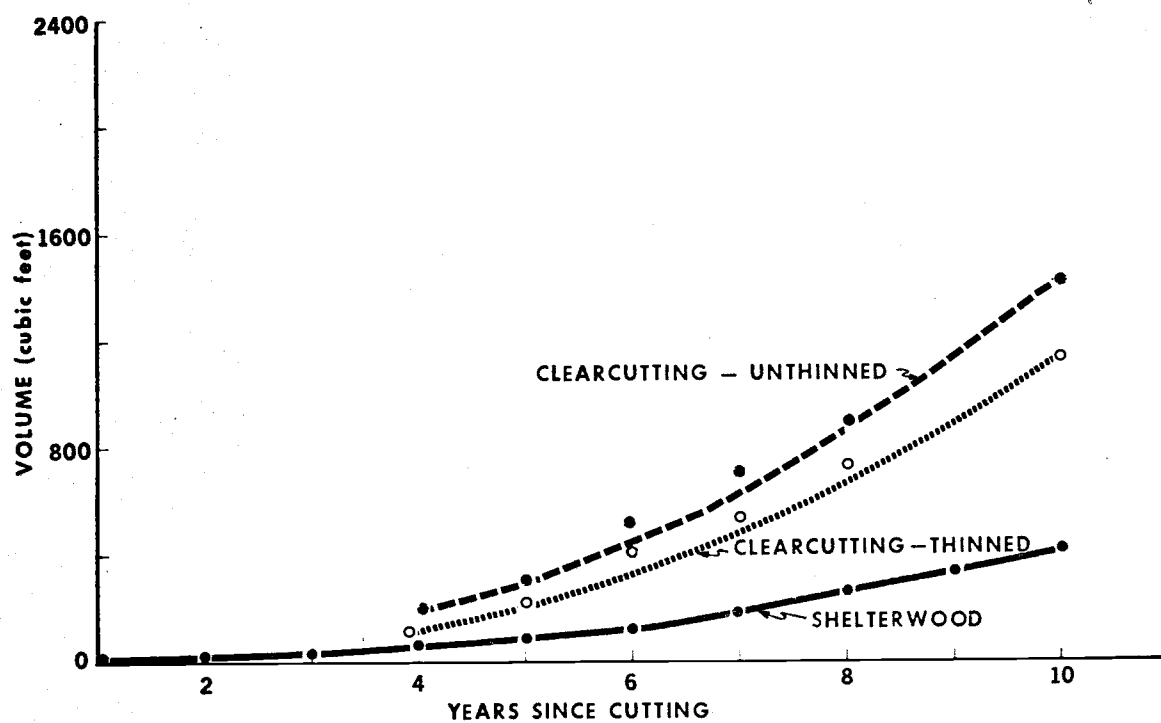


Figure 38.--Average annual volume of California black oak sprout clumps 10 years after cutting.

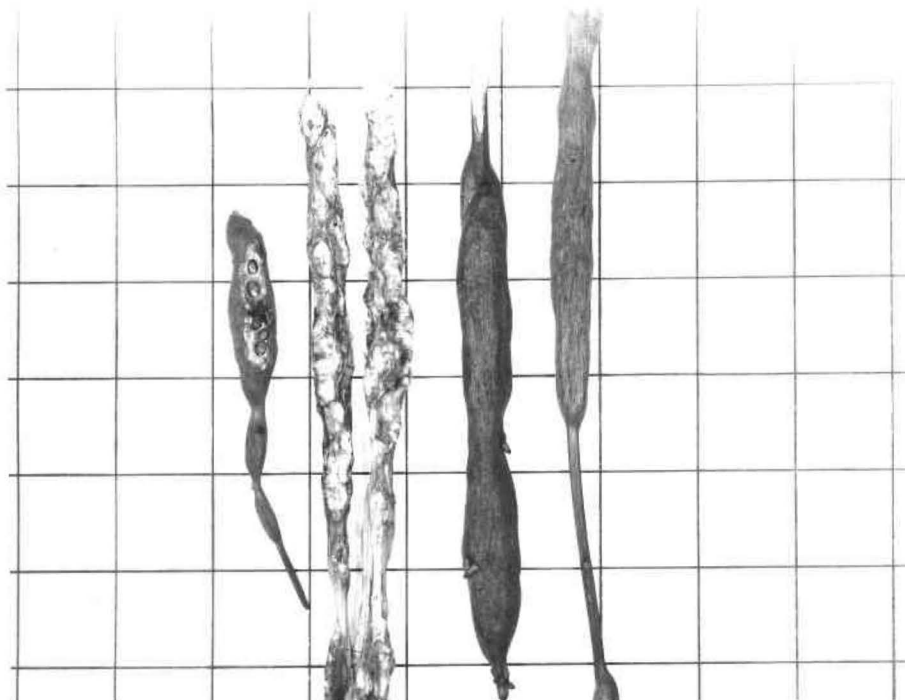


Figure 39.--Infested twigs cut by the California gray squirrel. The 3rd and 4th twigs from right show opened cavities from which the seed-like growths containing larva have been removed and eaten by the squirrel.

more frequent. For example, three sprout clumps in the shelterwood were damaged every year from 1969 to 1976 (Fig. 40). Damage to sprouts in the shelterwood was on both terminal and lateral twigs. In the clearcutting, most damage was to lateral twigs. Repeated death of the terminals resulted in poor height growth and excessive forking, which in turn caused poor form.

Freezing injury to elongating stems was another injury to the California black oak sprout clumps in both the shelterwood and clearcutting. Just as for seedlings, warm mid-April temperatures triggered bud burst and leaf flushing of the sprouts. Indeed, some sprout terminals had elongated 4 to 6 inches by April 19, 1970. On April 20, the minimum temperature reached 21 degrees F. and new shoots and leaves were killed. But freezing temperatures in May 1971 did not cause damage to sprouts in the study area but did elsewhere on the Experimental Forest. This is because the period of susceptibility to damage from late spring frosts is quite short--a matter of a few days--and then the new tissues are tough enough to withstand cold temperatures.

Elongating sprouts again were frozen in April 1972. Permanent damage or lowering of form could not be found one year later (Fig. 41). This lack of damage indicates the resilience of this oak to freezing injury.

The large sample size permitted additional testing of growth relationships for California black oak sprouts. Testing involved plotting data, examining linear, polynomial, or logarithmic regressions for best



Figure 40.--Slow height growth, poor form, and presence of many galls on terminals indicate repeated damage by C. perdens.



A



B

Figure 41.--A: Dead, drooping shoots and leaves of California black oak portray the effects of the hard freeze on April 13, 1972. B: No trace of freezing injury is visible on May 6, 1973.

fit, and then evaluating the degree of relationship between tested variables by means of correlation coefficients (Snedecor 1956, p. 174).

Most representative regression equations for unthinned California black oak sprouts were selected after examination of intercepts and correlation coefficients (Table 9). In the clearcutting, the highly significant relationship between stump vigor (width of last 10 rings) and stump diameter indicated that either can be used as a basis for predicting sprout growth. Stump diameter was chosen as best, however, because it is easiest to measure and relate to.

The regressions of number of sprouts, height, and crown width on stump diameter indicated that a highly significant amount of variation in these variables could be explained by changes in stump diameter. This proved true for sprout ages 4 and 10. For a relatively even-aged stand on a homogeneous site, this is as expected.

The regressions of number of sprouts and sprout height on crown width showed that much of the variation in these values could be explained by the width of the sprout crown. In general, the greater the crown width, the greater the number of sprouts that contributed to it. Likewise, as crown width expanded, its additional photosynthetic area fueled additional sprout height growth.

The tested effect of intracloonal sprout density on sprout height proved negligible at ages 4, 8, and 10 years. Obviously, the variation in sprout height continued to be caused by factors other than sprout density.

Table 9.--Regression equations and significance levels for various sprout ages and variables. California black oak, clearcutting

<u>Sprout age (years)</u>	<u>Regression of:</u>	<u>Regression Equation</u>	<u>r</u>	<u>Significance level</u>
4	Stump diam. on stump vigor	$Y = 7.99 + 6.92 x$	.69	.01
4	No. of sprts. on stump diam.	$Y = -56.20 + 36.76 \log x$	.48	.01
10	No. of sprts. on stump diam.	$Y = -3.08 + .44 x$	.62	.01
4	Sprt. height on stump diam.	$Y = 6.49 + .11 x$	.32	NS
10	Sprt. height on stump diam.	$Y = 14.11 + .47 x$	.60	.01
4	Crown width on stump diam.	$Y = -.52 + 2.06 \log x$	.62	.01
10	Crown width on stump diam.	$Y = -1.58 + 4.47 \log x$	.76	.01
4	No. of sprts. on crown width	$Y = -9.96 + 9.44 x$	.60	.01
10	No. of sprts. on crown width	$Y = -12.15 + 2.78 x$	.64	.01
4	Sprt. height on crown width	$Y = 4.15 + 2.44 \log x$	.50	.01
10	Sprt. height on crown width	$Y = 5.46 + 6.37 \log x$	.50	.01
4	Sprt. height on no. of sprts.	$Y = 7.28 + .017 x$	.23	NS
8	Sprt. height on no. of sprts.	$Y = 14.57 + .079 x$	.31	NS
10	Sprt. height on no. of sprts.	$Y = 18.06 + .106 x$	.31	NS

Similar analysis of sprout parameters in the shelterwood showed somewhat consistent trends, but reflected the effect of the cynipid gall wasp (Table 10). This is evident in the regressions of sprout height and crown width on stump diameter at ages 1 and 8, where almost no relationship was expressed.

Intraclonal sprout density and sprout height were highly correlated at age 1 and moderately so at age 8 in the shelterwood, but not at all in the clearcutting. This differential response possibly reflects the effect of the shelterwood overstory on the intolerant oak: beyond a certain threshold of light, a larger number of sprouts forces an early expression of dominance and an early upward reaching for light.

PLANT MOISTURE STRESS

Because differences in sprout characteristics were apparent for the clearcut and shelterwood environments, additional studies on plant moisture stress were carried out. Specifically, representative clumps of Pacific madrone, tanoak, and California black oak were selected for sampling in sun (clearcut) and shade (shelterwood) environments.

Sprouts were from the root crown and 7 years of age.

Sprouts in sunlight ranged from 5 to 10 feet tall, numbered 1 to 2 sprouts per clumps, and had crowns that were 2.5 to 4.5 feet wide. Current-year shoot elongation, a measure of plant vigor, was 2.5 to 4.0 inches. Shaded sprouts averaged 2.5 to 7.0 feet tall, numbered 3

Table 10.--Regression equations and significance levels for various sprout ages and variables. California black oak, shelterwood

<u>Sprout age (years)</u>	<u>Regression of:</u>	<u>Regression Equation</u>	<u>r</u>	<u>Significance level</u>
1	No. of sprts. on stump diam.	$Y = -12.39 + 3.54 x$	.52	.05
8	No. of sprts. on stump diam.	$Y = -37.76 + 22.08 \log x$	.69	.01
1	Sprt. height on stump diam.	$Y = .09 + .18 x$	.37	NS
8	Sprt. height on stump diam.	$Y = 2.23 + .34 x$	.23	NS
1	Crown width on stump diam.	$Y = .41 + .14 x$	.41	NS
8	Crown width on stump diam.	$Y = .18 + .58 x$	.44	.05
1	No. of sprts. on crown width	$Y = -2.23 + 13.66 x$	.70	.01
8	No. of sprts. on crown width	$Y = .99 + 6.91 \log x$	.61	.01
1	Sprt. height on crown width	$Y = -.32 + 1.20 x$	.86	.01
8	Sprt. height on crown width	$Y = -.27 + .99 x$	.88	.01
1	Sprt. height on No. of sprts.	$Y = .79 + .05 x$	.67	.01
8	Sprt. height on No. of sprts.	$Y = .57 + 2.14 \log x$	.45	.05

to 10 living stumps per clump, and possessed crowns 3.0 to 3.5 feet wide. New shoot elongation ranged from 1.5 to 6.0 inches.

Sampling procedure, twig collection technique, and date of sampling were as described in Part I. Xylem sap tension was monitored in each species for 24 hours to determine maximum and minimum moisture stress.

The horizon began to lighten slightly at about 5:20 a.m. PST; sunrise was at 8:10 a.m.; and the sun first shone directly on plant leaves at 9:12 a.m.

Predawn minimum moisture stress in Pacific madrone sprouts was about 5 atmospheres (Fig. 42). With increasing light, xylem sap tension increased steadily regardless if the plant was in sun or shade. A peak tension of 20.5 atmospheres was reached first in the shaded plant at about 9:25 a.m. PST. From then on, tension decreased almost linearly at the rate of about 1.3 atmospheres per hour. Peak tension (23.5 atmospheres) in the sunlit plant occurred at about 10:00 a.m. and from then on also decreased steadily. Overall, the shape of the moisture tension curves for both sunlit and shaded plants was quite similar.

Predawn minimum moisture stress in tanoak sprouts was slightly below 5 atmospheres (Fig. 43). Xylem sap tension in the sunlit plant apparently increased quite rapidly after first light and was nearly at peak by sunrise. By the time sunlight first illuminated the leaves, the plant was within 1 atmosphere of the maximum moisture stress (30.5 atmospheres) it would have to endure that day. Thus, the length of time the plant had to withstand high moisture stress was long--14 hours at over 25 atmospheres, or 10 hours at over 28.5 atmospheres.

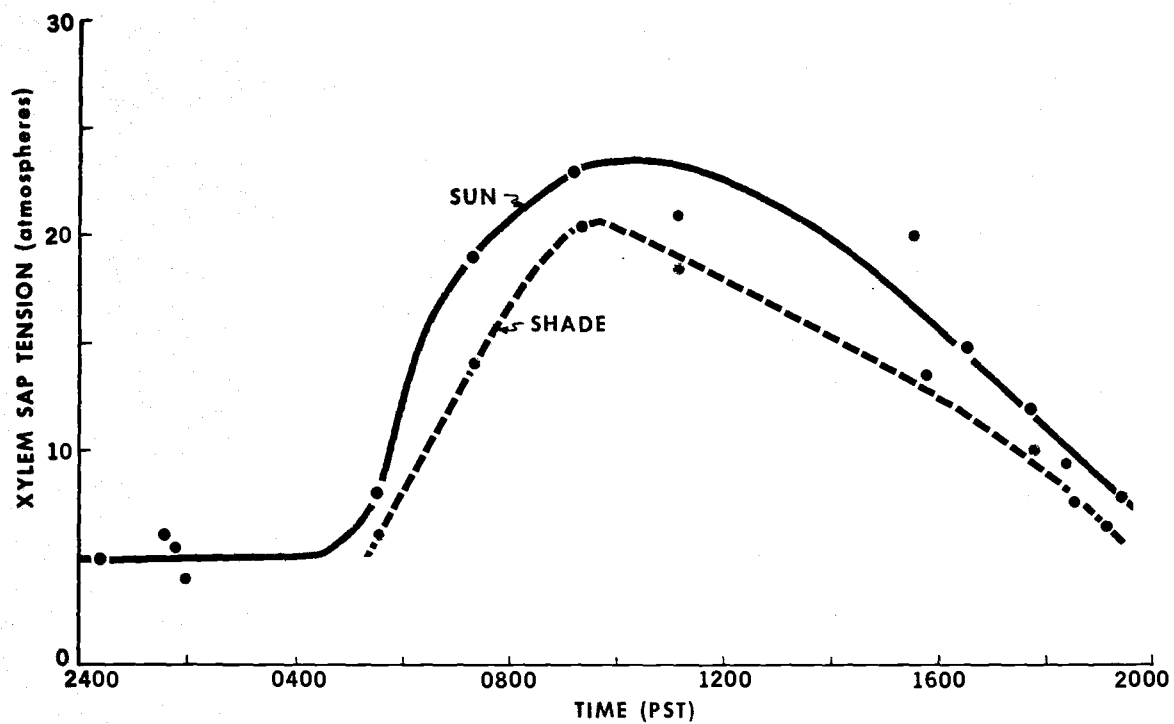


Figure 42.--Diurnal xylem sap tension pattern for Pacific madrone sprouts in sunny and shady environments.

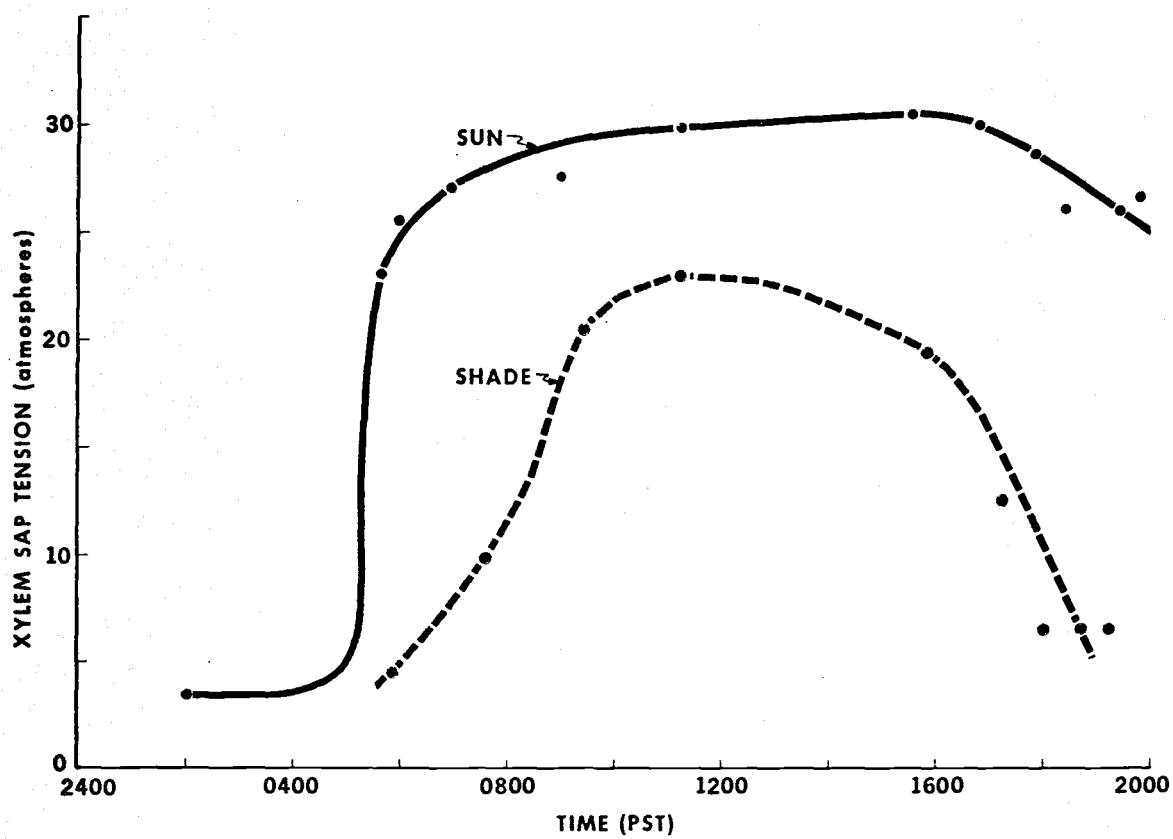


Figure 43.--Diurnal xylem sap tension pattern for tanoak sprouts in sunny and shady environments.

The tanoak sprout clump in shade also had to withstand rapidly increasing xylem sap tension from first light onwards. Peak tension was 23 atmospheres. More meaningfully, however, the shade plant did not have to endure high moisture stress for nearly as long as its sunlit counterpart.

Predawn minimum moisture stress in California black oak sprouts was about 8 atmospheres (Fig. 44). At first light, xylem sap tension increased rapidly in both sun and shade plants. In the shade plant, stress peaked at 28 atmospheres about 10:00 a.m. and decreased at an increasing rate thereafter. Xylem sap tension in the sunlit plant plateaued from about the time the sun shone directly on the leaves until 5:00 p.m. Thus, although peak stress was similar for plants in sun and shade, the sunlit plant endured higher stress for a longer timespan than its shade-grown brethren.

SUMMARY

After cutting, fire, or severe injury, Pacific madrone, tanoak, and California black oak sprout vigorously at or above the root collar from dormant buds. These buds connect directly with the primary xylem as opposed to adventitious buds which form in callus tissue at the end of the radial trace. In the hardwood species studied, the number of buds formed is tremendous, hence the sprout potential also is large.

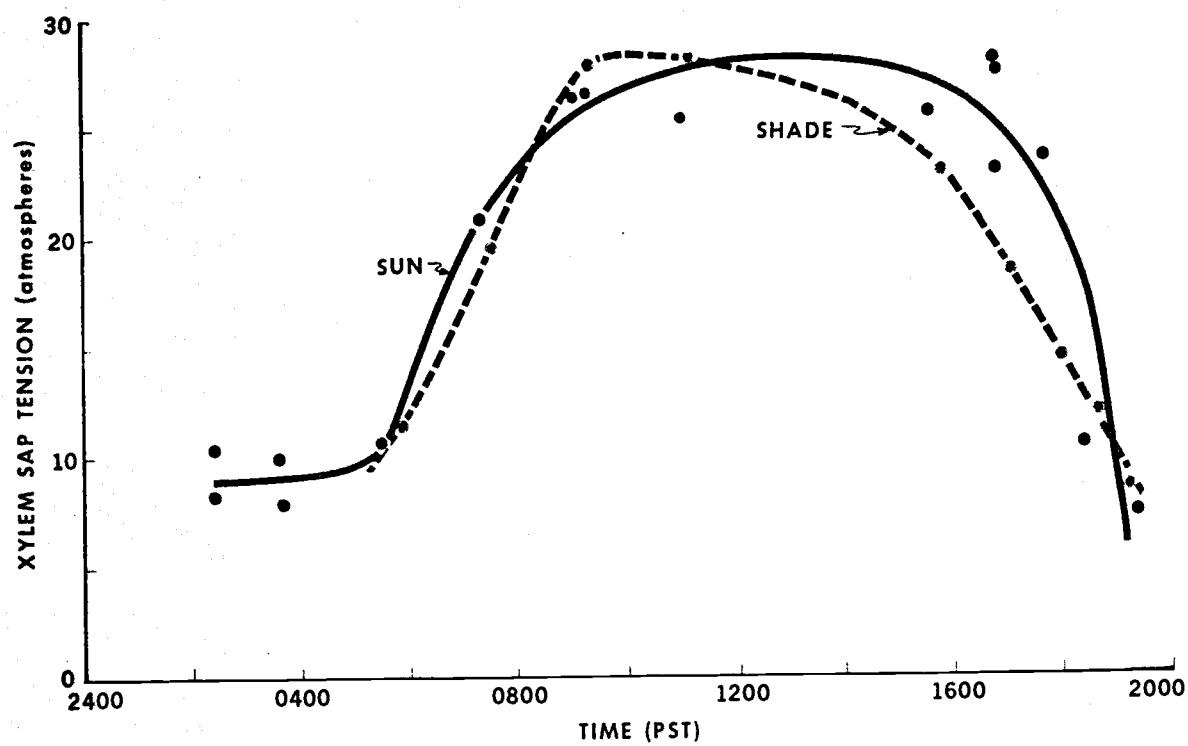


Figure 44.--Diurnal xylem sap tension pattern for California black oak sprouts in sunny and shady environments.

If cutting or injury leaves a high stump, sprouts form on it. Those highest up often become dominant. These "stool" sprouts, as they are called, are undesirable for two reasons: (1) they adhere weakly to the top and sides of the stump and get "peeled off" by side pressure from animals or heavy snow, and (2) the incidence of heart rot bridging from rotting stump to pith of sprout is high for stool sprouts. For root crown sprouts, however, the incidence of transmittal is almost nil.

Although regeneration of Pacific madrone, tanoak, and California black oak is made up of seedlings, advance reproduction, seedling-sprouts, and stump sprouts, stump sprouts are the primary reproductive mode. This is because of their ability to grow rapidly both vertically and horizontally. This allows them to quickly reoccupy a given site and dominate it for many years.

Comparison of number of sprouts per clump in the clearcutting and shelterwood environments showed intraclonal sprouting to be greater in the clearcutting for all species and years where comparisons were possible. After 10 years, the number of Pacific madrone sprouts per clump in the clearcutting was 15, and in the shelterwood, 6. For California black oak after 10 years, the number of sprouts was 15 in the clearcutting and 12 in the shelterwood. Tanoak averaged about 24 sprouts per clump in the shelterwood.

Height and crown growth rates of natural (unthinned) sprout clumps in a clearcut environment after 10 years were:

<u>Species</u>	<u>Height</u> (feet per year)	<u>Crown</u> (feet per year)
Pacific madrone	2.22	1.02
Tanoak	1.90	1.01
California black oak	1.97	0.94

In a contrasting shelterwood environment for a similar timespan average height and crown growth rates per clump were:

<u>Species</u>	<u>Height</u> (feet per year)	<u>Crown</u> (feet per year)
Pacific madrone	0.97	0.72
Tanoak	0.83	0.70
California black oak	0.69	0.72

These data give the land manager a basis on which to judge the competitive ability of these hardwood species in two differing environments on a high site.

The wildlife manager often needs data quantifying the browse potential of a given species at a certain time in its development. While Pacific madrone and tanoak are seldom browsed, California black oak often is. Cubic volumes of above-ground material, when fully leafed out, were calculated from height and crown width, using the formula of a cylinder. At age 4, average volume in cubic feet per clump by species in both the clearcutting and shelterwood were:

<u>Species</u>	<u>Clearcutting</u>	<u>Shelterwood</u>
Pacific madrone	220	90
Tanoak	370	74
California black oak	229	71

Most of this material would be available to browsing animals in the clearcutting, and because of lower height, all of it in the shelterwood.

The large differences in development between sprouts in the clearcutting and the shelterwood results from the interaction of inherent species characteristics and the differing environments created. In the clearcutting, intracloonal competition governs development the first few years, but as the crowns expand and begin to close, interclonal effects become increasingly important. Under the shelterwood canopy, available resources are more limiting, and the environment is less favorable for growth, even to tolerant Pacific madrone and tanoak. Intolerant California black oak fares even worse in the shady shelterwood. Height growth of this oak was worsened further by repeated attacks on terminal twigs by the cynipid gall wasp. This pest also attacked sprouts in the clearcutting, but damaged lateral twigs more heavily than terminals.

In every clump, much energy is channeled to sprouts which have no chance of becoming trees. If these poorer sprouts were removed, would the energy used by them be transferred to a few of the best-formed, most thrifty, dominant stems in each clump? To answer this question 1 to 4 of the best sprouts in each clump were selected for retention. All others were removed.

Thinning at age 1 proved difficult and ineffective. Tanoak promptly produced well over 100 additional sprouts, and California black oak and Pacific madrone a lesser number. Plainly, the root system of the residual sprouts was not in balance with that of the former tree. In addition, first-year sprouts were difficult to

eliminate. They were too numerous, showed little expression of dominance, and adhered so weakly to the stump that selected members inadvertently were lost. Also the boles of residual sprouts, especially Pacific madrone and California black oak, showed an increased tendency to sunscald.

For Pacific madrone and California black oak, thinning at age 4 proved much more practical and economical as the above problems were reduced greatly. As a whole, unwanted sprouts of Pacific madrone were easier to thin than those of California black oak. Because tanoak continued to produce large numbers of additional sprouts, it is not practical to thin this species for at least 10 years.

Thinned sprouts generally did not grow as well as their unthinned counterparts in either the shelterwood or clearcutting. For all three species, height growth of thinned and unthinned clumps differed by no more than 1.6 feet after 10 years. Crown width was where the effect of sprout thinning was manifest. After 10 years, the average width of thinned Pacific madrone, tanoak, and California black oak clumps was 68, 76, and 91 percent, respectively, of unthinned clumps. And a subjective evaluation showed thinned sprouts to fork more frequently and have poorer form than unthinned sprouts, particularly if of California black oak, and to a lesser extent, Pacific madrone. Thus, manipulating intraclonal sprout density is costly and provides no gain. It is not recommended.

In addition to quantifying various sprout growth characteristics over time, other developmental relationships were examined graphically

and by regression. For Pacific madrone, a weak but positive relationship was found between stump diameter and number of sprouts per stump in both shelterwood and clearcutting at ages 1 and 10. This was not expressed for tanoak sprouts in the shelterwood but was strongly expressed for California black oak sprouts in the clearcutting at ages 4 and 10, and in the shelterwood at ages 1 and 8.

For all three species, stump diameter did not relate well to sprout height in either the clearcut or shelterwood environments.

In order to better explain growth and development of California black oak sprouts, further testing of relationships in both the clearcutting and shelterwood was performed.

In the clearcutting, the regression of crown width on stump diameter indicated that much variation in the width of a sprout clump could be explained by changes in stump diameter. This relationship was expressed only at age 10 in the shelterwood.

The regressions of number of sprouts and sprout height on crown width indicated a meaningful relationship existed between these variables in both the clearcutting and shelterwood. Crown width increased in response to a larger number of sprouts per clump which created more photosynthetic area, and in turn fueled additional height growth.

For many hardwood species, it is recognized that height growth is affected directly by the density of surrounding vegetation, among other factors. This proved true for California black oak sprout clumps in the shelterwood, but not in the clearcutting. The difference could be caused by the lack of optimal light levels in the shelterwood forcing

an early expression of dominance and height growth. With time however, the number of sprouts that survive in each clump probably varies independently of sprout height. Thus the number of sprouts becomes an increasingly poorer independent variable with time.

Plant moisture stress was measured for 24 hours in Pacific madrone sprout clumps growing in contrasting environments--deep shade and strong sunlight. In general, the sunlit plant was under about 3 atmospheres more stress throughout the day than the shaded plant. Peak moisture stress occurred first in the shaded plant at 20.5 atmospheres and later in the sunlit plant at about 23.5 atmospheres. In both environments, plant moisture stress decreased steadily after the peak stress was reached. As stress peaked before 11:00 a.m., the plants actually were under decreasing stress during the hottest part of the day.

Tanoak sprout clumps also were tested for plant moisture stress in shaded and sunlit environments. Large differences in moisture stress were found. The sunlit plant underwent higher stress from the start and, indeed, was one atmosphere from peak stress (30.5 atmospheres) at the time sunlight first shone on the leaves. In general, moisture stress in the sunlit plant followed the same general pattern of the shaded plant. But it was about 7 atmospheres higher during the entire day. Thus the sunlit plant had to endure a much higher total daily stress than its shaded counterpart.

In California black oak, only minor differences in moisture stress were found between sunlit and shaded plants. Both endured a peak stress of 28.5 atmospheres, and the diurnal fluctuation of moisture

in both generally was similar. Moisture stress in the shade-grown plant peaked first; the sunlit much later--long after reaching a plateau of high tension. Therefore total stress for the period was greatest in the sunlit plant.

Implications for management of sprout stands of Pacific madrone, tanoak, and California black oak, aside from those presented by quantification of sprout density, height, crown width, and volume relationships, are many. It does not pay to thin sprout clumps or tolerate stool sprouts. The incidence of heart rot in root crown sprouts is so low that the manager does not need to worry about it. Sprout growth and form are best if all sprouts in each clump develop naturally and compete vigorously with each other, as well as neighboring sprout clumps and other vegetation, including vigorous woody shrubs.

Recognizing these implications leads to the conclusion that slash disposal in dense stands of these hardwood species can be either by (1) hand piling and burning, or (2) scattering slash evenly throughout the harvest area and burning it. In both methods, a thorough, clean burn is essential. Burning may stimulate germination of many shrub seeds but the slower height growth of the shrubs causes them to fall behind the burgeoning sprouts.

IV. STAND GROWTH AND YIELD

In this part of the study, existing young-growth hardwood stands were examined for response to various levels of thinning. In addition, diameter and volume growth relationships were examined by species, diameter classes, and intraclonal density. A major preparatory task was the creation of accurate volume tables for Pacific madrone, tanoak, and California black oak on high sites. Degree of epicormic branching also was evaluated for California black oak. Knowledge developed here will aid the landowner in deciding how to best manage his hardwood stands, and what yield he might expect from them.

DEVELOPMENT OF LOCAL VOLUME TABLES

Volume tables for native California hardwoods are scarce. Hornibrook and others (1950) formulated rather general tables for several California hardwoods, including the three study species, and Wiant and Berry (1965) published volume and tariff tables for tanoak in Humboldt County, California.

The hardwood stands on the Experimental Forest occupy a wide range of sites--on ridgetops, in draws, in old burns, in openings, and intermixed with conifers. Although overall site quality is high, specific site quality often varies considerably. Likewise, variation in tree form can be appreciable. When open-grown, forking in the three study

species can be excessive. When in dense stands trees exhibit the excurrent branching habit of conifers. Tree height also is sensitive to stand density and physiography. Dense stands or placement in a ravine usually results in tall trees with long, straight, gently tapering boles. Trees in openings and on ridgetops often are shorter and taper more severely. And height growth of California black oak has been shown to vary with aspect (McDonald 1969). If intraclonal sprout density remains high, surviving sprouts may have J-shaped stems and lean excessively. These factors make sampling and measurement of hardwoods much more difficult than for conifers.

Because growth and form of these species is sensitive to relatively minor changes in stand density and physiography, a large and well distributed sample is necessary. Also a precise instrument and much care in measurement must be used to accurately quantify tree dimensions.

Bark thickness was needed for each species and size of tree. Thus 136 trees in the diameter range of 4.8 to 41.0 inches were sampled by chopping into the bark and measuring its thickness on opposite sides of each tree.

Graphs of bark thickness on breast height diameter indicated a curvilinear relationship for the three species studied. This relationship then was tentatively expressed in three differing mathematical equations and examined for goodness of fit. A computer-based least squares curve-fitting technique was used. The most representative equation relating average single bark thickness to breast-height

diameter for each species was $Y = a + bx + cx^{-1}$ where y = average single bark thickness and x = d.b.h. (Figs. 45, 46, 47). Correlation coefficients, significant at the 1% level, by species, were Pacific madrone (.74), tanoak (.73), and California black oak (.84).

For tanoak, bark thickness increased as diameter increased up to about 18 inches. From then on, bark thickness varied from 0.6 to 1.3 inches regardless of tree diameter. Bark thickness of California black oak increased in an orderly manner within the d.b.h. range of 8.0 to 24.0 inches. After that, thickness of bark varied between 0.9 and 1.4 inches irrespective of diameter. For both species, high variation in bark thickness of larger trees appears to be a consequence of growth rate. Fast-growing trees have thick, deeply fissured bark, and badly suppressed and slower growing trees have shallow fissures and thinner bark. The bark of Pacific madrone sloughs off before it ever gets much thicker than 0.6 inches.

To meet the stipulated sampling conditions, the Barr and Stroud optical dendrometer was used. The sampling plan stressed a large sample, distribution throughout the Experimental Forest and adjacent area, and good representation of species, diameters, and physiographic settings.

Altogether, 333 trees from 3 to 30 inches in diameter were measured with the optical dendrometer. Sample size was: Pacific madrone 85 trees, tanoak 144, and California black oak 104 trees. Stand tables by species and diameter classes were constructed as sampling progressed. This facilitated a representative and well

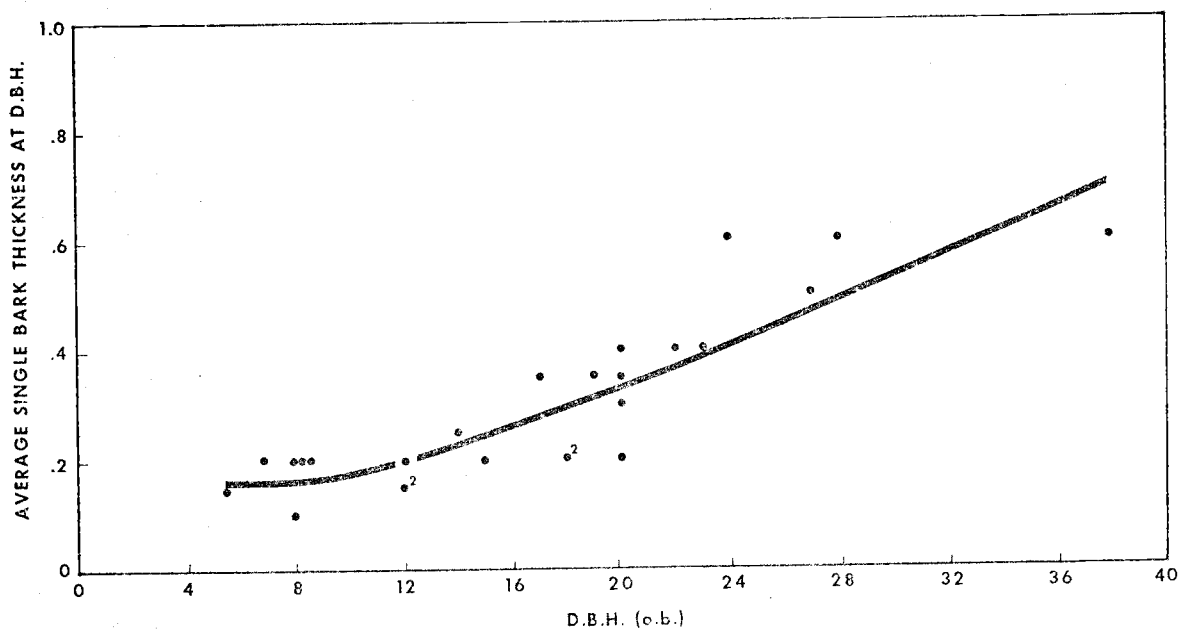


Figure 45.--Relationship of Pacific madrone bark thickness to diameter at breast height.

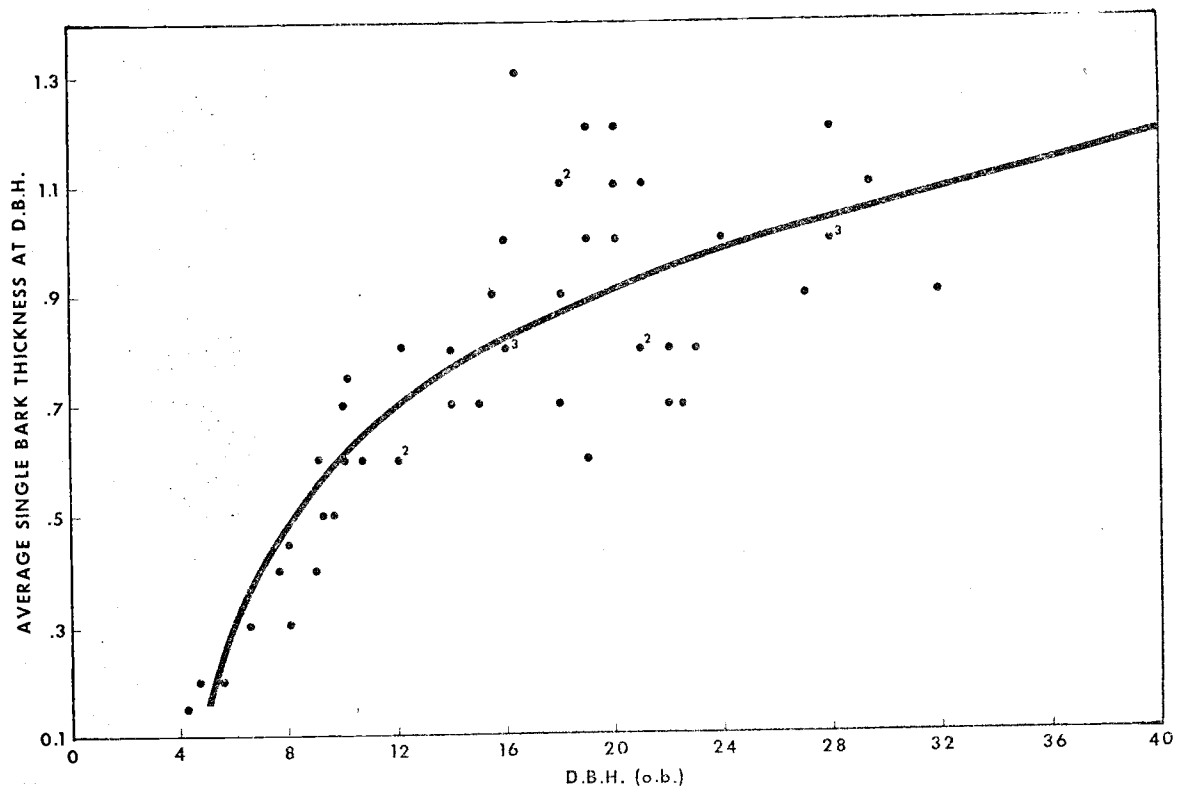


Figure 46.--Relationship of tanoak bark thickness to diameter at breast height.

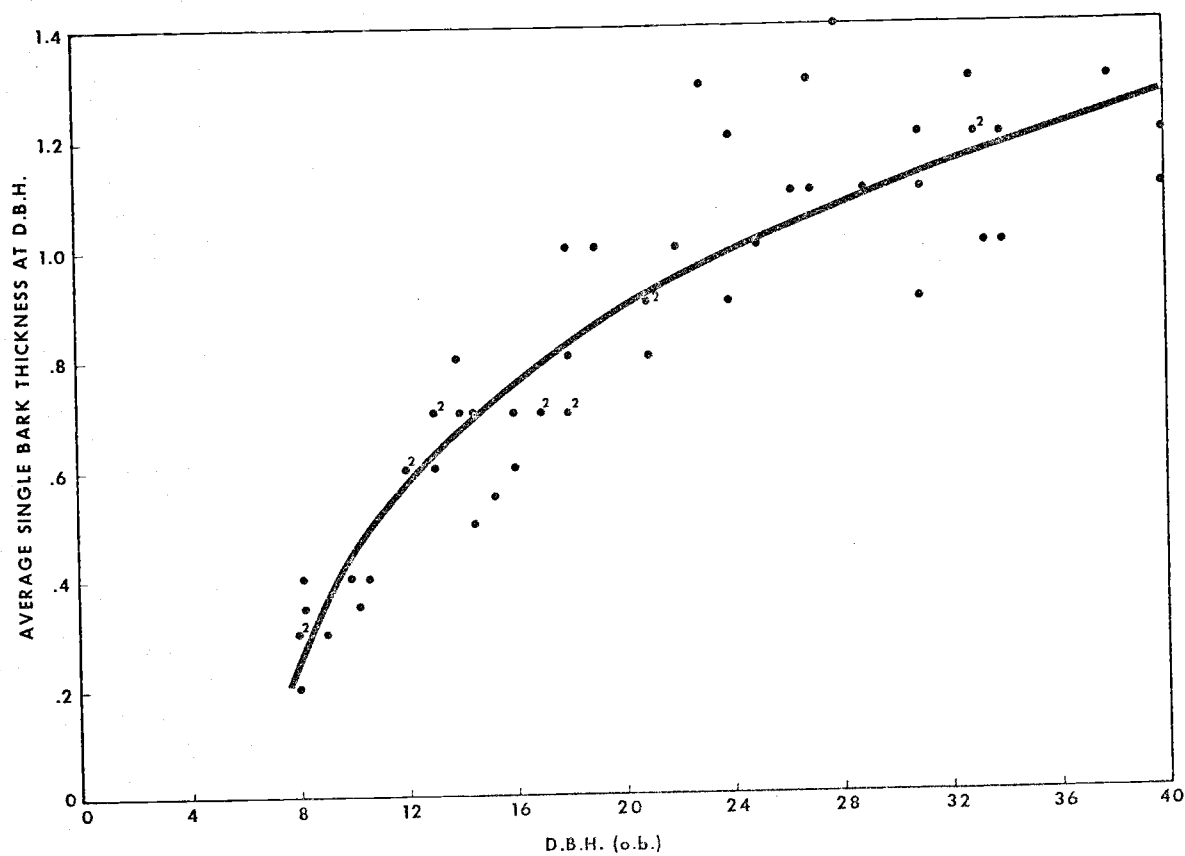


Figure 47.--Relationship of California black oak bark thickness to diameter at breast height.

distributed sample. Data were recorded at stump height, d.b.h. midway between d.b.h. and base of live crown, near base of live crown, midway in crown, and at top of tree. Many trees received additional measurements because of abrupt changes in bole diameter. Such abrupt changes are caused by large branches or forking. Every tree bole was defined by at least six measurements. Multiple-forked trees, however, received up to 14 measurements, with several measurements of each fork.

In many instances, base of live crown was poorly defined because of branches on one or more sides, and not on others. And an abrupt change in form often occurred here. For these reasons, the measurements related to base of live crown often were foregone.

After measurement, tree data were transferred to magnetic tape and processed by computer using Grosenbaugh's STXMOD program. Separate computer runs enabled volumes to be expressed for different species and utilization standards. Utilization standards were: cubic volume to a 0-inch top, cubic volume to a 4-inch top, and Scribner board-foot volume to a 4-inch top. Minimum log length was 8.0 feet.

Anyone who has observed the height and form of Pacific madrone, California black oak, and to a lesser extent, tanoak, knows how variable these species are. And when one considers that this sample deliberately contained straight-boled and forked trees, as well as trees in draws and on ridgetops, it is no surprise if strong variation in volume and height were indicated, especially in larger trees.

But variation wasn't bad. Volume-d.b.h. and height-d.b.h. relationships were plotted for each utilization standard. Mean volumes

and heights as well as standard errors and standard deviations by successive 2-inch diameter classes were calculated and examined. Those for California black oak to a 0-inch top and the volume-d.b.h. graph of this oak exemplify typical variation. As a whole, the range in volume for a given breast height diameter was rather small (Fig. 48). The standard error of mean cubic volume for 2-inch diameter classes varied from $1/5$ to $1/25$ of the mean with overall variation increasing with diameter enlargement. In general, the variance in volume of each 2-inch diameter class was less than half the mean.

The range in total height of California black oak trees varied somewhat at a given diameter (Fig. 49). The standard error of mean height by 2-inch diameter classes ranged from $1/12$ to $1/47$ of the mean, with no trend in variation relative to diameter class. The variance in tree height for each 2-inch diameter class ranged from $1/3$ to 3 times the mean.

After plotting indicated the general curve shape, the best mathematical expression of it was determined by a computer-based least squares curve-fitting procedure as was done for bark thickness. The most representative regression equation relating cubic volume to diameter was $\log(\text{volume}) = a + b \log(\text{d.b.h.})$. Because variation increased as diameter increased, $\log \text{d.b.h.}$ was used for weights in weighted regressions determining cubic volume to a 0-inch top for each species. Correlation coefficients, significant at the 1-percent level, by species, were Pacific madrone (.97), tanoak (.99), and California black oak (.99).

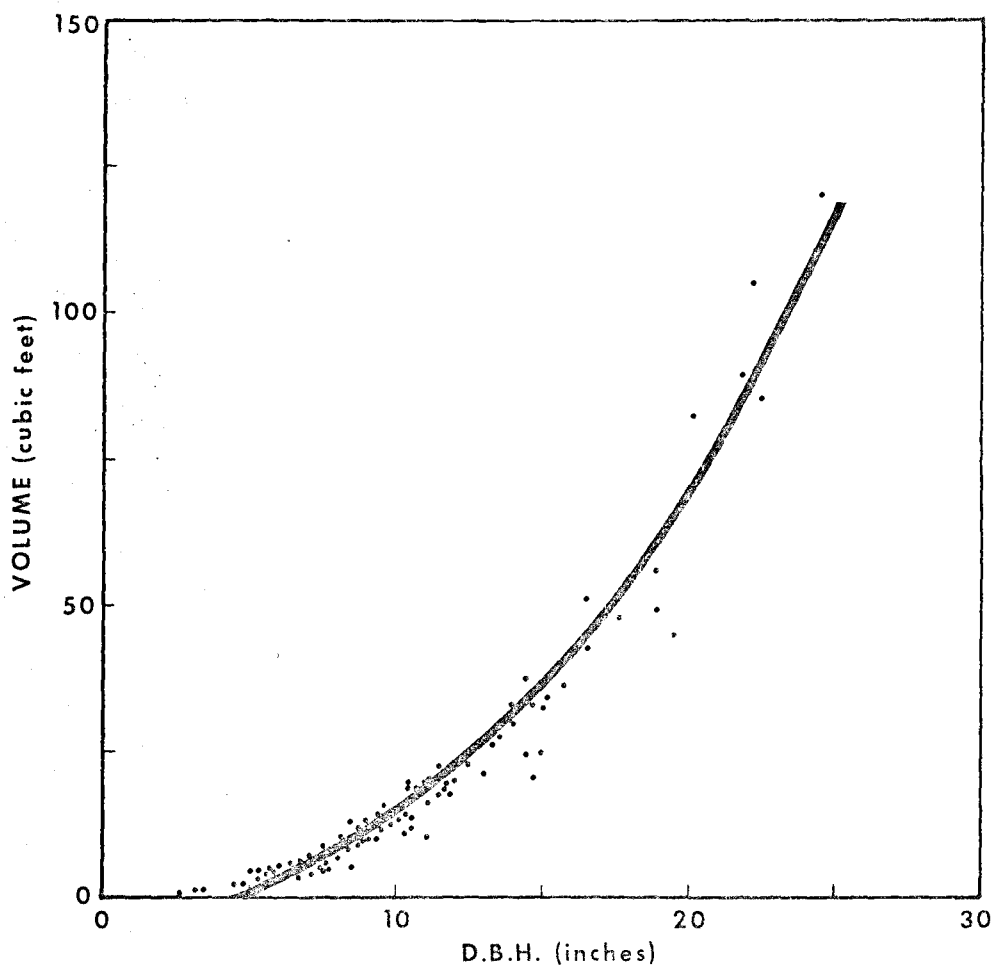


Figure 48.--Cubic volume-d.b.h. relationship for California black oak to a 0-inch top. 104 trees.

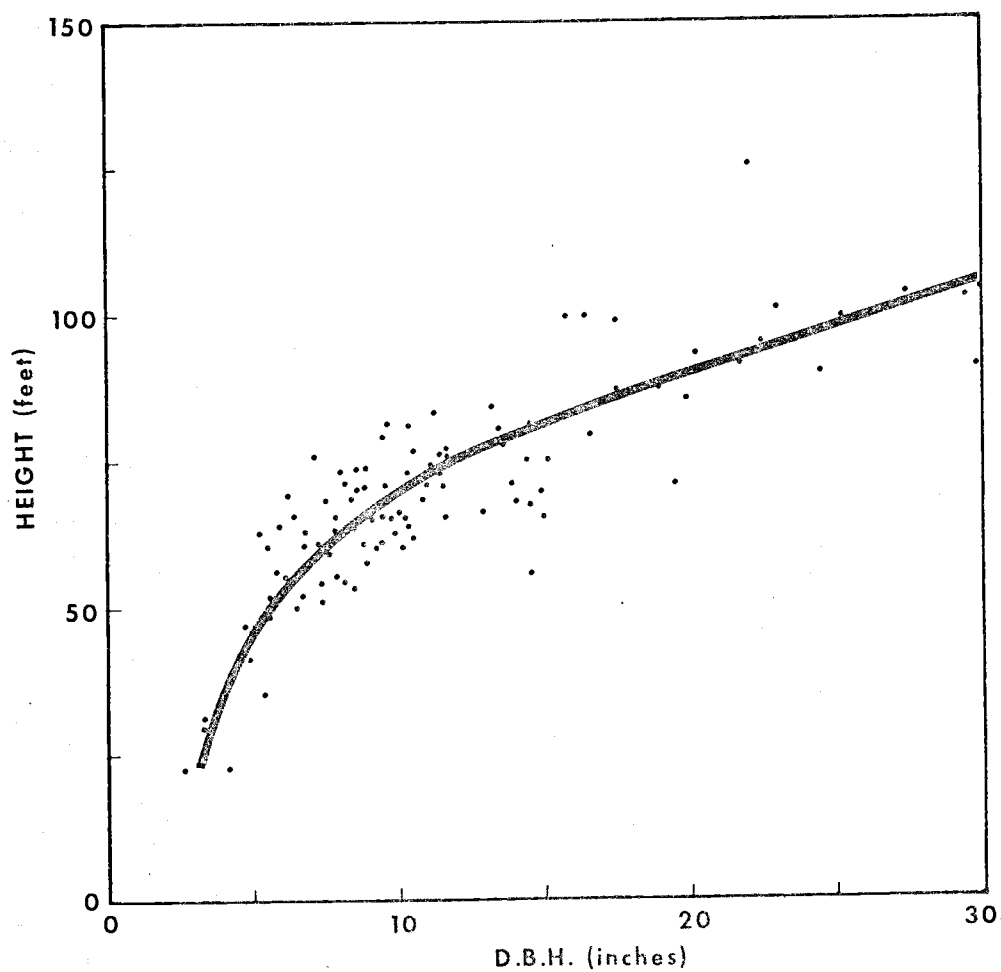


Figure 49.--Height-d.b.h. curve and plotted points for California black oak to a 0-inch top. 104 trees.

For cubic-foot volume to a 4-inch top, the log-log equation gave a poor fit. In fact, the plotted expression of the equation for the 4-inch top crossed that of the 0-inch top. Attempts to combine the two equations failed. This was because the log-volume equation attempted to fit lines that express a proportional relationship between the 0-inch and 4-inch volumes. Close examination indicated that the relationship was not proportional, but roughly constant. Linear regressions of volume difference between 0-inch and 4-inch on d.b.h. indicated slope coefficients that did not differ significantly from zero ($p = .05$). And this was true for all three species. Additional calculations indicated the mean volume difference for each species to be 0.73 cubic feet for Pacific madrone, 0.96 for tanoak, and 1.27 cubic feet for California black oak. A useful general rule of thumb, then, is that cubic volume to a 4-inch top is about one cubic foot less than that to a 0-inch top. The mathematical expression of the relationship between cubic volume to a 4-inch top and d.b.h. is $\text{volume} = 10^{(A + B \log \text{DBH})} - C$, where "C" is the mean volume difference between utilization standards. Correlation coefficients, significant at the 1 percent level, by species, were Pacific madrone (.97), tanoak (.98), and California black oak (.99).

The most representative Scribner volume equation for the three species proved to be $\text{volume} = a (\text{dbh} - d) + b (\text{dbh} - d)^2 + c (\text{dbh} - d)^3$ where "d" is a constant for each species based on an examination of the data. More specifically, it is that point, determined graphically, where each species has zero volume. For Pacific madrone the constant

was 5.0 inches, for tanoak 5.5 inches, and for California black oak 5.0 inches. Defining these constants and using them in the regression equations was necessary to control the curve in the region of zero volume. It was necessary to estimate each separately from the regression. Correlation coefficients, significant at the 1-percent level, by species, were Pacific madrone (.93), tanoak (.98), and California black oak (.98).

Volume tables by 1-inch diameter intervals for three utilization standards are presented for Pacific madrone, tanoak, and California black oak (Tables 11, 12, 13). For each of the tables, the average quadratic deviation of the individual tree volumes from those estimated from the equation (standard error of estimate), and the aggregated difference of the estimated values are shown as footnotes. Overall, they reinforce the fact that these tables are about as accurate and reliable as the inherently high variation in the species permits.

Height-diameter relationships were tested in a manner similar to those for volume and diameter. The most representative equation relating total tree height (0-inch top) to breast-height diameter for all species was $Y = a + bx + cx^2$ where Y = height in feet and x = d.b.h. in inches. Best-fit regression coefficients by species are:

Pacific madrone	$Y = 20.51 + 4.49x - .068x^2$
Tanoak	$Y = 9.62 + 6.87x - .14x^2$
California black oak	$Y = 24.59 + 5.33x - .096x^2$

Correlation coefficients, significant at the 1-percent level, by species, were Pacific madrone (.81), tanoak (.89), and California black oak (.86).

Table 11.--Volume table for young-growth stands of Pacific madrone
on high sites, three utilization standards

D.b.h. (inches)	Utilization Standard		
	0-inch top ^{1/} (cubic feet)	4-inch top ^{2/} (cubic feet)	4-inch top ^{3/} (board feet Scribner)
3	0.6	--	--
4	1.3	0.6	--
5	2.3	1.6	--
6	3.7	3.0	0.3
7	5.4	4.7	2.9
8	7.6	6.9	8.2
9	10.2	9.5	16.3
10	13.3	12.6	27.3
11	17.0	16.3	41.2
12	21.1	20.4	58.1
13	25.9	25.2	78.1
14	31.2	30.5	101.2
15	37.2	36.5	127.4
16	43.8	43.1	157.0
17	51.0	50.3	189.0
18	59.0	58.3	226.3
19	67.6	66.9	266.1
20	77.0	76.3	309.4
21	87.1	86.4	356.4
22	98.0	97.3	407.0
23	109.6	108.9	461.5
24	122.1	121.4	519.7
25	135.4	134.7	581.8
26	149.5	148.8	647.9
27	164.5	163.8	718.1
28	180.4	179.7	792.3
29	197.1	196.4	870.7
30	214.7	214.0	953.4

Average quadratic deviation of individual tree volumes from values estimated by the equation, and the aggregated difference of estimated values are:

^{1/} 6.67, + 0.06

^{2/} 6.86, 0.00

^{3/} 48.07, 0.00

Table 13.--Volume table for young-growth stands of California black oak on high sites, three utilization standards

- - - - - Utilization Standard - - - - -			
<u>D.b.h.</u> <u>(inches)</u>	<u>0-inch top^{1/}</u> <u>(cubic feet)</u>	<u>4-inch top^{2/}</u> <u>(cubic feet)</u>	<u>4-inch top^{3/}</u> <u>(board feet Scribner)</u>
3	0.8	--	--
4	1.6	0.3	--
5	2.7	1.4	--
6	4.1	2.8	1.7
7	5.9	4.6	5.7
8	8.1	6.8	12.1
9	10.7	9.4	20.9
10	13.6	12.3	32.2
11	17.0	15.7	46.2
12	20.9	19.6	62.7
13	25.2	23.9	82.0
14	29.9	28.6	104.1
15	35.1	33.8	129.0
16	40.8	39.5	156.8
17	47.0	45.7	187.5
18	53.7	52.4	221.9
19	61.0	59.7	258.1
20	68.7	67.4	298.2
21	77.0	75.7	341.4
22	85.8	84.5	387.9
23	95.2	93.9	437.8
24	105.1	103.8	491.0
25	115.6	114.3	547.8
26	126.7	125.4	608.1
27	138.4	137.1	671.9
28	150.6	149.3	739.5
29	163.5	162.2	810.8
30	176.9	175.6	885.8

Average quadratic deviation of individual tree volumes from values estimated by the equation, and the aggregated difference of estimated values are:

^{1/} 5.60, -0.34

^{2/} 5.73, 0.00

^{3/} 36.04, 0.00

Output from the STXMOD program included total tree heights for all trees. These data were separated into species and crown classes. Mean tree height in feet for these categories was:

Species	Crown Class		
	<u>Dominant</u>	<u>Codominant</u>	<u>Intermediate</u>
Pacific madrone	64.3	62.9	55.7
Tanoak	73.5	68.7	60.8
California black oak	73.1	68.4	61.5

Analysis of variance indicated significant differences in height among species ($p = .05$), and among crown classes for each species ($p = .05$).

Determination of site index is necessary for comparing growth of the stands on the Experimental Forest to those of eastern oaks. With a mean breast-height age of about 60 years and mean height of 70 feet, site index would be 60 at the index age of 50 years (Powers 1972).

RESPONSE TO THINNING

Before the effect of thinning can be evaluated, basic knowledge on natural stand density, basal area, volume, and effect of clumpy origin must be known.

Here one should pause for a moment and remember that young-growth hardwood stands of Pacific madrone, tanoak, and California black oak have special attributes in terms of origin, age, and density. Most, but not all, trees in these stands are from clumps. Usually the tallest and straightest stems triumph, but sometimes a stem will

curve away from the clump, turn upward, and dominate. When several stems per clump survive, one or more members often develop a leaning or J-shaped bole. Multiple-stemmed clumps of Pacific madrone and tanoak are common in young-growth stands; those of California black oak are much less so.

Most native hardwood stands on the west-facing slope of the Sierra Nevada and east-facing slope of the Coast Range are of comparatively recent origin. Hence, most trees are under 20 inches in diameter. Because of a sprouting tendency and short seed dissemination distance, most trees are found as individuals or in groves and small stands.

Stands of these hardwoods are dense, or even too dense, and growth rates are poor. Increment cores from several hundred dominant California black oaks throughout northern and central California showed diameter growth rates to average 12 to 15 rings per inch (McDonald 1969). Cores of Pacific madrone and tanoak on the Experimental Forest indicate a similar trend. This suggested that a thinning study that would provide additional resources to residual trees would be promising (Figs. 50 and 51). Thinning also would favor the best-formed trees and eliminate those with misshapen boles.

Virtually nothing is known about the growth response of these hardwood species. McDonald (1969) did extensive work in natural stands of California black oak and presented data for age-height-diameter relationships. Later Powers (1972) determined site quality relationships for this species. Roy (1957b) showed general diameter-height relationships for tanoak. Sundahl (1966) reported height-



Figure 50.--Looking into a partially thinned stand of mostly California black oaks, Challenge Experimental Forest.



Figure 51.--By thinning from 680 to 244 stems per acre, additional resources should accrue to remaining trees on this plot.

diameter relationships for a small sample of California black oak, tanoak, and Pacific madrone at the Challenge Experimental Forest.

To quantify the growth of these species, 12 quarter-acre circular growth plots were established throughout a 66-acre hardwood unit on the Experimental Forest. Two plots were randomly selected as uncut controls. The others were marked to establish a range of residual basal areas.

What range of basal areas to leave is a difficult decision. The stand cannot be severely opened up. California black oak is prone to epicormic branching along the bole. This malady is triggered by cutting, among other factors. Tanoak crowns suffer partial defoliation and twig dieback when suddenly exposed to strong light. And some Pacific madrone trees unexplainably die when stand density is reduced suddenly.

Careful consideration of these factors, and a desire to maximize growth, led to the establishment of residual basal areas ranging from 60 to 150 square feet per acre. These residual levels are high compared to eastern oak study levels in similarly-aged stands on medium to high sites, but seemed best in these circumstances. In Appalachian hardwoods and specifically northern red oak, Trimble (1968) created basal area levels ranging from 60 to 100 square feet per acre. In upland oak stands in the Missouri-Ohio-Kentucky area, Dale (1972) established growth response plots ranging from 25 to 110 square feet per acre. However, this author advocated keeping stocking in excess

of 50 percent to minimize adverse effects on stem taper, height growth, branch development and natural pruning.

Marking of leave trees was governed by several interacting factors: the required basal area level, leaving the best trees, and uniform spacing. Also, some trees were left as "guard" trees on the south side of California black oak crop trees to shield them from strong sunlight and consequent epicormic branching. And no more than four trees per clump were allowed as a larger number likely would be detrimental to growth and form.

In terms of classical thinning regimes, this thinning closely resembled a crown thinning; that is, residual trees were provided with "sky light" into which their crowns could expand. Each plot was surrounded by an extensive buffer zone, cut to its prescribed basal area level.

Thinning was done by local wood cutters. They did an acceptable job and the residual trees suffered little damage. The wood cutters removed all unmarked trees, left stumps shorter than eight inches, piled their slash, and promptly removed their wood.

In each growth plot, all leave trees larger than 3.5 inches in diameter were numbered and tagged 2 inches above breast height. Tree species, diameter, crown class, and clump density (1, 2, 3, or 4 members per clump) were recorded annually. Numerous cores from nearby trees, were studied to establish age and past stand history. The breast height age of dominant trees was 55 to 65 years.

Six growth plots and one control had data spanning 6 years.

These plots formed the basis for this part of the study.

Stand Structure and Species Composition

Basal area of the unthinned stands ranged from 165 to 230 square feet per acre. Thinning reduced these values an average of 41 percent:

<u>Plot</u>	<u>Basal Area per Acre Before Thinning (sq. ft.)</u>	<u>Basal Area per Acre After Thinning (sq. ft.)</u>	<u>Reduction (percent)</u>
1	165	102	38
2	194	110	44
3	208	125	40
5	230	141	39
6	206	136	34
7	<u>188</u>	<u>85</u>	<u>55</u>
Average	198	116	41
Control	209	209	0

To facilitate comparisons, all growth plots (each of which represented a stand) were combined into a composite stand. Before thinning, composite stand density and basal area levels averaged 659 stems per acre (Table 14) and 198 square feet per acre. These data emphasize the compactness of the hardwood stands. Ninety-year-old conifer stands on the Experimental Forest contain about 250 square

Table 14.--Composite stand tables before (B) and after (A) thinning

	- - - - - Trees per acre by diameter class (inches) - - - - -											
	4.0		4.1-8.0		8.1-12.0		12.1-16.0		16.1-20.0		Total	
	<B	A	B	A	B	A	B	A	B	A	B	A
Pacific madrone	4	0	52	4	27	9	6	6	1	0	90	19
Tanoak	46	0	231	14	99	50	38	34	1	1	415	99
California black oak	1	0	90	30	55	47	7	6	1	0	154	83
Total	51	0	373	48	181	106	51	46	3	1	659	201

feet of basal area, but only 270 stems per acre. After thinning, the average hardwood stand contained 201 stems per acre--a reduction of over 70 percent. The most striking reductions were in the 0 to 4- and 4 to 8-inch diameter classes.

Altogether, nearly 700 trees were removed from the growth plots. Examination of the freshly cut stumps revealed no evidence of heart rot. Young-growth stands of these species, if originating from seed or root crowns, are remarkably free of this infirmity.

In terms of crown classification, thinning removed the entire suppressed crown class, and part of the intermediate class, particularly of tanoak (Table 15). When calculated as a percentage of the composite stand, the proportion of trees in the codominant crown class doubled, and in the dominant class, tripled. Together, trees in these two classes constituted 79 percent of those remaining after thinning. As the before-thinning proportion of these two classes was only 34 percent, thinning provided a considerable improvement in stand structure.

Thinning also modified the species composition of the stand, favoring California black oak at the expense of tanoak and Pacific madrone. Species composition, in percent of the composite stand before and after thinning was:

<u>Species</u>	<u>Before</u>	<u>After</u>
Pacific madrone	14	9
Tanoak	63	50
California black oak	23	41

Table 15.--Crown classification of hardwood stands before (B) and after (A) thinning

<u>Species</u>	<u>Suppressed</u>		<u>Intermediate</u>		<u>Codominant</u>		<u>Dominant</u>	
	- - - - - percent of composite stand - - - - -							
	B	A	B	A	B	A	B	A
Pacific madrone	6	0	4	2	3	5	1	2
Tanoak	28	0	18	12	12	22	5	16
California black oak	4	0	6	7	8	20	5	14
Total	38	0	28	21	23	47	11	32

These changes reflect both the thinning rules and the relative number of well-formed trees in natural stands.

Changes in diameter class values further describe the thinning process. For each species, average tree diameter after thinning in every plot was much larger than its counterpart in the control (Table 16). Thinning favored the largest and tallest trees which in turn had the best form and straightest boles. This factor was mitigated, however, by the desire to have all three species represented in each growth plot. Even then, Pacific madrone was absent on two plots; trees were not present on one and of too poor a form to have economic potential on the other.

Analysis of tree diameter and number of stems per clump indicated that average tree diameter was similar whether 1, 2, 3, or 4 members per clump were present. This proved true for trees in the composite thinned plot both immediately after thinning and after 6 years.

Natural mortality on the growth plots for 6 years consisted of 8 trees or under 3 percent of the residual trees. It was fairly evenly divided among growth plots, crown classes, and diameter classes. No trends were apparent. Two California black oaks died from suppression on the most densely thinned plot (141 square feet of basal area). The other trees died from a root disease, probably Armillaria mellea. The overall effect of natural mortality on stand structure and species composition was small.

Natural mortality in the control differed markedly from that in the thinned plots. Twice as many trees or 9 percent of the stand

Table 16.--Differences in average stand diameter
by species in thinned plots and control

<u>Plot</u>	<u>Pacific madrone</u>	<u>Tanoak</u>	<u>California black oak</u>
- - - - - stand diameter (inches) - - - - -			
1	_____	11.6	10.1
2	12.3	11.3	9.2
3	11.2	9.3	8.9
5	10.3	11.1	9.1
6	_____	11.8	8.1
7	9.0	11.1	7.5
Control	8.7	7.5	6.6

died, all were California black oaks, and all died from suppression. Over 80 percent of these trees either were overtopped or had dead tops when the study began.

Diameter Growth

Diameter growth rates seem particularly appropriate as a descriptor of stand response. Trimble (1969) found that initial d.b.h. of northern red oak on a high site was highly correlated to diameter growth. In this part of the study, d.b.h. growth is discussed in relationship to: (1) species, (2) initial diameter in 4-inch classes, (3) crown class, (4) clump density, and (5) basal area.

In both the thinned plots and control, larger trees grew faster in diameter than smaller trees (Table 17). Larger trees, in general, have wider crowns, more crown volume, and more functional photosynthetic area.

On the thinned plots, and in the 4- to 8-inch diameter class, both Pacific madrone and tanoak grew faster than California black oak--reflecting the latter species reduced ability to function as a small tree in dense stands. By the time California black oak trees reach 8 inches in diameter, they grow faster than trees of Pacific madrone. This effect accelerated in the 12- to 16-inch class. Here, California black oak and tanoak were growing equally well. In the smaller diameter classes, tanoak was superior to the other species in adding width to its bole.

Table 17.--Comparative 6-year d.b.h. growth rates in thinned plots (P) and control (C) by species and diameter classes

	Tree growth by diameter class (inches)									
	4.1-8.0		8.1-12.0		12.1-16.0		16.1-20.0		All species	
	P	C	P	C	P	C	P	C	P	C
	- - - - - inches per tree - - - - -									
Pacific madrone	.50	.12	.61	.39	.78	.78	—	—	.64	.32
Tanoak	.68	.32	.91	.66	.96	.95	1.07	—	.90	.45
California black oak	.38	.26	.63	.52	.96	—	—	—	.57	.31
All species	.48	.26	.75	.53	.94	.83	1.07	—	.74	.36

In the control, small Pacific madrone and California black oak trees scarcely expanded in diameter in 6 years. All three species in the 8- to 12-inch category doubled their diameter growth rates over those in the 4- to 8-inch class. For Pacific madrone and tanoak trees larger than 12 inches d.b.h., diameter growth rates nearly equalled those of their thinned counterparts. Overall, the d.b.h. growth rate of each species in the control was about half that of each species in the thinned plots.

The relationship of d.b.h. growth to crown class is particularly revealing. Without exception, and in both thinned plots and control, the more favorably placed the crown, the better the diameter growth of the species (Table 18). Species differed in their response, however. For Pacific madrone and California black oak in the thinned plots, differences in growth rates were much smaller between dominant and codominant trees than between codominant and intermediate trees. For tanoak, the difference was greatest between dominant trees and those of the codominant and intermediate classes.

In the dense control, large differences in diameter growth rates of all three species developed between dominant trees and those with less advantageous crown positions. This suggests that once a tree in a natural stand becomes dominant, its ability to capture additional resources continues to expand, and thus a gap in diameter growth rate forms between crowns so placed and those of lesser position. Thinning however, aids codominant trees as well, and at least for Pacific

Table 18.--Relationship of 6-year d.b.h. growth rates to
crown class in thinned plots and control

<u>Species</u>	<u>Crown class</u>	<u>Thinned plots</u> --inches per tree--	<u>Control</u>
Pacific madrone	Dominate	.80	.85
	Codominate	.69	.40
	Intermediate	.38	.21
	Suppressed	—	.10
Tanoak	Dominant	1.04	.90
	Codominant	.86	.44
	Intermediate	.77	.48
	Suppressed	—	.28
California black oak	Dominate	.71	.48
	Codominate	.56	.29
	Intermediate	.27	.20
	Suppressed	—	.20

madrone and California black oak, the diameter growth-rate gap is greatest between the codominant and intermediate crown positions.

When considering the effect of clump density on diameter growth, the tendency is to think that individual trees will outgrow trees in clumps. In the thinned plots, this proved to be only weakly true--not enough so to make any real difference in predicting d.b.h. growth rates (Table 19). The finding that the diameter growth rate of clumps with four members exceeded that of two or three members, was more a function of the marking rules than any biological response to thinning. Specifically, in order to be retained as a clump of four, all trees had to clearly be exceptional in size and form. No wonder then, that trees in clumps of four, grew quite well. No trend of d.b.h. growth rate to clump density was discernible in the control.

Part of the reason for lack of correlation between clump density and d.b.h. growth rate is the wide range of diameters within a clump. For example, a random choice of a tanoak clump of three, indicated diameters of 11.4, 14.7, and 9.7 inches.

Growth of the different members of a clump tends to be inconsistent and unrestricted to tree size. One year, the smaller member will grow much more than the larger; the next year, the smaller member will grow a little more than the larger; the next, both grow the same; and the next, the larger grows more. Sometimes one member will scarcely grow for 2 or 3 years and the other spurts ahead. Then a reversal occurs and the slower excels. In a few clumps one member will consistently outpace all others. The prevailing pattern, however, is for

Table 19.--Effect of clump density on d.b.h. growth in
composite thinned plot (P) and control (C)
after 6 years

	Number of stems per clump							
	1		2		3		4	
	P	C	P	C	P	C	P	C
	- - - - - inches per tree - - - - -							
Pacific madrone	.5	.4	.4	.6	—	.2	—	.4
Tanoak	.8	.5	.7	.4	.6	.4	.9	.4
California black oak	.6	.4	.4	.7	.4	.0	.5	1.2
Combined	.7	.4	.7	.7	.6	.2	.8	.9

growth to accelerate on one member while the other(s) grows slowly, and then to alternate. In general, every possible combination of timing and amount of growth takes place on trees in clumps. And this holds true for all three species in both the thinned plots and control. A possible exception was California black oak in the control, however, as the largest member in the clump usually grew best, particularly if of the dominant crown class.

The practical significance of this finding is that 1 to 4 members per clump can be retained without loss of growth. Thus entire clumps of this number, can be left if so desired.

Thinning provided an opportunity to portray the various species response to different basal area levels. For Pacific madrone and tanoak, thinning to 85-110 square feet of basal area per acre allowed residual trees to grow best (Table 20). The d.b.h. growth rate for California black oak was best when the residual basal area was 85 square feet per acre. Overall, it appears that heavy thinning is best for stimulating diameter growth of these hardwood species.

Diameter growth rates of Pacific madrone, tanoak, and California black oak, taken together, were low relative to eastern oak species of comparable size and density, growing on comparable sites. Trimble and Mendel (1969) presented annual diameter growth rates in inches per tree (in parenthesis) for several oak species: northern red oak (1.3 - 1.7), chestnut oak (Quercus prinus L.) (1.1 - 1.4), and white oak (Q. alba L.) (0.9 - 1.1). Carvell (1969) noted individual northern red oaks to average between 1.29 and 2.08 inches of diameter growth per year.

Table 20.--Comparative 6-year d.b.h. growth rates by species
and residual basal areas

	Basal Area (square feet) - - - - -						
Species	85	102	110	125	136	141	209
	inches per tree - - - - -						
Pacific madrone	.57	—	.80	.62	—	.40	.32
Tanoak	1.14	1.14	.92	.86	.70	.73	.45
California black oak	.88	.66	.61	.53	.49	.51	.31
Total	.99	.91	.83	.66	.66	.56	.36

Timing and magnitude of release is of interest to silviculturists and land managers. But first the yearly growth patterns of each species in natural stands must be known. Accordingly, diameter growth in the control was calculated yearly for 9 years by species. Most trees increased in diameter at a rate commensurate with their size and crown class. This might be 0.1 inch every third year, 0.1 inch nearly every year, or 0.2 to 0.3 inches nearly every year. When diameter growth of the 24 fastest growing trees of all three species was examined, the growth pattern was more variable. Diameter growth varied from 0.1 to 0.3 inch per year irrespective of species or February-through-June precipitation.

In the thinned plots, some trees dramatically released immediately after thinning, others not until the third, fourth, or even fifth year. Some did not release at all, and others showed only a gradual improvement. Of the 33 fastest growing trees, the diameter growth pattern was highly variable. Typical variation was expressed by an 8.4 inch d.b.h. tanoak, single stem, that expanded in diameter each year after thinning:

<u>Year</u>	<u>D.B.H. increase</u>
1	0.3
2	0.5
3	0.3
4	0.4
5	0.2
6	0.3
7	0.2
8	0.1

The eighth year was dry with precipitation being only 42 percent of normal. As a whole, diameter growth of trees in the thinned plots varied from 0.1 to 0.5 inches per year.

Timing and magnitude of release in Pacific madrone, tanoak, and California black oak appears to be an unpredictable phenomenon. This is because of the alternating pattern of growth surge on trees within clumps, the effect of diameter and crown class, and possibly additional variation from February-through-June precipitation and epicormic branching.

Basal Area Growth

General relationships of basal area growth were investigated after converting tree diameters on the quarter-acre growth plots to basal area. All data were placed on magnetic tape and processed by computer. Output consisted of plot, species, and clump density groupings.

Gross basal area growth of all trees 3.5 inches d.b.h. and larger ranged from 2.00 to 3.52 square feet per acre per year for the six thinning treatments and control (Table 21). It was greatest in the uncut control and indicated no trend with residual basal area.

Net basal area growth was more a function of lack of mortality than of growth. Those plots with no mortality indicated the highest net growth rate. This is because the entire basal area (not just the periodic growth) of the dead tree is counted as a loss. Thus loss

Table 21.--Average annual and net basal area growth by residual basal area level and control (6-year basis)

	----- Residual basal area level (square feet)-----						
	----- Thinned Plots -----						Control
	85	102	110	125	136	141	209
	----- square feet per acre per year -----						
Gross	2.46	2.62	2.00	2.46	2.01	2.59	3.52
Mortality	.86	0	.43	0	.95	.37	1.16
Net	1.60	2.62	1.57	2.46	1.06	2.22	2.36

of even one tree amounts to a substantial subtraction from net basal area growth. And no ingrowth was present in cut plots and control to counter mortality. Because of these factors, no trend with residual basal area was discernible. There was some indication however, that 85 square feet of basal area was not enough to fully utilize the site.

On a gross growth basis, the high basal area growth of trees in the dense control would indicate that thinning does not pay. But the high losses from suppression reduced net growth below that of plots thinned to 102 and 125 square feet of basal area per acre. Death from suppression is a predictable phenomenon in the control, and will continue in the future. Death from disease, as in the thinned plots, is due more to chance than to residual basal area level. Thus from a growth standpoint alone, thinning does pay. When more of the study plots, especially those with low residual basal areas, have accumulated sufficient data, this fact should become more clear, as should the relationship between residual basal area and maximum basal area growth.

Cubic-Foot Volume Growth

Initial and 6-year cubic foot volumes for each tree were taken from the previously developed cubic-foot volume tables (0-inch top). Six-year volume growth data then were analyzed much as was basal area growth.

Gross cubic foot volume growth ranged from 70.4 to 93.3 cubic feet per acre per year in thinned plots and control (Table 22). Although volumes differed with residual basal area density, no trend to density was apparent after 6 growing seasons.

Mortality was less important in determining net cubic volume growth than it was for basal area growth. The two plots with lowest gross cubic volume growth had the highest mortality and hence lowest net growth. Average annual net cubic volume growth for the 6-year timespan ranged from 47.7 to 93.3 cubic feet in thinned plots and control. Net volume growth in the control was about 72 cubic feet per acre per year. The indication that too few trees occupied the plot cut to 85 square feet of basal area, was strengthened as gross and net volume growth ranked near-last and last, respectively, at this level. Other than this indication, it is still too soon to determine a relationship between cubic-foot volume growth and level of residual basal area.

Another indication of interest, and true of both basal area and cubic volume growth, was that the plot with the best growth had the most even growth contributions from all three species. For example, the 93.3 cubic feet per acre per year growth from the plot with 125 square feet of basal area showed species contributions to be: Pacific madrone, 25 percent; tanoak, 37 percent; and California black oak, 38 percent.

A comparison to eastern oak species reveals that Pacific madrone, tanoak, and California black oak, as a whole, grow quite well in terms of cubic-foot volume. Schnur (1937) found that even-aged, young-growth

Table 22.--Average annual and net cubic volume growth by residual basal area level and control (6-year basis)

	---- Residual basal area level (square feet) ----						
	----- Thinned Plots -----					Control	
	85	102	110	125	136	141	209
	----- cubic feet per acre per year -----						
Gross	70.4	87.5	80.7	93.3	73.3	81.7	93.0
Mortality	22.7	0	8.4	0	20.0	7.8	21.1
Net	47.7	87.5	72.3	93.3	53.3	73.9	71.9

natural stands of the five principal upland oak species (white, black [Quercus velutina Lam.], scarlet [Q. coccinea Muenchh.], chestnut, and northern red) averaged 43 cubic feet per acre per year on sites of similar quality. In the same general area, thinned stands of upland oaks added about 43 cubic feet per acre per year, net, when initial basal area was 90 square feet per acre (Dale 1972). Minckler (1967) found that pin oak (Q. palustris Muenchh.) produced about 50 cubic feet per acre per year when residual basal area was 94 square feet per acre.

Volume of natural California hardwood stands is of interest not only as an indicator of present productivity, but also as a basis for stand manipulation, growth, and yield (Fig. 52). When Pacific madrone, tanoak, and California black oak occur as stands in the Sierra Nevada, they contain a surprising amount of volume--4,090 cubic feet or nearly 43 cords of solid wood per acre (Table 23).

This average volume exceeds that of comparable oak stands. Schnur (1937) found that the composite yield of second-growth upland oak stands (all trees 0.6 inches d.b.h. and larger) on sites of comparable quality was nearly 2,600 cubic feet or 33 cords per acre. The volume of natural 48-year-old Appalachian hardwood stands on high sites that contain a high proportion of northern red oak, was about 3,500 cubic feet per acre (Trimble 1968).

Table 23.--Average cubic volume by species of natural and thinned
hardwood stands on high sites

Species	Natural		Thinned		Removed	
	cu. ft.	cords ^{1/}	cu. ft.	cords	cu. ft.	cords
Pacific madrone	638.4	6.7	277.4	2.9	361.0	3.8
Tanoak	2366.4	24.6	1460.9	15.2	905.5	9.4
California black oak	1084.8	11.3	908.3	9.5	176.5	1.8
Total	4089.6	42.6	2646.6	27.6	1443.0	15.0

^{1/} Utilization to a 2-inch top, and containing 96 cubic feet of solid wood.



Figure 52.--Dense young-growth hardwood stands in the Sierra Nevada yield a large volume of wood for product and energy uses.

EPICORMIC BRANCHING

Branches of Pacific madrone, tanoak, and California black oak in dense stands prune naturally at an early age. Consequently, well-formed trees generally have high potential for value growth. In California black oak, however, epicormic branching threatens high values.

Epicormic branching is a sudden and striking negative growth response to thinning (Fig. 53). Not only are these branches a degrade in themselves, but if they persist, knots develop and log and lumber quality are reduced. This is contrary to most management goals of producing high-value sawlogs and veneer logs in the shortest possible timespan.

The origin of epicormic branches in oak is mostly from dormant buds. These probably are from accessory buds formed at nodes on the current year's shoots. As such, they originate from or near axillary buds. But whether as accessory buds or axillary buds, both connect directly to the pith by vascular traces. Epicormics may arise from adventitious buds as well, but apparently are much less numerous.

Epicormic branches on California black oak in fairly dense stands on the Experimental Forest range in length from 0.1 to 3.0 feet. Their number seems to be in a constant state of flux. On a given tree, most will be alive and healthy, but some will be dead, some dying, and a few will just be bursting forth. In the environment created by thinning, they appear to be shortlived.



Figure 53.--Prolific epicormic branching has lowered the value of this otherwise well-formed California black oak.

Information on the propensity of Pacific madrone, tanoak, and California black oak to produce epicormic branches is scanty. Edwards (1957) reported that boles of California black oak "feathered" profusely after the stand was opened up by thinning, fire, or snow breakage. No information on the other two species is available although they are noted for not epicormic branching. On the growth plots, however, a few tanoaks produced a few epicormic branches. Almost always these were near healing branch scars on rapidly growing trees. None persisted for more than a year or two. No epicormics were revealed on Pacific madrone.

Trees in the six thinned growth plots and the control were ideal for quantifying the degree of epicormic branching in these species. The residual trees were growing at different density levels, were of different diameters, and were subject to different degrees of exposure. In a few instances thinning created small openings. Trees in the growth plots that faced these openings were designated as "border" trees.

Six to nine years after thinning, the epicormic branching study was performed. Shortly after, the boles of California black oak were observed to branch more profusely if injured, of small diameter, of a certain bole face, of the intermediate crown class, or bordering an opening. And more epicormics appeared with height up the bole. The effect of residual basal area was unknown. Trees with large numbers of dead epicormics also had large numbers of living branches. Consequently, a working hypothesis was that epicormic branching of this

oak was a function of these observations and variables.

Epicormic branches or clusters of branches were counted on each cardinal bole face of each California black oak. Short branches in a cluster were counted as one branch. Each cardinal bole face consisted of a quarter of the bole circumference centered around a cardinal direction. For example, a north face extended from northeast to northwest, a west face from northwest to southwest, etc. In addition, each bole face was divided into 8-foot segments (logs) beginning at stump height (12 inches). Two logs were defined on each tree.

The decision to concentrate on the basal 16 feet of tree bole was based on a report by Trimble and Mendel (1969). These investigators found that the rate of value increase was greatest when quality of the butt log of three eastern oak species was increased one grade by thinnings or improvement cutting.

Each bole face was outlined by two men each placing an 18-foot long slender aluminum rod at a face boundary (Fig. 54). A third crew member counted the epicormics. Breast height diameter, crown class, direction of face, inner or border tree, and exposure of border, plus log number and number of living and dead epicormic branches were recorded for each tree.

Sample size consisted of 93 inner trees on the growth plots with no open face, and 25 trees that bordered an opening and had one or more open faces, as well as 71 trees in the control.



Figure 54.--Narrow aluminum rods define a "face" for counting epicormic branches on a California black oak.

The number of epicormic branches in the control indicates the degree of epicormic branching in California black oak under natural conditions:

	<u>Living</u>	<u>Dead</u>
base log	0.8	0.4
log 2	1.6	1.7

Many of these epicormics grew on only a few trees, and these were dying from suppression. Suppression-caused death in this oak is from the top down. As dieback progresses, the number of epicormics increases dramatically in the basal 20 feet of bole. Eventually, these also die, and thus the relatively high number of dead epicormics in log 2 in the control. (A tree was not counted as dead until dieback had progressed below breast height.)

On the growth plots, inner and border trees produced many more epicormic branches:

	<u>Living</u>	<u>Dead</u>
base log	5.5	0.8
log 2	7.5	0.9

In the control, the mean number of living epicormic branches in the basal 16 feet of tree was 2.4 and in the thinned plots 13.0, or 5.4 times more living epicormics resulted from thinning.

These results also show that epicormic branching increased with height above ground. The mean number of living epicormics per tree for each log in each plot was compared by paired "t" test for inner trees and border trees. Significantly more epicormics occurred in

$\log 2$ ($p = .05$). A similar test confirmed that the mean number of epicormic branches per tree (both logs combined) was significantly higher on trees bordering openings than those in thinned stands ($p = .05$). Moreover, there was a distinct relationship of bole face on border trees to the opening. For example, if the south face of a tree was oriented toward the opening, it averaged more living epicormics than any other bole face:

	----- Bole Face -----			
	<u>North</u>	<u>South</u>	<u>East</u>	<u>West</u>
Border on South	2.8	10.1	4.8	7.1
Border on East	3.5	4.2	11.3	2.5
Border on West	6.0	6.5	8.0	9.5
Border on North	----- no openings -----			

Analysis of variance was used to test for significant differences in number of living epicormics among bole faces, diameter classes, and the interaction of these two variables. Trees in both thinned stands and on borders indicated that the number of living epicormics on each bole face differed significantly ($p = .05$). If the tree produced epicormic branches, it was more likely to produce them on south and east faces than on north and west faces (Tables 24 and 25). Perhaps this is an effect of the southerly aspect on which they grew.

When trees in the thinned stands were grouped by 4-inch diameter classes, the number of living epicormics differed most significantly among them ($p = .01$). Larger trees put forth the fewest epicormic branches, and those in the 8.1- to 12-inch class, the most (Table 24).

Table 24.--Number of living epicormic branches on
basal 16 feet of tree by bole face and
diameter class. Inner trees

Bole Face	----- Diameter Class -----			Total
	3.5 - 8	8.1 - 12	12.1 - 16	
	----- number -----			
North	0.4	0.9	—	1.3
South	1.0	2.0	0.4	3.4
East	0.9	2.0	0.3	3.2
West	<u>0.8</u>	<u>1.2</u>	<u>0.1</u>	<u>2.1</u>
Total	3.1	6.1	0.8	10.0

Table 25.--Number of living epicormic branches on
basal 16 feet of tree by bole face and
diameter class. Border trees

Bole Face	----- Diameter Class -----			Total
	3.5 - 8	8.1 - 12	12.1 - 16	
	----- number -----			
North	0.6	1.5	1.8	3.9
South	1.7	3.0	1.9	6.6
East	2.6	4.0	2.9	9.6
West	<u>0.7</u>	<u>1.7</u>	<u>1.6</u>	<u>4.0</u>
Total	5.6	10.2	8.2	24.1

Diameter class had no effect on number of living epicormics on border trees (Table 25). Obviously, the powerful effect of direct sunlight on a given bole face overrides the effect of tree size. For both thinned trees and border trees, the interaction of bole face and diameter size class was of no significance.

In the control, 89 percent of the sprouts occurred on trees in the 3.5- to 8-inch diameter class. And each bole face averaged about the same number of epicormics.

When rated by crown class, mean number of living epicormic branches in the first two logs of each tree varied consistently among control, inner trees, and border:

	<u>Dominant</u>	<u>Codominant</u>	<u>Intermediate</u>
Control	1.2	2.6	3.3
Inner trees	8.5	10.5	11.4
Border	22.8	25.8	25.0

No matter where growing, dominant trees had fewer epicormic branches than trees in other crown classes. Trees occupying the intermediate position in the stand generally produced the most epicormic branches.

Another test examined the trend of epicormic branching to residual basal area. Number of epicormic branches per log was plotted against residual basal area of the thinned stands. Plotting also was by inner and border trees. Within the residual basal area range of 75 to 150 square feet per acre, no relationship of epicormic branching to basal area of inner or border trees was exhibited. In the control, however, where basal area was 209 square feet per acre, 52 percent of the inner

California black oaks showed no evidence of epicormic branching. Such trees were independent of diameter size, but dependent on crown class. For example, 79 percent of the trees in the dominant class did not produce an epicormic branch, but only 21 percent of the intermediate trees lacked epicormics. Of the inner trees in the thinned plots, only 6 percent were devoid of epicormics and these were of the dominant and codominant classes.

Injured trees were observed to produce many epicormic branches. Sometimes, the weight of snow in the crown of a slender tree will cause it to bend in a great arc. The entire bole usually "feathers" when this happens. Another way to insure a plethora of epicormics is to scorch one side of the bole--the opposite side will be covered. Sunscalding leads to similar effects.

The question of buildup, decline, and persistence of epicormic branches in California black oak will be answered in a later study. Only subjective material is available now. While the number of epicormic branches increased over fivefold as a result of thinning 6 to 9 years ago, it appears that the number of epicormics now is static or declining. Tree crowns are expanding and closing, creating a less favorable environment for epicormics. Another factor affecting the number and persistence of epicormics is the cynipid gall wasp. Just as this wasp attacks terminal and lateral twigs of sprouts, so it also infests terminals of epicormic branches. Some branches are killed outright; others are shortened and malformed (Fig. 55). The overall effect is to hasten the epicormic's demise.

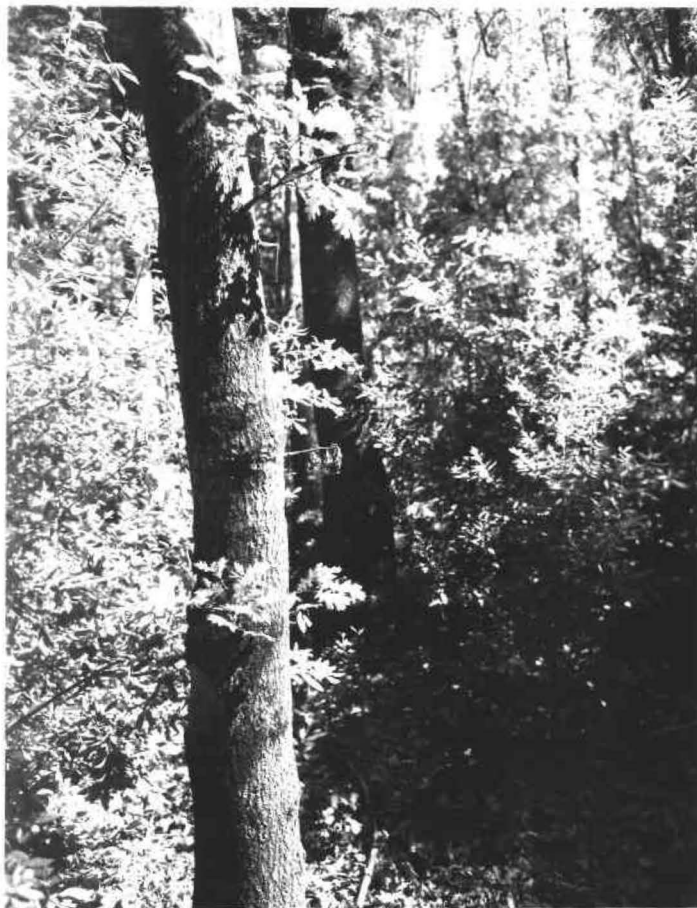


Figure 55.--Epicormic branches on a California black oak deformed by cynipid gall wasp. Note dead epicormic branch in center of photo and deformed terminals of upper branches.

The question of epicormic branching being governed by genetic influence cannot be answered without sampling other local races or ecotypes. It does appear, however, that the race of California black oak on the Challenge Experimental Forest has a high propensity for epicormic branching.

SUMMARY

Accurately measuring California hardwoods and estimating potential yield from them is more difficult than for conifers. Hardwood height and volume vary appreciably with a number of physiographic and biological factors. Tree form varies when trees are in open or closed stands, on different slopes and aspects, in different portions of a given slope, and if of sprout origin. Development of volume tables for Pacific madrone, tanoak, and California black oak to three different utilization standards emphasized the difficulty of defining height-diameter-volume relationships for these species.

Nevertheless, the job was done and now bole volumes to 0- and 4-inch tops, cubic measure, and to a 4-inch top, Scribner board foot measure, are available for trees on sites of high quality. Because the sample was large, and the measurements carefully taken with an accurate instrument, the volume tables for the species and utilization standards tested are quite accurate in terms of aggregate differences between predicted and actual volumes, as well as average bias of the prediction equations on which the volume tables were based.

Height-diameter and bark thickness-diameter relationships also were defined, and prediction equations formulated for height-diameter. Further analysis indicated that Pacific madrone averaged 4 to 9 feet shorter than tanoak and California black oak in the dominant, codominant, and intermediate crown classes. Tanoak and California black oak were of similar height in these classes.

Based on a common mean average height and common mean average age, a site index value for the three species combined was found to be 60 feet at an index age of 50 years.

To better understand the growth response of existing 60-year-old trees of essentially stump sprout origin, 12 quarter-acre circular growth plots were randomly installed on the Experimental Forest. Residual basal areas ranged from 60 to 150 square feet per acre. Information from the annual measurement of 7 of these plots with 6 years of data formed the basis for diameter, basal area, and volume growth analyses.

Because trees in natural stands often are of sprout origin, marking rules for leave trees are extremely difficult to express. Consequently, this thinning came to resemble a crown thinning--that is, one that would provide room for expansion of the crowns of residual trees. This thinning also favored retention of the largest and best formed trees of the dominant and codominant crown classes.

In the course of thinning, freshly cut stumps were examined for evidence of heart rot. None was found. Young-growth sprout stands resulting from natural disasters of fire, insects, and storm, or from short stumps cut by man have a very low incidence of rot.

In the thinned stands, diameter growth rates of trees 4 to 20 inches d.b.h., for 6 years, averaged 0.57 to 0.90 inches per tree per year. Tanoak grew faster than California black oak or Pacific madrone. Larger California black oaks (over 12 inches d.b.h.) equalled the diameter growth rate of tanoak, but smaller trees grew much more slowly. Further examination showed tanoak to grow best in all crown classes in both the thinned growth plots and the unthinned control. For all species, dominant trees grew best with codominant trees a close second.

Additional analysis indicated that diameter growth rates were independent of clump density, at least when members numbered up to four per clump. Whether 1, 2, 3, or 4 members per clump, diameter growth averaged about the same per member over the 6-year study. This is because growth is distributed fairly evenly on all members of the clump. One member may excell in growth for a year or two, but then another member, and finally another, excells. The significance of this finding is that entire clumps of up to four stems, if of reasonable form, can be retained with all having equal likelihood of growth.

Timing and magnitude of release of individual trees was analyzed closely. Some trees were found to release immediately after thinning,

some released years later, and still others released not at all. Many simply showed a slow, steady improvement in rate. The release response of Pacific madrone, tanoak, and California black oak apparently is an unpredictable phenomenon. Such influences as the alternating pattern of growth on trees in clumps, the effect of crown class and tree size, as well as species mix, makes this so.

Basal area growth also was quantified, and ranged from 2.00 to 3.52 square feet per acre per year. It was best in the control and indicated no real trend with residual basal area. Both basal area and diameter growth were less than that reported from eastern oak stands of comparable age on sites of similar quality.

Net cubic volume growth, however, was considerably higher than for eastern oaks on comparable sites. It ranged from 48 to 93 cubic feet per acre per year. Although no real trend of growth to residual basal area was revealed, indications were that 102 to 125 square feet of basal area per acre was best. When more growth plots accumulate more years of data, this relationship will become better defined.

Two other points are worthy of mention. The first is that net volume growth was best if all three hardwood species were fairly evenly represented in the stand. It could be that stands of such mixtures are best to maximize growth. The second point is that where these mixtures occur, stands contain a large volume of fiber--4,090 cubic feet or nearly 43 cords of solid wood per acre. In a world that is becoming increasingly short of energy, stands such as these are worthy of further investigation.

Volume considerations alone, however, are only half the decision when managing hardwoods. Quality of wood is the other half. All three of the hardwood species studied prune naturally at an early age in dense stands. Pacific madrone and tanoak rarely put forth epicormic branches after thinning or damage to the bole.

California black oak does put forth epicormic branches; sometimes just a few, sometimes a prolific number. A study of epicormic branching on this oak is necessary to evaluate this degrade of log quality, and to ascertain what factors influence its presence.

Living and dead epicormic branches on residual California black oak trees in the six growth plots and control were counted 6 to 9 years after thinning. This quantification was subdivided into the first two 8-foot logs above stump height and by cardinal bole faces.

Three different populations were recognized and compared. Each had a representative sample. These were inner trees on the growth plots (sample was 93 trees), border trees on the growth plots (25 trees), and the control (71 trees).

Based on the control, the number of living and dead epicormics before thinning was 2.4 and 2.1 per basal 16 feet of tree, respectively. Nearly 90 percent of all living epicormics occurred on trees in the 3.5- to 8-inch diameter class irrespective of bole face. Trees in the dominant crown class averaged 1.2 epicormics per tree, which was about one-half of those on codominant trees and one-third of those on intermediate trees. And 52 percent of the trees showed no evidence of

epicormic branching. Of these, dominant trees showed the least inclination to branch followed by trees in the codominant and intermediate crown classes.

Number of living epicormics per basal 16 feet of tree in the growth plots averaged 13, or over 5 times as many per tree as in the control. This is a direct consequence of thinning at 85 to 150 square feet of basal area per acre.

A number of factors were hypothesized as affecting the propensity for epicormic branching. These were injury, height on bole, bole face, bole diameter, border trees, crown class, and residual basal area. Various analyses indicated that all the above except residual basal area significantly affected the number of epicormic branches on young-growth California black oak. Residual basal area probably is more instrumental in governing persistence of the epicormics rather than their initiation.

Those variables that indicate tree vigor were particularly significant as quantifiers of the number of epicormics initiated. Analyses of diameter size and crown class clearly showed that dominant trees greater than 12 inches d.b.h. put forth fewer epicormic branches on that part of the bole where the greatest volume and value accrue--the lower 16 feet. These, then, are the trees the forest manager will want to select as crop trees.

The consistently and significantly higher number of epicormics on nearly every bole face in all diameter classes on border trees denotes

the problems associated with "edge." The need to maintain a low border-to-cut ratio is obvious. Thus, openings within a California black oak stand should be kept small.

That epicormic branching is a problem in the management of California black oak is irrefutable. But it can be minimized by compromising between maximum growth and bole quality. The best compromise can be obtained by thinning to 100-125 square feet of basal area per acre. At this level, dominant and codominant trees of low epicormic branch potential will predominate and most intermediate and all suppressed trees will have been eliminated. Except for a few guard trees sheltering crop trees, those trees that remain are the largest trees and probably among the fastest growing, have the best form, the fewest existing epicormics, and the lowest potential for new epicormics. And they are the best phenotypes in the stand. Thinning to this level of stocking is recommended for initial cutting in young-growth hardwood stands on high sites.

From these relationships and those from the chapter on sprouting, a method for managing stands of these hardwood species evolves. It essentially is a 2-stage shelterwood. The first stage is similar to that in this study: thinning the stand to a recommended basal area level and leaving the largest and best trees. Pruning at an early age should be considered as it could provide quality wood at low initial cost.

The second stage involves the sprouts. They are in-place and established--waiting for overstory removal to burst forth. Mortality has occurred and only the most vigorous stems in each clump remain. These usually are of good form as well, because they are reaching for sunlight and are forced upward by competition. This competition tends to minimize lateral branch development. Along with the sprouts are a few straight and slender trees from seed. These should be recognized and care taken to keep them undamaged. Eventually the sprouts become the overstory, are thinned, and the process is repeated. At all times the best formed and fastest growing trees are retained.

When to remove the overstory is partly an economic question based on growth rate and the quality and quantity of the wood. Seldom should the overstory be retained for over 80 years, however, as the incidence of heart rot increases rapidly beyond this age. This is true at least of the California black oak component of the stand (McDonald 1969).

V. SPECIES ADAPTATION AND STRATEGY

As arborescent members of the unique group of plants called "broad sclerophylls," Pacific madrone, tanoak, and California black oak possess a number of adaptations that are common to most of the species in the group. In this part of the study, some of these collective adaptations are examined in greater detail, and discussed in terms of the individual species' strategies to adapt and survive in an ever-changing environment. Material for this closer examination of collective adaptation is based on the original data in the preceeding sections.

The Pacific madrone-tanoak-California black oak community was present as a community along with other species as long as 20 million years ago. In fact, Cooper (1922) lists 9 of the 13 dominants in the Oak-Madrone forest of today as being represented in the Mascall flora of the upper and middle Miocene epoch. Thus these trees represent ancient species that have survived in spite of cataclysmic vulcanism, glaciation, uplifting, subsidence, and drought.

The Miocene equivalents of Pacific madrone, tanoak, and California black oak, are well represented throughout the range of the Mascall flora. The fossil progenitors of today's species extended from eastern Washington throughout eastern Oregon and southwestern Idaho into northwestern Nevada. In California, fossilized Miocene counterparts have been found to the north (Pitt River), south (Tuolumne County), and southwest (Santa Rosa and San Pablo)

(Chaney 1925). By far the most relevant placing of these species in the Miocene epoch is the finding of their fossilized remains at Remington Hill--a middle-elevation Sierra Nevada site a relatively few miles southeast of the Experimental Forest (Axelrod 1973).

Thus it is likely that the area once occupied by the community, of which these species were a major part, has shrunk considerably from former times (Axelrod 1958; Whittaker 1961). This area and the regressive successional changes in the flora that have occurred are a consequence of progressive aridity which has been taking place throughout much of the Cenozoic era. Logically then, these species have had sufficient time to develop a polymorphic gene base--one that is especially adapted to aridity.

A thorough gleaning of the literature reveals 14 collective adaptations of broad sclerophylls for survival in arid and harsh environments or where major disturbance is frequent. These are:

(1) Hard, thick, flat, leathery leaves that possess transpiration inhibiting mechanisms such as sunken stomates, pubescence, and waxy coatings (Cooper 1922),

(2) A deep and extensive root system (Lewis & Burgoyne 1964), and more biomass in roots than in shoots (Hellmers et al. 1955),

(3) The ability to withstand severe moisture stress (Waring 1969),

(4) The ability to photosynthesize throughout the year in spite of low internal moisture, high temperatures, and low CO₂ intake levels (Harrison et al. 1971),

(5) The ability to minimize cuticular water losses by having thick cuticular tissue on leaves and twigs (Cooper 1922),

(6) A high respiration cutoff threshold that leaves the plants adequate energy and fluid reserves to maintain life functions (Mooney and Dunn 1970),

(7) The ability to minimize overheating during high radiation loads by having small leaves that possess a relatively large amount of water conduction tissue relative to total blade tissue (Kummerow 1973),

(8) Toxic substances in plant leaves and stems that inhibit herbaceous competition (McPherson and Muller 1969; Hanes 1971),

(9) Ability to persist and grow on soils of low nutrient availability (Mooney and Dunn 1970),

(10) The production of copious pollinator-attracting inflorescences and heavy seed crops nearly every year,

(11) Seeds which stay viable in duff and surface soil layers for scores of years (Quick 1956),

(12) The ability of seeds to break dormancy and germinate after severe disturbance when competition has been reduced greatly (McDonald 1976),

(13) The propensity to trap moisture on leaves and stems and transport it by stemflow to the ground below,

(14) The ability to sprout quickly and vigorously from the root crown, and thus get "the jump on" competing vegetation (Mooney and Parsons 1973).

The ability to produce large seed crops frequently, or to produce seed each year, insures that at least some seed of the species will fall into microsites favorable enough to increase the chances of the seed becoming trees.

Pacific madrone, tanoak, and California black oak produce huge seed crops frequently. And a large seed crop is just that--one 15.7-inch diameter Pacific madrone produced 2.15 million seed and a 16-inch d.b.h. tanoak had the equivalent of over a million seed per acre beneath it. California black oak also produces bumper seed crops, but not of the frequency or magnitude of Pacific madrone or tanoak in young-growth trees. Another indicator of the importance of seed to a species is the age at which it is first produced. In Pacific madrone and tanoak this is age 4 and 5 respectively. Not until age 30 or so does California black oak produce much seed in narrow-crowned trees.

Obviously, a significant part of these trees' energy is devoted to the production of reproductive material. The theoretical reason for this is clear enough, but the means for accomplishing regeneration from seed are not as clear. Part of this paradox is that the primary reproductive mode of all three species is by sprouting, not by seed. Seed, however, by virtue of its tie to animal and bird disseminators, allows the species to invade and occupy new areas; the sprouts keep the species on previously occupied ground.

In the case of the oaks, acorns fall directly beneath the trees and do not bounce or roll very far from them. The environment beneath

the trees is characterized by deep shade, heavy litter accumulation, and a generally more moist, humid regime.

For tanoak, this is a near-ideal environment. Acorn germination is good and seedling survival is high. Over time, vast numbers of advance seedlings and seedling-sprouts accumulate and persist on the forest floor. Their height growth, however, is slow.

Seed of Pacific madrone, either as seed alone, or as seeds in berries, also falls into this cool moist environment. But it is anything but ideal for seedling propagation. Damping-off and root-rotting fungi abound, and together with slugs and sometimes drought, form a deadly combination from which few, if any, seedlings survive.

Another factor affecting Pacific madrone seedling establishment is the presence of toxic substances from leaf, litter, and bark. These gave rise to high inhibition values in laboratory experiments as well as lessened herbaceous plant populations beneath tree crowns (Del Moral and Cates 1971). And stemflow could be an important mechanism of toxic transport in this smooth-barked species. The chance of autotoxicity to germinating seeds or young seedlings is quite high.

Still another factor is the negative effect of exfoliating bark and fallen leaves. Both fall to the ground in July and smother tiny new seedlings (Pelton 1962). Shedding leaves at this time coincides with the onset of moisture stress from summer drought. But shedding bark and baring the smooth stem saves no water and might even increase its loss. Smothering by exfoliated bark seems to be yet another

means of lessening competitive vegetation beneath tree crowns.

California black oak acorns germinate well in the cool shady environment beneath parent trees. But too much shade is present and seedling survival is poor. Eventually however, the living crown of parent trees retreats up the bole and light levels increase on the forest floor. By then, the parent tree crown has expanded, acorn production has increased, and seed falls into a habitat more conducive to seedling survival.

It should be noted, however, that even in the cool shady habitat beneath a dense stand, acorn survival of both tanoak and California black oak is low. For example, not one seedling resulted from the fabulous acorn crop beneath the 16-inch d.b.h. tanoak tree. This was because late afternoon sunlight slanted in under the tree and "cooked" the newly fallen acorns. Acorns are extremely sensitive to temperature and moisture content. And not just high temperatures either--acorns also freeze in winter if not covered by insulating leaves or soil. It is safe to say that exposed acorns, no matter where they fall, rarely result in seedlings. Lethal temperatures, low moisture content, and consumers see to that.

The reproductive strategy of Pacific madrone, California black oak, and to a certain extent, tanoak, is two-fold: (1) to discriminate either directly or indirectly against its own reproduction, and to favor sprout production in occupied areas, and (2) through a host of bird, rodent, and animal consumers (and seed disseminators) to favor more long range seed dissemination by them.

For Pacific madrone, dissemination by birds is near-ideal. The colorful fleshy berry is attractive, nutritious, and apparently tasty. But it inhibits germination of the seeds within. After digestion by the bird, however, the berry no longer is a problem. With luck, the bird has flown well beyond the parent tree and deposited the seed in an area of bare mineral soil. If germination conditions are not right, the small hard seed gets buried in the upper soil and duff, and becomes dormant. Here it stays viable for scores of years. If conditions are right, cool temperatures and adequate moisture induce after-ripening and dormancy is broken. The seed germinates and prospers in the bare mineral seedbed free of fungi, slugs, and toxic metabolites.

Long-term seed dormancy and viability as in Pacific madrone are to the species advantage. They enable it to "wait out" times of unfavorable circumstances--times when germination would mean certain loss of seed. Such times are those when vegetative competition is intense and the site is covered with organic material. Gross disturbance, which decimates competition, removes the organic covering, and bares the soil. It also places the seed near the soil surface where increased levels of light, temperature, and oxygen combine to stimulate germination.

For tanoak and California black oak, dissemination by birds and squirrels also can be advantageous--placing acorns and resultant seedlings in a more free-to-grow environment than whence they came.

But why so many seeds? One possible strategy is to keep the seed disseminating agents closeby. This means providing them with shelter and food, year after year. Rather than extravagance, it is a good investment for the tree species to provide sustenance for a continuous population of bird and animal associates.

There also is a long-term advantage for maintaining the bird-animal-tree community. In the past it was the birds and animals that moved when the climate first changed. Likely they took the seeds of these tree species with them for mutual benefit. Eventually, the climate may change again, and again these associates will extend the species.

Those seeds that survive through the winter to produce seedlings, also benefit from various survival strategies. Acorns of both tanoak and California black oak provide a good example.

Germination of acorns is a highly variable phenomenon. Microclimate, depth buried, amount of mold, and damage from insects all influence when the hypocotyl appears above ground. In general, the germination period is strung out for three or four months. This increases the chance for emergence to occur at an opportune time and ultimately, for the emerging seedling to survive.

When acorns fall, most end up resting on their sides. Others become oriented vertically, and still others repose at various angles to the ground. Some roll into little depressions and come to rest with their pointed end up. These acorns with reversed polarity

germinate much earlier than those resting on their sides or having their pointed end down. Early germination can help the seedling get off to a strong start by keeping it in adequate soil moisture for a longer period. Late spring frosts, however, can counter this advantage. Because acorn position partially governs speed and completeness of germination, and because acorns lie at all positions in the forest, the timing of hypocotyl emergence inevitably will be variable, and at an opportune time for at least a few individuals.

When an acorn germinates, the radicle emerges first and grows straight downward. As the energy reserves of the large and nutritious cotyledons are high, they can fuel this downward development for up to 30 days before the hypocotyl cleaves the soil surface and begins the manufacture of photosynthate. But 10 to 30 days of root growth help the plant to get and stay in a region of adequate soil moisture, and hence is a powerful survival strategy.

Once the hypocotyl and tender new leaves emerge above ground, they are subject to depredation, consumption, and climatic extremes. In the open plantation, tanoak is subject to unaccustomed climatic stress. Even though site quality is extremely high, and site preparation has created a competition-free surface, light and temperature apparently are at the mortality threshold for this species.

Young tanoak seedlings are strong and robust and though only 3 to 4 inches tall, are 7 or 8 times that length below ground. But given the slightest excuse, the plant opts for multiple stems, rather

than a single stem. And it can put forth multiple stems as early as 7 days after emergence and freezing injury. Drought or injury also cause development of multiple stems. Why multiple stems? Mutual shading is the logical reason. But this is not a complete answer either.

Dieback on shoots in young sprout clumps commonly occurs and is of all magnitudes from slight to complete. Take a normal, healthy tanoak seedling in an opening, provide it with shade, and it will grow taller than normal and lean away from the shade (Fig. 56)--seemingly in a hurry to get into the sunlit and stressful environment where it probably will dieback or even die completely (Figs. 57 and 58). Perhaps the species' strategy is to sacrifice endless numbers of seedlings for a few successful seedlings that find a favorable microenvironment and quickly capture the site (Fig. 59).

Early growth of seedlings disproportionately favors seedling roots over shoots. California black oak provides a good example of this phenomenon and the competitive value it gives the species.

As noted earlier, the radicle grows straight down for 2 to 4 weeks before plant parts appear above ground. On high sites and in favorable microclimates, the seedling root often reaches a length of 9 inches in 28 days, and 30 inches at the end of the first growing season. Lateral root development is practically nonexistent--the longest lateral on a 30-inch taproot being only 1 inch (Fig. 60).



Figure 56.--By being taller than normal and leaning away from the shingle, this year-old tanoak seedling seems to be striving for the dubious value of direct sunlight.



Figure 57.--This 4-year-old tanoak seedling now has 15 stems and has suffered from partial dieback at least once.



Figure 58.--After the last dieback, only a few leaves at the base of the plant remained green. These and the root stock are now dead at age 6.



Figure 59.--This 6-year-old tanoak seedling has found a favorable microenvironment (probably an old root channel) and is "shooting" skyward.

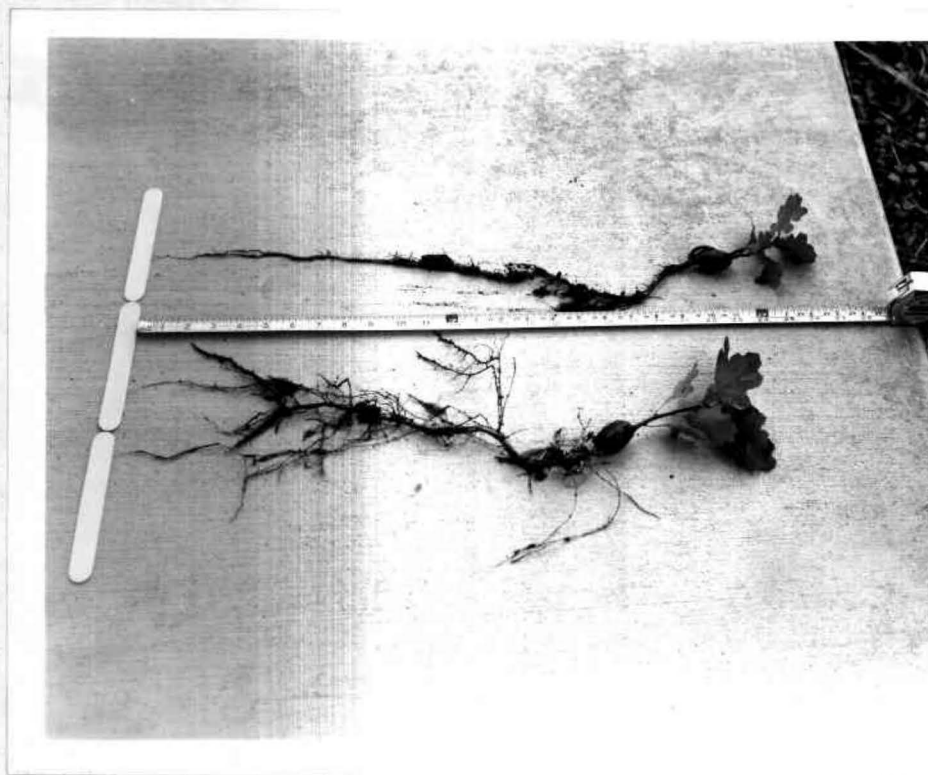


Figure 60.--Root-shoot development in the laboratory of a 105-day-old California black oak seedling. The first growing season is not yet complete.

Under favorable conditions, this downward extension of roots continues for years, and not until the root system is deep and well formed does extensive above-ground development take place.

In less favorable microclimates, and particularly those with too much shade, California black oak develops special adaptations for persistence. The seedlings or more accurately, advance seedlings, develop a surprising degree of adaptation to shade. Even when death is imminent, the advance seedling persists. It will undergo dieback, or even skip a growing season, at least above ground. Still it remains viable. This could be because the thickened rootstock functions as a food-storage organ (Fig. 61). At any rate, California black oak advance seedlings, with the majority of their biomass in roots, are able to persist for years in an unfavorable environment--biding their time until disturbance eliminates their competitors and frees them to resprout and capture the area.

It has been stated many times that plants on harsh and infertile sites tend to develop adaptations which allow them to tolerate low nutrient levels. And regardless of site quality, they eventually lose their ability to respond when added nutrients become available. For California black oak, this was not so. Levels of nitrogen and phosphorous in the plant increased significantly after fertilization. And, except for potassium, were comfortably above poverty levels at the time of maximum nutrient usage.

For tanoak, however, acquisition of adequate nutrients was much more difficult. During the period of maximum nutrient stress,

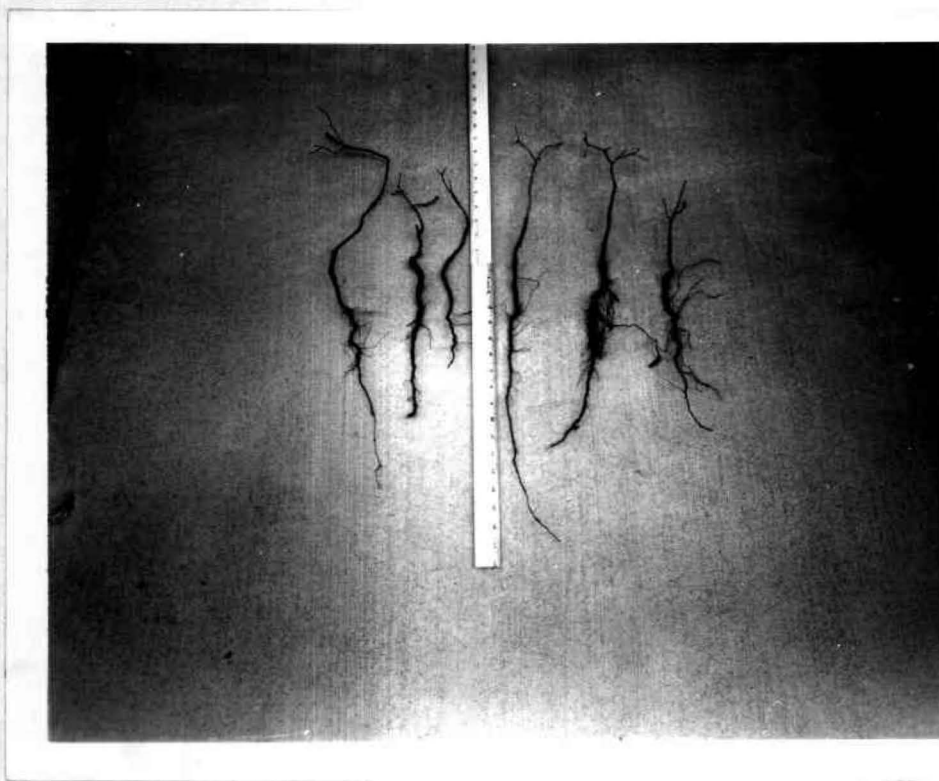


Figure 61.--Thickened rootstocks from California black oak advance seedlings in a deep-shade environment.

nitrogen, phosphorous, potassium, and calcium were all near poverty levels for plants of this species. Fertilization with nitrogen and phosphorous aided in plant nutrition, but not nearly as much as when extra water was provided as well. This water apparently facilitated nutrient entry into the plant as well as translocation and assimilation. Tanoak then, is not as efficient as California black oak in nutrient utilization, possibly because it is less efficient in its use of water.

Quantification of plant moisture stress in seedlings and sprouts of Pacific madrone, tanoak, and California black oak revealed evidence of a most interesting survival strategy. This apparently is a combination of (1) ability to photosynthesize efficiently at very low light levels, (2) ability to undergo high moisture stress for long time-spans, (3) possession of a remarkable fail-safe mechanism that reduces respiration in spite of reduced transpiration and high temperature and light loads, and (4) the ability of roots to efficiently gather moisture and recharge the plant at night.

As the plant must photosynthesize to manufacture the necessary substrate, the best time for it to do so is early in the morning when all tissues have rehydrated, temperatures are coolest, and light loads are low. Even on a hot day at the end of a long dry summer, predawn moisture stress of sprouts was quite low for all species (Table 26). Root systems efficiently recharged the plants with water.

Because plant moisture stress in both sun and shade plants increased rapidly from first light in the morning, nearly all

Table 26.--Comparison of plant moisture stress for Pacific madrone, tanoak, and California black oak sprouts in sun and shade

<u>Item</u>	<u>Species</u>					
	<u>Pacific madrone</u>		<u>Tanoak</u>		<u>California black oak</u>	
	<u>sun</u>	<u>shade</u>	<u>sun</u>	<u>shade</u>	<u>sun</u>	<u>shade</u>
Predawn minimum						
moisture stress	5.0	5.0	4.0	4.0	8.0	8.0
(atmospheres)						
Peak moisture						
stress (atmospheres)	23.5	20.5	30.5	23.0	28.0	28.0

stomates must have opened fully. By the time sunlight first shone directly on the leaves, the plants were close to being at maximum stress. For all but the tanoak plant in the sun, plant moisture stress then actually leveled off and began to decrease. With this one exception, differences between plants in sun and shade were minor. Likewise, the overall shape of the plant moisture stress curves also was quite similar. The tanoak plant in the sun, however, endured a stress of slightly over 25 atmospheres for 14 hours. And it did so with no ill effects. Obviously, these tree species possess the collective fail-safe mechanism that permits retention of sufficient energy and moisture reserves to sustain vital functions. Plants of most other species would have respired to death.

These tree species, then, simply open most of their stomates, photosynthesize at maximum rates until water becomes lacking, close their stomates without respiratory consequences, have the roots recharge the plants, and then begin the process anew the next morning.

This remarkable survival strategy may not be fully developed in four-month-old tanoak seedlings however, as at least one seedling underwent 34 atmospheres of stress and died, presumably from drought. Likewise, repeated dieback and eventual death of young tanoak sprout clumps also illustrates that limits exist even to this remarkable strategy. And the fact that newly exposed tanoak trees also suffer from chronic loss of leaves in the upper crowns suggests that this species is not as well adapted to aridity as Pacific madrone and California black oak.

The ability to produce dormant buds and to sprout is a well known adaptation that enables a plant species to consistently occupy a site. This is accomplished largely through the action of the already established and well developed root system, which in turn promotes rapid shoot growth and early capture of the site. But just how rapidly sprout clumps expand, and hence the magnitude of this adaptation as a survival strategy, is not fully appreciated.

Of the three species studied, tanoak is the most vigorous sprouter. It produces the most dormant buds per stump and needs the least excuse to trigger their development. When it does sprout, more sprouts are produced, which persist longer. Not only that, but the stump root system apparently stays alive longer, and actually produces additional sprouts after the initial surge.

Relative to the other species studied, however, all of these early advantages give tanoak no real competitive advantage. In terms of clump density, height, crown width, and cubic volume, tanoak rates intermediate among these species both at age 4 and age 10. And this is true in both the clearcut and shelterwood environments.

As a whole, however, species with sprout ability have a decided reproductive advantage over those that do not. In the clearcutting, rates of height and crown expansion for the species studied averaged about 2 feet and 1 foot per year, respectively, over a 10-year period. Few other plant species, and certainly not naturally established conifers, can match these rates. In the shelterwood, height and crown growth rates were reduced over half of those in the clearcutting

for all species. But even then, these rates are highly competitive in this environment.

The need for mutual shading such as that from multiple stems exists. Lack of shading led to sunscald of stems in thinned clumps of Pacific madrone and California black oak. Less forking and a tendency for J-shaped stems characterized unthinned sprout clumps of all species. And, although differences were slight, the overall height growth of Pacific madrone and California black oak was greater if the clump was unthinned. For tanoak, a slight, but logical advantage in height growth occurred if the relatively large number of sprouts was thinned heavily. It appears then, that in Pacific madrone and California black oak at least, the inherent vigor of the parent stump is channelled to all sprout members. Reducing their number results in no gain to the survivors. This suggests that each sprout claims more or less equal portions of the parent-tree root system, and develops its own system from that. The fact that a few stems become dominant is more a function of this development than that which is inherited.

Just as a tremendous amount of energy was directed in vain to acorns and berries, so is tremendous energy vainly channelled toward sprout production. Projections of initial sprout density data from the clearcut environment, together with the number of trees of each species in the average hardwood stand at Challenge, show Pacific madrone, tanoak, and California black oak together to produce about 65,900 sprouts per acre. And this is a conservative estimate because

it assumes that the initial sprout crop will stock the stand. All subsequent sproutings, and those from seedlings and saplings under 3.5 inches d.b.h. are not considered. Of the 65,900 sprouts, only 659 per acre remain by the time the stand reaches age 60. These hardwood species' strategy, then, is to direct large amounts of energy toward continuous site occupation, as well as toward capturing new sites.

Like the seedlings, the sprouts of California black oak were damaged by frosts. Both quickly resprouted. Stump sprouting often is considered an adaptation of a species to an environment where fire is commonplace. But Axelrod (1973) notes that most broad sclerophyll species evolved in a cool, presumably frosty, climate long before the Mediterranean climate (and the advent of drought and numerous fires) evolved. The ability to sprout, then, probably is a more general adaptation to both cool and droughty environmental stresses (Mooney 1977). And evidence of the gene complex in these tree sclerophylls being polymorphic, is reinforced.

Epicormic branching of California black oak also is a survival strategy. Small, suppressed, and injured trees sprout dramatically when the stand is opened-up. These are the very trees that need additional resources, and this is one way of getting them. Large, dominant, full-crowned trees don't need additional resources as badly, and epicormic branching is significantly less in them.

The tendency for these hardwood species to grow in dense stands either as single species or as mixtures is common. Below ground, the

site is totally occupied; and above, the ground is besieged with a rain of thick leathery leaves and exfoliated bark. These decompose slowly. Cool temperatures and dense shade insure an environment so lacking in light, moisture, and nutrients, that competitive plants are few.

The apparent trend of cubic volume growth being best when all three species were fairly evenly represented in the stand indicates the species long-term coevolution as community associates. Apparently, each species occupies a specific, but slightly different niche in the hardwood forest. And together the three species capture more of the total available resources of the site than does each alone.

Although Armillaria mellea is endemic in the hardwood stands of the Sierra Nevada, Pacific madrone, tanoak, and California black oak appear to have evolved with this pathogen over millenia to the point that losses from it are small. Likewise, the presence of heart rot in young-growth trees is low. For species whose primary reproductive mode is sprouting, strong resistance to the bridging of disease from rotting stump to pith of sprouts is critical. In the hardwood species studied, sufficient protective mechanism obviously has evolved, as no heart rot was noted in root crown sprouts or young-growth trees.

The advantages of sprout origin continue as the sprouts grow to tree size. The area captured early continues to be enlarged both above and below ground. And should one or two members of a clump die or become broken from wind and storm, the others remain and keep

the species in that area. The broken stems, if of California black oak, will epicormic branch; if of Pacific madrone or tanoak, are likely to sprout from root crowns. Generally, fewer sprouts result, however, if one or two tree members of a clump remain and keep the area shaded. Growth of sprouts put forth by broken members is extremely slow--again demonstrating the species' strategy of minimizing competition beneath tree crowns.

Like many species, California black oak becomes increasingly intolerant with age. Its need for light mandates that at least the crown receive toplight. Trees will grow tall and skinny to achieve this end and members 70 feet tall and 10 inches in diameter at breast height are not uncommon. The need for light is so strong that skinny trees will forgo necessary buttressing of the bole to achieve it. Bending in a great arc from storms or heavy snows often is the fate of such trees.

Even when hopelessly suppressed, this oak stays alive for several years. How it does so is a unique survival strategy. Overtopped trees die from the top down. After the top is dead, epicormic branches appear on the bole. Leaves on these branches are abnormally large and flat, and better able to receive light from sunflecks. With continued suppression, these branches also die, until only a few near the ground remain. Thus, even though hopelessly overtopped, the tree stays alive--in a position to take advantage of a major disturbance. Should this disturbance occur, the tree then will regain its former area through its epicormic branches or its root crown sprouts.

The alternating growth pattern among members of a clump spreads diameter growth over healthy members in it, at least when 1 to 4 members remain. This is a remarkable adaptation which insures that no member falls behind to the point of death. As death of all members in the clump is rare, having several present practically guarantees the species presence in that spot.

Taken together, Pacific madrone, tanoak, and California black oak possess a host of collective and specific adaptations that serve them well in a harsh environment. Through all life stages from acorns to seedlings to saplings and finally to trees, their special adaptations keep them in occupied areas and allow them to colonize new ones. Natural selection over countless millenia, and development of a polymorphic gene base have led to these remarkable adaptations and successful survival strategies.

After noting the role of light in delineating the shape of a tree's crown and its position in the stand, Horn (1971) called certain tree species "crafty green strategists." Certainly Pacific madrone, tanoak, and California black oak qualify for this description.

BIBLIOGRAPHY

Anonymous.

1963a. Industry business. Forest Ind. 90(8):11.

Anonymous.

1963b. Californians pioneer tanoak. Forest Ind. 90(11):66-67.

Anonymous.

1969a. Slammers--An assist by radar. Oakland Tribune, July 13, 1969.

Anonymous.

1969b. Microwave drying revives commercial use of tanoak. Can. Forest Ind. 89(9):11.

Anonymous.

1972a. Northern hardwood removal increases. Forest Ind. 99(4):11.

Anonymous.

1972b. Hardwood market is flourishing. Forest Ind. 99(8):9.

Anonymous.

1972c. New business from black oaks. San Francisco Chronicle Nov. 10, 1972.

Amen, R. D.

1963. The concept of seed dormancy. Am. Sci. 51:408-424.

Anderson, Walter C.

1973. Preservation and timber too. J. For. 71(1):38-40.

Axelrod, D. I.

1958. Evolution of the Madro-Tertiary geoflora. Bot. Rev. 24: 433-509.

Axelrod, Daniel I.

1973. History of the Mediterranean ecosystem in California. In Mediterranean type ecosystems--origin and structure. F. di Castri and H. Mooney, (eds.) p. 225-277. Springer-Verlag, New York, Heidelberg, Berlin.

Balls, E. K.

1962. Early uses of California plants. 103 p. Univ. of Calif., Berkeley and Los Angeles.

Barrette, B. R., D. R. Gedney, and D. D. Oswald.

N.D. California timber industries 1968. Mill characteristics and wood supply. Calif. Div. For. 117 p.

- Barrette, Brian.
1971. Markets for woodland products in California. Calif. Div. For. Rep. 6, 39 p.
- Bloch, Ivan.
1964. Western markets for red alder from specified counties in Oregon and Washington: A preliminary and partial examination prepared for the U.S. Area Redevelopment Administration. 56 p.
- Bolsinger, Charles L.
1976. Timber resources of northern interior California 1970. USDA Forest Serv. Resour. Bull. PNW-65, 75 p. Pacific Northwest Forest and Range Exp. Stn., Portland, Oreg.
- Bonner, Franklin T.
1967. Germination of sweetgum seed in response to light. J. For. 65:339.
- Bonner, J., and J. E. Varner.
1965. Plant biochemistry. 1054 p. Academic Press, New York.
- California Department of Fish and Game.
1961. The effects of hunting pressure on the gray squirrel in California. Rep. to the Fish and Game Comm. April 6-7, 1961. 8 p.
- Campbell, C. J., and C. P. Pase.
1972. Pressure bomb measures changes in moisture stress of birch-leaf mountainmahogany after partial crown removal. USDA Forest Serv. Res. Note RM-221. 4 p. Rocky Mountain Forest and Range Exp. Stn., Ft. Collins, Colo.
- Carvell, Kenneth L.
1969. The growth response of northern red oak following partial cutting. West Virginia Univ. Agric. Exp. Stn. Bull. 577, 11 p.
- Chan, F. J.
1971. Establishment of woody plants by direct seeding in California. 81 p. Univ. Calif., Davis.
- Chaney, Ralph W.
1925. II. The Mescal Flora--its distribution and climatic relation. Carnegie Inst. Publ. 349, p. 25-48.
- Cooper, W. S.
1922. The broad-sclerophyll vegetation of California. An ecological study of the chaparral and its related communities. Carnegie Inst. Publ. 319, 124 p.

Dale, Martin E.

1968. Growth response from thinning young even-aged white oak stands. USDA Forest Serv. Res. Paper NE-112, 17 p. Northeastern Forest Exp. Stn., Upper Darby, Pa.

Dale, Martin E.

1972. Growth and yield predictions for upland oak stands. USDA Forest Serv. Res. Paper NE-241, 21 p. Northeastern Forest Exp. Stn., Upper Darby, Pa.

Del Moral, Roger, and Rex G. Cates.

1971. Allelopathic potential of the dominant vegetation of western Washington. Ecology 52(6):1030-1037.

Dickinson, F. E.

1958. Factors contributing to the increased use of west coast hardwoods. Proc. Soc. Am. Foresters 1957:3 p.

Dieter, Alice.

1975. Wood technology: Honing a new edge. Boise Cascade Quart. 3(1):6-8.

Dixon, J. S.

1934. A study of the life history and food habits of mule deer in California. Part II. Food habits. Calif. Fish and Game 20(4): 315-354.

Dixon, W. J., and F. J. Massey, Jr.

1957. Introduction to statistical analysis. 2d ed. 488 p. McGraw-Hill Book Co., New York.

Dost, William A., and W. P. Bemis.

1966. Markets for woodland products in California. Calif. Div. For. Rep. 5, 23 p.

Edwards, Milton B.

1957. California black oak--its management and economic possibilities. J. For. 55:506-510.

Emery, Dara.

1964. Seed propagation of native California plants. Santa Barbara Bot. Gard. Leaflet 1(10):81-96.

Estes, K. M., and D. A. Blakeman.

1970. Foliar spraying of sprouting tanoak plants best in late summer. USDA Forest Serv. Res. Note PSW-207, 4 p. Pacific Southwest Forest and Range Exp. Stn., Berkeley, Calif.

Fowells, H. A.

1941. The period of seasonal growth of ponderosa pine and associated species. *J. For.* 39:601-608.

Friend, D. T. C.

1961. A simple method of measuring integrated light values in the field. *Ecology* 42:577-580.

Galston, A. W., and P. J. Davies.

1969. Hormonal regulation in higher plants. *Science* 163:1288-1297.

Grant, J. A. C.

1951. The relationship between stocking and size of quadrat. *Univ. Toronto For. Bull.* 35 p.

Griffin, James R.

1973. Xylem sap tension in three woodland oaks of central California. *Ecology* 54:152-159.

Hamilton, Martin A.

1965. Multiple comparison procedures. USDA Forest Serv. Res. Note RM-44, 12 p. Rocky Mountain Forest and Range Exp. Stn., Ft. Collins, Colo.

Hanes, T. L.

1971. Succession after fire in the chaparral of southern California. *Ecol. Monogr.* 41:27-52.

Harrison, A. T., E. Small, and H. A. Mooney.

1971. Drought relationships and distribution of two Mediterranean-climate California plant communities. *Ecology* 52:869-875.

Hatano, Ken-ichi, and Sumihiko Asakawa.

1964. Physiological processes in forest tree seeds during maturation, storage, and germination. In *International Review of Forestry Research*. Vol. 1, 404 p. Academic Press, New York.

Heilman, P. E., and S. P. Gessel.

1963. The effect of nitrogen fertilization on the concentration and weight of nitrogen, phosphorus, and potassium in Douglas-fir trees. *Soil Sci. Soc. Am. Proc.* 27:102-105.

Hellmers, H., J. S. Horton, G. Juhren, and J. O'Keefe.

1955. Root systems of some chaparral plants in southern California. *Ecology* 36:667-678

Hinckley, T. M., M. O. Schroeder, J. E. Roberts, and D. N. Bruckerhoff.

1975. Effect of several environmental variables and xylem pressure potential on leaf surface resistance in white oak. *Forest Sci.* 21:201-211.

Horn, Henry S.

1971. The adaptive geometry of trees. 144 p. Princeton Univ., Princeton, N. J.

Hornibrook, E. M., R. W. Larson, J. J. Van Akkeren, and A. A. Hasel.

1950. Board-foot and cubic-foot volume tables for some California hardwoods. U.S. Forest Serv. Calif. Forest and Range Exp. Stn. Res. Note 67, 31 p., Berkeley.

Horton, Jerome S.

1960. Vegetation types of the San Bernardino Mountains. USDA Forest Serv. Tech. Paper 44. 29 p. Pacific Southwest Forest and Range Exp. Stn., Berkeley, Calif.

Ingles, Lloyd G.

1947. Ecology and life history of the California gray squirrel. Calif. Fish and Game 33(3):139-158.

Jaeger, Edmund C.

1920. The mountain trees of southern California. 116 p. Post Printing and Binding Co., Pasadena, Calif.

Jensen, Herbert A.

1939. Vegetation types and forest conditions of the Santa Cruz Mountains unit of California. U.S. Forest Serv. Calif. Forest and Range Exp. Stn. Surv. Release 1, 55 p. Berkeley, Calif.

Johnson, C. M., and Albert Ulrich.

1959. II. Analytical methods for use in plant analysis. Calif. Agric. Exp. Stn. Bull. 766, p. 27-78.

Jones, A. R. C., and R. A. Lord.

1970. Studies of private forest ownership in southwestern Quebec. For. Chron. 46(1):34-38.

Kaufmann, Merrill R.

1968. Evaluation of the pressure chamber technique for estimating plant water potential of forest tree species. Forest Sci. 14: 369-374.

Keen, F. P.

1958. Cone and seed insects of western forest trees. U.S. Dep. Agric. Tech. Bull. 1169, 168 p.

Kellogg, Albert.

1882. Forest trees of California. 148 p. State Print. Off., Sacramento.

Kummerow, Jochen.

1973. Comparative anatomy of sclerophylls of Mediterranean climatic areas. In Mediterranean type ecosystems--origin and structure. F. di Castri and H. Mooney, (eds.) p. 157-167. Springer-Verlag, New York, Heidelberg, Berlin.

Leach, H. R., and J. L. Hiehle.

1957. Food habits of the Tehama deer herd. Calif. Fish and Game 43(3):161-178.

Leopold, A. Starker, T. Riney, R. McCain, and Lloyd Tevis, Jr.

1951. The Jawbone deer herd. Calif. Div. Fish and Game Bull. 4, 139 p.

Lewis, D. C., and R. H. Burgy.

1964. The relationship between oak tree roots and ground water in fractured rock as determined by tritium tracing. J. Geophys. Res. 69:2579-2588.

Malcolm, F. B.

1962. California black oak--a utilization study. U.S. Forest Serv. Forest Prod. Lab. Rep. 2237, 17 p.

Martin, A. C., H. S. Zim, and A. L. Nelson.

1961. American wildlife and plants. A guide to wildlife food habits. 354 p. Dover Publ. Inc., New York.

Mast, Fred R.

1968. Tanoak utilization story: New applications pay off. Forest Ind. 95(9):31-33.

May, Richard H.

1957. Wood charcoal in California. U.S. Forest Serv. Calif. Forest and Range Exp. Stn. Forest Surv. Release 28, 12 p. Berkeley.

May, Richard H.

1958. Development of the veneer and plywood industry in California. U.S. Forest Serv. Calif. Forest and Range Exp. Stn. Forest Surv. Release 34, 26 p. Berkeley.

McDonald, Philip M.

1969. Silvical characteristics of California black oak (Quercus kelloggii Newb.) USDA Forest Serv. Res. Paper PSW-53, 20 p. Pacific Southwest Forest and Range Exp. Stn., Berkeley, Calif.

McDonald, Philip M.

1973. Cutting a young-growth, mixed-conifer stand to California Forest Practice Act standards. USDA Forest Serv. Res. Paper PSW-89, 16 p. Pacific Southwest Forest and Range Exp. Stn., Berkeley, Calif.

McDonald, Philip M.

1976. Forest regeneration and seedling growth from five major cutting methods in north-central California. USDA Forest Serv. Res. Paper PSW-115, 10 p. Pacific Southwest Forest and Range Exp. Stn., Berkeley, Calif.

McDonald, Philip M.

1977. Tanoak--a bibliography for a promising species. USDA Forest Serv. Gen. Tech. Rep. PSW-22, 8 p. Pacific Southwest Forest and Range Exp. Stn., Berkeley, Calif.

McDonald, Philip M., and William E. Sundahl.

1966. Pacific madrone . . . a general bibliography for a promising species. USDA Forest Serv. Res. Note PSW-98, 8 p. Pacific Southwest Forest and Range Exp. Stn., Berkeley, Calif.

McDonald, Philip M., and William E. Sundahl.

1967. California black oak . . . a general bibliography on an increasingly valuable species. USDA Forest Serv. Res. Note PSW-134, 7 p. Pacific Southwest Forest and Range Exp. Stn., Berkeley, Calif.

McPherson, J. K., and C. H. Muller.

1969. Allelopathic effects of *Adenostoma fasciculatum*, "chamise" in the California chaparral. Ecol. Monogr. 39:177-198.

Minckler, Leon S.

1967. How pin oak stands respond to changes in stand density and structure. J. For. 65(4):256-257.

Mirov, N. T., and Charles J. Kraebel.

1939. Collecting and handling seeds of wild plants. Civ. Conserv. Corps. For. Publ. 5, 42 p.

Mogensen, H. Lloyd.

1975. Ovule abortion in *Quercus* (Fagaceae). Am. J. Bot. 62(2): 160-165.

Molotkovskii, G. K.

1955. Germination energy and germination capacity of fruits of oak and Persian walnut relative to their position in the soil. Doklady Akademii Nauk SSSR 102(3):637-639. (Trans. from Russian)

Mooney, Harold A.

1977. Frost sensitivity and resprouting behavior of analogous shrubs of California and Chile. Madroño 24(2):74-78.

Mooney, Harold A., and E. Lloyd Dunn.

1970. Convergent evolution of Mediterranean-climate evergreen sclerophyll shrubs. *Evolution* 24:292-303.

Mooney, Harold A., and David J. Parsons.

1973. Structure and function of the California chaparral--an example from San Dimas. In *Mediterranean type ecosystems--origin and structure*. F. di Castri and H. Mooney, (eds.) p. 83-120. Springer-Verlag, New York, Heidelberg, Berlin.

Muerle, G. F., and E. M. Hornibrook.

1965. Timber harvest in California, 1962. USDA Forest Serv. Res. Bull. PSW-2, 29 p. Pacific Southwest Forest and Range Exp. Stn., Berkeley, Calif.

Oswald, Daniel D.

1970. California's forest industries--prospects for the future. USDA Forest Serv. Res. Bull. PNW-35, 55 p. Pacific Northwest Forest and Range Exp. Stn., Portland, Oreg.

Overholser, James L.

1968. Oregon hardwood sawtimber. For. Res. Lab. Rep. G-9, 52 p. Oreg. State Univ., Corvallis.

Paul, Benson H., Alfred W. Dohr, and John T. Drow.

1955. Specific gravity, shrinkage, and strength of tanoak. U.S. Forest Serv. Forest Prod. Lab. Rep. 2041, 8 p., Madison, Wis.

Peattie, Donald Culross.

1953. A natural history of western trees. 751 p. Houghton Mifflin Co., Boston.

Pelton, John.

1962. Factors influencing survival and growth of a seedling population of Arbutus menziesii in California. *Madroño* 16: 237-276.

Pfeiffer, J. R.

1957. Oregon hardwood plywood. Forest Prod. Lab. Info. Circ. 10, 32 p., Oreg. State Univ., Corvallis.

Pfeiffer, Jack R.

1960. Northwest hardwood industry. *The Lumberman* 87(3):44-46.

Powers, Robert F.

1972. Site index curves for unmanaged stands of California black oak. USDA Forest Serv. Res. Note PSW-262, 5 p. Pacific Southwest Forest and Range Exp. Stn., Berkeley, Calif.

- Quick, Clarence R.
1956. Viable seeds from the duff and soil of sugar pine forests. Forest Sci. 2(1):36-42.
- Robinson, Cyril S.
1937. Plants eaten by California mule deer on the Los Padres National Forest. J. For. 35:285-292.
- Robinson, Dan D.
1948. Utilization of Oregon hardwoods. Sch. For. Inf. Circ. 2, 22 p., Oreg. State Univ., Corvallis.
- Roth, E. R., and G. H. Hepting.
1943. Origin and development of oak stump sprouts as affecting their likelihood to decay. J. For. 41:27-36.
- Roy, D. F.
1955. Hardwood sprout measurements in northwestern California. U.S. Forest Serv. Calif. Forest and Range Exp. Stn. Res. Note 95, 6 p., Berkeley.
- Roy, D. F.
1957a. A record of tanoak acorn and seedling production in northwestern California. U.S. Forest Serv. Calif. Forest and Range Exp. Stn. Res. Note 124, 6 p., Berkeley.
- Roy, D. F.
1957b. Silvical characteristics of tanoak. U.S. Forest Serv. Calif. Forest and Range Exp. Stn. Tech. Paper 22, 21 p., Berkeley.
- Roy, Douglass F.
1962. California hardwoods: Management practices and problems. J. For. 60:184-186.
- Sampson, Arthur W., and Beryl S. Jespersen.
1963. California range brushlands and browse plants. Calif. Agric. Exp. Stn. Man. 33, 162 p.
- Sander, G. H.
1958. Oregon hardwoods: Management, marketing, manufacture. Ext. Bull. 775, 16 p., Oreg. State Univ., Corvallis.
- Schnur, G. Luther.
1937. Yield, stand, and volume tables for even-aged upland oak forests. USDA Forest Serv. Tech. Bull. 560, 87 p. Washington, D.C.

- Scholander, P. F., H. T. Hammel, E. D. Bradstreet, and
E. A. Hemmingsen.
1965. Sap pressure in vascular plants. *Science* 148:339-346.
- Schopmeyer, C. S.
1974. Seeds of woody plants in the United States. U.S. Dep.
Agric., Agric. Handb. 450, 883 p.
- Siegel, William C., and Clark Row.
1965. U.S. hardwood imports grow as world supplies expand. USDA
Forest Serv. Res. Paper SO-17, 25 p. Southern Forest Exp. Stn.,
New Orleans, La.
- Silen, Roy R.
1956. Use of temperature pellets in regeneration research.
J. For. 54:311-312.
- Smith, Harvey H.
1952. Utilization of western hardwoods. *J. Forest Prod. Res.*
Soc. 2:52-54.
- Smith, Harvey H.
1956. Improved utilization of western hardwoods by modern drying.
Forest Prod. J. 6:121-124.
- Smith, Walton A.
1968. The band-tailed pigeon in California. *Calif. Fish and Game*
54(1):4-16.
- Snedecor, G. W.
1956. Statistical methods. 534 p. Iowa State Coll. Press, Ames.
- Society of American Foresters.
1954. Forest cover types of North America. 67 p., Soc. Am. For.,
Washington, D.C.
- Stienecker, Walter, and Bruce M. Browning.
1970. Food habits of the western gray squirrel. *Calif. Fish and*
Game 56(1):36-48.
- Sudworth, George B.
1908. Forest trees of the Pacific slope. 441 p., U.S. Government
Print. Off., Washington, D.C.
- Sundahl, William E.
1966. Crown and tree weights of madrone, black oak, and tanoak.
USDA Forest Serv. Res. Note PSW-101, 4 p. Pacific Southwest
Forest and Range Exp. Stn., Berkeley, Calif.

- Sundahl, William E.
1974. Fine cleaning of small seeds by static electricity. Tree Plant. Notes 25(2):2.
- Tamm, C. O.
1964. Determination of nutrient requirements of forest stands. Int. Rev. For. Res. 1:115-170.
- Tarrant, Robert F.
1958. Silvical characteristics of Pacific madrone. USDA Forest Serv. Pacific Northwest Forest and Range Exp. Stn. Silvical Ser. 6, 10 p., Portland, Oreg.
- Taylor, Walter P.
1956. The deer of North America. Their history and management. 668 p. Wildlife Management Institute, Washington, D. C.
- Trimble, George R., Jr.
1968. Growth of Appalachian hardwoods as affected by site and residual stand density. USDA Forest Serv. Res. Paper NE-98, 13 p. Northeastern Forest Exp. Stn., Upper Darby, Pa.
- Trimble, George R., Jr.
1969. Diameter growth of individual hardwood trees. USDA Forest Serv. Res. Paper NE-145, 25 p. Northeastern Forest Exp. Stn., Upper Darby, Pa.
- Trimble, George R., Jr., and J. J. Mendel.
1969. The rate of value increase for northern red oak, white oak, and chestnut oak. USDA Forest Serv. Res. Paper NE-129, 27 p. Northeastern Forest Exp. Stn., Upper Darby, Pa.
- U.S. Department of Commerce.
1968. The Hoopa Valley Reservation hardwood study report. Econ. Devel. Admin. 162 p.
- U.S. Forest Service.
1954. Forest statistics for California. U.S. Forest Serv. Calif. Forest and Range Exp. Stn. Forest Surv. Release 25, 66 p., Berkeley.
- U.S. Forest Service.
1973. The hospitable oak. Coordination guidelines for wildlife habitats 3. Calif. Reg. U.S. Forest Serv. 11 p.
- Van den Driessche, R.
1974. Prediction of mineral nutrient status of trees by foliar analysis. Bot. Rev. 40:347-394.

- Van Dersal, William R.
1938. Native woody plants of the United States, their erosion-control and wildlife values. U.S. Dep. Agric. Misc. Publ. 303, 362 p.
- Wang, B. S. P.
1974. Tree-seed storage. Can. For. Serv. Publ. 1335, 32 p. Ottawa.
- Waring, R. H.
1969. Forest plants of the eastern Siskiyous: Their environmental and vegetational distribution. Northwest Sci. 43(1):1-17.
- Wheeler, Philip R.
1970. The South's third forest. J. For. 68(3):142-146.
- Whittaker, R. H.
1961. Vegetation history of the Pacific Coast States and the "central" significance of the Klamath Region. Madroño 16:5-23.
- Wiant, Harry V., Jr., and William S. Berry.
1965. Cubic-foot volume and tariff access tables for tanoak in Humboldt County, California. Div. Nat. Resour. For. Rep. 2, 10 p., Humboldt State Coll., Arcata.
- Woods, F. W., and J. T. Cassady.
1961. Sprouting of sandhills scrub oaks following cutting. In Hardwood sprout development on cleared sites. 6 p. USDA Forest Serv. Southern Forest and Range Exp. Stn., New Orleans, La.
- Worrell, Albert C.
1969. What can we expect small private forests to produce? J. For. 67:865-867.