Valley Oak Seedling Growth Associated with Selected Grass Species[1]

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Abstract: Valley oak (*Quercus lobata* Née) has exhibited inadequate regeneration since the last century. Seedlings become established, but few develop into saplings. We hypothesized that the invasion of alien annual grasses into native perennial grasslands has increased oak seedling mortality by decreasing soil moisture availability. We conducted greenhouse experiments to test if the alien annual grass *Avena fatua* L. and the native perennial grass *Stipa pulchra* Hitchc. differentially effect soil moisture and valley oak seedling growth. Results showed that valley oak seedlings in the *A. fatua* treatments grew significantly smaller than seedlings in the *S. pulchra* treatments. In addition, valley oak seedling growth showed a positive correlation with soil moisture during the growing season. The results suggest that the introduction of alien annual grasses has reduced valley oak seedling growth and survivorship by limiting soil moisture availability.

It appears that, since the early 1900's, valley oaks have shown limited regeneration because of high seedling mortality (Griffin 1976, Bartolome and others 1987). Just prior to this time period, settlers introduced alien annual plants both accidently and purposely. These alien plants replaced much of the native plant species composition which, according to some researchers (Clements 1934, Beetle 1947, Barry 1981), consisted primarily of perennial bunchgrasses. Presently, alien annual grasses dominate valley oak habitat (Swirsky and Halvorson 1984, Swirsky 1986). Some researchers have suggested that this replacement of native grasses by alien grasses may be linked to the observed high seedling mortality (Welker and Menke 1987, McCreary 1989).

Field surveys revealed that soil moisture generally measured lower in alien grasslands than in native grasslands during the growing season (White 1967, Hull and Muller 1977). Jackson and Roy (1986) demonstrated that annual grasses grow and utilize soil moisture faster than perennial grasses. This faster rate of decline in soil moisture associated with alien annual grasses may be a significant factor effecting valley oak seedlings.

Phytophysiological studies demonstrated that when soil moisture declines slowly oak seedlings avoid water stress by accumulating solutes in their cells which promotes the influx of water. The accumulation of solutes lowers cell water potential without significantly reducing cell water content. If soil moisture declines too rapidly, however, water content decreases before cellular solutes can accumulate and water stress ensues (Osonubi and Davies 1981, Flower and Ludlow 1986, Welker and Menke 1987, Gordon and others 1989). Water stress limits plant growth (Kramer 1969, Matthews and Boyer 1984) and eventually results in the collapse of cell walls and senescence of the plant (Flower and Ludlow 1986). Consequently, competition for water by alien annual grasses may induce severe water stress in valley oak seedlings that results in slowed growth and ultimately death.

This paper reports on a greenhouse experiment designed to determine if valley oak seedlings established with alien grasses experience reduced growth as compared to those established with native grasses. We conducted a second greenhouse experiment to compare the soil moisture associated with alien and native grasses.

METHODS

Seeds of valley oak; the native perennial grass, *Stipa pulchra;* and the alien annual grass, *Avena fatua,* were collected from the Santa Monica Mountains of the Transverse Ranges north of Los Angeles, CA. The experiments were conducted in the greenhouse of California State University, Los Angeles.

In the first experiment, we measured valley oak seedling growth using waxed cardboard tubes lined with polyethylene bags as planting containers.

During the first week of December 1987, we planted *A. fatua* seeds into each of 50 containers (density = 2000/m^2), and we transplanted one-year-old *S. pulchra* plants into each of another 50 containers (basal cover = 11 percent). Density and basal cover approximated field conditions (Heady 1958, White 1967, Gordon and others 1989). Last, we left 50 containers devoid of grasses for controls. During the last week in December, after the grasses had become established, we planted one germinated acorn per container.

Throughout the experiment, we watered 75 of the containers to simulate dry years (25 for each grass treatment) and 75 to simulate wet years. Dry year treatments received 5 times less water than wet year treatments. Precipitation data from the Santa Monica Mountains (U.S. Weather Bureau) served as a basis to determine this watering regime.

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In February 1988, as valley oak seedling shoots emerged, we initiated the biweekly recording of the growth measurements: height, number of leaves, and length of the largest leaf. In September 1988, we removed the valley oak seedlings and recorded final root and shoot lengths and dry weights.

In the second experiment, we measured soil moisture between December 1988 and May 1989. We used an experimental design similar to that used in the growth experiment. However, we did not use controls, and we reduced the sample size of each grass treatment to 10 containers. Each month we extracted two soil samples from different levels from each container. We measured the soil moisture (water potential) of the samples using a thermocouple psychrometer (Decagon SC-10). For further details on methodology and data analysis refer to Danielsen (1990).

RESULTS

Growth Experiment

In all treatments, valley oak seedling shoots emerged during February and March (*fig. 1*). Though all acorns were viable and developed roots, some never developed shoots; particularly in the *Avena fatua* treatments.

Seedling Growth Experiment

Simultaneous analysis of seedling height, number of leaves, and length of largest leaf for the sampling dates combined (*fig. 2* and *3*) showed that seedlings in the controls grew significantly larger than seedlings in the grass treatments for both the dry and wet year regimes (canonical variates test, sample size = number of emerged shoots, probability <.05). Between grass treatments, seedlings in the *S. pulchra* treatments grew significantly larger than seedlings in the *A. fatua* treatments.

A comparison of the maximum averages for each growth variable (*table 1*) further illustrates that seedlings grew largest in the controls and smallest in the *A. fatua* treatments. Data for each growth variable and sampling date were analyzed separately (Kruskal-Wallace test). For all three growth variables in both the dry and wet year regimes, significant differences between the controls and the grass treatments and between the differing grass treatments occurred during March and April.

From May through August, significant differences continued to occur for all three growth variables between the control and grass treatments. Between the grass treatments, significant differences continued to occur for the height and length of largest leaf variables.

Seedling Root and Shoot Measurements

Seedling roots and shoots in the controls were significantly longer and heavier than those in the grass treatments in both the dry and wet year regimes (*tables 2* and *3*). Between the grass treatments, in the dry year regime, seedling shoots in the *S. pulchra* treatments were significantly longer and heavier than those in the *A. fatua* treatments.

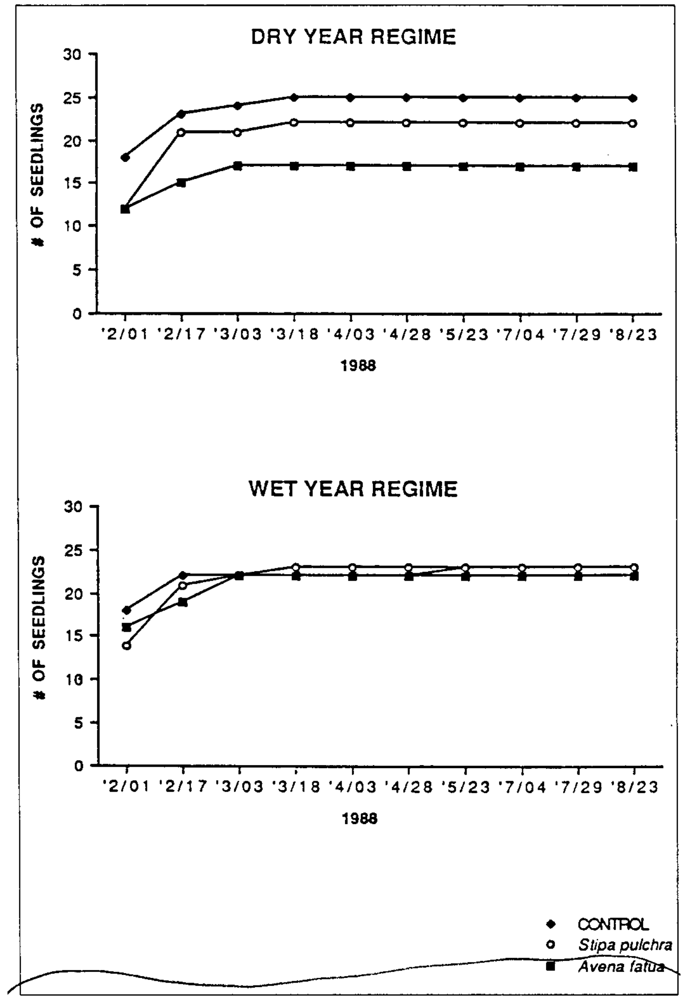

Figure 1—Number of valley oak seedlings with emerged shoots for each sampling date.

Root/shoot ratios were calculated to determine allocation of biomass. Valley oak seedlings in the *A. fatua* treatments showed greater root/shoot ratios than seedlings in the controls or *S. pulchra* treatments. Dry weight root/shoot ratios, in the dry year regime, averaged 10.0 in the *A. fatua* treatments, 3.7 in the *S. pulchra* treatments, and 5.9 in the controls. In the wet year regime, dry weight root/shoot ratios averaged 6.0 in the *A. fatua* treatments, 2.6 in the *S. pulchra* treatments, and 4.0 in the control treatments. Length root/shoot ratios, in the dry year regime, averaged 8.3 in the *A. fatua* treatments, 3.9 in the *S. pulchra* treatments, and 2.8 in the controls. In the wet year regime, length root/shoot ratios averaged 5.1 in the *A. fatua* treatments, 3.4 in the *S. pulchra* treatments, and 2.2 in the controls.

Soil Moisture Experiment

Soil water potentials remained high in both grass treatments from December through February. The maximum mean soil

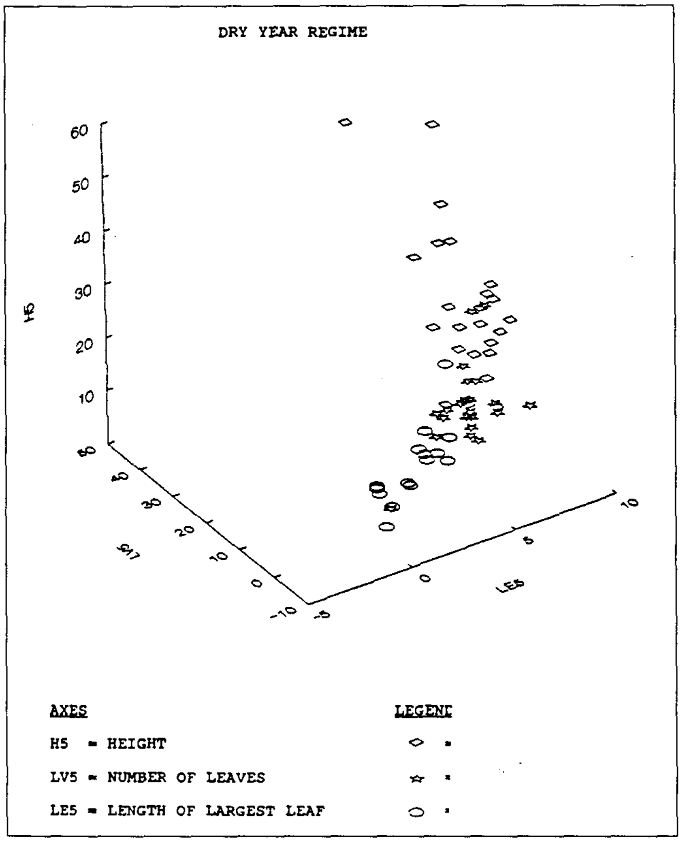

Figure 2—Overall growth in dry year regime: height, number of leaves, and length of largest leaf were plotted for each valley oak seedling with respect to grass treatment for sampling date, 3 April 1988. Simultaneous analysis of these growth variables for the sampling dates combined showed significant differences between the control and grass treatments and between the differing grass treatments (canonical variates test, N=# of seedlings with emerged shoots, p<.05).

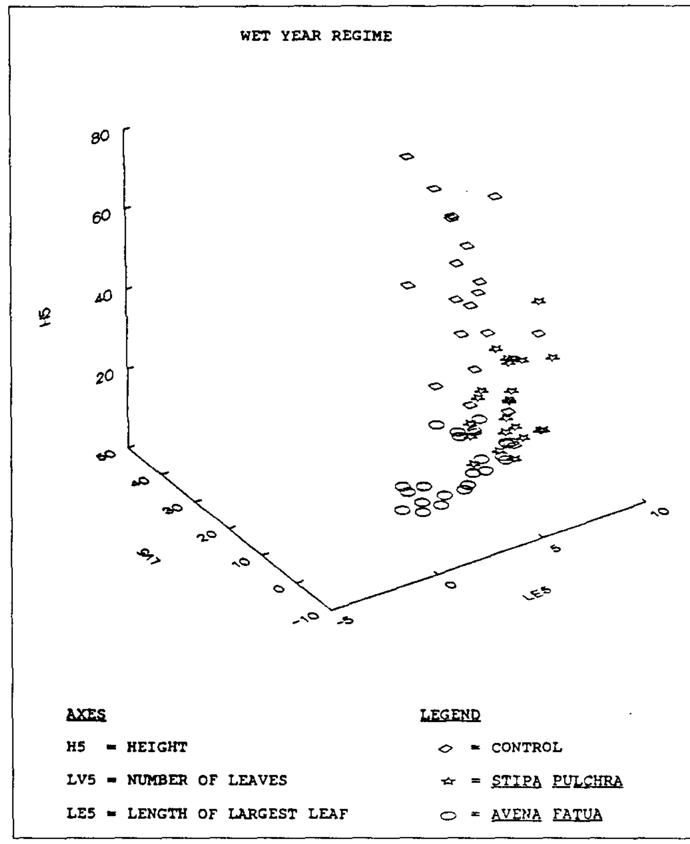

Figure 3—Overall growth in wet year regime: height, number of leaves, and length of largest leaf were plotted for each valley oak seedling with respect to grass treatment for sampling date, 3 April 1988. Simultaneous analysis of these growth variables for the sampling dates combined showed significant differences between the control and grass treatments and between the differing grass treatments (canonical variates test, N=# of seedlings with emerged shoots, p<.05).

water potential during December measured -425.6 (38.08 SE) J/kg.

During March, potentials decreased; particularly in the *A. fatua* treatments. In the dry year regime, upper level mean potentials measured only 3 percent of the maximum measured in December in the *A. fatua* treatments and 6 percent in the *S. pulchra* treatments. Lower level mean potentials measured 6 percent of the maximum measured in December in the *A. fatua* treatments and 8 percent in the *S. pulchra* treatments. In the wet year regime, upper level mean potentials measured 9 percent of the maximum in the *A. fatua* treatments and as much as 58 percent in the *S. pulchra* treatments. Lower level mean potentials measured 9 percent of the maximum in the *A. fatua* treatments and 70 percent in the *S. pulchra* treatments. Analysis of the soil water potential data in March showed significant differences between the grass treatments at both levels in the wet year regime (Mann-Whitney U-test, sample size = 5, $p<.05$).

During April, in the wet year regime, mean potentials remained lower in the *A. fatua* treatments than those in the *S. pulchra* treatments (2 percent and 5 percent of the maximum, respectively, at the upper level; and 7 percent and 12 percent of the maximum at the lower level). In the dry year regime, mean potentials in the *A. fatua* treatments actually increased at the lower level. The senescence of the *A. fatua* resulted in potentials equal to or higher than those in the *S. pulchra* treatments (upper level: 1 percent of the maximum in both treatments; and lower level: 12 percent of the maximum in the *A. fatua* treatments and 7 percent in the *S. pulchra* treatments). Analysis of the soil water potential data in April showed no significant differences between the grass treatments.

DISCUSSION

Indications of water stress in valley oak seedlings were most prevalent in the *Avena fatua* treatments, followed by the *Stipa pulchra* treatments, and finally the controls. Oak seedlings allocate water and, subsequently, biomass in order of roots, stems, and leaves. Consequently, during the growing season, oak seedlings initially respond to water stress with reduced leaf growth (Kramer 1969). Seedling leaves measured significantly smaller in the *A. fatua* treatments than in the *S. pulchra* treatments or the controls. Furthermore, seedlings in the *A. fatua*

Table 1—***Maximum averages of valley oak seedling height (measured in centimeters), number of leaves, and length of largest leaf with respect to grass treatment. Standard error in parentheses. For all three growth variables in both the dry and wet year regimes, significant differences occurred between the control and grass treatments and between the differing grass treatments (Kruskal-Wallace test, N=# of seedling emerged, p<05).***

	HEIGHT (CM)	# OF LEAVES	LENGTH (CM)
PRY YEAR REGIME			
Control	28.7 (2.41)	20.8 (l.75)	7.5 (0.22)
S. pulchra	12.3 (l.34)	8.8 (0.71)	6.0 (0.17)
A. fatua	6.7(l.16)	6.2 (0.55)	4.0 (0.47)
WET YEAR REGIME			
Control	38.1 (4.56)	29.0 (2.89)	7.3 (0.28)
S. pulchra	17.2(l.72)	9.7 (0.67)	6.6 (0.32)
A. fatua	10.8 (1.31)	6.8 (0.57)	4.0 (0.26)

Table 2—***Valley oak seedling average root and shoot lengths (cm); final measurements. RL=root length and SL-shoot length. Standard error in parentheses.***

	RL	SL	RS/SL
DRY YEAR REGIME			
Control	92.8 (3.89)	33.7 (3.55)	2.8
S. pulchra	69.7 (3.79)	17.9 (2.04)	3.9
A. fatua	65.5(l.97)	7.9(l.47)	8.3
WET YEAR REGIME			
Control	89.5 (4.23)	39.9 (4.96)	2.2
S. pulchra	74.3 (3.64)	21.7 (2.22)	3.4
A. fatua	72.2 (3.01)	14.1 (1.55)	5.1

Table 3—***Valley oak seedling average root and shoot dry weights (gm); final measurements. RW=root dry weight and SW-shoot dry weight. Standard error In parentheses.***

	RW	SW	RW/SW
DRY YEAR REGIME			
Control	13.0 (0.88)	2.2 (0.22)	5.9
S. pulchra	1.1 (0.07)	0.3 (0.03)	3.7
A. fatua	1.0 (0.07)	0.1 (0.02)	10.0
WET YEAR REGIME			
Control	13.3(l.55)	3.3 (0.45)	4.0
S. pulchra	1.3 (0.19)	0.5 (0.08)	2.6
A. fatua	1.2 (0.12)	0.2 (0.03)	6.0

treatments produced the fewest number of leaves.

A high root-to-shoot ratio also indicates water stress (Gordon and others 1989). The valley oak seedling root/shoot ratio for the length measurement averaged highest in the *A. fatua* treatments and lowest in the controls. The root/shoot ratio for the dry weight measurement averaged highest in the *A. fatua* treatments and, interestingly, lowest in the *S. pulchra* treatments; not in the controls. Roots of seedlings in the controls, unlike in the grass treatments, developed woody tissue. Therefore, in the controls, secondary growth, not necessarily water stress, produced higher weight root/shoot ratios. Nevertheless, the resulting root/shoot ratios demonstrate that seedlings in the *A. fatua* treatments experienced the greatest water stress.

As previously mentioned, oak seedlings exposed to a rapid decline of soil moisture experience water stress and display reduced growth during the growing season. Oak seedlings exposed to a slower decline of soil moisture are subjected to less water stress, through physiological adjustments, and continue growth. *A. fatua* grew rapidly in February and March, and reduced available soil moisture. *S. pulchra* grew more slowly and utilized less soil moisture. The valley oak seedlings grew largest in the controls, next largest in the *S. pulchra* treatments and smallest in the *A. fatua* treatments.

In April, *A. fatua* became senescent and soil water absorption decreased. *S. pulchra* growth accelerated with an accompanying increase in soil water absorption. In the dry year regime, soil water potentials were higher in the *A. fatua* treatments than in the *S. pulchra* treatments. In the wet year regime, available soil moisture in the *A. fatua* treatments allowed the development of new leaves on four valley oak seedlings. However, seedlings remained significantly larger in the *S. pulchra* treatments than in the *A. fatua* treatments.

In this experiment, valley oak seedlings grew most rapidly in February and March. During this growing season, soil water potentials corresponded with valley oak seedling growth. After the growing season, soil water potentials failed to significantly alter established seedling growth patterns. Consequently, the phenology of the different grass species, and the resulting soil moisture availability during the growing season, determined the ultimate size of the valley oak seedlings.

Other studies have obtained similar results. Adams and others (1987) observed reduced seedling survival of valley oak and blue oak (*Quercus douglasii* H.& A.) in the presence of alien annuals. Gordon and others (1989) documented a significant positive correlation between soil moisture availability associated with alien annuals and blue oak seedling growth. Welker and Menke (1987) noted that soil moisture loss caused by decreased amounts of mulch resulting from cattle grazing also limits blue oak seedling growth.

CONCLUSION

In this research, associated grasses inhibited the growth of valley oak seedlings. The particular species of grass, however, determined the degree of inhibition. Seedlings in the *Stipa pulchra* (a native grass species) treatments grew significantly larger than seedlings in the *Avena fatua* (an alien grass species) treatments. Furthermore, soil moisture measured lower in the grass treatments, particularly in the *A. fatua* treatments, and thus correlated with seedling growth. Therefore, these results suggest that the replacement of native perennial grasses by alien annual grasses has reduced valley oak seedling growth and survivorship by limiting soil moisture availability.

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Effect of Acorn Planting Depth on Depredation, Emergence, and Survival of Valley and Blue Oak[1]

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Abstract: During 1989 in east-central San Luis Obispo County, California, we studied the relationship of valley oak (*Quercus lobata*) and blue oak (*Q. douglasii*) acorn planting depth and number of acorns per planting site to acorn depredation, seedling emergence, survival, and height. Acorns were planted at three depths (1.3, 5.1, and 10.2 cm) at each of 960 planting sites with one or three acorns per site. Animal depredation of acorns was significantly ($P < 0.05$) greater for valley oak and seedling emergence and survival were significantly higher for blue oak. Depredation of valley oak acorns decreased significantly with deeper planting; depredation of blue oak acorns was significantly greater at the most shallow planting depth than at the two deeper depths where it was about the same. Although between-depth differences were not significant ($P > 0.05$), seedling emergence and survival of valley oak seedlings at the two deepest planting depths were better and almost identical. Conversely, blue oak seedling emergence and survival were significantly better at the two most shallow planting depths, and there was a strong, but insignificant, trend toward the best blue oak emergence and survival at the 5.1-cm depth. Regardless of planting depth, planting several acorns per planting site significantly decreased depredation and increased seedling emergence and survival for both oaks, and height for valley oak. Study results indicate that under the environmental conditions at the study site, the 5.1 cm (2 in) planting depth provided the best balance between lesser acorn depredation and greater seedling emergence and survival for blue oak; the 5.1 cm and 10.3 cm (4 in) depths provided the best balance for valley oak.

Poor natural regeneration of several of California's native oaks (*Quercus* spp.) has increasingly been recognized. Blue and valley oak are not regenerating sufficiently to maintain current stand densities. Factors that contribute to the regeneration problem include conversions of oak woodlands to urban and agriculture lands, increased fuelwood cutting, and competition from introduced Mediterranean annual grasses.

Artificial regeneration is an important option available for replacement of lost oaks. Although successful oak regeneration techniques have been developed (Griffin 1971; Russell 1971; Wright and others 1985; Johnson and Krinard 1985; Johnson and others 1986; Vande Linde 1987; McCreary 1989), animal depredation of direct-planted acorns is a common problem. Studies have examined several methods to reduce animal depredation. Johnson and Krinard (1985) concluded that a large-sized clearing around the planting site minimized animal damage. Russell (1971) believes that effective repellents would be a cost-efficient animal deterrent which needs to be developed. Cages surrounding planting sites keep animals out (Adams and others 1987), but are also expensive and take time to install.

Acorns planted at or just under the soil surface are more likely to be depredated than acorns planted at deeper depths (Russell 1971; Griffin 1971; Johnson and Krinard 1985; Borchert and others 1989). Optimal planting depth, however, has not been determined, at least not for California oaks. This paper reports on the response, in terms of animal depredation, seedling emergence, survival, and growth to valley and blue oak acorn planting depth and number of acorns planted per planting site.

STUDY AREA

The study site was established on the Santa Margarita Ranch in east-central San Luis Obispo County about 23 km northeast of San Luis Obispo (fig. 1). The climate of the area is Mediterranean, characterized by warm, dry summers and cool, wet winters. Average monthly temperatures range from 8° C in January to 23° C in July. Average annual rainfall totals about 53 cm. Typically, no rain falls during May to October.

Topography of the area is gently rolling to hilly. Residual soils, formed in place on sedimentary or secondary rocks, predominate. The dominant vegetation community is foothill oak woodland (Barbour and Major 1988). Dominant tree species in the oak woodlands include blue and scrub oak (*Quercus dumosa*) on xeric sites and coast live oak (*Q. agrifolia*) and valley oak on the more mesic sites. Gray pine (*Pinus sabiniana*) is frequently interspersed with the oaks. A variety of brush, forbs, and annual grasses occupy the oak woodland floors and grassy openings.

Since European settlement of coastal central California, the predominant land use of the Santa Margarita Ranch has been livestock production. Currently, the ranch is stocked moderately with cattle. All data were collected on the ranch during January to October 1989 within a 1.8-m tall welded-wire fence exclosure constructed around 0.6 ha of grazed pastureland. Forbs, predominantly filaree (*Erodium* spp.) and annual grasses covered the exclosure; no trees or brush occurred within the exclosure.

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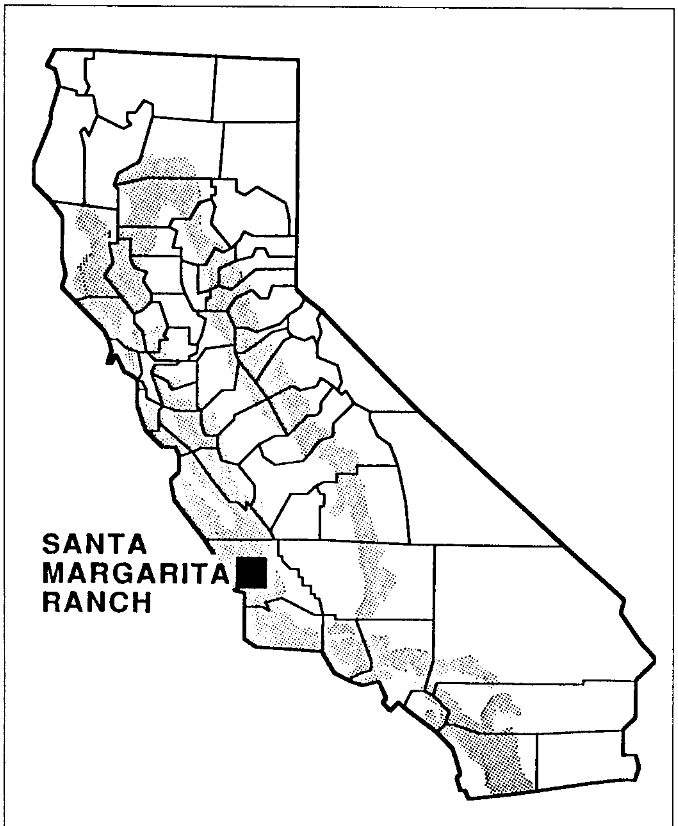

Figure 1—Location of the Santa Margarita Ranch in west-central San Luis Obispo County, California.

METHODS

Acorn Collection and Storage

In October 1988, valley and blue oak acorns were collected from trees on the Santa Margarita Ranch. The fungicide Captan was applied to the valley oak acorns, but not to the blue oak. All acorns were then refrigerated at 2° C until planting.

Site Preparation

In January 1989 in the 0.6-ha exclosure, 960 planting sites were laid out in a 2.4- by 2.4-m (8- by 8-foot) grid divided into four replicates of 240 planting sites each (randomized complete block design). The large distance between planting sites was used in an attempt to reduce the likelihood of a potential acorn depredator which, if it happened to find one planting site, would be more likely to find another. Twelve treatments were assigned randomly to each replication using the following variables: blue oak or valley oak; planting depths of 1.3, 5.1, or 10.2 cm (0.5, 2.0, or 4.0 in, respectively); and one or three seeds per planting site.

Each planting site was marked permanently with an aluminum identification tag wired to a steel rebar stake. In all replications, treatments were assigned randomly in groups of five planting sites. During 2-11 January 1989, acorns were planted the same compass direction and distance from the steel stakes by use of a template in the shape of an equilateral triangle with 10.2-cm sides. For one-acorn sites, an acorn was planted at the top angle and at each angle at three-acorn sites.

Two tools were used to plant the acorns at the proper depth. Whenever possible, a 2.5-cm diameter soil-sampling tube, marked with depth gradations (1.3, 5.1, and 10.2 cm) was used. At unusually rocky planting sites, holes were dug with a 3.8-cm diameter soil auger. The augered holes were measured with a ruler to ensure proper depth for planting. Soil removed with the soil-sampling tube or auger was replaced and firmed against the seed.

To minimize competition from grasses and forbs, herbicides were applied to the site twice: 1.1 kg atrazine and 0.7 kg oxyfluorfen per ha on 14 and 15 February and 1.1 kg glyphosate per ha on 10 March 1989. A backpack spray pump was used to make 1.5-m swaths centered on each row.

Site Monitoring

On-site rainfall was measured with a Taylor rain gauge. Rainfall data was taken after each storm from January to May 1989. Rainfall data for the same months was obtained from the US Weather Bureau, Salinas Dam Weather Station (3 km east of the study site). Average annual rainfall for the study site was obtained from the US Weather Bureau, Paso Robles, California (33 km north of the site).

Two soil samples were taken from the site in March 1989 and analyzed by the Soil Science Department, California Polytechnic State University, San Luis Obispo. The two locations for the samples were determined ocularly to represent the extremes in soil that occurred.

In order to document the kinds of animals present on the site, live trapping and observational animal scans (Fagerstone 1984) were conducted during March and April 1989. Trapping sites were laid out on a 11- by 11-meter grid. There were 49 trap sites consisting of forty 7.6-cm and nine 12.7-cm Sherman live traps. Trapping was done twice: 8-9 and 21-23 March.

During 15 March to 3 April, a total of 1710-minute periods of observation was made with a pair of field binoculars from a vehicle parked along a blacktop road about 20 m from the exclosure. Number of animals seen on and around the 0.6-ha study plot was recorded. Animal sign and species occurrence was not documented prior to study start up and planting, but cursory observations did not indicate any appreciable differences from during the study.

Oak Monitoring

Above-ground animal depredation was monitored twice a week during January to March. Acorn depredation was determined by examining each planting site for digging and other signs of animal activity, such as acorn shell remains. Suspected depredation was confirmed ocularly at 1.3-cm planting sites and by examining manually the digging for acorns planted 5.1 cm deep. Since the 10.2-cm depth was too deep for these methods, a ruler was inserted into the hole to measure the depth of digging and to feel for an acorn.

Seedling emergence data was collected weekly from the time the first seedling emerged in March and until emergence of the last seedling in July. Seedlings were located by ocular examination of each planting site. Upon emergence, each seedling was protected from animal damage with a 13-cm diameter aluminum-screen cage pinned to the ground.

Seedling survival and growth data were recorded in October 1989. Survival was determined ocularly. Each seedling was placed in one of two categories: alive or dead. All leaves had to be completely brown for the seedling to be dead. Seedling height was measured (nearest cm) from ground level to the tip of the terminal bud. One outside row (32 planting sites) was omitted from the analysis of height data because of heavier herbicide application.

Fate of Acorns Not Emerged

Since acorns could have been depredated from underground, a sample of acorns that did not appear to be depredated, but did not produce a seedling, was dug up to determine their fate. In December 1989, 20 planting sites in each of the four replications (118 acorns) were selected randomly for sampling. Each site was dug to the proper planting depth with a shovel and the soil sifted to help ensure finding the acorns, if present.

Data Analysis

For analysis of animal depredation, the three-acorn planting sites were considered depredated only when all three acorns were gone. For seedling emergence analysis, only one seedling had to come up at a site for it to be successful. If more than one seedling emerged at a three-acorn site, the tallest living seedling in October 1989 was used to assess seedling survival and height. This approach seemed reasonable at three-acorn sites because a practical application of planting multiple acorns is to increase the chance that one vigorous seedling is produced.

General trends of the data were determined using Macintosh EXCEL. Macintosh Statview II (Feldman and others 1987) was used to perform ANOVA to test the treatment effects on percent depredation, emergence, and survival. A multiple-factor factorial, non-repeated measures, balanced model (Winer 1971) was used to compute the ANOVA table shown at top of next column:

Source	degrees of freedom
Planting Depth	2
Species	1
Number of Seeds	1
Planting Depth by Species	2
Planting Depth by No. of Seeds	2
Species by No. of Seeds	1
Planting Depth by Species by No. of Seeds	2
Blocks	3
Error	33
Total	47

If there were significant interactions among any of the treatments (species, planting depth, and number of acorns per planting site) for any variable (acorn depredation; seedling emergence, survival, and height), the table of interaction means was examined to determine the cause of the interaction and how it may affect interpretation of the significant main effects. For each variable, a Duncan's multiple-range test (Steel and Torrie 1960) for the main effects was conducted to determine which treatment means were significantly different at the $P \leq 0.05$ level. Since seedling height data had an unequal number of observations, Student's *t*-tests were used to test the significance of seedling height differences for each of the three treatments.

In table 1, rainfall is compared between 1988 and the year of the study, 1989. Table 2 shows the means of the variables (acorn depredation; seedling emergence, survival, and growth) for the treatments (acorn species, planting depth, and number of acorns per planting site). Figure 2 illustrates the differences in means of the acorn depredation and seedling emergence variables for the species, acorn depth, and number of acorns per planting site treatments.

RESULTS

Site Monitoring

The year 1989 was very dry for San Luis Obispo County (US Weather Bureau, Sacramento, California). At the Salinas Dam Weather Station only 26 cm of rainfall were recorded compared to an average annual rainfall of 53 cm. During the first five months of 1989, 14.6 cm of rain fell on the study plot

Table 1—*Rainfall (cm) recorded at the Salinas Dam Weather Station during January to May in 1988 compared to rainfall recorded during the same months in 1989 on the study site.*

	Year	
Month	1988	1989
January	7.2	3.6
February	5.1	4.1
March	4.7	5.3
April	7.1	0.8
May	0.2	0.8

Table 2—Average fate of 960 sites planted at three depths: 1.3 (0.5 in), 5.1(2 in), or 10.2 cm (4 in), with either one (1) or three (3) valley (V) or blue (B) oak acorns per site during January to October 1989 on the Santa Margarita Ranch study plot, San Luis Obispo County, California.

Acorn Planting Depth (cm)	Depredation (pct)[d]				Emergence (pct)[d]				Survival (pct)[d]				Height (cm)			
	V		B		V		B		V		B		V		B	
	1	3	1	3	1	3	1	3	1	3	1	3	1	3	1	3
1.3 (0.5 in)	100 ^{a}	86	75 ^{a}	45	0 ^{a}	4	23 ^{a}	51	0 ^{a}	4	20 ^{a}	50	- ^{a}	9	6 ^{a}	8
5.1 (2.0 in.)	75 ^{b}	50	18 ^{b}	0	9 ^{a}	23	34 ^{a}	63	5 ^{a}	20	25 ^{a}	55	4 ^{a}	10	6 ^{a}	7
10.2 (4.0 in.)	29 ^{c}	28	6 ^{b}	6	5 ^{a}	28	13 ^{b}	28	5 ^{a}	25	10 ^{b}	25	7 ^{a}	9	5 ^{a}	6

[a,b,c] Pairs of means (averaged over number of seeds) not followed by the same letter within a column are significantly different ($P \leq .05$) by Duncan's multiple-range test and, for height, by Student's *t* tests.
[d] All percentages are based on 960 planting sites.

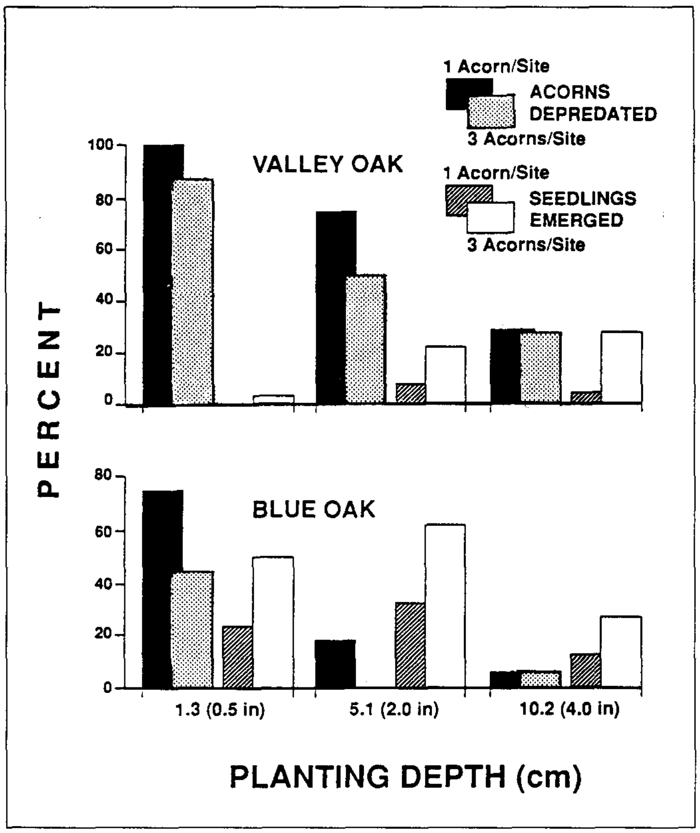

Figure 2—Percent valley oak and blue oak acorns depredated and seedlings emerged from three planting depths (1.3, 5.1, and 10.2 cm) at one- and three-acorn planting sites on the Santa Margarita Ranch study plot, San Luis Obispo County, California.

compared to 24.3 cm recorded at the Salinas Dam Weather Station during the same months in 1988 (table 1).

Since the results of the two soil tests were similar, they are averaged here. The soil texture was a sandy loam comprised of 75 pct sand, 12 pct silt, and 13 pct clay. It held only 24 pct water at saturation. The pH was 6.2. Organic matter (nitrogen: 89 kg per ha) was more than average for the soils of the area and, due probably to the residual from grazing, the phosphorus was very high (69 ppm dry weight). Potassium, calcium, and magnesium (123,623, and 41 ppm dry weight, respectively) were all low due to leaching of the sandy soils and because the soils had low ability to retain nutrients.

In March 1989 during the first trapping period, 28 deer mice (*Peromyscus maniculatus*) were caught in Sherman live traps (98 trap nights) and nine during the second period of trapping (147 trap nights). No other animals were captured. Fresh California ground squirrel (*Spermophilus beecheyi*) digging was common after March within and around the study plot. The fact that ground squirrels were not trapped in any of the 12.7-cm Sherman live traps may be due to trap design: the live traps had aluminum rather than woven-wire sides. Ground squirrels are relatively wary of entering the aluminum traps (R. Schmidt, pers. comm.).

California ground squirrels were observed during the seventeen 10-minute observational scans: three times on the study site and 32 times on the surrounding area. No other potential mammal acorn depredators were sighted within or around the study plot. Potential avian depredators were not seen on the site. Although periodic checks were made during January to October 1989, pocket gopher (*Thomomys* spp.) mounds were observed only on the area outside the study plot.

Oak Monitoring

There were significant differences for the variables acorn depredation, seedling emergence, survival, and height for most levels of the three treatments (oak species, depth the acorns were planted, and the number of acorns planted per planting site) of this study. There were also significant species by planting-depth interactions; valley oak and blue oak did not respond (in terms of acorn depredation, seedling emergence, and survival) in the same way to the depth the acorns were planted. Each variable is explained below.

Acorn Depredation.— Of the 960 planting sites, nearly half (43 pct) were depredated. Valley oak acorns were depredated significantly more (61 pct) than blue oak (25 pct).

Depredation was also much different among planting depths, ranging between 100 pct at one-acorn sites for valley oak planted 1.3 cm deep to 0 pct at three-acorn sites for blue oak planted 5.1

cm deep. Depredation of valley oak acorns decreased from 93 pct at 1.3-cm planting depth to 29 pct at 10.2 cm; with one and three-acorn sites combined, these differences were significant. In contrast, blue oak depredation decreased significantly from 60 pct at the 1.3-cm depth to 9 pct at 5.1 cm, but did not change significantly between the 5.1 and the 10.2-cm (6 pct) depths. The fact that animal depredation of valley oak acorns decreased about equally between planting depths but blue oak did not, resulted in a significant oak species by planting depth interaction. Finally, for blue oak and valley oak acorns planted at 1.3 and 5.1 cm, depredation was significantly less at three- than one-acorn planting sites. This difference did not occur at the 10.2 cm planting depth where depredation was nearly equal.

Depredation of acorns began within about a week of planting and continued until mid-March, when emergence of non-depredated acorns began. Occasional depredation of acorns occurred until the end of July. At most planting sites that were depredated, a small hole about 3 cm in diameter was dug, apparently by deer mice, to the depth the acorn was planted. A much greater amount of digging at other depredated planting sites suggested the acorns were taken by ground squirrels. There was no evidence of digging at planting sites by any other kind of animal.

Seedling Emergence.—Valley and blue oak seedlings emerged from mid-March to the end of June. A seedling came up at 23 pct of the 960 planting sites. Seedlings grew at significantly more blue oak (35 pct) than valley oak (12 pct) planting sites.

Few valley oak seedlings emerged (4 pct) at the 1.3-cm sites. At the 5.1- and 10.2-cm planting sites, about equal proportions emerged (16 pct and 17 pct, respectively). On the other hand for blue oak, the most (49 pct) seedlings emerged at the 5.1 cm planting depth; significantly fewer (21 pct) emerged at the 10.2-cm depth. This between-species difference in seedling emergence accounts for the significant species by planting depth interaction—the lowest seedling emergence for valley oak was at 1.3 cm planting depth but at 10.2 cm for blue oak. Finally, one-acorn sites produced significantly fewer seedlings than three-acorn sites: 5 pct vs. 18 pct and 23 pct vs. 47 pct for valley oak and blue oak, respectively.

Seedling Survival.—Nearly all the blue oak and valley oak seedlings that grew in spring 1989 (a seedling at 23 pct of the 960 planting sites) were still alive the following October (a seedling at 20 pct of the planting sites) when the last data on seedling survival were taken. Therefore, results of the ANOVA for seedling survival are nearly identical to those for seedling emergence: the same significant differences on survival were detected between species, acorn planting depth, and numbers of acorns planted per planting site. Also similar to the emergence results, there was a significant species by planting depth interaction for seedling survival.

Seedling Height.—The average height of all seedlings in October at the end of their first growing season was 7.0 cm. Valley oak seedlings were significantly taller than blue oak seedlings (8.3 cm and 6.5 cm, respectively) but, importantly, average heights of valley and blue oak seedlings from acorns planted at 1.3-, 5.1-, and 10.2-cm depths were about the same (9.0, 8.2, and 8.3 cm tall, respectively, for valley oak; 6.8, 6.7, and 5.8 cm tall, respectively, for blue oak). Finally, average seedling height was greater at three- compared to one-acorn planting sites (9.2 and 5.2 cm tall for valley oak; 6.8 and 5.8 cm tall for blue oak); the difference was significant for valley oak.

Fate of Acorns Not Emerged

In December 1989, we searched for 118 acorns (80 planting sites) that had not apparently been depredated nor produced a seedling. Of these, 70 pct had produced both a root and a sprout, but the sprout had not grown above the surface of the ground, and 12 pct appeared inviable. The fate of the remaining 18 pct, which were not found, could not be determined, but there was no evidence of animal depredation.

DISCUSSION

Planting Depth: 1.3 vs. 5.1 vs. 10.2 cm

Acorns planted at 1.3 cm were more easily detected by deer mice and ground squirrels present in the study plot than those planted deeper (5.1 or 10.2 cm). Observational scans and live trapping on the study plot indicated these surface-feeding rodents were quite common. The acorns planted just below the soil surface were especially susceptible to depredation from above ground. But, even if the acorns had not been depredated, other studies (Griffin 1971; Russell 1971; Johnson and Krinard 1985) indicate they might not have germinated due to adverse soil conditions near the surface: temperatures average higher and evaporation of soil moisture occurs at a faster rate. In this study, these conditions were compounded by the low rainfall and the sandy soils with low water-holding capacity.

On the other hand, the deeper-planted acorns, especially those planted at 10.2 cm, were depredated less because they were less easily detected by smell and the small rodents present on the study plot generally do not dig deep to get acorns (Russell 1971; Johnson and Krinard 1985; Borchert and others 1989). Had gophers been active in the study site, depredation of the more deeply-planted acorns would have likely been greater (Russell 1971).

It is not completely clear why many of the acorns that germinated at a depth of 10.2 cm did not come up. The long-term grazing of the study site has likely compacted the soil, making soil penetration more difficult. Matsuda and McBride (1987) attributed mortality of germinated blue and valley oak acorns to hard soils that did not allow root penetration. But, in this study, it seems that compacted soil would have equally impeded seedling emergence of acorns planted at depths of 1.3 and 5.1 cm. Especially for blue oak, planting 10.2 cm deep apparently resulted in such a large distance for the shoots to penetrate that many were not successful in emerging from the soil.

It is of interest that in spite of the environmental conditions at the study site and acorn physiological constraints, in contrast to blue oak, valley oak seedling emergence and survival did not decrease between the two deeper planting depths. Our data do not provide enough evidence to adequately judge this observation, but it suggests that the relatively large valley oak acorns may produce a seedling from acorns planted quite deep. Moreover, especially for valley oak, had rainfall been average and/or the soil had higher water-holding capacity, seedling emergence from the deepest planting depth (10.2 cm) may have been much better. Because of the advantage of lesser animal depredation that planting acorns at deeper depth affords, it may be useful to test success of deep-planted acorns under several water (rainfall) and soil conditions.

Species: Valley Oak vs. Blue Oak

The planting depth by oak species interactions in the ANOVA tests indicated that these factors acted together on acorn depredation, seedling emergence, and seedling survival. A possible explanation for greater depredation of valley oak acorns compared to blue oak, even at deeper planting depths is, simply, that valley oak acorns are larger. Barnett (1977) did a study with pignut hickory (*Carya glabra*) and white oak (*Quercus alba*) in which the hickory was depredated at a higher rate than the oak. Barnett attributed this to the stronger odor of the hickory nut due to its larger size; it was easier than the smaller white oak for predators to locate. Similarly in this study, the larger valley oak acorns may have exuded a stronger odor which attracted predators more, even at the deepest planting depth. It seems unlikely that use of the fungicide Captan on the valley oak, but not on blue oak acorns, increased depredation differentially. According to Sid Sakamoto (pers. comm.), Captan does "not attract small mammals." In fact, for seed-eating birds, Captan has been used as a repellent.

Number of Seeds: One vs. Three

This study confirms the validity of the acorn-planting technique: several acorns per spot. Three-acorn planting sites had less acorn depredation and better seedling emergence, survival, and height. Notably, apparently 10.2 cm (4 in) was adequate space between acorns to minimize the likelihood of finding all three once one was located—at least for the kinds of animal depredators on the study plot. The higher emergence and survival rates at three-acorn sites indicates that competition between seedlings was not a problem during the first growing season. Greater average height, moreover, of seedlings at three-acorn sites was due, simply, to the opportunity to select the tallest of three seedlings. The advantages of planting multiple acorns are noteworthy because acorns are easy to collect and planting several per planting site is not much more expensive or difficult than planting one.

RECOMMENDATIONS

The following management recommendations are suggested:

(1)Plant acorns about 5.1 cm (2 in) deep. This will help reduce animal depredation but not be too deep for seedlings to come up. Somewhat deeper planting may be better in areas or years of high rainfall and/or soil with good water-holding capacity.

(2)Plant several seeds per planting site, spaced at least 7 cm (several inches) apart.

(3)Plant the oak species which is most suited to the rainfall and soil conditions of the area.

Planting at the recommended depth does not preclude the need to protect the planting site. Planting at the optimal depth may increase the chance of success of protected sites, and may make successful planting more likely when protection of the planting site is not practical.

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Effects of Shade on Blue Oak and Coast Live Oak Regeneration in California Annual Grasslands[1]

Pamela C. Muick [2]

Abstract: Canopy effects and annual vegetation have been shown to strongly influence oak seedling survival. From the many elements composing canopy, shade was selected for experimental manipulation. A split-plot, multifactorial experiment was designed to test whether blue oak (*Quercus douglasii*) and coast live oak (*Q. agrifolia*) could establish seedlings in annual grasslands outside of canopy influence, and if there were differences in the responses of the two species to shade and sun treatments. All herbivory was excluded from three plots. All plots were constructed outside of direct canopy influence, and the annual herbaceous vegetation was not manipulated. Even under conditions of prolonged, severe drought, blue oaks and coast live oaks were able to establish seedlings from acorns in annual grasslands. Although the initial emergence of coast live oak seedlings from acorns was greater than that of blue oak in the first year, more blue oak seedlings were alive a year later. The survivorship of both species was significantly enhanced by the shade treatment.

The statewide oak regeneration survey concluded that in many locations, regeneration was inadequate to maintain existing stands. Additionally, the occurrence of regeneration was considered highly site specific. Seedlings of blue oak (*Quercus douglasii)* and coast live oak (*Q. agrifolia*) occupied the canopy understory quite successfully. Yet taller, sapling-sized blue oaks were rarely located under tree canopies and were found on the edge of the canopy and in the open. In contrast, coast live oak seedlings and saplings were both found beneath tree canopy (Muick and Bartolome 1987).

During the survey and subsequent field work I observed another phenomena. Evergreen oak species—coast live, interior live (*Q. wislizenii*), and canyon live (*Q. chrysolepis*)—appeared to be regenerating more successfully throughout the state. In certain locations live oak saplings, which looked like maiden trees rather than stump sprouts, were growing under the canopy of mature blue oak stands. The presence of live oak saplings, plus the absence of deciduous oak saplings, suggested that locally important changes in oak woodland species composition were taking place.

Shade tolerance is a term, most commonly used by foresters, to describe the relative ability of a species to grow and thrive under a forest canopy. A tolerant species can grow and thrive under tree canopy, whereas an intolerant species can thrive only away from the main canopy or in the open. The major canopy effect limiting species in arid environments is thought to be reduced soil moisture; light is rarely limiting in temperate forests (Spun: and Barnes 1980). Sudworth (1908) described coast live oak as highly tolerant of canopy condition and blue oak as highly intolerant. Based on data, observations, and relative tolerance ratings, I hypothesized that blue oaks were unable to grow to sapling size under tree canopy.

In evaluating the effects of canopy, I considered the relationship between canopy and shade. The effects of shade and tree canopy are best considered as overlapping, but not equivalent, variables. Tree canopy intercepts solar irradiance resulting in a zone of reduced light beneath and around the tree. However, shade is only one of several components comprising canopy effects.

The effects of canopy include other attributes besides reduced light. Soil moisture, nutrient status, soil texture, and pathogens are usually quite different beneath a tree than in a comparable site without tree cover. Shade itself is variable, and depends upon the amount of light blocked, and areal, daily, and seasonal patterns. Although tree canopy may be a dominant source of shade in oak savannas and woodlands, shade can also result from topographic relief, rock outcrops, and shrubs and herbaceous vegetation.

At the Sierra Field Station, Momen (1987) evaluated the effects of canopy on water potential of blue oak seedlings in grazed and ungrazed locations. The lowest values of seedling water potential occurred in grazed areas beneath tree canopy, which also had the higher densities of annual grasses. Momen concluded that the prospect of blue oak seedling survival is greater in the grazed, open environment than beneath canopy.

Cruzan (1981) found that all coast live oak seedlings growing in the full sun died. In the shade and vegetation removal experiments, increased shade and/or decreased annual vegetation led to higher percentages of seedling survival. The negative effects of annual grass and forb species on oak seedling survival have been reported by many authors (Griffin 1980, Welker and Menke 1987, Gordon and others, 1989).

Other researchers have tested the effects of herbivore exclusion (Borchert, and others 1989) and compared the effects of canopy with non-canopy areas (Momen 1987, Welker and Menke 1987). To date no California researchers have tested blue oak canopy components away from the canopy environment. Therefore I decided to manipulate a single effect of the canopy, shade, while holding annual vegetation, seed source, and rodent populations constant. For the purposes of this study, shade can be considered as either a canopy effect or a variable independent of canopy.

This paper reports on my investigations to determine 1) if blue oak and coast live oak could establish in annual grasslands

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outside of canopy influence, and 2) if, at the seedling stage, the species exhibited different responses to shade or sun outside of canopy influence. The experiments were carried out in exclosures which protected the seedlings from all vertebrate herbivores. Vertebrates have been demonstrated to consume both acorns and seedlings in many locations (Borchert and others 1989, Griffin 1980).

THE EXPERIMENT

Field experiments were conducted at the Hastings Natural History Reservation, Carmel Valley, Monterey County, in the Inner South Coast Ranges. At Hastings I selected three annual grassland sites, formerly "old fields", each within about 10 meters of an existing oak stand. Sites were located at similar elevations but on different soils representing a spectrum of Hastings' soil types. Robertson Saddle (2) is the most arid site and also receives the most insolation. Tire Flat (3) is the most mesic site and receives the least insolation. North Field (1) is mid-way between the other two sites in terms of insolation, but is more similar to Tire Flat in terms of soil type and moisture.

In order to eliminate the influences of vertebrate herbivores, exclosures were thoroughly fenced, both above and below ground. A backhoe was used to dig a trench around a rectangular area measuring approximately 6 meters by 8 meters. Trenches were excavated to a thick, claypan that was considered to define the lower limit for burrowing rodents. Depth to claypan varied across the plots and ranged from 1 to 3 meters. During construction and fence building, soil disturbance and compaction on plot surfaces was minimized. Most of the rodents remaining within the plot after construction were removed by trapping. The top of the exclosure was not fenced. Exclosures were rested for about one year and the plots were planted in December, 1988.

I used a split-plot, multifactorial experimental design. Each 6 m by 8 m exclosure plot was divided into four quarters of similar size, with buffer strips defined between plots and next to the fences. Two diagonally opposed quarters were assigned to the shade treatment, while the other two were unshaded and served as controls. An evenly spaced grid of sixteen cells, each cell measuring about 30 cm on a side, was superimposed on each quarter-plot. Species and treatments were assigned to each cell according to a pre-determined, interspersed random pattern. The 16 acorns in each cell were from the same parent tree, in the case of blue oak, or from the same population, in the case of coast live oak.

Planting was accomplished by wedging the soil open with a trowel, then dropping an acorn, sideways, into the 5 to 7 cm deep crevice. The opening was closed and about 100 ml of water was poured over each spot after planting. All acorns were planted within two days in December of 1988.

For the shade treatment shadecloth tarps were positioned over the two shade treatment quarter plots, in each of the three exclosures, in February of 1989. The six tarps were sewn from shadecloth which was rated to block out 50 pct of overhead sunlight (®Weathashade). Each tarp was suspended horizontally, about 1 to 1.25 meters above the ground, and three corners were fastened to the exclosure fence. The fourth and inside corner of the tarp was attached to a fencepost driven into the middle of the plot.

Data were collected monthly. I counted the number of seedlings emerged and alive, calculated average number of leaves and stems, and measured the height of seedlings and annual vegetation. I also noted and quantified other data including evidence of arthropod herbivory.

RESULTS

The following results are based on the emergence and above ground mortality data. Emergence was defined as the presence of a shoot or stem with leaves by June 1989. Survival was defined as the presence of a stem with green leaves or a green stem, in June 1990. The responses of the seedlings varied

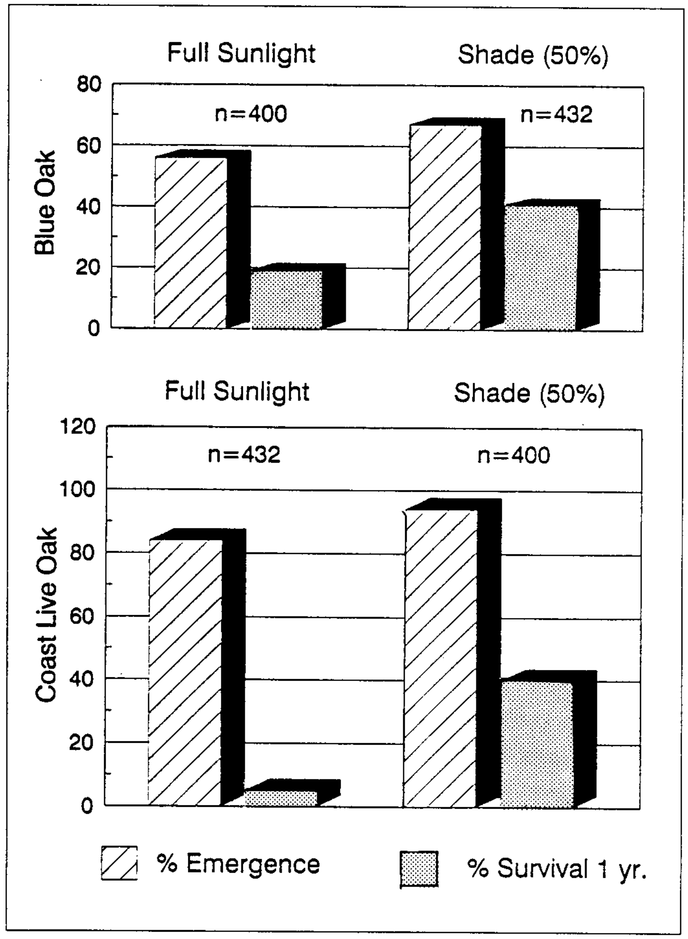

Figure 1—A graph of emergence and survival of blue oak and coast live oak seedlings by treatment.

between plots, however, several general and significant patterns emerged (figure 1).

Emergence and Survival by Species

A very high percentage of coast live oak, on both sun and shade plots, emerged (table 1). Of the 832 acorns planted in December of 1987, 739 (89 pct) had emerged by June of 1989. However, a year later in June of 1990, the population of coast live oak seedlings had decreased dramatically. Only 181(22 pct) coast live oak seedlings survived and of those 89 pct (all but 20) were found under the shade treatment.

Only 515 (62 pct) of the 832 blue oak acorns produced an above-ground stem by June 1989. However, a year later in June 1990, 30 pct of those planted or almost half of those that had emerged were alive. Of the 251 surviving blue oak seedlings 75 pct were located under the shadecloth.

Patterns of Emergence and Survival

Coast live oak acorns gave rise to many more seedlings than did blue oak acorns. Using two-way analysis of variance (ANOVA), species and seedling emergence were significantly related ($p = 0.05$). This may well be related to differences in viability between the two species.

Shade treatments were strongly and significantly related to seedling survival ($p = 0.05$). On the extremely arid Robertson Saddle plot, only 2 (3 pct) of the previous year's blue oak seedlings and 1 (1 pct) of the previous year's coast live oak seedlings leafed out, all under the shadecloth. On the two more mesic plots, North Field and Tire Flat, greater numbers of blue oak seedlings survived on the sun plots, 32 pct and 26 pct respectively. There was no significant difference between species in their response to the treatments.

DISCUSSION

Shade tolerance of a species can vary over the lifetime of a plant and between individuals. Black oak (*Q. kelloggii*) can persist in the understory for many years, but in order to reach maturity it must have its canopy in the sun (McDonald 1978). Although Sudworth characterized blue oak as highly intolerant, results presented here suggest that blue oak does display some tolerance to experimentally produced shade at the seedling stage. Other authors (Momen 1987 and Welker and Menke 1987) also mention the presence of naturally occurring blue oak seedlings under tree canopy.

The mean annual precipitation at Hastings is 535 mm (21 inches), which usually falls as rain and occasionally as snow during the winter months. As the record shows, drought is not an uncommon event at Hastings (figure 2). In the previous 62 years precipitation was below average thirty-six or 58 pct of the time. Precipitation measured less than 400 mm (15.7 inches) for thirteen of those below average years. During this study, Hastings was undergoing the second and third years of an extreme drought, and precipitation has been below 14 inches annually since the 1987-88 season. Rainfall during 1987-88, the year prior to planting, was 347 nun (13.7 inches). Rainfall during the 1988-89 season, when seedling emergence was counted, was only 328 mm (12.9 inches). Precipitation during 1989-90, the year survival was observed, measured 347 mm (13.7 inches).

No additional water was brought onto the plots after the 100 ml poured over each acorn seed spot at the time of planting in December, 1987. The effects of the shadecloth tarp on the accumulation of additional condensation is unknown; however, snow and fog are uncommon at Hastings.

The high levels of moisture stress measured on blue oak seedlings growing under tree canopy (Momen 1987) and high percentages of seedling mortality measured by Welker and Rice (1987) suggest this a one possible mechanism for the exclusion of blue oak saplings from the beneath the canopy environment (Muick and Bartolome 1987). The strong **positive** relationship between shade and blue oak seedling survival as presented in this study suggests that blue oak regeneration may be enhanced

Table 1—*Summary of seedling emergence and survival by species and treatment.*

Planted in Species	Acorns in 12/1988	Seedlings Emerged Surviving in 6/1989		Seedlings Surviving 1.5 Years 6/1990		Overall Survival 1988-1990
	No.	No.	Pct	No.	Pct	Pct
Blue oak						
FULL SUN	400	222	56	74	33	19
SHADE	432	290	67	177	61	41
Total	832	512	62	251	49	30
Coast live oak						
FULL SUN	432	363	84	20	6	5
SHADE	400	376	94	161	43	40
Total	832	739	89	181	25	22

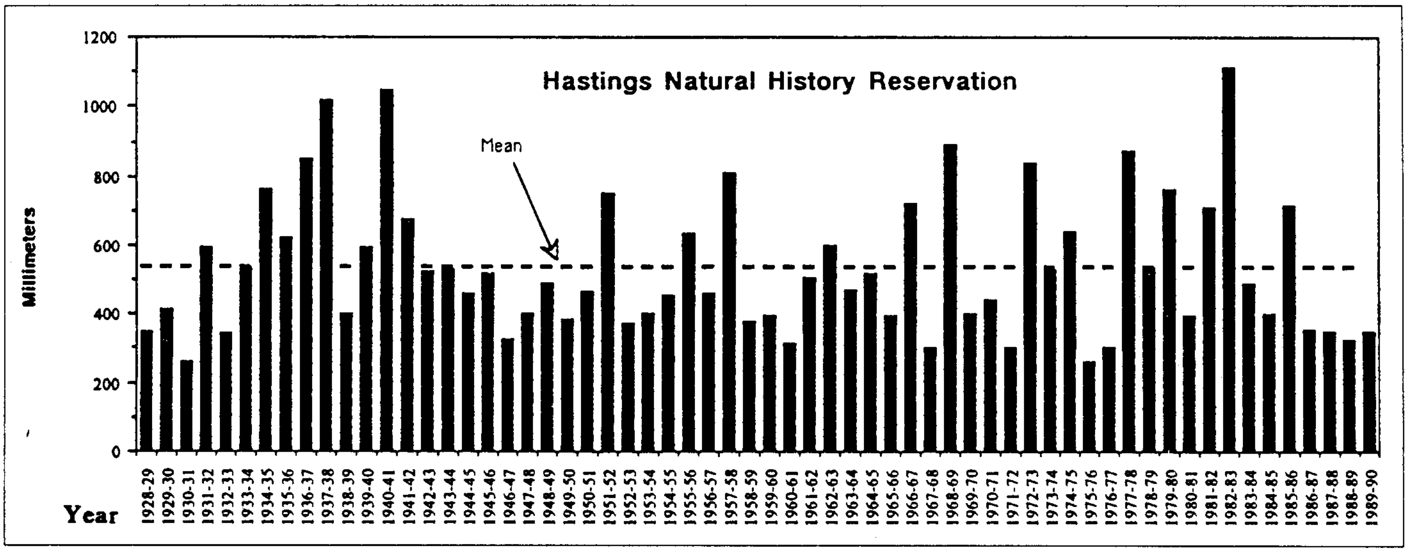

Figure 2—Total annual precipitation measured at Hastings Natural History Reservation: 1928-1990.

by shade. This suggests that one quality of a blue oak regeneration site is non-canopy shade. It may well be that the least likely location for successful blue oak regeneration to occur is under tree canopy.

CONCLUSIONS

Naturalized annual grasses and forbs are frequently associated with the lack of oak regeneration, particularly for blue oaks (Gordon, and others 1989, Welker and Menke 1987). However, even under conditions of prolonged, severe drought, blue oak and coast live oaks were able to establish seedlings from acorns in annual grasslands, when protected from vertebrate herbivory. Both oak species were able to successfully establish seedling populations, based on shoot emergence in the first year. Coast live oak required shade for seedling survival into the following year whereas blue oak seedlings survived on both sun and shade plots. Blue oak survivorship was significantly enhanced by the shadecloth treatment, and blue oak seedlings survived in greater numbers than coast live oak.

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Oak Seedling Establishment in Relation to Environmental Factors at Annadel State Park[1]

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Abstract: As part of an ongoing study of oak ecology in Sonoma County, California, we have begun to evaluate various environmental factors relative to oak seedling establishment at Annadel State Park. These factors, identified at three spatial scales (macro, meso and microscales), were corelated with the presence of oak seedlings in two contrasting northern oak woodland understory types - annual and perennial grass. No significant statistical correlations were found, but this is probably due to the small sample size. Preliminary analysis suggests that positive correlations will be found between seedling densities and late spring and summer soil moisture levels maintained by one or more factors at each scale.

This paper is a preliminary report on an ongoing study of oak seedling establishment at Annadel State Park. The objective of the study is to evaluate environments for oak seedling establishment at three spatial scales in order to identify an appropriate scale for making decisions about regeneration projects. A supplementary objective was to see if we could identify environmental factors at different scales which correlate with oak seedling establishment. Management decisions regarding oak planting, restoration of oak woodlands, and the control of grazing livestock to reduce herbivory must be based on an understanding of the relationship between various environmental factors and oak seedling establishment.

The three spatial scales used in this study will be referred to as the macro, meso, and micro scales. The macro-scale is the scale at which plant communities segregate out over the landscape. This scale is determined by local climate, surficial geology, soil types, drainage patterns, land use history, and fire frequency. The mosaic of plant communities in an area is the best expression of the interaction of environmental factors at the macro-scale. Wells (1962) has analyzed the distribution of oak woodlands near San Luis Obispo working at this scale.

The meso-scale environment for seedling establishment is the scale of variation of environmental factors within the boundaries of a plant community. This scale is to a large degree controlled by the modification of environmental factors by the dominant species in the plant community. Environmental factors to be considered at this scale include biotic factors such as tree crown cover, shrub cover, ground cover, and abiotic factors like soil depth, soil moisture, and slope. Analysis of meso-scale factors has been used in many studies of oak seedling establishment (Griffin 1971).

The micro-scale environment for seedling establishment corresponds to the operational environment proposed by Mason and Langenheim (1957). This is the immediate environment surrounding the acorn and developing seedling which impinges directly upon the seedling. Mason and Langenheim saw this operational environment in terms of physical (e.g., heat, atmospheric moisture, etc.) and biotic (e.g., herbivory, pollination, etc.) factors which impinge directly on the physiology and morphology of the plant. We have attempted to characterize the micro-environment in terms of physical and biological conditions we observed in the immediate proximity to seedlings. Such characteristics as distance to nearest object (rock, tree, log), seedling cover by perennial grass leaves and evidence of herbivory and/or drought were used to define the micro-environment of seedlings.

It has occurred to us that the divergent opinions regarding natural seedling establishment in California oaks might be related to differences in the environmental scale at which different investigators approached the study. Muick and Bartolome (1987) working at what we consider the macro-scale suggested that a number of macro-scale factors (e.g., grazing history, precipitation, soil type) are related to variations in seedling establishment. Snow (1972) and McBride (1974) investigated the relationship between some meso-scale factors and seedling establishment in coast live oak (*Quercus agrifolia*). Their work suggests that the degree of crown cover, moisture availability, and livestock grazing in oak woodlands are key factors in seedling establishment. Griffin (1976; 1980) working at what we consider the micro-scale proposed micro-scale factors such as herbivory by pocket gophers as the primary factor controlling seedling establishment.

This paper reports on how a better understanding of oak seedling regeneration may be obtained by properly focusing on the appropriate environmental scale. It was the expectation of this project to identify that scale in the case of Oregon oak (*Quercus garryana*) in Annadel State Park near Santa Rosa, California.

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STUDY AREA

Annadel State Park is located immediately southeast of Santa Rosa, Sonoma County, California, in the Sonoma Mountains. This north-south trending range, primarily composed of Pliocene Sonoma Volcanics above older sediments (Jenkins 1951) is in the eastern portion of the county ca. 30 km from the Pacific coast. Climate patterns are typically Mediterranean with mild winter temperatures (January mean daily minimum 2-3 °C) and hot summer temperatures (July mean daily minimum 28-29°C) which are often moderated by morning fog. Total annual precipitation is ca. 750 mm/year with dry summers and wet winters (January mean 150 mm) (National Oceanographic and Atmospheric Administration 1989).

The vegetation of the park, typical of that found throughout the southern North Coast Range, is a complex mosaic of communities including coastal prairie, chaparral, northern oak woodland, mixed evergreen forest and coniferous forest. The coniferous forest type is most common in the northeastern third of the park. Mixed evergreen forest occurs on northerly slopes and moist drainages throughout the park, integrating with northern oak woodland, particularly in the center of the park. Northern oak woodland is predominant in the southwestern two-thirds of the park, although tree densities and composition vary with aspect. Oregon oak occurs in relatively high densities on north-facing slopes, while south-facing slopes support more open savannas of Oregon oak-blue oak hybrids (*Q. garryana* x *douglasii*). The northern oak woodlands may also be characterized by understory conditions. Perennial grasses dominate the understories of stands on steep, rocky slopes. Northern oak woodlands occurring on less steep slopes and soils without rocks generally support understories of annual grasses. Chaparral occupies relatively small areas throughout the park, usually on southern or western exposures and on rock outcroppings. The prairie type forms small to fairly extensive meadows throughout the park. It is important to note that these vegetation types form a mosaic; areas occupied by a given type are often small and boundaries between types often abrupt.

The area in which Annadel is located was extensively utilized by European settlers and their descendents (Futini 1976). Major types of activities included cattle grazing (intermittent since 1830s), cobblestone quarrying around the turn-of-the-century and extensive cutting of hardwood for cordwood and charcoal in the 1920s. Cattle ranching was the dominant activity from 1930 to 1970. The park was established in 1972.

Several recent studies have focused on the oak woodland and hardwood forest types in Sonoma County with particular reference to Annadel State Park. Anderson and Pasquinelli (1984) described the northern oak woodland at several sites along a moisture gradient within the county, including two sites in Annadel. They concluded that high oak canopy densities and lack of oak regeneration may result in the future dominance of mixed evergreen forest species at the more mesic end of the gradient. Tunison (1973) investigated the distribution of oak woodland and mixed evergreen forest types on Bennett Mountain in Annadel State Park. Noting the dominance of young Douglas-fir (*Pseudotsuga menziesii*) and Bay (*Umbellularia californica*) in the understory of many oak dominated stands, he tentatively concluded that all of these oak types are seral to mixed evergreen forest. Barnhart (1978) suggested a similar vegetation change, although he pointed out that the complex nature of the coast range vegetation makes it difficult to document successional trends. Wainwright and Barbour (1984) demonstrated the diverse nature of the mixed evergreen forest type in Annadel. Barnhart et al. (1987) examined Douglas-fir invasion into the northern oak woodland type at Annadel State Park. They did not, however, report on oak regeneration in these stands.

METHODS

Two oak dominated woodland types were selected for this study as expressions of the macro scale environmental factors at Annadel State Park. These types were the northern oak woodland with perennial grass understory (perennial grass woodland) and the northern oak woodland with annual grass understory (annual grass woodland).

Five 10m by 10m plots were established in September, 1990 at random in each type and the following data were collected:

1. Oak seedlings
   species, number, height, diameter
2. a. Meso-scale factors
   - species, diameter at breast height (DBH), and height of trees > 1.4m tall
   - total crown cover on plot
   - pct. ground cover by perennial grass
   - pct. ground cover by annual grass
   - pct. ground cover by litter
   - pct. ground cover by rocks
   - pct. ground cover by logs
   - pct. bare ground
   - litter depth
   - soil depth
   - soil moisture percentage at 0 to 10cm and 20 to 30cm
   - ground slope
   - aspect of plot

   b. Micro-scale factors
   - distance from seedling to nearest rock
   - distance from seedling to nearest tree
   - distance from seedling to nearest clump of perennial grass
   - distance from seedling to nearest log
   - seedling coverage by leaves of perennial grass
   - litter depth at base of seedling
   - evidence of seedling drought
   - evidence of herbivory on seedling

In addition to the micro-scale factors listed above, the distances from 10 points located at random to the nearest rock, tree, clump of perennial grass, and log were measured within each 10m by 10m plot. The litter depth at these random points and the "coverage" of the ground at these points by perennial grass was also recorded.

Data analysis procedures involved comparison, using Student's "t" test, of the average numbers of seedlings found on each vegetation type. Spearman's Rank Correlation was run to establish whether or not the meso-scale variables were correlated with the number of seedlings occurring on the plots. Regressions were initially run for each vegetation type, then the data from both types were combined for a second set of regression analyses. The micro-scale factors occurring at seedlings were compared to the same factors at randomly located points using Student's "t" test and Wilcoxon Rank Sum test.

RESULTS

An average of 23.0 and 11.8 seedlings were found respectively on the perennial grass woodland and the annual grass woodland plots. The majority of these seedlings were Oregon oak; however, hybrids of Oregon oak and blue oak (*Q. douglasii*), California black oak (*Q. kelloggii*), and coast live oak were also present (table 1). Seedlings were larger on the plots located in the perennial grass woodland.

Comparison of the average number of oak seedlings observed in each type, using Student's "t" test, showed no significant difference. Similar comparisons between the two vegetation types of the average number of Oregon oak seedlings or hybrid oak seedlings also showed no significant difference. The results of these statistical comparisons are due to the wide range in seedling densities on the plots. Plot number 3 (perennial grass woodland) supported 73 seedlings while plot number 5 had 6 seedlings; the range was from 0 to 24 seedlings on the annual grass woodland plots. We believe this wide range in seedling densities may reflect both local differences in seed production from plot to plot and random variation in seed production from one tree to another. Statistical comparison of average height and average diameter of seedlings likewise showed no significant differences between the perennial and annual grass woodland plots.

Meso-scale Environmental Factors

Average values were calculated for the meso-scale environmental factors measured in this study on five plots within each vegetation type (table 2). None of these averages was significantly correlated with seedling density in either of the oak woodland types. The lack of significant correlation may be due to the small sample size at this preliminary stage in our study. When data from both sets of northern oak woodland plots were combined, Spearman's Rank Correlation Test showed a significant correlation only between the number of seedlings per plot and litter depth.

The lack of a demonstrable correlation between seedlings and crown cover of either trees or perennial grass may be due, in part, to a curvilinear relationship between these two variables, cover and seedling establishment. Spearman's Rank Correlation Test measures the correlation between the independent and dependent variable assuming a linear relationship. The lack of correlation between soil moisture percentage and the number of seedlings may be spurious because of the unusual characteristics of precipitation in spring, 1990. A heavy storm at the end of May brought soil moisture levels back to near field capacity. This precipitation fell after the annual grasses were senescent. This added soil moisture in the annual grass woodlands was slowly

Table 1—*Number, height, and diameter of seedlings on $100m^2$ plots to Oregon oak woodlands at Annadel State Park*

Plot Number	Understory Type	Species	Number	Average Height (cm)	Average Diameter (mm)
1	perennial grass	Quga	3	13.6	3.0
		Hybrid	7	13.0	3.0
		Total	10	13.2	3.0
2	“	Quga	3	8.6	2.0
		Hybrid	4	10.0	2.5
		Total	7	9.4	2.2
3	“	Quga	42	12.2	2.6
		Hybrid	30	9.7	2.4
		Quag	1	30.0	10.0
		Total	73	11.0*	2.5*
4	“	Quga	15	21.0	4.0
		Hybrid	4	13.0	3.5
		Total	19	19.4	3.9
5	“	Quga	6	8.5	2.6
		Total	6	8.5	2.6+
Average	“	Quga	13.8	12.8	2.8
		Hybrid	9.0	11.4	2.8
		Quag	0.2	30.0	10.0
		Total	23.0	12.3*	2.8*
6	annual grass	Quga	6	12.5	2.8
		Hybrid	10	9.1	2.3
		Total	16	10.5	2.5
7	“	Total	0	0	0
8	“	Quga	5	8.4	2.4
		Total	5	8.4	2.4
9	“	Hybrid	24	9.6	3.0
		Total	24	9.6	3.0
10	“	Quga	6	10.2	2.2
		Hybrid	8	8.2	2.0
		Total	14	9.0	2.1
Average	“	Quga	3.4	10.1	2.5
		Hybrid	8.4	9.0	2.4
		Total	11.8	9.4	2.5

* Quag height and diameter omitted from calculation of the average
Quga = Quercus garryana
Hybrid = Quercus garryana X douglasii;
Quag = Quercus agrifolia

Table 2—*Average values for Meso-scale environmental factors measured on 100m² Plots in Oregon oak woodland at Annadel State Park*

Environmental Factor	Understory Type: Perennial Grass	Understory Type: Annual Grass
1. Number of trees/plot	Value	Value
Quga	6.0	4.6
Hybrid	0.2	0.4
Quke	0.2	0.2
Arma	0.4	0.2
Total	7.0	5.2
2. Tree diameter (cm)		
Quga	22.2	31.5
Hybrid	16.0	31.0
Quke	21.0	22.0
Arma	7.0	13.0
Total	20.6	28.5
3. Tree basal area (m^2)		
Quga	0.252	0.307
Hybrid	0.004	0.033
Quke	0.020	0.008
Arma	0.001	0.002
Total	0.277	0.350
4. Tree crown cover (pct)	57.0	67.0
5. Height of dominant trees (m)	11.8	11.2
6. Perennial grass cover (pct)	60.0	5.1
7. Annual grass cover (pct)	5.0	68.0
8. Litter cover (pct)	16.3	15.0
9. Average log cover (pct)	0.1	0.9
10. Average rock cover (pct)	18.1	9.0
11. Bare ground (pct)	0.0	0.2
12. Litter depth (cm)	3.8	3.1
13. Soil depth (cm)	20.1	18.9
14. September soil moisture (pct)		
10 cm depth	9.2	9.0
30 cm depth	12.1	10.3
15. Slope (pct)	23.2	14.6

Quke = *Quercus kelloggii*
Arma = *Arctostaphylos manzanita*
Quga = *Quercus garryana*
Hybrid = *Quercus garryana X douglasii*

depleted during the ensuing summer months by evaporation and transpiration by the overstory oaks and the oak seedlings. The added spring soil moisture in the perennial grass woodland was depleted during the summer by a combination of evaporation and transpiration, primarily from the perennial grasses. In a normal rainfall year we would anticipate lower soil moisture levels in the annual grass woodland because of the normally early depletion by the annual grasses.

Micro-scale Environmental Factors

Analysis of micro-scale environmental factors was focused on local micro-site factors which were assumed to protect oak seedlings from evaporative stress and from herbivory by deer and pocket gophers. Distances to nearby (within 100cm) objects which might afford protective shade and visual or physical barriers to herbivory were measured for each seedling and for 10 points located at random in each plot. Litter depth adjacent to each seedling and at the random points was also measured as was the percentage of seedlings showing browse damage and drought damage. Results of these measurements are shown in table 3. The distance from random points to the nearest object of any type on the plots which might interfere with deer browsing was less than the distance from seedlings to similar adjacent objects. Comparison of the difference in distances using Student's "t" test and Wilcoxon Rank Sum test showed that the difference in each vegetation type was not significant. A greater number of objects, particularly rocks and perennial grass clumps, occurred in the perennial grass woodland. However, the differences in the distances between nearby objects and random points and the differences in the distances between nearby objects and seedlings were not significant when the two vegetation types were compared. Coverage of seedlings by perennial grass leaves, although greater than coverage of random points, was not significantly different in either vegetation type. Likewise, differences in average litter depths at random points were not significantly different from average litter depths adjacent to seedlings. Drought damage was lower in annual grass woodlands than in perennial grass woodlands. Browse damage was greater on plots in the annual grass type. Differences, however, were not significant.

CONCLUSIONS

The lack of any statistical correlation between environmental factors at either the macro, meso, or micro-scale is, we believe, a function of the small sample size available for analysis

Table 3—*Micro-scale environmental factors measured on 100m² plots in Oregon oak woodlands at Annadel State Park*

Environmental Factor	Perennial Grass: Oak Seedling	Perennial Grass: Random Point	Annual Grass: Oak Seedling	Annual Grass: Random Point
1. Average distance (cm) to nearest				
rock	60.6	57.5	92.2	80.7
perennial grass clump	21.5	18.8	71.4	93.2
log	94.7	97.6	86.9	93.2
tree	95.6	97.6	85.0	97.7
object (rock, perennial grass, etc.)	17.3	14.7	58.2	55.4
2. Coverage by perennial grass leaves (pct)	86.4	50.4	6.6	2.0
3. Litter depth (cm)	3.8	3.8	3.1	3.1
4. Drought damage seedlings (pct)	44.3	—	17.5	—
5. Browsed damaged seedlings (pct)	57.4	—	80.0	—

at this time in our study. The variability between plots will most likely be reduced as the number of samples increases. We are convinced from our field observations at Annadel State Park that relationships do exist between seedling establishment and some environmental factors at each of the three spatial scales used in this study.

At the macro-scale we anticipate that an increased sample size will confirm a significant difference between the numbers and sizes of oak seedlings observed on the two northern oak woodland types. The larger number of seedlings and their larger size (height and diameter) suggested by the average number and average seedling size on the perennial grass woodland plots is, we believe, a function of the macro-scale environmental factors which distinguish the northern oak woodland types. We believe these factors to be soil type and aspect, both of which influence water availability to oak seedlings.

Meso-scale environmental factors which we anticipate will show a significant correlation with seedling establishment are soil moisture, rock cover, and litter cover. In a typical rainfall year we should anticipate higher soil moisture in perennial grass woodlands. The unusual pattern of late spring precipitation in 1990 accounts for a leveling of the differences in soil moisture both between the two vegetation types and among plots of each vegetation type. We believe that higher soil moisture levels at the end of the growing season will correlate with greater numbers of oak seedlings.

With increased sample size, the percentage of rock cover should show a significant correlation with seedling density and survival in perennial grass woodlands. Rock cover is significant because it facilitates increased soil moisture due to run-off from the impervious surfaces to the surrounding soil. Rock cover also reduces soil moisture loss due to evaporation, since soil beneath the rocks is protected from solar radiation, thus providing pockets of available moisture later into the growing season. Rocks below ground serve as condensation surfaces for water vapor in the soil, thus concentrating soil moisture near their boundary with the soil. The presence of rocks on the ground may reduce the use of an area by deer.

Percentage of the ground covered by litter should also be shown to correlate with seedling numbers as our sample size increases. We believe that litter cover is significant because it protects acorns from predation and desiccation prior to germination and it reduces evaporation of moisture from the soil. It also is a measure of the area of ground that is not occupied by plants, and therefore under reduced loss of soil moisture to transpiration.

At the micro-scale of environmental factors a larger sample size is not expected to change our observation, based on the current data, that objects such as rocks, logs, or perennial grass leaves protect oak seedlings from herbivory. In both woodland types, the distances from random points to nearby objects were closer than the distance from seedlings to the nearest object. Although the trends in herbivory were greater on annual grass woodland plots, where protective objects occurred less frequently, we do not think that more data will demonstrate the protective effect of nearby objects. The evidence of herbivory we observed was assumed to be the result of deer browsing. This may not be the case. Smaller herbivores, less affected by nearby objects, may be responsible for the herbivory we recorded. If, however, deer are responsible for the observed browsing, their behavior may be more influenced by vegetation type than nearby objects.

Data from the current plots showed a trend toward greater drought injury to seedlings in oak woodlands with perennial grass understories. We think this trend is the result of the unusual pattern of late spring precipitation in 1990 and is not typical. The resulting additional moisture available to oak seedlings on plots with annual grass understories minimized drought injury to the seedlings on these plots. Competition for soil moisture between the perennial grasses and oak seedlings following the late spring rain may account for the trend in greater drought injury to seedlings on the plots with perennial grass understories.

The data base available at this point in our study is insufficient to make conclusions concerning the relative value of the three scales of environmental factor analysis. We look forward to an elucidation of this question when a greater data base is assembled.

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Evaluating Tree Protection Devices: Effects on Growth and Survival-First-Year Results[1]

L. R. Costello R. H. Schmidt Gregory A. Giusti[2]

INTRODUCTION

The protection of seedlings from animal browsing is critical for the survival and growth of many tree species. This is particularly true in wildland areas and arid areas (McAuliffe, 1986), and oftentimes in urban areas. A variety of techniques and devices have been used to protect seedlings, from using straw stubble to milk cartons to plastic or metal screens. Recently, Tuley (1985) reported the successful use of "tree shelters" to protect oak seedlings in England. Tuley's tree shelters are essentially translucent plastic tubes (up to 6 feet in height and approximately 3 inches in diameter) which are placed over young seedlings. Tree shelters were found to significantly accelerate seedling height growth as well as protect them from animal injury. More recent reports (Frearson, 1987; Potter, 1989; and Bainbridge,1990)have found similar results for other species. Although other protection devices improve survival of young trees, their effects on growth (positive or negative) are not notable or not documented.

This paper reports on the effects of three protection devices on the survival and growth of four tree species. Tree shelters, plastic mesh screens, and wire screens were selected. Since many reforestation and revegetation sites in California occur in areas with little or no summer rainfall, and which frequently are not irrigated, tree survival and growth were evaluated under both irrigated and nonirrigated conditions. The study was designed to address the following questions:

1) are there notable (positive or negative) effects from these tree protection devices on survival and growth?

2) when soil moisture is limiting, are effects equivalent to the irrigated condition?

3) are effects consistent for all test species, or do species -specific effects occur?

4) do any of the devices increase or diminish seedling injury by insects or diseases?

[1] Presented at the Symposium on Oak Woodlands and Hardwood Rangeland Management, October 31 - November 2, 1990, Davis, California.

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METHODS AND MATERIALS

Experiments were conducted at the University of California Hopland Field Station, Hopland, California (elevation 800 feet). A half-acre plot of pasture land (Sequel loam) was fenced to exclude livestock and deer. All pasture vegetation was controlled with glyphosate prior to planting. The two study plots, irrigated and nonirrigated, were separated by a 20 foot unplanted buffer strip. Using a randomized complete block design, six blocks were established in the irrigated plot and 10 in the nonirrigated plot. Seedlings of blue oak (*Quercus douglasii*), valley oak (*Q. lobata*), interior live oak (*Q. wislizenii*) and Douglas-fir (*Pseudotsuga menziesii*) were planted into auger-dug holes (5 foot centers) on March 15 and 16, 1990. Blue and valley oak-seedlings were 6 months old and growing in leach tubes (germinated Fall, 1989) while interior live oaks were 1-year-old seedlings germinated in Fall, 1988. Douglas fir were 1-year-old bare-root seedlings provided by the California Dept. of Forestry. All seedlings were irrigated and fertilized (Osmocote 14-14-14) after planting. All plants were checked for viability after 2 and 5 weeks, and dead plants were replaced. Once initial establishment was complete, treatments were installed as follows:

1) Ventilated Tree Shelters (VTS) - Tubex(R) tree shelters (2 ft. high) with six 1-inch diameter ventilation holes drilled into sidewalls at 6, 12, and 18 inch levels;

2) Nonventilated Tree Shelters (NVTS) - Tubex(R) tree shelters without ventilation holes;

3) Hopland Tents (HT) - molded plastic mesh screens (1/16 inch diameter openings) which are sealed at one end (18 inches high by 8 inches wide);

4) Wire Screens (WS) - window screening cut and fastened to form a cylinder around a seedling with the top sealed (18 inches high by 9 inches wide);

5) Controls (C) - no protection device.

All devices were secured in place with appropriate stakes. Treatments in the irrigated plot began 4/24/90 while those in the nonirrigated plot began two weeks later.

A drip irrigation system was installed to supply water in the irrigated plot. Single emitters were placed at the base of each plant, delivering water at the rate of 1 gallon per hour. Irrigation began in mid May and continued weekly through October (2 gals/plant/week). Nonirrigated plants were hand-watered three times after planting, with the last irrigation occurring in early June.

Plant height (cm) and stem diameter (mm) measurements were taken 4/24/90 and 9/12/90. Diameter measurements were taken 2 inches above ground. Height measurements were made from ground level to the apical bud or meristem of the dominant stem. In cases where codominant stems occurred, competing stems were lightly headed to promote the development of a single stem.

Weed control was maintained by mowing and hand-pulling. Planting basins were kept weed-free.

Soil moisture potentials were measured periodically in the irrigated and nonirrigated plots, and air temperatures inside and outside all tree protection devices were measured on 7/31/90 and 8/1/90.

RESULTS

Survival

Survival of all species was generally good in the irrigated plot (Fig. 1). All valley and live oak seedlings survived, as did 96 percent of the blue oaks. At 83 percent, Douglas-fir survival was lowest. Survival did not appear to be related to treatments.

In the nonirrigated plot, survival was lower (Fig.2). Across treatments, valley and blue oak survival was highest (84 and 82 percent, respectively), while live oak survival was 63 percent. Only two of 50 Douglas-fir seedlings survived. It appears that some irrigation in the summer months is critical for Douglas-fir survival. Among treatments, survival was least in unprotected control plants (45 percent), while protected plants ranged from 53 to 68 percent survival. Excluding Douglas-fir, oak survival ranged from 70 to 90 percent with protection, and 58 percent without protection.

Growth

a. Irrigated Plot

After 5 months, growth response was somewhat variable for both treatments and species (Figs. 3 to 10). In most cases there was a substantial range in height and diameter growth among replicates. Some trees grew a lot while others grew very little. Height growth of controls for all species was less than that of protected plants, while diameter growth was less in most cases. Douglas-fir showed the least increase in height for all species, while valley oak was largest in height and diameter increase.

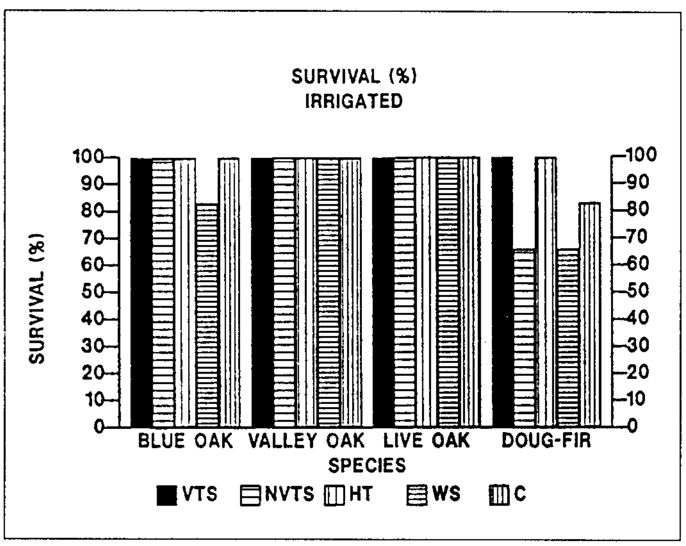
In comparing treatments, a variable diameter response occurred: largest diameter increase was found for a different treatment in each of the species. Across the species, plants in wire screens (WS) were found to have largest diameter increase, while those in non-ventilated tree shelters (NVTS) were least.

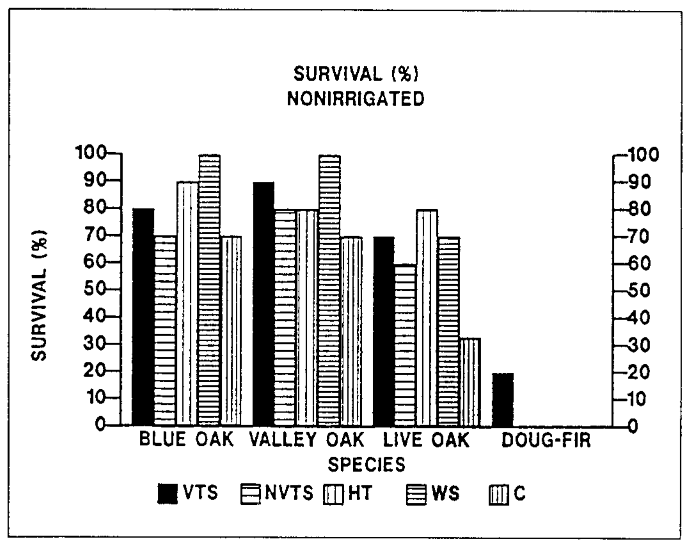
Height increase was largest in tree shelters (both NVTS and VTS) for most species. Greatest growth was found in NVTS in valley and live oak, while least occurred in Hopland tents for blue oaks. Again, all controls were less than treatments.

b. Nonirrigated Plots

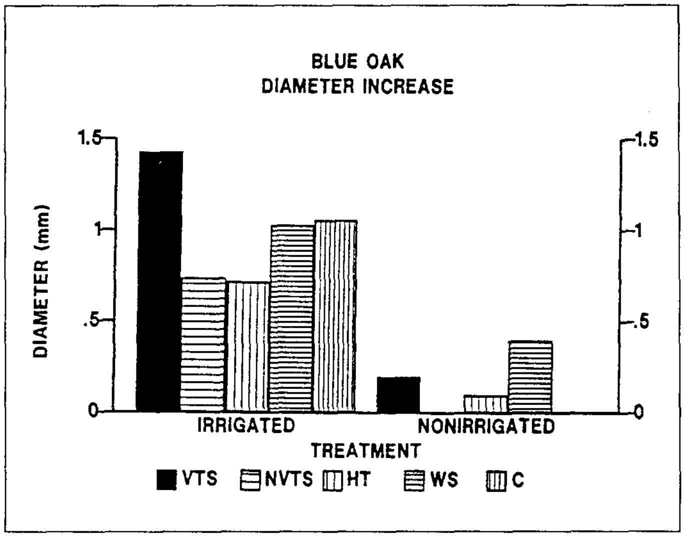
Since only two of 50 Douglas-fir seedlings survived in the nonirrigated plot, analysis of results is confined to oak species. Little growth occurred in the nonirrigated plot. Mean diameter and height differences were approximately 20 and 15 percent, respectively, of the growth found in irrigated plots. Interior live oak generated the most growth with an average 5.2 cm height increase and 0.5 mm diameter increase, while blue oak was slowest, growing only 0.5 cm in height and 0.14 mm in diameter.

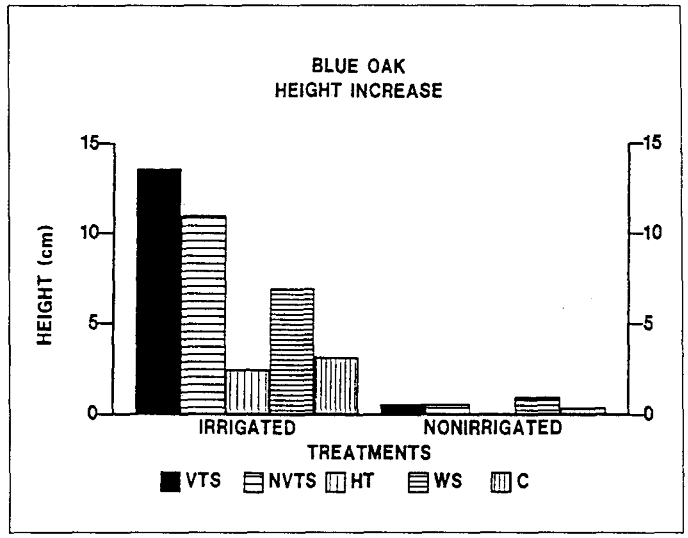
Treatment effects found that wire screens (WS) generated greatest height increases for all species. Least growth was found in ventilated tree shelters (VTS), i.e., aside from control plants which grew less than all treatments.



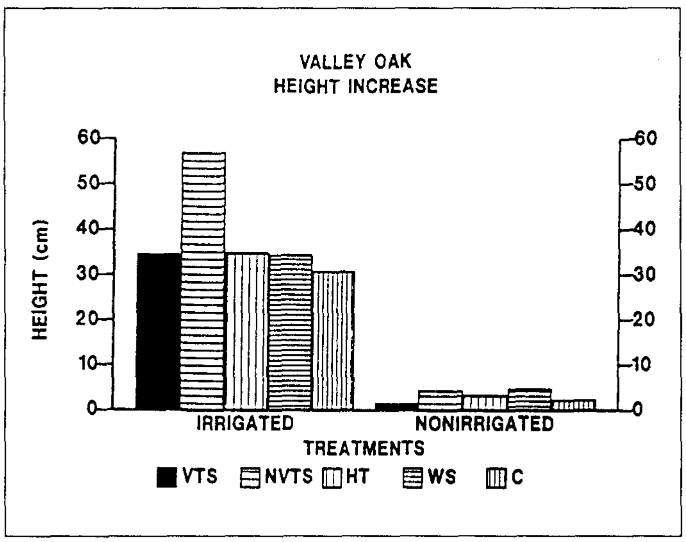


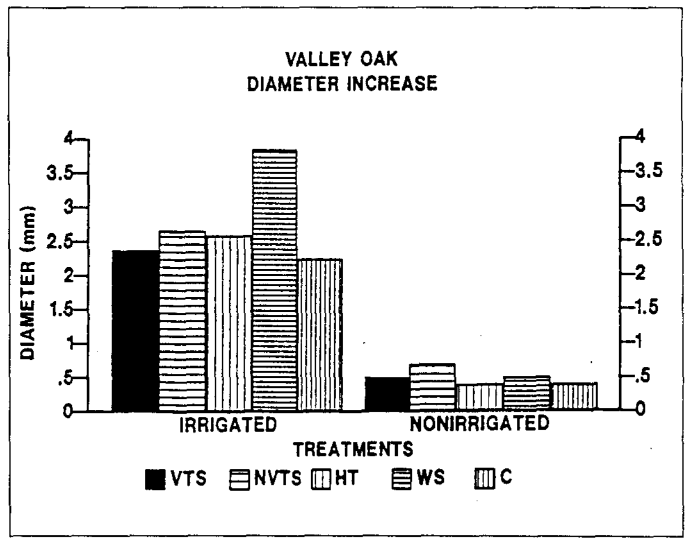
Figures 1 and 2—Percent survival of test species in irrigated and nonirrigated plots. See "Methods" for description of treatments.



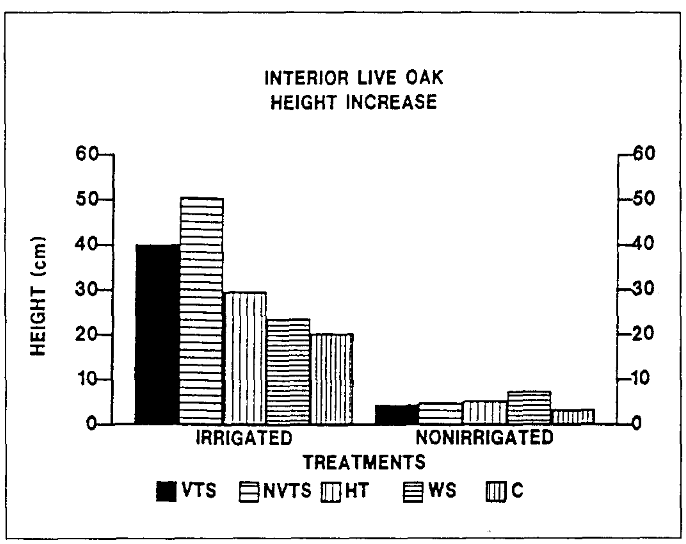


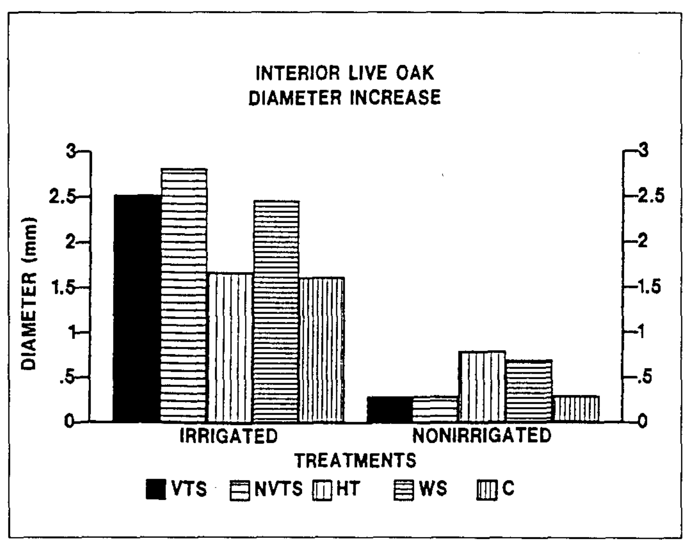
Figures 3 and 4—Height and diameter growth increase of blue oak seedlings *(Q. douglasii)* in irrigated and nonirrigated plots. See "Methods" for description of treatments.



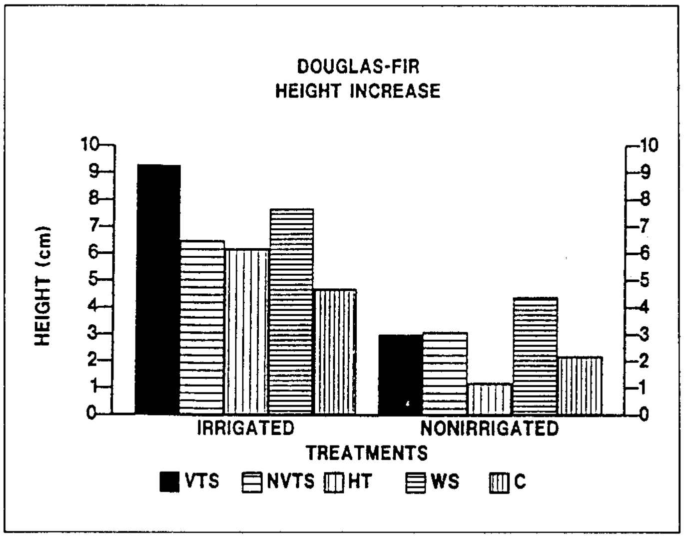


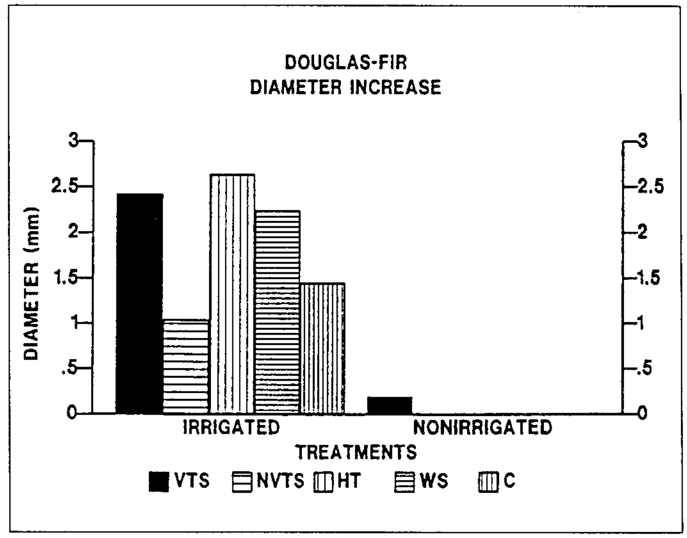
Figures 5 and 6—Height and diameter increase of valley oak seedlings *(Q. lobata)* in irrigated and nonirrigated plots. See "Methods" for description of treatments.





Figures 7 and 8—Height and diameter increases of interior live oak *(Q. wislizenii)* in irrigated and nonirrigated plots. See "Methods" for description of treatments.





Figures 9 and 10—Height and diameter increases of Douglas fir seedlings *(P. menziesii)* in irrigated and nonirrigated plots. See "Methods" for description of treatments.

Temperatures and Soil Moisture

Temperatures inside Hopland tents and wire screens were approximately 4°F higher than the outside temperature (95°F) in both irrigated and nonirrigated plots. Temperatures inside treeshelters (both VTS and NVTS) were approximately 4°F higher and 7°F higher than outside temperature (97°F) in irrigated and nonirrigated plots, respectively.

Soil matric potentials were found to reach a maximum 25 cb at 10 inches in the irrigated plot, and were greater than 100 cb at 10 inches in the nonirrigated plot.

Insects and Diseases

Although grasshoppers were found in several of the protection devices, regardless of type, no significant insect or disease injury was found on any of the plants, protected or unprotected.

DISCUSSION

In nonirrigated areas, survival of all three oak species appears to be enhanced by the protection devices used. Survival of Douglas-fir was very poor without summer irrigation, regardless of whether they are protected or not. This suggests that protection devices can serve two roles:

1) physical protection from animal browse, and

2) modification of the plant environment to reduce factors contributing to plant dehydration. This second role may be particularly important in harsh environments (windy, hot, dry) where both "physiological" and physical protection may be needed.

Results of treatment effects on growth must be considered preliminary at this time. The first five months after planting is often considered an "establishment" period, where root growth is likely a "higher priority" during this phase than top growth. It is interesting to note, however, that protection devices generally did enhance top growth during this time. Of particular interest is the indication that tree shelters accelerate height growth in the oaks studied. This effect would be of significant value in reducing the time required for oaks to develop shoots above the deer browse line. Once established to this point, little or no protection may be needed. This would certainly accelerate many reforestation or revegetation timetables.

In nonirrigated areas, some protection appears helpful in promoting growth. The implication being that these devices allow plants to maintain a more satisfactory internal water balance than unprotected plants. Perhaps water deficits are not as frequent and/or severe when plants are protected. Considering the response of Douglas fir to irrigation, however, this is likely a species specific response, i.e., water deficits which merely slow the growth of one species may be fatal to another.

Treatment effects on growth may be more pronounced in subsequent years. Tuley (1985) found a dramatic increase in height growth of *Quercus petraea* protected by tree shelters in the second and subsequent years. In this study, height and diameter growth will be monitored for another two years.

FURTHER RESEARCH

Naturally occurring seedlings should also benefit from protection. Certainly, physical protection from animal injury would be of value, while growth enhancement would accelerate the establishment period for many species. Studies are, therefore, planned to evaluate the usefulness of these devices on naturally-seeded tree species.

ACKNOWLEDGMENTS

Assistance provided by Amy Peters and the staff at the Hopland Field Station is gratefully acknowledged.

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Seasonal Growth Patterns of Blue and Valley Oak Seedlings Established on Foothill Rangelands[1]

Douglas D. McCreary[2]

Abstract: Blue (*Quercus douglasii* Hook. & Am.) and valley (*Quercus lobata* Née) oak seedlings were planted on a foothill rangeland site in 1987 and 1988. Both species were watered their first year but received no irrigation thereafter. They were evaluated during each subsequent spring and summer for survival, weekly height growth and total year-end height. Seedling survival was extremely high for both species and height growth was rapid and vigorous. Blue oak seedlings four growing seasons after planting averaged over 2.3 m and valley oaks after three seasons averaged 2.0 m in height. Yearly height growth occurred in a series of flushes beginning around the end of March. Typical seedlings had either two or three flushes, although the average number per year has been declining. During flush periods, growth was rapid, often exceeding 15 cm per week. The greatest height increment occurred during the second flush. These results suggest that both blue and valley oaks have the capacity to grow rapidly as young seedlings if suitable environmental conditions are maintained.

Two native oak species reported to be regenerating poorly in portions of California are blue oak and valley oak (Bolsinger 1988, Muick and Bartolome 1987). While concern about the natural regeneration of these species has been voiced since the turn of the century (Sudworth 1908), only during the last five years has a large amount of research focused on understanding and solving this problem. Results from these studies have greatly increased our knowledge of the causes of poor regeneration and have demonstrated a variety of techniques for successfully growing and planting seedlings. To date, however, most of the studies have evaluated field performance in terms of survival or year-end size, and little has been reported about phenological development or seasonal growth patterns. Such information can be vital to understanding basic physiological mechanisms operating within seedlings, and can help clarify some of the factors limiting field performance of both natural and planted seedlings. This paper describes the results of an intensive two-year evaluation of blue and valley oak seedlings planted on a foothill rangeland site. It is hoped that this information will provide some insights into the factors influencing juvenile seedling growth and help promote greater establishment success in regeneration plantings.

[1] Presented at the Symposium on Oak Woodlands and Hardwood Rangeland Management, October 31-November 2, 1990, Davis, California.

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METHODS

Blue Oak Trial

The first field plot was established in April 1987 with the planting of 120 blue oak seedlings at the Sierra Foothill Range Field Station near Browns Valley, California (elev. 200 m). These seedlings came from acorns collected near Rescue, California (elev. 425 m) and had been grown for one year in plastic boxes approximately 6 cm square by 13 cm deep. They were transplanted into a bare field plot into holes that had been augered to a depth of 90 cm and backfilled. The soil at the site was an Auburn-Las Posas-Argonaut rocky loam and was between 60 and 100 cm deep. Prior to planting, a 21 g fertilizer tablet (20-10-5) was placed approximately 30 cm deep in each hole. Immediately after planting, seedlings were covered with 40 cm tall pieces of aluminum screen to prevent browsing and insect damage. As the seedlings grew taller, these cages were opened at the top and were eventually replaced by 90 cm tall screen cylinders. Several seedlings which died during the first 2 weeks were replaced.

At the time of planting, seedlings were thoroughly watered and were irrigated regularly with drip irrigation throughout their first summer. However, no irrigation was provided during the three subsequent years.

Valley Oak Trial

These seedlings were planted a year later, adjacent to the blue oak plot. The same number of seedlings was planted with the same spacing, augering and fertilization treatments. Seedlings were from acorns collected in Briones Park in Contra Costa County (elev. 100 m) the previous fall and had been grown for approximately four months in 4 by 4 by 15 cm containers. After planting, seedlings were watered during the subsequent summer with varying levels of irrigation as part of another experiment (McCreary 1989). However, no irrigation was provided in 1989 or 1990.

Measurements

At the end of the 1987 growing season (blue oaks only) and the 1988, 1989, and 1990 growing seasons (blue and valley oaks) the survival and year-end height of each seedling were recorded. In addition, in both 1989 and 1990 leaf-out date of each seedling was determined, as well as the weekly height increment of the terminal branch of each seedling during 24week periods beginning in early April. Since both species tended to have droopy leaders, terminal height was determined by straightening out the main branch and recording either total seedling height or height increment of the actively growing shoot. If there was no single obvious terminal shoot, the height of the tallest branch was recorded.

In addition to height measurements, the number of flushes in each growing season was also recorded. This was determined by evaluating height increment patterns, as well as examining the terminals for buds, bud swelling, and if flushing occurred, for evidence of bud scars on the stem. From the collected data several variables were also calculated including average weekly height increment, the number of seedlings actively growing during any week (those that grew 2 cm or more), and height increment per flush.

RESULTS

Blue Oak — Survival, Height Growth and Leaf-out Date

Seven seedlings died during the first summer, but no mortality has occurred since. Average height increment during the first year was approximately 25 cm. Since then, however, seedlings have grown rapidly and now average over 2.3 m in height (fig. 1). There was a very consistent pattern of growth during 1989 and 1990. In both years seedlings began leafing out (leaves emerging through the bud scales of the most advanced bud) during a two-week interval, beginning in the last week in March. Average leaf-out date was March 30 in 1989 and March 25 in 1990. There was also a consistent pattern for growth initiation among seedlings within the plot. For both years the difference between the date the first and last seedling leafed out was only 11 days.

Flush Pattern

For both years the first flush of growth lasted about two weeks, with relatively little height increment (fig. 2). By the middle of April, most seedlings had stopped elongating and set a resting bud. The period between the first and second flush varied considerably among seedlings but the average time, about five weeks, was fairly consistent between years. However, while all seedlings had at least two flushes in 1989, there were four seedlings that only had one flush in 1990. By the end of May in both years most seedlings had resumed active growth and were elongating rapidly. The greatest height increment occurred during this second flush. For instance in 1989, second flush increment accounted for 68 percent of the total height growth, while in 1990 it accounted for 83 percent (fig. 3). Not only was

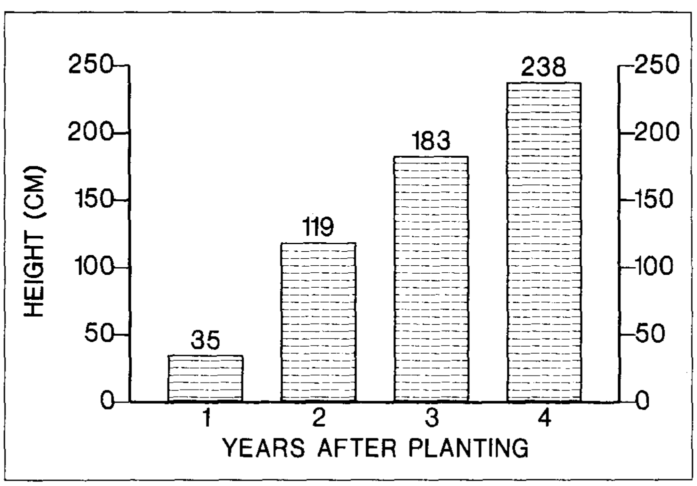

Figure 1—Average total height of blue oak seedlings 1, 2, 3 and 4 years after planting.

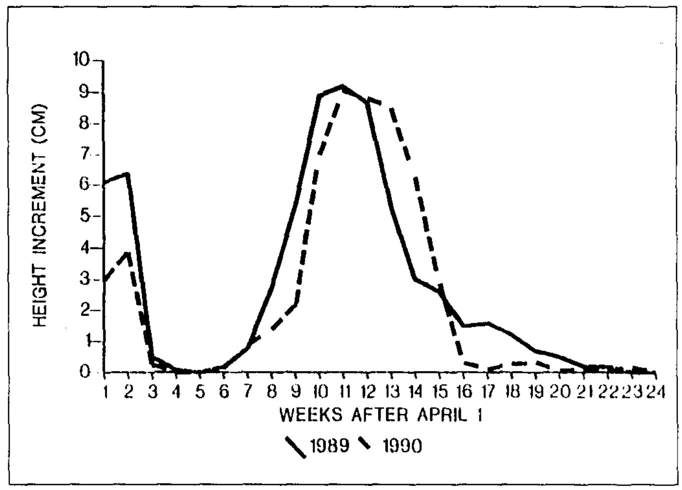

Figure 2—Average weekly height increment of blue oak seedlings in 1989 and 1990.

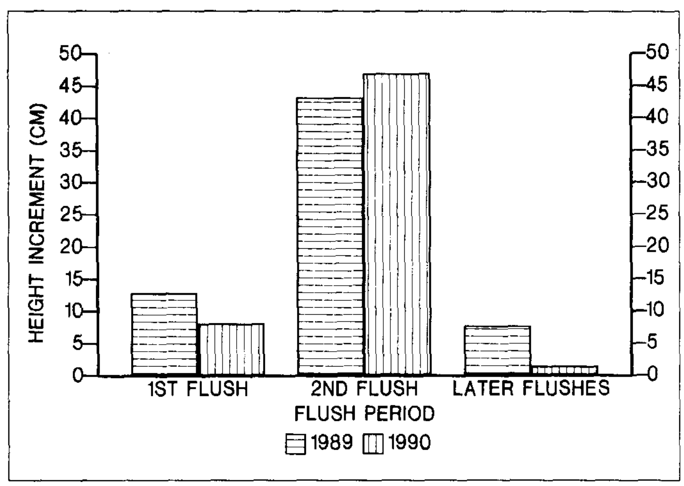

Figure 3—Average height increment per flush (averaged over all seedlings) of blue oaks in 1989 and 1990.

there a large total amount of growth during this period, but the growth rate was exceedingly rapid. During the peak growth period, average height growth of all seedlings in the plot was nearly 10 cm a week, while many individuals grew more than 15 cm. The elongation interval was also far longer than for the first flush, averaging about six weeks. Almost half of the seedlings also had a third flush in 1989. However, the initiation of this flush varied tremendously, from mid-summer until early fall. In general, this flush period was relatively brief and contributed little to total height increment. In 1990, only a handful of seedlings had a third flush, however. The average number of flushes in 1989 was 2.41, compared to an average of 2.08 in 1990.

Valley Oak — Survival, Height Growth and Leaf-out Date

After three seasons, all of the valley oak seedlings that were planted are alive. Average yearly height growth was slightly greater than that of the blue oaks (fig. 4) and seedlings are now just under 2 m tall. Average leaf-out date for the valley oaks was March 30 in 1989, and March 21 in 1990.

Flush Pattern

The same general growth pattern observed for blue oaks was also followed by the valley oaks, with a relatively weak first flush followed by a rapid, vigorous second flush (fig. 5). However, there was greater variability among valley oak seedlings in the growth patterns than for blue oaks. For instance, there was a three-week period beginning around mid-April in both years when not a single blue oak seedling was actively elongating. For valley oaks, on the other hand, at no time between April and mid-June of either year were all seedlings inactive.

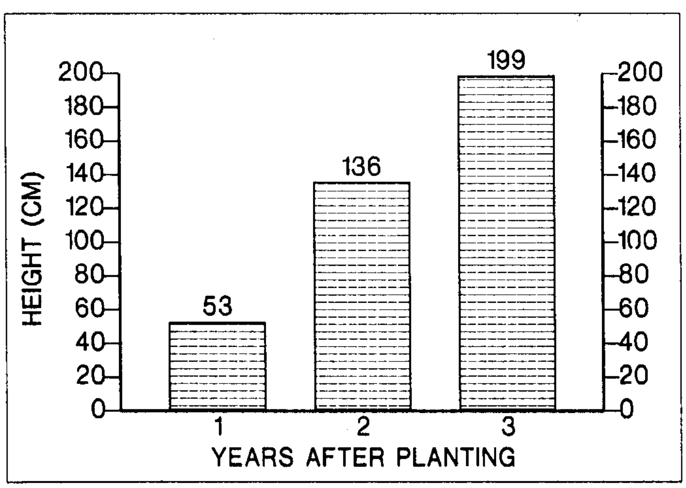

Figure 4—Average total height of blue oak seedlings 1, 2, 3 and 4 years after planting.

The pattern between years was also much more inconsistent for valley oaks. In 1989, the pattern was quite similar to that for the blue oaks, with most seedlings flushing early, setting a bud and then initiating a second flush in early June. In 1990, however, 14 percent of the seedlings did not set a bud in April and continued elongating into the summer. These longer first flushes also resulted in a higher percent of the overall growth accounted for by the first flush than it was in 1989 (fig. 6). As with the blue oaks, the average number of flushes per seedlings was greater in 1989 (2.57) than in 1990 (1.88).

DISCUSSION

One of the most surprising results of this study was the high survival and rapid growth rate of both species, even though no

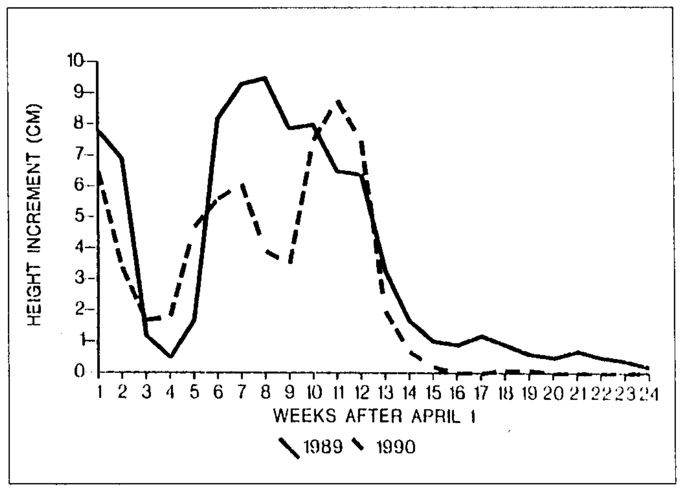

Figure 5—Average weekly height increment of valley oak seedlings in 1989 and 1990.

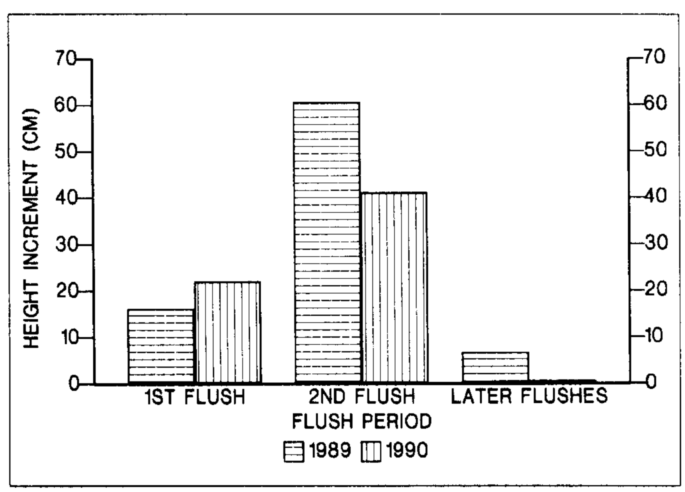

Figure 6—Average height increment per flush (averaged over all seedlings) of blue oaks in 1989 and 1990.

irrigation was provided after initial establishment. This growth occurred in spite of the fact that some seedlings were repeatedly browsed by deer, covered by powdering mildew, and/or chewed on by a variety of insects. Thus, even though both species have been found to have problems naturally regenerating, results from these trials indicate that once established, seedlings are very resistant to mortality factors. Of 240 total seedlings planted, only seven died the first year, and none have died since.

Growth rate for blue oak has also been dramatically greater than expected. While valley oak is reported to grow fairly rapidly under favorable conditions, blue oak is generally characterized as an extremely slow growing species. In this field trial, however, yearly height growth of blue oaks averaged well over 50 cm a year, and there has been no evidence of a significant slowdown. While it is impossible to predict field performance at other sites based upon this one trial, these results suggest that slow growth of blue oaks in the field is probably a result of environmental limitations, rather than an inherent propensity to grow slowly. This is encouraging since one of the greatest barriers to successfully regenerating native oaks is browsing of young plants by deer and livestock before they become tall enough to withstand these pressures. If seedlings can be planted, protected, and maintained in such a way that the growth rate can be significantly increased, the interval during which plants are vulnerable could be greatly reduced. While such intensive management (weed control, augering, screen protection, etc.) is currently costly, it may be ultimately less expensive than repeated plantings, slow growth, and in some cases, land being unavailable for other uses (i.e., livestock production).

Another dramatic finding of this study was the marked periodicity of terminal growth and the great disparity between first- and second- flush increment. This pattern contrasts with that of many conifers grown in similar environments, where the first (and sometimes only) flush results in the majority of height growth and subsequent flushes contribute little. This result was surprising since the buds preceding the first flush for both species were so much larger, robust, and appeared to be more developed than those preceding the second flush.

There are several possible explanations for these growth patterns. In contrast to most conifers, both oak species evaluated are deciduous and were just starting to leaf out when terminal elongation began. It is possible that the initial height growth was therefore limited by lack of photosynthesis. By the time the second flush began, on the other hand, the leaves were fully expanded and able to generate more photosynthate to support terminal growth.

Environmental conditions when these flushes took place were also quite different and may have further contributed to the observed growth differences. At the time of the first flush, soils were very wet, but soil and air temperatures were still relatively cool. By the time the second flush began, however, there was still abundant soil moisture (since the competing vegetation was controlled) but temperatures had increased substantially. For instance in 1989 average air temperatures were 18°C during the first two weeks in April and 22°C during the first two weeks in June, while soil temperatures 15 cm beneath the surface were 17°C and 23°C respectively. Such increases could have substantially influenced growth rates since these temperatures are closer to the optimum range for photosynthesis and other processes favoring growth (Salisbury and Ross 1969).

The final factor which may also have contributed to height growth differences between flushes was competition from root growth. During periods of active root growth, roots act as a sink and can reduce the energy available for the above ground part of the plant. While it is known that there is a periodicity to root growth patterns for most woody species (Kramer and Kozlowski 1979) and there is often a marked peak of root activity in the early spring, not enough research has been done on the two species evaluated here to determine if this was occurring.

A final observation from these trials was that both species seemed very resilient and able to withstand a wide range of environmental conditions. When both species were browsed by deer before mid summer, they quickly resumed growth from previously dormant lateral buds. They also tolerated a tremendous range of temperatures from a low of -9°C to a high of 43°C and even survived a rare foothill snow storm which seriously damaged an adjacent planting of eucalyptus. As young seedlings they were also able to remain actively growing under what appeared to be very harsh conditions. In 1988, for instance, 40 percent of the blue oaks were flushing in August, even though there had been very little rainfall since April and almost all other vegetation on the hillsides had turned brown.

CONCLUSIONS

These trials indicate that planted blue and valley oak seedlings can have high survival and are capable of extremely rapid juvenile growth under favorable environmental conditions. Seedings planted in augered holes containing a slow release fertilizer tablet, and maintained in a weed-free plot, grew an average of over half a meter, a year, even though no irrigation was provided after initial establishment. Only seven of the 240 seedlings died during the first year, and none died thereafter.

Both species also exhibited a determinate growth pattern with stem elongation occurring as a series of flushes separated by periods of inactivity. By far the greatest growth took place during the second flush which commenced near the end of May and lasted for approximately six weeks. Height growth during this period often exceeded 15 cm a week for certain seedlings. The average number of yearly flushes per seedling was generally between two and three, but tended to decrease as the plants became older.

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Blue and Valley Oak Seedling Establishment on California's Hardwood Rangelands[1]

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Abstract: Factors contributing to poor establishment of blue oak (*Quercus douglasii*) and valley oak (*Q. lobata*) in California oak-grassland savannas were studied in a series of acorn seeding experiments initiated in 1985. Exclusion of large herbivores permitted examination of herbaceous interference and small mammal and insect depredation. Herbaceous interference was the most important factor. Average emergence in all blue oak seedings with and without herb control was 45 percent and 29 percent, respectively. The respective values for all valley oak seedings were 60 percent and 46 percent. Average first year survival, expressed as a percentage of acorns planted, was significantly improved by elimination of herbs in both blue oak (30 percent vs. 11 percent) and valley oak (45 percent vs. 25 percent) seedings. Limited data suggests the differential in survival is maintained over time as overall survival declines. With few exceptions, the addition of screen protection to discourage predation significantly enhanced survival and growth. Shade provided by window screen cages is suspected of making an unmeasured positive contribution. Interaction between herbaceous control and protection appears to develop with time.

In the most recent and comprehensive inventory of California's hardwoods, Bolsinger (1988) reports that livestock graze the majority of nearly 3 million hectares of noncommercial woodland where oaks (*Quercus* spp.) are the dominant trees and blue oak (*Q. douglasii*), occupying about 1.2 million hectares, is the dominant hardwood type. The author also states that recruitment in blue oak stands is relatively sparse and almost nonexistent in valley oak (*Q. lobata*) stands. Results of a germination study in Monterey County suggest that unsuccessful blue and valley oak recruitment results from mortality in seedling and sapling stages rather than from inadequate germination and seeding emergence (Griffin 1971). In a later study of regeneration based on analysis of tree rings, McClaran (1985) suggests that the transition from a seedling to sapling and tree stages is more critical in limiting regeneration than acorn germination and early seedling survival.

Clearing of woodlands in rangeland improvement projects and poor natural regeneration were two of 19 concerns identified by the Hardwood Task Force of the California Board of Forestry in its December 1983 draft report (Passof and Bartolome 1985). Development of artificial restocking techniques and identification and quantification of problems associated with these techniques are needed to address the concerns raised and preserve management options in oak woodlands.

This paper examines the potential of artificially sown acorns for establishment of oak in oak woodlands of California. Specifically, we evaluated the impacts of herbaceous interference and small mammal and insect herbivory on emergence, survival, and growth of seedlings. Included is an evaluation of selected techniques for reducing negative impacts.

STUDY SITES

Over a period of 5 years, blue and valley oak acorns were directly seeded in field plots in six counties lying between latitudes 35°15' and 39°15'N (fig. 1). These oak woodland sites in California's Mediterranean-like climate have understories

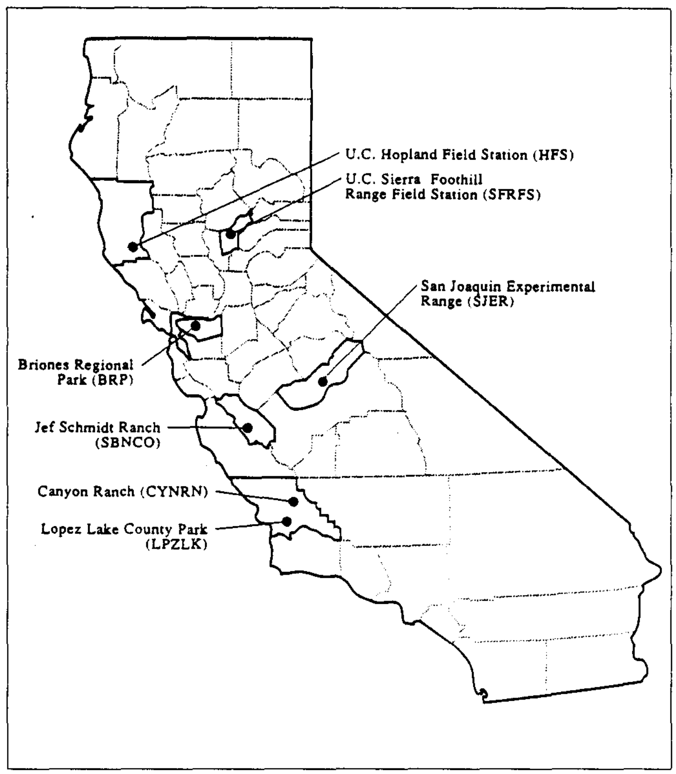

Figure 1—Location of 7 oak-grassland study sites.

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dominated by annual grasses. Throughout the study area, annuals continue to grow until all available soil water is exhausted. A discussion of the ecology and composition of California annual grasslands is presented by Heady (1977). Menke (1989) describes the influence of biomass management (grazing) on productivity and composition.

San Luis Obispo County was the most southerly site for acorn plantings of the two oak species. Valley oak was planted at Lopez Lake County Park (LPZLK) and blue oak on the Canyon Ranch (CYNRN). The San Benito County plantings of both oaks were made on the Jef Schmidt Ranch (SBNCO). In Madera County, blue oak was planted on the U.S. Forest Service San Joaquin Experimental Range (SJER). In western Contra Costa County, the two oaks were planted in Briones Regional Park (BRP), part of the East Bay Regional Park District. In Mendocino County, the two oaks were established at the University of California Hopland Field Station (HFS). In Yuba County, blue oak was planted on the University of California Sierra Foothill Range Field Station (SFRFS). Elevation, rainfall, and soil characteristics (table 1) represent conditions typical of those occurring in natural stands of the oaks found in the Coast Ranges, interior coastal ranges of the San Joaquin Valley, and western foothills of the Sierra Nevada in the Sacramento and San Joaquin Valleys.

METHODS

Acorns were collected from trees in late summer through early fall, dusted with captan and placed in 0.08 mm clear plastic bags with material at the bottom to absorb excess moisture from respiration. The acorns were then placed in cold storage (4°C) until planting. Storage between 1°-4°C is recommended by Korstian (1927) and Harrington (1972) to retard germination without a reduction in emergence potential.

Plantings of blue and valley oak acorns were made in late fall each year (November-December) from 1985-1989. Not all locations were included each year because annual acorn production was irregular and sometimes inadequate for establishment of plantings.

Acorns were sown in open areas away from canopy effects and on terrain as flat as possible to reduce effects of slope exposure and inclination. All work was conducted within deer-proof enclosures to exclude browsing of seedlings by deer and livestock, an acknowledged problem (Franco 1976, Longhurst and others 1979, Menke and Fry 1980) and to prevent depredations by feral pigs (*Sus scrofa* Linnaeus).

At each site, treatments were the factorial set of two levels of herbaceous plants (none and the naturally occurring vegetation) and two levels of protection against small mammal and insect damage (screens and no screens). The experimental design was a randomized complete block with the two levels of herbaceous plant control as main plots and protection applied as a split on main plots.

Main plot treatment each consisted of 100 acorns planted in four rows of 25 each with 30 cm between acorns and rows. Planting depth was 5 cm, a depth suggested for use in controlled environments (Lobel and George 1983) and one considered a minimum to discourage disturbance by mice (Griffin 1971). In other research, this depth has been found to be a good compromise between improved protection from predation and reduced emergence that occurs from planting at a greater depth (Tietje and others 1991).

During planting, acorns with obvious insect damage, usually consisting of exit holes created by larvae of the filbert weevil (*Curculio occidentis* Casey) and filbertworm (*Melissopus latiferreanus* Walsingham), were discarded. Acorns that had

Table 1—Physical parameters at locations included in blue and valley oak seeding studies.

			Soils		
Location	Elevation (m)	Avg. Annual Precip (cm)	Depth (cm)	Estimated AWC[1] ($cm\ cm^{-1}$)	Series[2] and Surface Texture
			Blue Oak		
BRP	188	48	86	0.15-0.18	Los Osos clay loam
CYNRN	545	28	155	0.14-0.17	Ayar clay loam
HFS	273	94	183	0.14-0.17	Hellman loam
SBNCO	394	36	61	0.10-0.14	Santa Lucia shaly loam
SFRFS	182	72	53	0.11-0.16	Argonaut gravelly loam
SJER	333	48	74	0.09-0.12	Ahwahnee sandy loam
			Valley Oak		
BRP	124	48	193	0.16-0.18	Botella clay loam
HFS	273	94	152	0.14-0.17	Yorkville loam
LPZLK	158	51	183	0.10-0.15	Elder sandy loam
SBNCO	394	36	61	0.10-0.14	Santa Lucia shaly loam

[1]AWC = Available Waterholding Capacity
[2] All are upland soils except Botella and Elder which are alluvial.

germinated in storage were distributed among treatments and replicates to insure uniformity of potential emergence.

During the study, two blue oak seedings had to be planted twice because of depredation. At CYNRN in 1985, feral pigs dug up many acorns before fencing was erected. In the second instance at SFRFS in 1987, deer mice (*Peromyscus maniculatus* Wagner) were the suspected problem. This assumption is based on live trap records at the site.

Measurement of emergence was confounded by small mammal depredations. Some acorns were destroyed early at all locations, both before and after emergence. One seeding at SJER was destroyed in 1985-86 and could not be reseeded. The high population of ground squirrels (*Spermophilus beecheyi* Richardson) present at the time suggests this rodent was responsible. Subsequent seedings at SJER were made after the population was reduced, but control at this site was maintained throughout the study.

Pocket gophers (*Thomomys bottae* Eydoux & Gervais) were common at all sites, and control was practiced where populations were a significant threat. However, no level of control was adequate to prevent losses to this rodent. These depredations may have been encouraged by the geometric planting pattern and relatively close spacing of acorns. In addition, we noted that control of herbaceous plants discouraged depredation.

Emergents in each main plot were randomly split into two groups, protected and unprotected, with protection provided by window screen cages (closed cylinders 15 cm in diameter and approximately 40 cm high) or Foregon (formerly Vexar) 14-strand rigid plastic seedling protectors (screens) 5 cm in diameter and 30 cm high. The large mesh plastic screens were substituted for window screen cages in new plantings when the threat from grasshoppers (*Melanoplus devastator* Scudder) was minimal. As a consequence, the efficacy of this less expensive protection was evaluated in six seedings, two blue oak seedings each at CYNRN and SJER (1987 and 1988) and two valley oak seedings at LPZLK (1987 and 1988). At CYNRN and LPZLK, black tailed jackrabbits (*Lepus californicus* Gray) and rabbits (*Sylvilagus* spp.) are the suspected major predators, and ground squirrels are a threat at SJER. Protection was applied beginning in Spring 1987 to all one-year seedlings and new emergents.

Following 1986 emergence in the 1985 SFRFS seeding, hairnets used in the food processing industry were applied to seedlings in each treatment to protect against defoliation by grasshoppers. In subsequent seasons, window screen cages were used as described.

During the 1985-86 growing season, glyphosate, a systemic herbicide, was applied after planting to control herbaceous growth until oak seedling emergence. After emergence, herbs were hoed. In subsequent seasons, initial herb control in new seedings was obtained using both glyphosate and a soil active herbicide, atrazine, to eliminate existing herbaceous growth and most such growth that might appear after application. The combination was used to reduce labor. In established plantings, two soil active materials, atrazine and oxyfluorfen, were applied annually during winter dormancy for more effective control of herbaceous growth. Potential for damage to emerging oak seedlings discouraged use of the latter chemical during the season of planting.

In one blue and one valley oak seeding, each established in 1985 (CYNRN and LPZLK), herbaceous plant interference was eliminated in all treatments after the first season. This was necessary to provide access. A third seeding at CYNRN in 1986 was established only with control of herbaceous plants.

Observations evaluated by analysis of variance (ANOVA) included emergence, survival measured in the spring of each growing season, and height of plants each fall. When measuring height, the longest stem was used if branching occurred. Unless otherwise noted, significant differences are reported at the 95 percent level of confidence.

Since data were collected over several time intervals, time was a third factor in survival and was considered a second split (Steel and Tome 1960). When there was a significant time interaction, ANOVAs for each time interval were used to assess the treatment effects. This was done to insure a conservative interpretation of data.

When necessary for the ANOVA, raw data were transformed to maintain homogeneity of variances. The results presented are treatment averages for the original measurements.

RESULTS AND DISCUSSION

Emergence

Overall emergence of 14 blue and 10 valley oak seedings was improved through herb control (table 2). Average emergence of blue oak with control was 45 percent. Without control, it was 29 percent. The values for valley oak were 60 percent and 46 percent, respectively.

Effect of Herb Interference on Survival

Average first-year seedling survival of both oak species, expressed as a percent of acorns planted, was significantly greater without herbaceous interference. In 11 blue oak plantings, survival was 33 percent of acorns planted without herbs while 11 percent survived in the control. Survival in eight valley oak seedings with and without herb control was 45 percent and 25 percent, respectively. These significant differences occurred despite some variability among plantings (table 3). SBNCO was not included because herbs could not be controlled, and no survival was recorded in either treatment.

Information on survival over time is limited, but figure 2 shows average survival of 3-year-old blue oak seedlings growing with and without herbs in three plantings. Herb interference clearly has a negative impact on seedling survival. Differences recorded each spring were highly significant ($P \leq 0.01$) and there was a highly significant ($P \leq 0.01$) interaction between treatment

Table 2—*Emergence (percent) with and without herbaceous plant control in 14 blue oak and 10 valley oak seedings and the associated precipitation patterns.*

				Emergence (pct.)			
				Blue Oak		Valley Oak	
Location	Planting Season	Seasonal Precip (cm)	Percent Avg Annual Precip	No Herbs	Herbs	No Herbs	Herbs
CYNRN	1985-86	33	118	72a[1]	75a	—	—
	1987-88	27	96	64b	41a	—	—
	1988-89	15	54	71b	15a	—	—
SBNCO	1985-86	45	125	15b	4a	81a	88a
			65	20b	4a	—	—
SJER	1987-88	31					
	1988-89	33	69	59b	41a	—	—
BRP	1987-88	37	77	—	—	72b	15a
	1988-89	35	73	25b	la	84a	87a
	1989-90	37	78	50a	38a	18a	11a
LPZLK	1985-86	63	124	—	—	69a	59a
	1987-88	40	78	—	—	56b	34a
	1988-89	43	84	—	—	55b	30a
SFRFS	1985-86	86	119	78b	53a	—	—
	1986-87	48	67	43a	31a	—	—
	1987-88	54	75	35a	40a	—	—
HFS	1986-87	62	66	60b	41a	32a	26a
	1987-88	73	78	12b	0a	86a	75a
	1988-89	68	72	29b	18a	44a	35a
MEAN				45b	29a	60b	46a

[1]For each seeding and each species, values in rows not followed by the same letter are significantly different ($P \leq 0.05$).

and time. After 3 seasons, control of herbaceous plant interference resulted in survival of 40 percent more seedlings.

Effect of Screen Protection on Blue Oak Survival

The addition of screen protection after emergence to blue oak seedlings produced mixed results the first year. In two seedings (SFRFS 1987 and SJER 1988), screens had no effect on first year survival, possibly due to the episodic nature of some depredation. Average survival with and without protection was 26 percent. Seedling survival in three seedings (CYNRN 1987, HFS 1986 and 1988) was significantly enhanced with screen protection. Average survival with screens at the three locations was 33 percent of acorns planted compared to 26 percent without screens.

Limited information on survival over 3 seasons from four plantings shows that blue oak seedlings survive in higher numbers with screen protection when growing with herb control (fig. 3). The value of protection was apparent at the end of the first season and was highly significant ($P \leq 0.01$) through the 3rd season with a highly significant ($P \leq 0.01$) interaction between treatment and time.

Screen protection and herb control in three seedings (CYNRN 1987, HFS 1986, and SFRFS 1987) were compared over 2 seasons (fig. 4). Interaction between herbs and screens was recorded at the beginning of the 3rd season. Application of

Table 3— *Survival (percent of acorns sown) in 11 blue oak and 8 valley oak seedings after 1 season with and without herbs.*

		Survival (pct.)	
Location	Seeding	Herbs	No Herbs
		Blue Oak	
CYNRN	1985	23a[1]	33a
	1987	21a	36a
	1988	<1a	61b
BRP	1988	0a	18b
HFS	1986	22a	55b
	1988	7a	16b
SFRFS	1985	18a	47b
	1986	7a	25b
	1987	35a	33a
SJER	1987	0a	4b
	1988	2a	35b
MEAN		11a	33b
		Valley Oak	
BRP	1987	14a	62b
	1988	70a	71a
HFS	1986	3a	11b
	1987	38a	69b
	1988	7a	30b
LPZLK	1985	34a	39a
	1987	18a	42b
	1988	13a	34b
MEAN		25a	45b

[1]For each seeding, values not followed by the same letter are significantly different ($P < 0.05$).

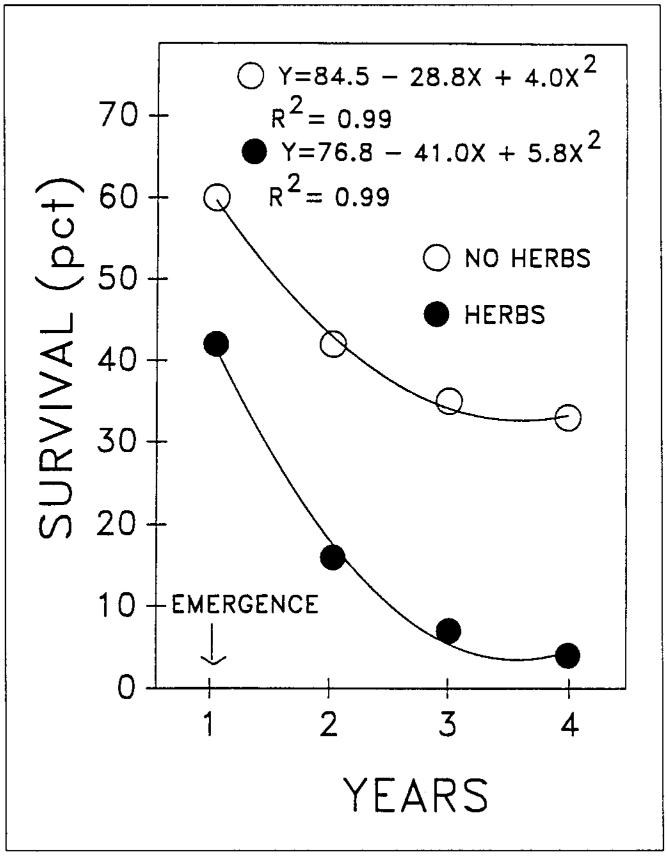

Figure 2—Three-season survival (percent of acorns sown) of blue oak combined over 3 seedings (HFS 1986, SFRFS 1985 and 1986) for plants growing with and without herbs. Observations made in spring after bud break. Difference in survival is highly significant ($P \leq 0.01$), and the progressive differential represents a highly significant ($P \leq 0.01$) linear interaction between treatment and time.

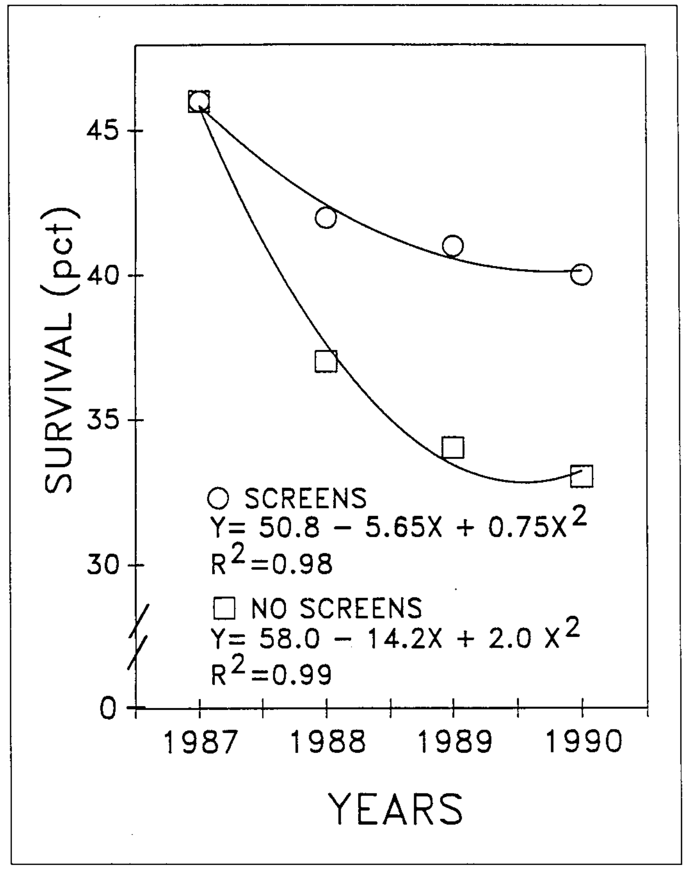

Figure 3—Three-season survival (percent of acorns sown) of blue oak combined over 4 seedings (CYNRN 1985 and 1986, HFS 1986, and SFRFS 1985) for plants growing without herbs and with and without screen protection. Observations made in spring after bud break. Difference in survival is highly significant ($P \leq 0.01$), and the progressive differential represents a highly significant ($P \leq 0.01$) linear interaction between treatment and time.

screens to seedlings growing with herbs nearly doubled survival. Screens increased survival only one-sixth where herbs were excluded.

Shade, as provided by window screen cages protecting blue oak in two seedings above, may have contributed to the large difference in survival between levels of protection where herbs were uncontrolled. Only 46 percent of incident sunlight is transmitted through window screen cages (measured in $\mu E/m^2/s$ by a quantum sensor). As a result, the environment beneath screens may provide an element of protection against excessive transpiration. That blue oak seedlings are tolerant of reduced sunlight beneath the screen cages is supported by data from other research in which the measured amount of transmitted sunlight did not significantly reduce net carbon gain (Kevin Rice, pers. comm.).

Effect of Screen Protection on Valley Oak Survival

The effect of screen protection on valley oak seedling survival the first season also varied by site. At BRP in 1988, survival was not influenced by window screen cages. Average survival with and without screens was 40 percent. However, use of screens in three seedings at HFS in 1987, 1988 and 1989 did produce significantly higher survival. On average, survival of protected and unprotected seedlings was 42 percent and 26 percent, respectively. Again, no interaction with level of herb control was detected.

In the 1987 and 1988 seedings at LPZLK, a significant difference in first year survival with and without screens (Foregon rigid plastic protectors) was recorded in both seedings, but in this case, survival without screens was greater. Without screens, average survival was 27 percent of acorns seeded compared with 22 percent for protected seedlings. Since most loss at this location occurred from gophers (88 percent in the 1988 seeding), the difference may have been due to their ability to identify and select protected plants.

Levels of both screen protection and herb control in 3 seedings were compared over 2 growing seasons (fig. 4). As with blue oak, interaction between levels of herbs and screens was recorded at the beginning of the third season. After 2 seasons, screens nearly doubled survival where herbs were excluded, but for the same period, survival of protected seedlings growing with herbs was three times that of unprotected seedlings. The greater difference in survival where herbs were

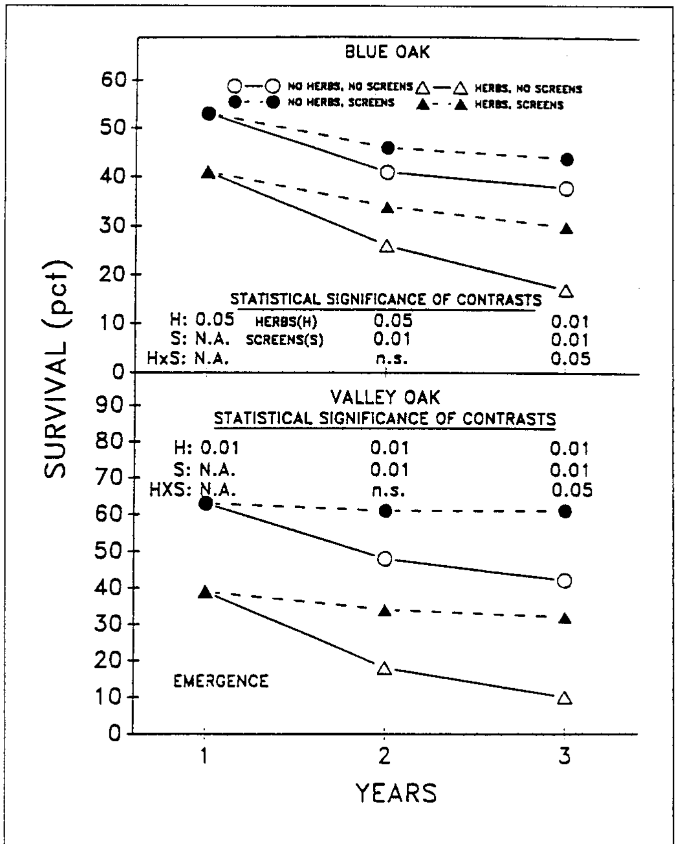

Figure 4—Two-season survival of blue oak combined over 3 seedings (CYNRN 1987, HFS 1986, and SFRFS 1987) and valley oak combined over 3 seedings (BRP 1987 and HFS 1986 and 1987) for all treatment combinations. Observations made in spring after bud break.

uncontrolled repeats the performance observed in blue oak seedings.

Effect of Screen Protection on Growth

Average height of 2-year blue and valley oak seedlings in 3 seedings was compared over all treatment combinations (table 4). The addition of screens in blue oak seedings more than doubled seedling height under the 2 levels of herb control at CYNRN, HFS and SFRFS. This response strongly suggests an interaction between screens and herbs.

The response of valley oak at HFS (two seedings) and LPZLK was equally as dramatic but not consistent between levels of herb control. Screens doubled seedling height where herbs were absent but increased height more than five times where herbs were present.

CONCLUSIONS

Control of herbs appears essential to achieve adequate emergence and first-year survival of blue and valley oak seedlings. Limited data on long-term survival suggests seedling mortality over time is reduced by herb control.

Screens protected seedlings against insects and small mammals and significantly improved survival and growth of both oaks at most locations. Window screen cages provided the best protection against grasshoppers, the principal insect herbivore on seedlings. Screens are recommended for all plantings.

Window screen cages not only protect seedlings from predation but modify the seedling microenvironment. They provide shade, the effects of which we could not separate from protection.

Other predators also appear to be affected by control of herbs (Wright 1985). The elimination of herbs around seedlings seemed to discourage pocket gopher predation. Control of this rodent is recommended in all plantings.

Predation in our studies may have been affected by concentrated planting patterns and characteristics of the exclosures.

We suspect the negative effects of herbaceous interference and predation can be modified by using livestock for phytomass control in carefully managed systems that would limit damage to oak seedlings. Such systems will reduce herbaceous cover and may effectively modify habitat, thus reducing potential predation. Such a strategy needs evaluation.

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Table 4—Average fall height of 2 year-old blue and valley oak each in 3 seedings (blue oak: CYNRN 1987, HFS 1986, and SFRFS 1987; valley oak: HFS 1986, HFS 1987, and LPZLK 1987) growing with and without both herbs and screens.

	Fall Ht. (cm)			
Species	Herbs and No Screens	Herbs and Screens	No Herbs and No Screens	No Herbs and Screens
Blue Oak	4.1a[1]	9.9b	10.1b	20.7c
Valley Oak	2.4a	13.5bc	10.1ab	21.0c

[1]Treatment values for each species not followed by the same letter are significantly different ($P \leq 0.05$). Those for blue oak represent an interaction (Herbs X Screens).

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Acorn Size As A Factor in Early Seedling Growth of Blue Oaks[1]

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Abstract: Field performance was evaluated for blue oak (*Quercus douglasii* Hook. & Am.) acorns of different size classes (weights) and from different trees which produced predominantly small, medium, or large acorns. Emergence, height, and survival were monitored for two growing seasons. A parallel evaluation, mainly of root characteristics, was conducted in an observation growth box. Acorn size significantly influenced emergence, survival, and height the first year, and influenced height growth the second year. Large acorns produced taller seedlings with heavier total root weight. Acorn size also affected other variables in a significant manner. Parent tree influence was significant for some variables but not for height growth.

In diverse tree species researchers have reported that seed size affects seedling germination and growth (Bonner 1987, 1988). Given the rather large size range one encounters in any acorn collection, the question arises if there could be some advantages to selecting large acorns for artificial regeneration of oaks. Larger acorns are presumably correlated with greater quantities of stored nutrients which might be convertible to larger, more vigorous seedlings with better chance of early survival.

Acorn size has been related to seedling performance with some differing opinions. Korstian (1927) reported "unmistakable advantage in total germination and survival in favor of large acorns" in four eastern oaks, two of which were in the subgenus Quercus, the white oaks. But he maintained these early effects may not be persistent. Others have reported a positive correlation between acorn size and root weight (McComb 1934), and between acorn size and total seedling size and weight in various subgenera (Matsuda and McBride 1986). Yet others have reported no acorn size advantage with regard to germination (Aissa 1983). Bonner (1988) reviewed several studies that cautioned such size advantages may not persist and that genetic factors may be more important than seed size. The present study investigated acorn size and seedling performance of blue oaks (*Quercus douglasii* Hook. & Am.) in California.

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METHODS

The study consisted of two parts, both conducted at the University of California Sierra Foothill Range Field Station (elevation 200 m), 20 miles northeast of Marysville. Part 1 was an outplanting of 720 acorns in a field plot fenced to exclude deer and cattle. Part 2 was a growth box study of planted acorns which allowed periodic harvest and measurement of seedlings.

Field Plot

Acorns were knocked or picked from branches of three trees during September, 1988 near Bangor, California, a location 25 kilometers from the field plot and of similar elevation. Tree 1 had acorns that were predominantly small; Tree 2 had predominantly medium-sized acorns; and Tree 3 had large acorns. Representative samples determined the range of acorn fresh weights for each tree collection, and each was sorted into three size classes. The ranges and size classes selected are shown in table 1. Acorns were soaked for 24 hours, air dried, and then stored in plastic ziplock bags at 0-4°C. Prior to soaking, samples of six acorns were taken from each of the size classes to determine moisture content by weighing before and after oven drying. Moisture content of each acorn size class was consistent within the single tree collections regardless of tree source. Trees 1, 2, and 3 differed, however, with moisture contents of 41.9 percent, 47.3 percent, and 50.4 percent, respectively. There were also apparent differences in ripeness as indicated by ease of picking from the different source trees.

Prior to planting, some acorns in every size class began to germinate in cold storage, and these were separated out. The remaining ungerminated acorns were placed on moist vermiculite in germination boxes at lab room temperature of 15-23°C. Once germinated, as defined by an emerging radicle .5 cm or longer, they were returned to the cooler with those previously germinated until planting.

Table 1—***Ranges in acorn fresh weight (gm) for each tree-size combination***

	----------------Acorn Size / Class	-----------		Average
Parent Tree	Small	Medium	Large	Weight
Tree 1, Small Acorn Tree	1.00—2.50	2.51—3.50	3.51—5.00	2.9
Tree 2, Medium Acorn Tree	2.00—3.50	3.51—4.50	4.51—6.00	4.0
Tree 3, Large Acorn Tree	4.00—6.00	6.01—7.50	7.51—9.50	6.8

The field plot was on a northeast facing 15 percent slope, in Sobrante-Las Posas, very rocky loam. Competing vegetation had been glyphosate treated in early fall and the dead plant cover and top few centimeters of soil carefully scalped off by tractor blade. A uniform planting area was thus created, with 720 planting spots arranged in eight blocks of nine rows each, a randomized complete block design. Each row had 10 planting spots on 30-cm centers; the rows were 60 cm apart. Rows were randomly assigned to acorns from the nine different tree source-acorn size classes. Acorns were planted over a 3 week period beginning December 20, 1988. All but 80 acorns were planted in the first week; 40 from Tree 1 and 40 from Tree 3 were slower to germinate in the germination boxes and were planted two weeks later than the rest. All were planted on their sides at 2-3 cm depth with radicles pointing in natural downward position. Only acorns with radicles less than 2 cm were planted.

Beginning in March and continuing throughout the summer the plot was evaluated twice weekly for seedling emergence, which was defined as first visible sign of the shoot. The plot was hand weeded on occasion, but competing vegetation was very slow to return. No irrigation was provided. Year-end survival and height measurements were taken, and the plot was similarly monitored the following year.

Growth Box

A selection of acorns from Tree 2, the medium sized acorn tree, was reserved for planting in two plywood growth boxes. Each box measured 50 cm by 90 cm by 100 cm deep. The boxes were each partitioned into ten compartments 8 cm wide using polyethylene covered sliding partitions. Each compartment was filled with soil from the field plot site, sifted through a 1.3 cm screen, and compacted by thoroughly watering to promote settling. The planting design was a split plot, so that each removable compartment contained four replications of randomly assigned small, medium, or large pre-germinated acorns. All acorns were planted on December 19, 1988, with points up and then covered with 2-3 cm soil. This planting position was necessary to fit in all the acorns, with 2-3 cm spaces between them. It differed from the on-side position of our field plantings. Extra acorns were planted on outside planting spots to serve as buffers and were not included in the data. The outermost compartments, which corresponded to the first and last harvest dates, were also considered buffers. The boxes were kept outdoors except for a brief period (two nights) of sub-freezing temperatures when they were moved to an unheated warehouse.

It was possible to harvest the acorns in each compartment by removing the entire compartment and either carefully excavating the acorn and its root system (early stages only), or gently removing all soil with a fine water spray. Roots were thus recovered in very clean condition, nearly 100 percent intact. We measured and calculated acorn fresh weight prior to planting, dry weight at harvest to fresh weight ratio (an index of nutrient depletion), total length of root system, number of branched roots vs. tap root configuration, dry weight of root in 20 cm segments, numbers of laterals emanating from the first segment, length of longest lateral, length and weight of shoot, and date of shoot emergence. The first compartment was harvested one month after planting. So little growth had occurred that the next harvest occurred one month later on February 21, 1989, and every two weeks thereafter until June 13.

Data were analyzed by ANOVA and, when significant differences ($P \leq 5.05$) were detected, by a Fisher's Protected LSD test. Harvest dates were treated as random variables, but by necessity the compartments had to be harvested in a serial, non-random fashion. We believe this not to have been a serious violation of the design since the differences measured between harvest dates were in all cases very great.

RESULTS

Field Trial

In the field, the timing of acorn emergence was unusual. Generally, the emergence pattern was not typical of our experience for this site. The main emergence period was April 1- June 1(fig. 1). Fast germinating species like blue oak typically show emergence curves considerably steeper in slope and much earlier in the year after late fall planting (McCreary 1990). Furthermore, the 64 percent emergence for the first year was somewhat low, although not unusually low from the experience of others for this site. Unusual weather patterns could account for these results. We would have expected greatest emergence during February - March. During these two months, the Field Station recorded minimum temperatures for several days as low as -10 and -5°C; and February's mean low was 1.7°C, compared to the 20 year norm of 5°C. Precipitation in March 1989 was in excess of 30 cm, compared to the norm of 9 cm. McClaran (1986) observed poor emergence under wetter conditions, and Matsuda and McBride (1989) noted delayed shoot development associated with decreasing temperatures of higher elevations. What was noteworthy in our study was a very delayed emer-

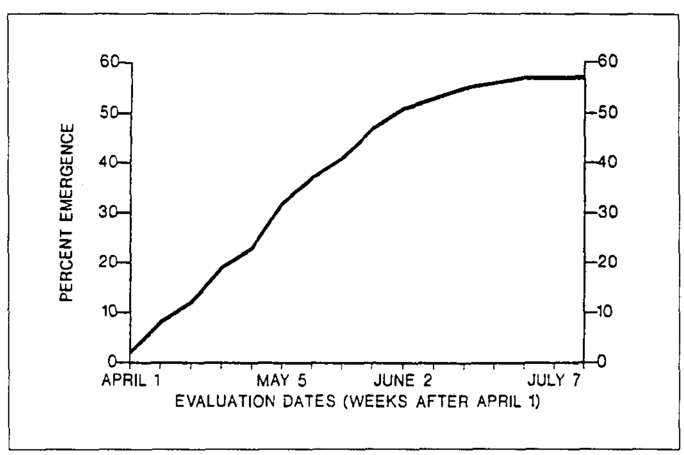

Figure 1—Cumulative emergence of acorns in 1989.

gence of 14 percent of the acorns. Four percent of the acorns emerged in the fall after an unseasonably wet September. The following spring and summer 10 percent (70 acorns) more emerged for the first time, bringing our total plot emergence to 74 percent. We are not aware of reports of such extensive delayed emergence in the literature.

Table 2 summarizes results for different sized acorns, disregarding parent tree. For 1989, significantly more seedlings from the largest acorns emerged. A greater proportion of these seedlings also survived than did those from the smallest acorn size class. While the largest acorns also had the highest percent survival in 1990, the differences were not statistically significant. Larger acorns also produced taller seedlings, and this relationship lasted into the second year of growth, with an increasing magnitude of height difference between large-acorn seedlings and small-acorn seedlings. The incremental growth differences from 1989-90, while greatest for the largest acorns, were not significant at the P≤05 level (ANOVA).

Table 3 summarizes our data for acorn size differences in relation to their parent trees. While there are trends toward increasing emergence, survival, and height depending on parent tree, the significance of these differences do not present a clear pattern, and there were no significant differences between the parent trees with regard to shoot emergence date or seedling height. Since large acorn size was found to make a difference in emergence and survival, we expected to observe significant differences between the small acorn tree and the large acorn tree, because the small acorn tree's acorns weighed 1.0-5.0 gms, while the large acorn tree's weighed 4.0-9.5 gms. This was not the case. While the large acorn tree tended to have greater emergence, survival, and height growth, the only significant patterns for parent tree were for survival in 1990 (table 3). The 1990 survival analysis also showed a tree by acorn size interaction that complicates the parent tree significance for this variable. But when we examined the parent tree by acorn size class combinations, we found that the large acorn tree in all cases had the highest survival. We would, thus, still accept parent tree effect as significant for survival.

Acorns which emerged for the first time in the second year were distributed throughout the plot in a spotty fashion. There were too many missing values for whole rows to do a valid ANOVA analysis. However, table 4 summarizes our findings for this interesting phenomena. There seems to be a trend for greater year-end height related to acorn size. Parent tree seems also to be important, as seen in table 5, with the large acorn tree producing most of the new emergers.

Growth Box

Table 6 summarizes the result of our analysis. The most interesting finding was that total root weight was significantly related to acorn size. The average weights of roots from large acorns were almost double those of the small acorns. This relationship was also true for the first 20 cm root segment, which merely indicates that this was where most of the root mass was located. Over the course of this study, 72 percent of the total root weight was, on average, accounted for by this root segment. Root weights, regardless of acorn size, increased in a somewhat similar manner over time (fig. 2), the differences in magnitude

Table 2—*Field plot average for different sized acorns, regardless of parent tree - 1989-90*[1]

Acorn Sizes	Pct emergence 1989	Pct year end survival 1989	1990	Year end height (cm) 1989	1990[2]	Average emergence date (1989)
Small	59[a]	57[a]	67	5.2[a]	19.3[a]	May 4
Medium	63[b]	62[ab]	68	5.1[a]	17.4[a]	May 8
Large	71[b]	70[b]	76	7.1[b]	24.5[b]	May 5

[1]Values for each variable are not significantly different (P ≤ 0.05), Fisher's LSD test, if they are followed by the same letter or none.

[2]Data for this variable tracks those seedlings emerged in 1989 only.

Table 3—*Field plot averages of all acorn size classes from different parent trees*

Parent Tree	Pct emergence 1989	Pct year end survival 1989	1990	Year end height (cm) 1989	1990[1]	Average emergence date (1989)
Small Acorn tree	67[a]	65[ab]	70[a]	5.2	17.9	May 4
Medium Acorn tree	57[b]	55[a]	61[b]	5.6	20.8	May 5
Large Acorn tree	70[a]	69[b]	80[c]	6.5	22.5	May 9

[1]Data for this variable tracks those seedlings emerged in 1989 only.

Table 4—*Averages of acorns newly emerged in second year by size class*

Acorn sizes	Number emerged	Pct vacant spots w/new emergers	Emergence date	Year end height
Small	29	29	April 20	3.4
Medium	22	25	April 14	6.0
Large	19	28	April 12	6.4

Table 5—*Averages of acorns newly emerged in second year by parent tree*

Parent Tree	Number emerged	Pct vacant spots w/new emergers	Emergence date	Year end height
Small Acorn tree	21	26	April 12	4.6
Medium Acorn Tree	16	15	April 16	5.1
Large Acorn Tree	33	46	April 18	6.1

Table 6—*Averages for variables measured in growth box trial for 8 harvest dates*[1]

Variable	Acorn Size: Small	Medium	Large
Total Root Weight (g)	.278a	.376b	.498c
First 20 cm segment of root (g)	.203a	.268b	.359c
Root Length (cm)	47.5	49.6	51.2
Shoot Weight (g)	.119a	.184b	.196b
Shoot Length (cm)	5.09	6.61	6.43
Length of Lateral Root Zone (cm)	56.0	57.2	59.3
No. of Laterals >1 cm in 1st Root Sgmt	38.9	44.8	50.3
Length of Longest Lateral (cm)	6.8a	8.7ab	11.3c
Acorn Fresh Weight (g)	2.98a	3.94b	5.09c
Acorn Dry Weight (g)	1.03a	1.36b	1.81c
Ratio Dry Weight/Fresh Weight	.35	.35	.36

[1]Values for each variable are not significantly different (P≤0.05), Fisher's LSD test, if they are followed by the same letter or none.

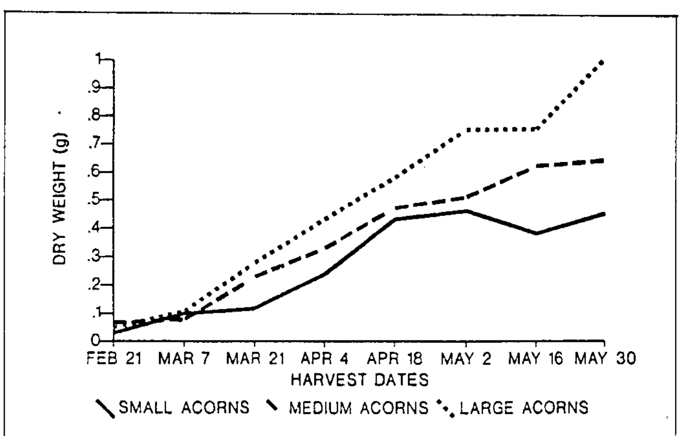

Figure 2—Average root weights for 3 sizes of acorns harvested on different dates.

increasing, especially after the tenth week when most above ground shoot growth commenced. Root lengths, on the other hand (fig. 3), were very similar for all acorn sizes and increased at a similar rate. There were no significant differences for average root lengths.

A similar pattern was observed for shoot weight and shoot length; large and medium sized acorns produced significantly heavier shoots than did small acorns, while shoot lengths were not significantly different.

There were no significant differences between acorn size classes as regards the length of the lateral root zone or the number of laterals in the first root segment. However, the subjective impression that large acorn roots were "bushier" was supported by the significant difference between the longest laterals of the large and small acorns.

When we consider the index of depletion of the acorn's cotyledon reserves as measured by the ratio of acorn dry weight at harvest over initial fresh weight (fig. 4), it is clear that these reserves are utilized similarly over time independent of acorn size. There were no significant differences and ratios were almost identical.

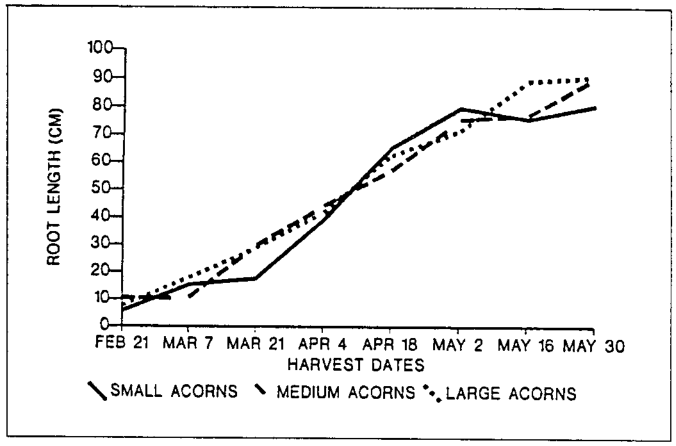

Figure 3—Average root lengths for 3 sizes of acorns harvested on different dates.

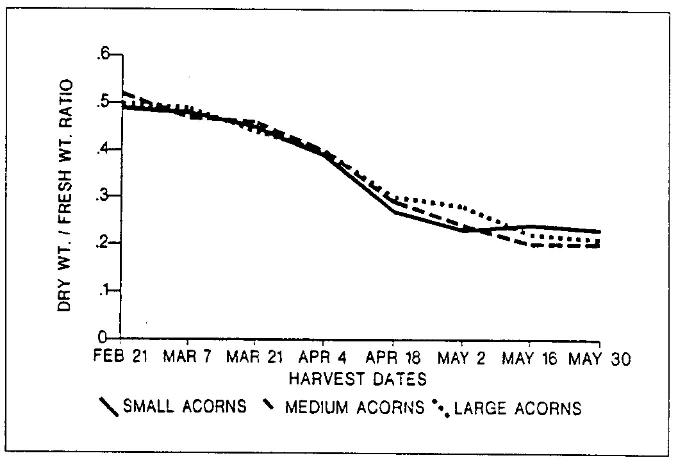

Figure 4—Average acorn dry weight/fresh weight ratio for 3 sizes of acorns harvested on different dates.

DISCUSSION

The data indicate that acorn size in blue oaks is significantly related to initial seedling growth. The field trial demonstrated that larger acorns convey an advantage to seedlings which is reflected especially in the ability to produce taller seedlings. Larger acorns also produced heavier and more developed root systems in the box trial. It was somewhat surprising that root length was not affected by acorn size in our growth box. We had initially reasoned that larger acorn size would be advantageous since larger acorns could rapidly grow deeper root systems, thus accessing soil moisture unavailable at shallower depths. The simulated field conditions of our box data did not support this hypothesis. However, the growth box limited our investigation to depths <100 cm, and differences might have been detected had we been able to track root growth for a longer period to greater depths. Still, the greater mass and branching of root systems produced by larger acorns would seem to promote uptake of both moisture and nutrients and account for the greater seedling heights observed.

The growth box component of this study was intended to shed light on the below ground development which might be occurring in the field plots. We did not expect such rapid root growth. When the last compartment was harvested on June 13, roots had already reached beyond the one meter depth of our box. Most of this growth began after January 19. Extensive root development preceded shoot emergence, and we were unable to obtain shoot growth comparable to that in our field plot because our seedlings outgrew the box depth, terminating observation. Root growth was not affected by the low temperatures we experienced, which was to be expected from the findings of Matsuda and McBride (1986). Average root lengths for February and March,1989 (fig. 3), for instance, when air temperatures were especially low, increased in roughly the same manner as for periods when temperatures were much higher.

The average emergence date for the box can only be considered an estimate- since compartments were destructively harvested over time and any acorn that hadn't emerged by harvest date was therefore not recorded for emergence. However, if we consider the last six harvest dates, where emergence was nearly complete in all compartments, average emergence date was April 1. This compares to April 20 for the field plot. Twenty-nine out of a total 144 acorns in these last six harvest compartments failed to emerge but were still alive. Of these non-emergers, 59 percent had a multi-branched root system rather than a normal tap root system, compared to 24 percent occurrence of such root systems among those which emerged. Multi-branched systems result from damage to the radicle early in development and can be artificially induced by simulated injury (Carpenter and Guard 1954). It is therefore probable that the delayed emergence observed in both box and field plot was related to early radicle injury.

It would appear that the root system serves an important storage function as a reserve for seedling resprouting. Blue oak seedlings readily resprout (Griffin 1971) and have an enormous potential to remain alive for long periods without photosynthetic support or other above ground functions. After complete stem clipping of seedlings, for example, an entire year may pass before above ground functions resume (Welker and Menke, in press). This could be seen as an adaptation to herbivory, fire, and xeric or other harsh environmental conditions. Our results indicate that this ability is established before the seedling ever receives any photosynthetic support. The rapid translocation of nutrients to below ground storage in blue oaks may even give an acorn a two growing season potential for successful shoot emergence under favorable environmental conditions as we observed in our field plot. Large acorn size would logically be an advantage in this regard, and while we have indications that this might be the case, we cannot say with certainty that acorn size provides a significant advantage for such delayed emergence or resprouting. The potential for delayed emergence of acorns also suggests caution in interpreting survival or emergence results from a one-year study.

The large volume of the first 20 cm segment of our seedling root systems in the growth box, coupled with its significant relationship to acorn size for all harvest dates of our box study, point to this root segment as the principal storage region or recipient of translocated nutrients from the acorn. The segment resides in the most competitive part of the soil profile, has the least amount of active root growth, and the most suberization, and would appear to be most favorably situated for a more passive storage function.

CONCLUSION

The results of these trials suggest that increased growth and survival may be obtained by selecting acorns from trees that produce large acorns, as well as by selecting the largest acorns within single tree collections. Large acorns tended to produce taller seedlings with roots of greater mass. However, there was considerable variation in field performance between the three trees tested. For the medium acorn tree, greater acorn size resulted in a clear pattern of increased survival. For the other two trees, however, there was relatively little difference between acorn size classes. This suggests that the benefits in artificial regeneration of selecting larger acorns within single tree collections could vary greatly depending upon the parent tree. In general, the height gains from increased acorn size, while not great in the first year, do show significant persistence. Only further tracking of our field plot will reveal how persistent these advantages may be, and at this time, based on the limited evidence, we would not recommend selecting large acorns as a regeneration prescription. However, researchers should be aware of possible acorn size effect when conducting comparisons of seedlings to ascertain various treatment effects on planted acorns.

Finally, it should be noted that other considerations may influence decisions concerning which acorns to select for planting. Even if larger acorns are deemed superior from a growth and survival standpoint, smaller acorns may be preferred to meet other objectives, such as the use of local seed sources and maintaining adequate genetic diversity by planting acorns from a large number of parents.

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Soil Water Effects on Blue Oak Seedling Establishment[1]

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Abstract: A field experiment was conducted to examine the effects of soil water availability on blue oak (*Quercus douglasii*) seedling establishment. Acorns were planted either into cleared plots of 0, 10, 20, or 40 cm diameter. The cleared plots were located in two grazed and one ungrazed site. Half of the plots received drip irrigation in a split plot design. Soil water and plot size, depending on the site, and initial acorn weight and parent tree all influenced oak seedling growth. Survival and height in subsequent growing seasons was dependent on early growth. Soil water availability in the first growing season, therefore, influences both oak seedling establishment and growth in subsequent years.

Earlier work (Gordon and others 1989, Gordon and Rice 1990, Rice and others these proceedings) indicates that blue oak (*Quercus douglasii* Hook. & Am.) seedling establishment, water relations, and growth depend on the rate of soil water depletion. Further, this rate has been demonstrated to depend on the composition of the herbaceous neighborhood in which a blue oak seedling is planted. In addition to the effects of the competitive environment, seedling growth varies with tree of acorn origin and initial acorn weight (Rice and others these proceedings). Thus, maternal or genetic differences in source material interact with the competitive characteristics of the environment to influence the probability of oak seedling establishment and survival.

The above experiments were all conducted in containers. This paper describes a field experiment in which soil water availability and proximity of herbaceous competitors were varied around establishing blue oak seedlings to examine the questions: 1) Are seedling emergence and growth in the field reduced under rapidly drying soil water conditions? 2) Do parent tree and initial acorn weight interact to influence seedling response to environmental conditions? 3) Does seedling growth in the first growing season influence survival and growth in subsequent years?

METHODS

The experiment was conducted at the University of California Sierra Foothill Range Field Station (SFRFS) in Yuba Co., California. A 1 ha area encompassing grazed land and adjacent land which had not been grazed since 1972 was fenced to exclude both livestock and deer. Soils are derived from metamorphic parent materials and consist of reddish Alfisols and brownish Ochrepts. Annual precipitation averages 740 mm; temperature extremes range from -2 to 40°C.

This experiment examined the growth, water status, and survival of oak seedlings in cleared circular plots of 1, 10, 20, and 40 cm diameter, with or without irrigation in the spring. The watering treatment was established as the main plot in a split-plot design, with plot size as a subplot treatment. Ten blocks were established in each of three sites: grazed with oak canopy removed, grazed open, and ungrazed low canopy sites. The canopy-removed site was established so that the effects of canopy-influenced soil could be examined without a confounding reduction in light availability.

The surface 1-2 cm of soil and litter were removed from the plots in fall, 1986. Plots were weeded as necessary during the first 2 years of the experiment. Blue oak acorns, collected from four trees at the SFRFS, were planted in the center of each subplot in winter, 1987. All acorns showed healthy radicle development of up to 10 mm when planted. Parent tree and initial acorn weight in 0.5 g classes were recorded for use as covariates in the analysis. Tree and weight were randomly distributed among the subplots. To reduce herbivory on seedlings, each subplot was caged with aluminum screening.

Soil water content was increased for 2 months with drip irrigation tubing in one main plot of each block. Each watered plot received about 7 liters of water weekly starting April 23. Soil water potential at 40 cm depth was measured biweekly with calibrated screen-cage thermocouple psychrometers (J.D. Merrill Specialty Equip.) placed in 2 replicates each of the 0, 20, and 40 cm unwatered plots and in the 20 cm watered plots.

Shoot emergence, stem height, leaf number, and estimated leaf area of oak seedlings were measured weekly. Mid-day leaf conductance and transpiration rates (Licor null-balance porometer) were also taken weekly. Initial and final seedling height in 1988, and final height in 1989 and 1990 were also recorded to determine the relationship between initial seedling growth and subsequent survival.

BMDP logistic regression (Dixon 1985) was used to examine the effects of watering treatment and plot size on oak

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seedling emergence in 1987 and 1988. Chi-square analysis examined the influence of parent tree and acorn weight class on emergence. The general SAS linear model analysis of split plot designs (Freund and others 1985) was used to compare oak growth responses to treatments. Acorn weight and parent tree identity were included as covariates in these analyses. Parameters measured over time were tested in ANCOVA models through an orthogonal polynomial decomposition of the time effect. Main and interactive effects and Tukey tests were thus tested against specified nested Type I error terms (Gordon and Rice 1990). Correlations of seedling growth within and among seasons were also examined. Continuous variables were log-transformed while count variables were square root-transformed to increase consistency with linear model assumptions.

RESULTS

The watering treatment maintained the water potential above -1.5 MPa at the 40 cm depth in cleared plots during most of June (fig. 1). Plot size did not affect the rate of soil water decrease through the season at any of the sites (fig. 1). Average water potential tended to increase with plot diameter, but significant differences were not detected.

By early April, 23, 4, and 0 percent of the acorns had produced shoots in the grazed canopy-removed, ungrazed, and grazed open sites, respectively. In mid-May, 48, 33, and 36 percent had emerged in the three sites. However, between the second and third weeks of May, 94 percent of the new shoots emerging were in irrigated plots. Actual numbers of plots with acorns were lower than the percentages indicate, however, because of shoot mortality and disappearance from several plots. Gopher activity (focussed on irrigated plots) appeared to be the major cause of this loss. Overall, only about 40 percent of the acorns planted produced shoots in the plots.

Logistic regression of block, plot size, and water treatment effects on seedling emergence within each of the three sites revealed significant effects of watering in the grazed open (F=3.88, p=.05) and the grazed canopy-removed (F=4.3 1, p<.05) sites. These effects were most dramatic in the grazed open site, where 30 percent of the unwatered and 59 percent of the watered acorns showed shoot growth (fig. 2). Conversely, the main and interactive effects of block and plot size significantly influenced emergence in the ungrazed site (F=6.48, p<.0001); emergence was significantly lower than expected in the 10 cm (p<.005) and higher than expected in the 20 cm (p<.004) diameter plots.

Interactions between planting site and acorn weight (F=2.97, p=.05) and site and parent tree (F=3.81, p<.0005) influenced the probability of oak shoot emergence. Smaller acorns from three of the four parent trees emerged later than did larger acorns; the opposite relationship between size and emergence date existed for the remaining tree (fig. 3). When sites were evaluated separately, emergence was positively dependent on acorn size

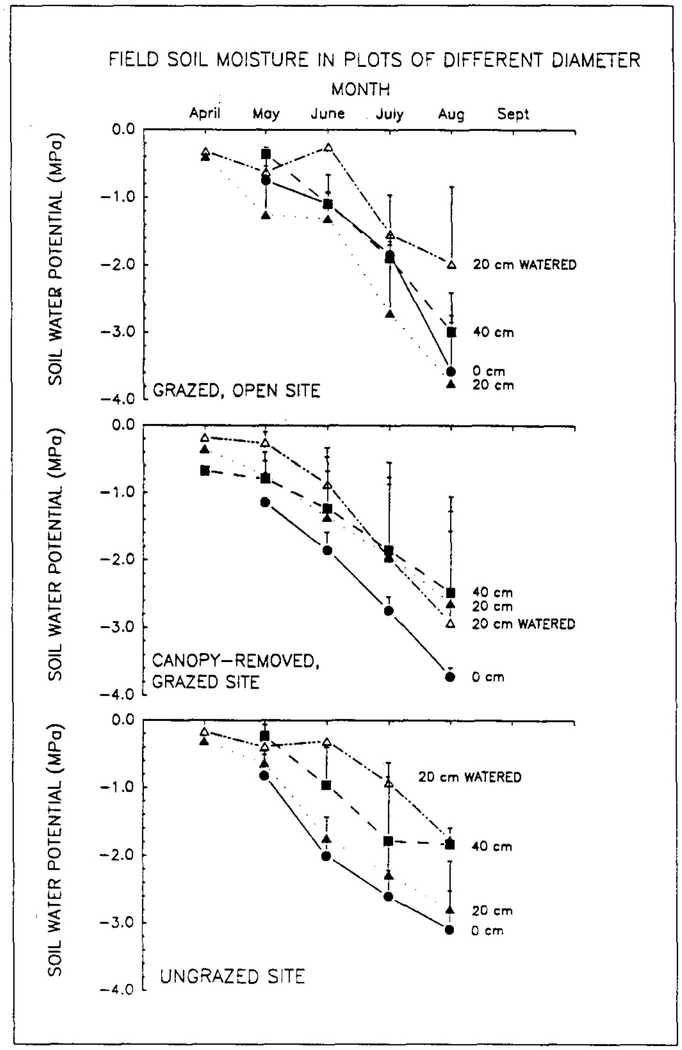

Figure 1—Soil water potential (mean and 1 s.e.) at 40 cm depth in cleared plots by site, plot size, and irrigation treatment.

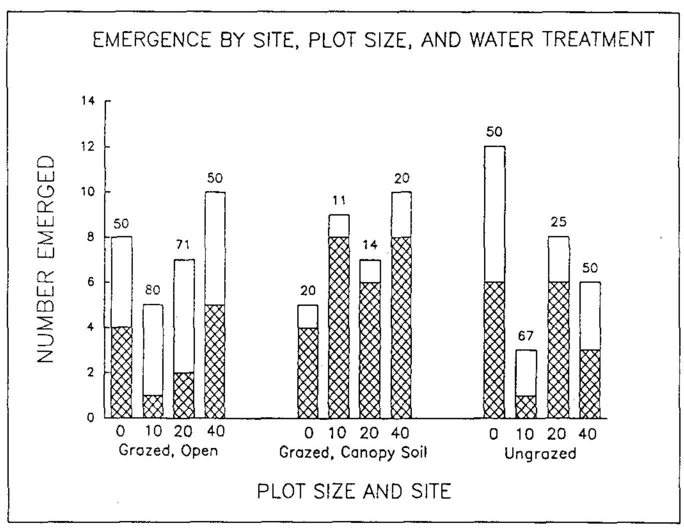

Figure 2—Number of shoots which emerged from acorns planted in plots of different size in each of three sites. Open bars are total number emerged; hatched bars show the number which emerged prior to irrigation. The numbers above the bars are the percent emergence following irrigation.

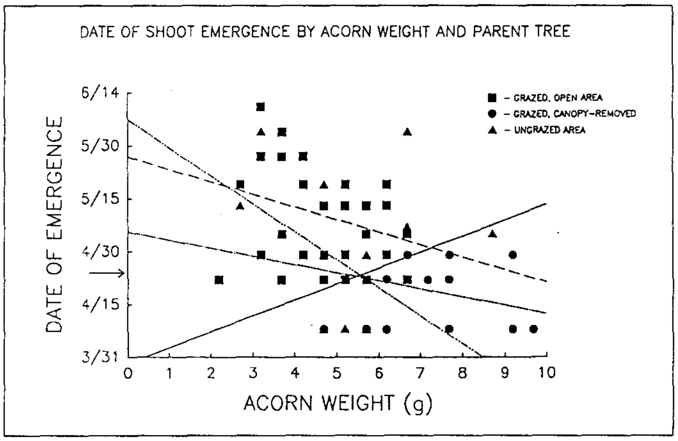

Figure 3—Emergence dates of seedlings from acorns of different weights by parent tree. Planting sites are designated by symbol. The arrow on the y- axis indicates the date on which irrigation started.

only in the ungrazed site: 73 percent of the seedlings emerged from acorns larger than the mean sowing weight. Parent tree identity significantly (X^2=9.49, p<.025) influenced the probability of shoot growth only in the open grazed site. Following emergence, however, neither acorn weight nor parent tree had further effects on height or leaf growth.

All seedling growth and gas exchange responses measured were significantly dependent on soil water potential over time (table 1). Seedlings in irrigated plots were larger than were those in non-irrigated plots. Plot size had significant but inconsistent effects on seedling growth (table 1). Leaf number, for example, was higher (p<.05) in 0 and 20 cm irrigated plots than in 0 or 10 cm non-irrigated plots. Seedlings in irrigated 40 cm plots had more leaves than did those in 0, 10 or 20 cm non- irrigated, or 10 cm irrigated plots. Final height was correlated with the number of leaves (r=.90, p<.0001).

About 60 percent of the 1987 seedlings showed further growth in 1988, with the probability of regrowth being dependent only on emergence in 1987 (F=46.18, p<.0001) across all sites and treatments. An additional 7 percent of the acorns in the grazed open site, and 2 percent in the ungrazed site which had not grown in 1987 showed shoot growth in 1988. These delayed emergences were independent of plot size or watering treatment.

Excavation of those plots from which no shoots emerged in either 1987 or 1988 revealed that acorns in 56 percent of the plots had either been eaten or attacked by fungi and showed no evidence of root growth. Acorns were missing from 27 percent of the plots. Only 8 percent of the plots had acorns present which showed root development prior to death. More acorns were missing from the ungrazed site relative to the 2 grazed sites.

Seedling height and leaf number were significantly correlated in both 1987 and 1988 (r=.90, p<.0001 and r=.96, p<.0001, respectively). Final height in 1988 was correlated with that in 1987 (i-.56, p..0001), although neither the length of the 1987 growing season nor the experimental treatment influenced 1988 growth. Height in 1989 was also correlated with that in 1988 (r=.86, p<.0001). Only those seedlings which emerged in 1987 were included in these analyses.

Table 1—*Summary of ANCOVA results of the dependence of blue oak seedling growth and stomatal conductance on soil water potential over time. Seedlings were grown in cleared plots of various size (plot), in the Sierra Nevada foothills.*

	Stem Height (cm)	Number of Leaves	Leaf Area (cm^2)	Stomatal Conductance (mmol $m^{-2}s^{-1}$)
Overall model F	9.07	14.34	12.21	9.09
p	.0001	.0001	.0001	.0001
Block*	0.58	0.39	0.59	1.35
	.80	.92	.78	.33
Soil Water	62.51	48.55	70.56	4.83
Potential*	.0001	.0001	.0001	.06
Tree*	0.01	0.14	3.62	3.34
	.94	.73	.09	.10
Acorn Weight*	0.46	0.55	0.14	0.53
	.52	.48	.72	.48
Plot(block)	2.73	5.41	3.21	6.37
	.005	.0001	.001	.0001
Date	0.29	1.25	1.54	17.94
	.59	.26	.23	.0001
Water Potential	5.04	6.39	4.90	1.66
x Date	.02	.01	.03	.20

*tested against the Type I error term Plot(block)

Seedlings senesced their leaves earlier in the grazed canopy-removed and the ungrazed sites than in the grazed open site in 1988. Close to 50 percent of the seedlings in the two former sites had no remaining green tissue in early October, 1988, while 75 percent of the seedlings from the grazed open site retained green leaves.

Chi-square analysis revealed that the probability of surviving through 4 growing seasons was independent of height at the end of the first growing season across all sites. However, individuals greater than 8 cm in height by the end of 1987 tended to survive through 1990 at greater than expected frequency than did those below that height (fig. 4). Small sample sizes preclude confident evaluation of these data. Seedlings which were taller than 7.5 cm after their first growing season had a significantly higher probability of surviving through 3 growing seasons in another field experiment (Gordon unpub. data).

DISCUSSION

Results from this experiment support the hypothesis that water availability significantly affects blue oak seedling recruitment in the field. Shoot emergence of the pre-germinated acorns

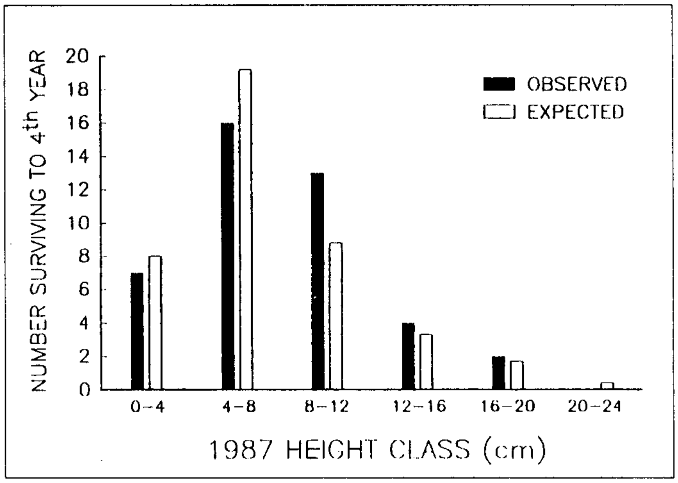

Figure 4—Expected and observed number of seedlings surviving through the 1990 growing season by height class at the end of the first growing season (1987).

was significantly enhanced by late season water availability in grazed areas. The reduced response of seedlings in cleared plots in the ungrazed area may be partially explained by gopher depredation of watered plots in that site.

Plot size effects, though significant, were secondary to those of irrigation. These results are explained by the insignificant effect of plot size, or proximity of competitors for soil water, on the resource. Plot size appeared to have the greatest influence in the ungrazed site, where plant densities were already the lowest (unpub. data) and where soil water tended to be highest. Root encroachment into the plots may have reduced plot size treatment effects.

Following emergence, water potentials continue to determine the extent of growth and stomatal conductance in oak seedlings. These results are consistent with others for both blue oak (Borchert and others 1989, Gordon and others 1989, Gordon and Rice unpublished draft, Welker and Menke 1990) and for valley oak (*Q. lobata*) (Danielsen 1990) in California. Further, influences of soil water potential on growth in the first growing season continue to influence seedling growth in subsequent seasons. Griffin (1971) also reported enhanced blue oak survivorship when competing grasses were experimentally removed.

The results from the blue oak experiments discussed here and elsewhere (Gordon and Rice 1990, Rice and others these proceedings) also suggest that blue oak sensitivity to competition for soil water has a genetic component. Acorns were collected from trees ranging in elevation and aspect at the SFRFS. Both the distribution of acorn weights and the responses of acorns to the environment varied among these parent trees: acorn weight and parent tree interacted with site conditions to influence seedling emergence and growth. Significant variation in acorn size distributions and influence of acorn weight and parent tree on seedling establishment have been documented for *Q. petraea* (Jarvis 1963), *Q. kelloggii* and *Q. agrifolia* (Hunter and van Doren 1982), and *Q. rubra* (Kolb and Steiner 1989). Thus, potential genetic influence on such characters as leaf number holds implications both for survival and growth over several growing seasons, and for regrowth following browsing because axillary buds for lateral branches are formed at the base of the petiole.

These data indicate that the interaction between maternal characters and the water environment surrounding establishing blue oaks may influence the success of establishment. A more gradual decline of soil water when the oak understory was dominated by perennial rather than annual grasses (White 1967, Welker and Menke 1990) would allow higher oak growth rates for longer into the summer drought. The larger seedlings developed would be better able both to exploit soil resources not available to the herbaceous understory and to survive into subsequent growing seasons. This scenario may partially explain why reduced recruitment in oak populations coincides with the conversion of the oak woodland understory to annual grassland.

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Intraspecific Phenotypic Variation and Ecological Genetics of Blue Oak *(Quercus douglasii* Hook. & Arn.)[1]

Kevin J. Rice   Doria R. Gordon   Jeanine L. Hardison   Jeffrey M. Welker[2]

Abstract: We examined potential variation in water use efficiency (WUE) in both mature trees and seedlings of blue oak by measuring the carbon isotope composition of plant tissue collected from populations arrayed along a latitudinal rainfall gradient. We also conducted common garden studies to determine the potential genetic basis for phenotypic variation in seedling WUE, growth and phenology. We planted acorns from both xeric and mesic populations into herbaceous neighborhoods characterized by different rates of soil water depletion.

Acorns from the mesic site were significantly smaller. While the probability of emergence increased with acorn size in the xeric population, there was no effect of acorn size on emergence in the mesic population. Seedling WUE was influenced significantly by herbaceous neighborhood composition. Average leaf size and stem weight increased with acorn size in the mesic population. Differences among maternal families in the mesic population suggested significant within-population genetic variation for seedling traits. Further, leaf weight responded differently among families to variation in neighborhood composition, suggesting genetic variation for plasticity in leaf morphology.

Conservation concerns about California's blue oak (*Quercus douglasii* Hook. & Arn.) woodlands focus on the recent documentation of low seedling survival over the entire range of blue oak (Muick and Bartolome 1987, McClaren and Bartolome 1989). Although seedlings are relatively common, successful recruitment to sapling age classes (common before the mid-1800's), now appears rare. Concern about this apparent lack of recruitment is heightened by the fact that the woodland community created by blue oak populations has decreased in area by over 43,000 ha since 1973 and is currently being lost to human development at a rate of over 4,000 ha/yr (Bolsinger 1988). These woodlands are extremely important as wildlife habitat (Verner 1987); for example, among Mediterranean ecosystems world-wide, blue oak woodlands have the highest diversity of bird species (Cody 1986). In addition, the importance of the nutrient cycling role of blue oaks in maintaining the productivity of oak woodland and oak-savanna ecosystems has been documented (Holland 1973, Holland 1979, Kay 1987).

Given the obvious importance of conserving blue oak woodlands and the general recognition that consideration of genetic diversity is critical in any conservation effort (Schoenwald-Cox and others 1983), we have initiated a research program on the ecological genetics of blue oak. The study reported here used both a regional survey and a common garden approach to examine how phenotypic expression in several seedling traits is influenced by the interaction of acorn source and competitive environment.

METHODS

Regional Variation in Blue Oak Water Use Efficiency (WUE)

Leaf and stem material produced during the 1987 growing season was collected from three adult blue oak trees in each of four regional sites in September, 1987. Samples of approximately 50 gm fresh weight were taken from four branches in the lower canopy of each tree and pooled by tree. Samples were collected from the 1ower tree canopy to minimize the differences in atmospheric moisture conditions experienced by trees and seedlings. Simultaneously, three blue oak seedlings under each tree were collected and pooled.

The collection sites were chosen along a latitudinal rainfall gradient that is based on both total rainfall accumulation during 1986-1987 and differences in 30 year rainfall averages. The most northern, mesic site (University of California Hopland Field Station, Mendocino County) is located 20 km inland from the north-central California coast and receives an average of 90.4 cm of rainfall each year (71.2 cm in 1987). The most southern, xeric collection site (San Joaquin Experimental Range, Madera County) receives an annual average of 48.0 cm of rainfall (28.3 cm in 1987). The two intermediate sites were the Hastings Reserve (Monterey County) located 21 km inland from the Pacific Ocean in the Carmel Valley (average annual rainfall of 53.8 cm; 38.1 cm in 1987), and the Sierra Foothill Range Field Station (Yuba County) located along the western foothills of the Sierra Nevada mountains (average annual rainfall of 73.1 cm; 46.0 cm in 1987). Although rainfall accumulation at all sites during 1986-1987 was lower than the 30 year average, the two extreme sites (Hopland and San Joaquin) still differed by 50 pct.

Plant material was dried at 65 °C for 48 hours, ground through a 60 mesh screen and analyzed for $^{13}C/^{12}C$ ratios (Ehleringer and others 1987). Carbon isotope analysis consists

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of sample combustion with a catalyst to generate the CO_2 gas which is then analyzed for isotopic differences with an isotope-mass_ spectrometer. The carbon isotope ratio of the sample is then compared to the ratio in a standard and a $\delta^{13}C$ value is calculated (Farquhar and others 1989). This ^{13}C value is expressed as parts per thousand or "per mil"; as this value becomes less negative, reduced discrimination against ^{13}C is indicated. In turn, a lower degree of isotope discrimination is an indication of higher plant WUE (Farquhar and others 1988).

The $\delta^{13}C$ values for stem and leaf material in tree and seedling samples were analyzed separately using linear regression analysis. An average $\delta^{13}C$ value per tree or composite seedling sample was used as an indication of whole plant physiological performance. The power of non-significant ($p>0.05$) statistical tests was calculated using tables provided in Cohen (1988).

Common Garden Study

Potential genetic variation on local and regional scales in blue oak seedlings were examined in a common garden experiment by collecting acorns from oak populations occupying the southern, xeric site (San Joaquin Experimental Range, Madera County) and the northern, mesic site (Hopland Field Station, Mendocino County). Seedlings germinated from these collections were grown outdoors at University of California Davis in 12 specially designed large volume containers, each having one slanted glass side for root growth observations. The containers were 1 m in height, 48 by 24 cm at the top and 48 by 12 cm at the base. The potential for maternal tree effects as manifested by differences in acorn size were assessed by weighing each acorn before planting. Acorns were planted into three types of herbaceous neighborhoods: an introduced annual grass, *Bromus diandrus* Roth.; an introduced annual dicot, *Erodium botrys* Cav.; and a native perennial grass, *Stipa pulchra* Hitchc. These different neighborhoods induce different rates of soil water depletion; soil moisture is exhausted more rapidly by the introduced annual species (Gordon and Rice, unpublished data). We examined the potential influence of the local soil water regime on phenotypic expression of population differences in seedling WUE, morphology, growth, and survival. Relative estimates of seedling WUE were obtained by measuring the ratio of ^{13}C to ^{12}C in leaf and stem material (Farquhar and others 1988).

Contingency table analysis was used to detect differences between populations in the relationship between acorn weight and emergence probability. The General Linear Model (GLM) procedure of the SAS statistical package (Freund and others 1986) was used to calculate linear correlations between acorn weight and various seedling traits. Analysis of variance procedures within the GLM were used to examine the interactive influence of germplasm (population or family) and competitive environment on phenotypic variation in seedling traits. If necessary, data were appropriately transformed to conform with the assumptions of the analyses within the parametric GLM procedure.

RESULTS

Regional Variation in Blue Oak WUE

Regression analysis indicated that the $\delta^{13}C$ values of leaves and stems of adult blue oak trees were significantly related to annual rainfall ($p=0.018$, $r^2=0.44$). Along the decreasing rainfall gradient from Hopland in the north to San Joaquin in the south, carbon isotope discrimination in adult plants decreased. This strong pattern across regional boundaries suggests higher WUE in trees from dry habitats and lower WUE in trees from more mesic sites.

In contrast, there was not a significant relationship between blue oak seedling tissue $\delta^{13}C$ and rainfall ($p=0.23$, $r^2=0.13$). The power to detect a significant relationship for seedlings was low (i.e. for r^2 = 0.13, power = .22); however if the relationship between seedling tissue $\delta^{13}C$ and rainfall had been as strong as that found for adult trees, the power to detect this relationship would have been relatively high (power = .72).

Common Garden Study

On average, acorns were smaller in size in the mesic population and the acorn size distribution within this population was heavily skewed to the right (fig. 1). Probability of seedling emergence increased with acorn size in the xeric population, but was independent of acorn size (contingency table analysis; $p > 0.50$) in the mesic population (fig. 1). There were significant differences between populations in the relationship between acorn size and seedling morphology and growth. In the mesic population, both average leaf size ($r = 0.68$) and final stem weight ($r = 0.79$) increased with acorn size, while in the xeric population these seedling traits were not significantly correlated with acorn size. There was no detectable difference in seedling WUE between the two populations ($p>0.50$). However, herbaceous neighborhood composition had a significant effect on WUE; in the native *Stipa* neighborhood, where soil water is depleted more slowly, the seedlings exhibited significantly lower WUE ($p<0.05$)than in the annual neighborhoods.

Within the mesic population there were significant differences in acorn size among families ($p<0.001$); family averages ranged in size from a high of 8.4 to a low of 2.7 gins. Analogous to the results reported for between-population variation, the effect of within-family variation in acorn size varied among maternal families. Significant differences among trees in the direction and magnitude of the linear correlation between acorn size and seedling average leaf size and stem weight are indicated by a significant family by acorn weight interaction (ANOVA; $p < 0.02$) and the interaction plots for both seedling traits (fig. 2A and 2B). Thus, the relative importance of acorn size on seedling morphology and growth differs significantly among families within this population. Significant interaction (ANOVA; p <

0.01) of maternal family and neighborhood composition in average leaf weight (fig. 3) indicates that the magnitude and direction of phenotypic response in seedling leaf weight to changes in herbaceous neighborhood varies from one tree to the next.

DISCUSSION

The higher $\delta^{13}C$ values for blue oak tree populations in the drier regions suggests greater WUE because of greater regulation of diurnal and seasonal stomatal conductance. Phenotypic variation in gas exchange characteristics that regulate water use may result from either genetic differentiation or acclimation. The possibility of genetic differentiation among blue oak populations in water use characteristics is supported by recent reports of heritable variation for carbon discrimination and WUE in agronomic species (Farquhar and others 1989).

In contrast to the strong linear relationship between tree WUE and rainfall, we were unable to detect a comparable relationship for seedlings. This difference in response to the rainfall gradient may result from differences in growth phenology between trees and seedlings. In blue oak seedlings, stomatal conductance and growth are very sensitive to reductions in soil water potential (Gordon and others 1989). Seedling conductance and growth are minimal at the pre-dawn water potentials of $\geq$ -3.0 MPa that have been observed in the field by late May and early June (Welker 1988, Gordon and others 1989). As a result, seedlings avoid drought by actively growing only during the spring when both temperature and moisture are favorable. In contrast, adult blue oak trees continue to transpire and grow well into the summer drought (Elliott 1958, Griffin 1973, Baker and others 1981). During late summer when soil water potentials exceed -5.0 MPa at the xeric sites, higher WUE may significantly improve drought tolerance in adult oaks (Levitt 1980).

The common garden study represents an initial attempt to examine the interactive effects of germplasm, maternal effects (e.g. acorn size), and local competitive environment on phenotypic variation in blue oak seedlings. The importance of germplasm source or phenotypic plasticity, or both, in shaping oak seedling phenotypes appears to be trait-dependent. For example, seedling WUE is characterized by a plastic response to drought induced by different herbaceous neighborhoods and does not appear significantly affected by acorn source. In contrast, probability of emergence is determined by an interaction of regional acorn source, maternal effects (i.e. acorn size), and competitive environment (Gordon and others 1989).

These differences between the regional acorn sources suggest that significant racial or subspecific variation may exist in blue oak. These results for quantitative traits contrast with the results obtained by Millar and others (1990) for electrophoretic variation in blue oak. Although their results indicate that there is no geographic pattern in blue oak allozyme variation, they point out that electrophoretic variation may be a poor indication of genetic variation in quantitative traits (Gottlieb 1981, Hamrick 1983) and suggest that common garden studies are needed to fully understand the role of genetic variation in blue oak adaptation.

In addition to significant variation between populations, differences among trees within the mesic population in both acorn size and seedling growth and morphology suggest that there may be significant within-population genetic variation for traits of potential adaptive significance. This within- population variation provides the genetic raw material for selection to act upon; it represents, in a sense, the evolutionary potential of a population to respond to selective challenges in the future. Evidence for genetic variation in phenotypic plasticity is also indicated by the differential response among families in leaf weight to changes in the competitive neighborhood. If this variation has a significant additive genetic component, selection for plastic responses in seedling leaf traits may also be possible in this population (Via and Lande 1985, Schlichting 1986).

Conservation and restoration biologists are in general agreement on placing high priority on the conservation of critical or keystone species within ecosystems (Wilcox and Murphy 1985, Terborgh 1986). As noted by Thomas and Salwasser (1989), the conservation of keystone species such as blue oak that occur in multiple-use lands represents one of greatest challenges but also one of the greatest opportunities for maintaining biological diversity. The challenge is to conserve diversity in a manner compatible with multiple-use demands; the opportunity arises from the fact that conservation practices developed within multiple-use arenas can be applied to a wide range of public lands. However, the conservation of species and habitats requires understanding of the determinants of phenotypic expression. Common garden studies are helpful in partitioning the relative influences of genetic variation and environment on phenotypic development. Whether the apparent genetic variation detected between and within populations of blue oaks is adaptive remains to be tested; to this end we have initiated a series of reciprocal transplant experiments to detect spatial scales of local adaptation, if it exists. Because the importance of acorn size in phenotypic expression was demonstrated for several traits in this study, a series of reciprocal grafting studies are also currently planned to help evaluate the influence of genotype and environment on adult blue oak traits such as acorn size and WUE.

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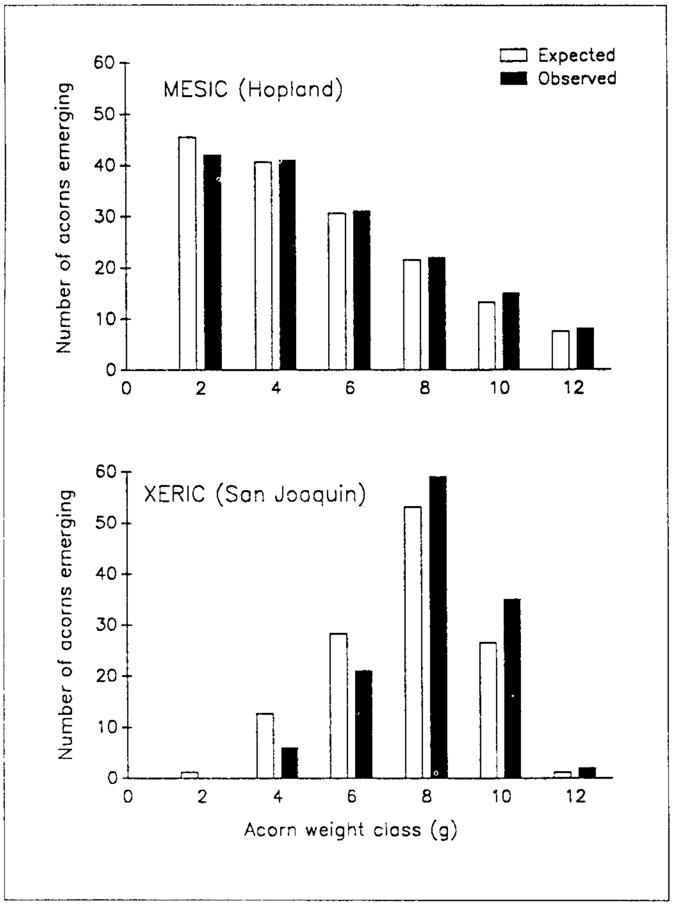

Figure 1—Between-population differences in the effect of acorn size on emergence.

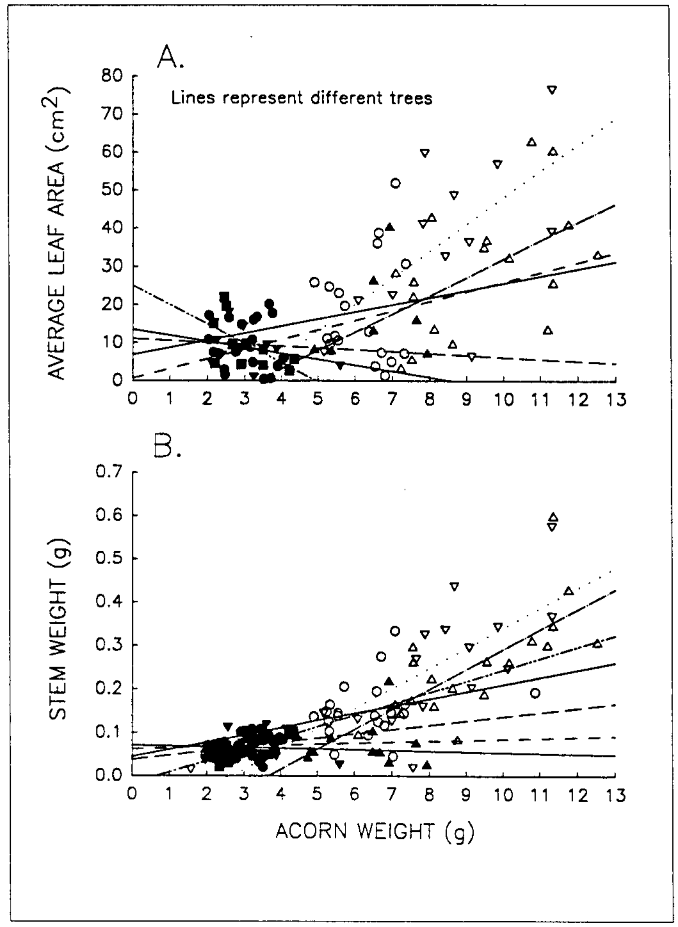

Figure 2—Within-population (among tree) variation in the effect of acorn size on A) seedling leaf size and B) shoot growth.

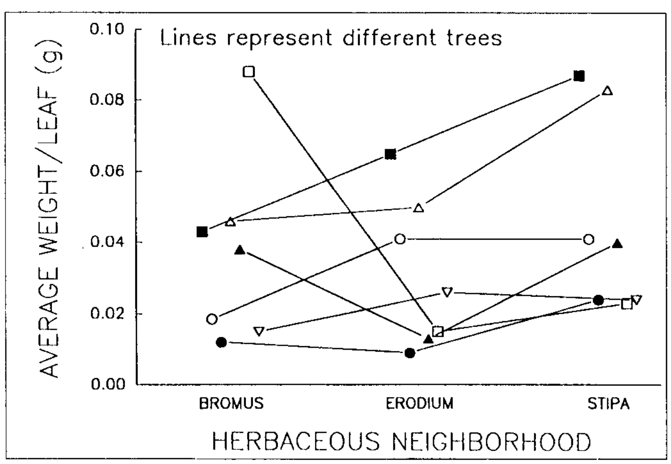

Figure 3—Within-population variation for plasticity in leaf weight in response to competitive neighborhood.

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Stump Sprouting of Blue Oaks in California[1]

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Abstract: A study was conducted at five sites in California to determine the sprouting response of blue oak (*Quercus douglasii* Hook. & Am.) to varying harvest dates, stump heights, and fencing treatments. First- and second-year results indicated that harvest date had relatively little influence on sprouting, while stump height had a great impact. Nearly twice as many 90-cm stumps sprouted as did ground-cut stumps. Site also had a large influence. The average percent of stumps with live sprouts after two years ranged from 76 percent at one site to 37 percent at another, and average shoot length ranged from over a meter to less than 40 cm. While fencing had relatively little effect on the percent of stumps that sprouted, it greatly reduced browsing injury and increased sprout length. These results suggest that sprouting by blue oak will result in the reestablishment of many harvested trees, but that a number of factors can influence sprouting success.

Recent inventories of California oaks indicate that blue oaks are not regenerating well in portions of the state (Bolsinger 1988; Muick and Bartolome 1987). A variety of factors are known to limit natural regeneration, including predation of acorns, browsing of seedlings, clipping of roots, and drought-induced mortality caused by dense, competing vegetation. In some of the areas where recruitment by seedlings is apparently limited, it is believed that many of the existing blue oaks have originated from sprouts following fire or cutting (McClaran 1986). For a variety of reasons, stump sprouts are thought to have a competitive advantage over seedlings. First, since no acorns are involved, there is less risk of losses to insects, birds, or rodents. Second, since the root systems of established trees are massive in comparison to those of newly germinated acorns, they have a greater ability to tap soil moisture and maintain a more favorable water balance during the hot, dry summers that characterize the blue oak region. Finally, the initial growth rate of sprouts is likely to be greater than that of seedlings since stored carbohydrates in the roots provide an abundant food reserve unavailable to small seedlings. Rapid initial growth may be critical to successful establishment since it allows plants to grow above the level where they are susceptible to clipping or repeated browsing. Trees originating from stumps are also obviously located in areas suitable for growing blue oaks.

Previous research indicates that sprouts grow much faster than seedlings. Zahner and Myers (1984) found that sprout origin oak stands grew rapidly even on poor sites. A study of four species of oaks in the South reported that seedling growth was only 12 percent of sprout growth ten years after clearcutting (McQuilkin 1975). And Johnson (1978:p. 115) stated that "probably the most important silvicultural trait of stump and root sprouts is their rapid early growth".

While oaks are known for their ability to sprout (Hannah 1987), there has been very little research on sprouting of California species including blue oak. The following study was initiated to evaluate the effects of harvest date, site, stump height and protection from browsing on sprouting of this species.

METHODS

In 1987, 1-hectare study sites were selected at five locations (fig. 1) in dense (about 500 stems per ha) blue oaks stands representing a range of site conditions (table 1). At each study site, four plots were established. Each plot ranged in size from 0.15 to 0.30 ha and contained at least 96 trees. Two of the four plots were enclosed within 1.8-m tall fences to exclude deer and livestock. All study sites were grazed by either cattle or sheep.

Within each plot, 96 blue oak trees ranging in size from 7- to 40-cm DBH (Diameter Breast Height) were marked with numbered aluminum tags. On each of four dates (July, October 1987, January, April 1988) 12 trees were harvested per plot. Of these 12, six were cut at or near ground level (basal stump), and six were cut approximately 90 cm from the ground. Trees selected for harvest were chosen randomly. At the time of harvest, tree DBH and height were recorded. After felling, tags were nailed to the tops of stumps for permanent identification.

At the end of the 1988 and 1989 growing seasons (late September or early October), the number of sprouts, length of the longest sprout and browsing damage were recorded for each stump. A stump was given a positive browse rating if there was evidence of browsing or clipping on any of the living sprouts. Unfortunately, it was usually not possible to determine the animals responsible for injury.

Data were evaluated using analysis of variance for a doubly nested randomized block design, with sites as the main plots, fences as the sub-plots, and combinations of harvest dates and stump heights as the sub-sub plots. Where we found significant

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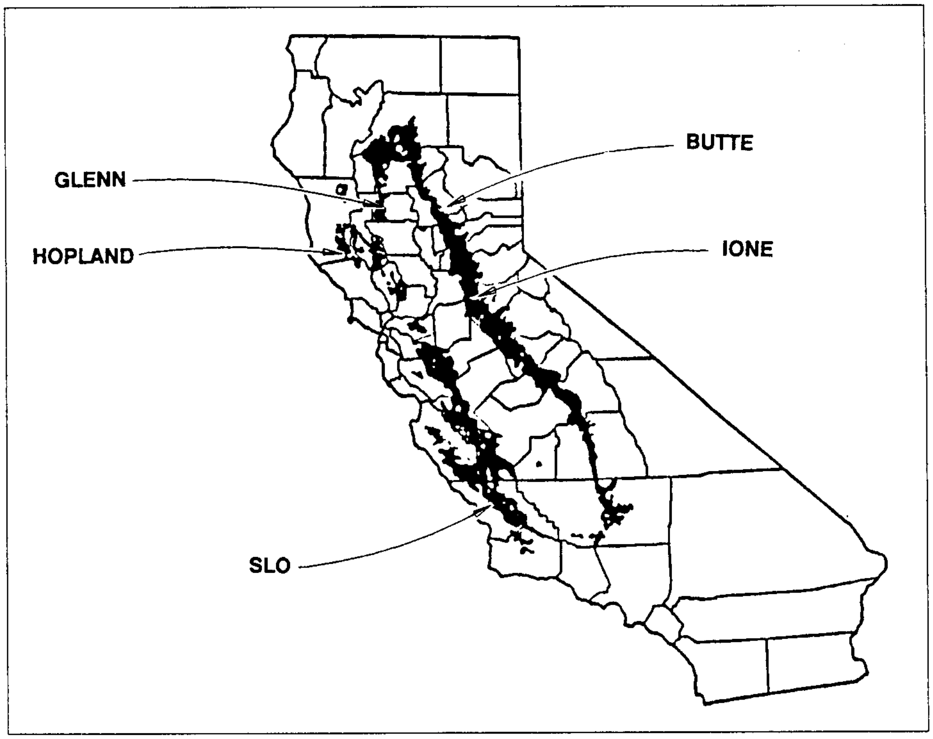

Figure 1—Location of the study sites. Shaded areas show the distribution of blue oak in California.

Table 1 — ***Characteristics of blue oak study sites***[1]

	Site				
Site Characteristics	Hopland	Glenn	Butte	Ione	SLO
Elevation (m)	490	240	170	82	550
Density (stems/ha)	483	518	464	470	485
Basal area (m2/ha)	17	9	15	12	11
Annual precipitation (cm)[1]	93	55	52	46	55
Soil:					
Depth (cm)	60	70	45	100	42
Texture	silt loam	clay loam	clay loam	grav.loam	grav.loam
Series	Laughlin	Sehorn	Auburn	Red Bluff	Millsholm
Subgroup	Ultic Haploxeroll	Entic Chromoxerert	Lithic Xerochrept	Ultic Palexeralf	Lithic Xerochrept

[1] Precipitation data are from the nearest NOAA weather station. Soils information is from U.S. Soil Conservation Service reports for Glenn, Butte, Amador (lone), San Luis Obispo (SLO) and Mendocino (Hopland) Counties.

differences ($P < 0.05$), individual treatment means were compared using a Fisher's protected LSD test. In addition, average diameter and height of trees whose stumps sprouted were compared with those that did not sprout using t-tests. Finally, regression analysis was used to determine if there were significant relationships between preharvest tree measurements and sprout growth.

RESULTS

Percent of Stumps Sprouting

In both 1988 and 1989 more than half of the stumps sprouted at all study sites except Glenn (table 2). In 1988, sprouting ranged from a high of 73 percent at San Luis Obispo (SLO) to a low of 34 percent at Glenn. By 1989, overall sprouting percent increased at each site and ranged from 76 to 37 percent. Sprouting at the Glenn site was significantly lower than sprouting at all

Table 2 —*The average values of sprouting variables for different sites and evaluation years*[1]

	--- Sprout Percent ---		---Sprout Number ---		---- Sprout (cm) ---	
Stand Location	1988	1989	1988	1989	1988	1989
Hopland	62a	72a	25.3	54.1	36.7c	52.6c
Glenn	34b	37b	26.5	22.0	37.3c	41.6d
Butte	63a	65a	34.0	30.1	74.7a	107.2a
lone	59a	65a	21.2	20.2	51.6b	77.8b
San Luis Obispo	73a	76a	24.7	25.0	29.8c	39.9d
Totals	58	63	26.5	30.6	46.5	64.8

[1]Values within a column are significantly different (P<0.05) if they are followed by a different letter (Fisher's protected LSD test).

other sites, which were not significantly different from one another.

The most striking difference in the percent of stumps sprouting resulted from stump height (fig. 2). Nearly twice as many 90-cm stumps sprouted both years. While tall stumps had greater sprouting than basal stumps at all sites, the proportion in these two groups varied by site, resulting in a significant site by stump height interaction for 1988.

Although there was no significant difference the first year, in 1989 a significantly greater percent of protected stumps sprouted compared to unprotected stumps (67 versus 59 percent). There were no significant differences in sprouting percent either year for dates of harvest. These percentages ranged from 55 to 63 percent in 1988, and from 60 to 65 percent in 1989 (fig. 3).

Number of Sprouts

In contrast to the sprouting percent, the number of sprouts per stump was not significantly affected by site (table 2). It was also not affected by harvest date in 1989, but it was in 1988. In the first year, there were significantly fewer sprouts on stumps from the last harvest date (April 1988) than from any of the other harvest dates.

There were also significant differences in the number of sprouts growing on tall and short stumps both years, with a greater number of sprouts growing on the 90-cm stumps (36 versus 15 in 1988, and 33 versus 28 in 1989). However, there was no consistent pattern in number of sprouts inside or outside the fences; in 1988 there were significantly more sprouts inside while in 1989 there were more outside. In 1989 there were several significant interactions for the number of sprouts. These were due primarily to one basal stump at Hopland which had 600 sprouts! - more than double the number of any other tree in the study.

Length of the Longest Sprouts

For both years there were significant differences among study sites in the average lengths of the longest sprouts (table 2). In 1989, average sprout lengths varied from 75 cm at Butte to 30 cm at SLO. For 1989, average sprout lengths at these respective sites were 107 cm and 40 cm. There were also significant differences in sprout lengths inside and outside the fences (fig. 4). In 1988, average length inside was 59 cm, compared to 33 cm outside. In 1989, these averages were 85 cm and 42 cm.

Date of harvest also influenced sprout lengths. For both years, stumps from the April harvest produced significantly shorter sprouts than those from the other harvest dates. There were no significant differences in sprout lengths between stump heights.

There was also a significant fence by site interaction for

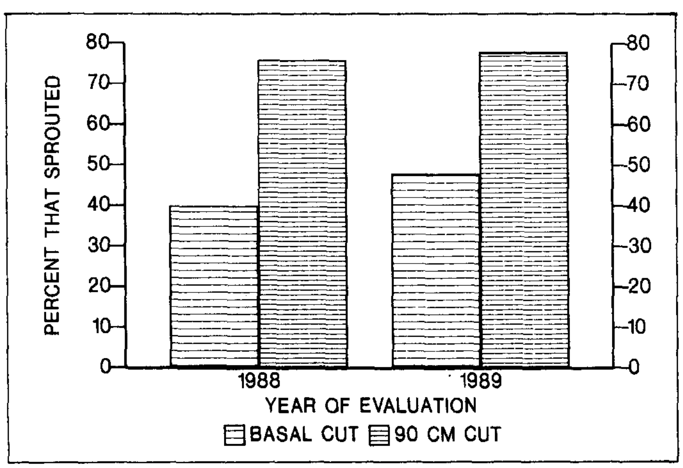

Figure 2 —The percent of stumps from each stump height that sprouted in both 1988 and 1989.

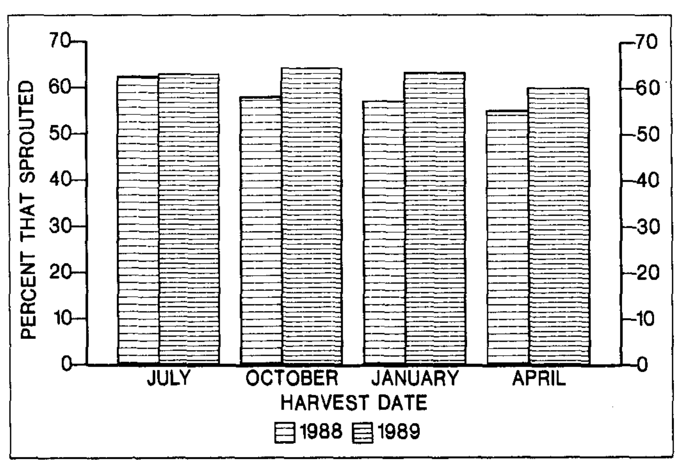

Figure 3—The percent of stumps from each harvest date that sprouted in both 1988 and 1989.

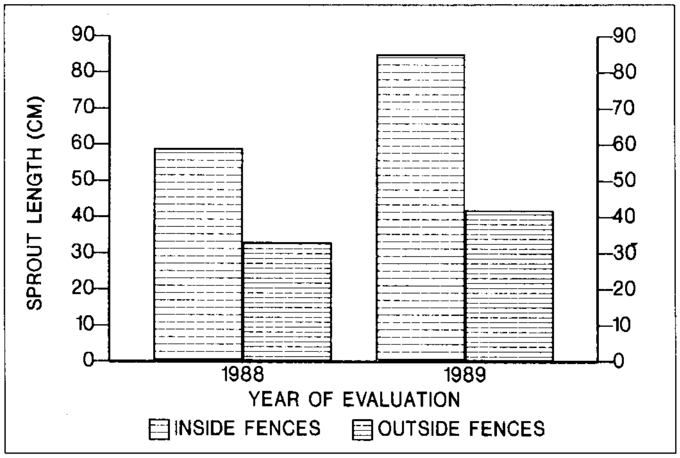

Figure 4 — The average length of the longest sprout per stump in 1988 and 1989, both inside and outside fenced exclosures.

sprout length, primarily because at Hopland both years the lengths inside fences were more than 10 times those outside due to unusually heavy browsing. At the other sites, however, lengths inside were generally less than double those outside.

Browse Damage

The only significant difference in browse damage in either year was between protected and unprotected stumps. Eighty-two percent of stumps outside fences were browsed in 1988 compared to 18 percent inside. For 1989 these figures were 88 and 14 percent, respectively. It appeared that mice and/or rabbits browsed or clipped the sprouts inside the fences, while deer and livestock were primarily responsible outside.

Relationship between Tree Size and Sprouting

For both 1988 and 1989 trees that sprouted were significantly smaller, averaging 15.5 cm in diameter. Non-sprouting trees averaged 17.8 cm both years. While these differences were fairly small and there were trees of all size classes in each group, there was a clear trend for small trees to sprout more than large trees. For instance, for trees less than 13-cm DBH, 71 percent sprouted in 1988 while, for trees greater than 26-cm DBH, only 41 percent sprouted. However, there were no significant differences in initial tree height between sprouting and non-sprouting trees.

We also tried to find out if initial tree diameter affected subsequent sprouting characteristics by correlating the DBH of trees that sprouted with the number of sprouts and length of the longest sprout that were produced each year. There was a significant positive correlation for all of these combinations, except for DBH and number of sprouts in 1988. These results indicate that, of the trees that did sprout, larger initial diameter promoted the growth of more sprouts and longer sprouts.

DISCUSSION

A dramatic result from this study was the tremendous influence of stump height on sprouting. More 90-cm stumps from each harvest date at each site sprouted than did basal stumps, although stump height did not have a consistent effect on sprout number or length. The reasons for the greater sprouting of the 90-cm stumps are unclear but are probably related to the fact that tall stumps have more dormant buds than short stumps, as well as more stored carbohydrates in their stumps.

This finding contradicts research on oaks by Roth and Hepting (1943:p.29) who reported that "the height at which stumps are cut has little effect upon the sprouting capacity, because the great majority of sprouts arise about the root collar." In this study, sprouts on the 90-cm stumps often originated up and down the stump, but few came from the roots.

Even though tall stumps may produce more sprouts than basal stumps, Hannah (1987) asserted that oak sprouts originating high on stumps are inferior to those growing from the root crown or low on the stump. He concluded that the best sprouts originated from buds at or below the ground line and, consequently, recommended cutting stumps low. The common perception is that sprouts originating high on stumps are at greater risk from decay which moves from the decaying stump to the new. sprouts. Shigo (1986), however, argued that decay does not move freely from an old wound into the new sprouts since the heartwood core of the stump and the heartwood of the sprout are not connected. He pointed out that sprouts originating at all locations on the stump and roots can still be killed from below by root rots taking advantage of the weakened host, or from above through wounds resulting from the death of low-vigor sprouts or branches. He also noted that stool sprouts - those originating from buds along the cambial zone on the surface of the cut stump - are inherently weak and generally do not last long. We will continue to monitor the stumps and evaluate the differences in sprouting of high and low-cut stumps over time to determine if there are differential rates of survival, growth and decay.

One surprising result of this study was that harvest date had very little influence on sprouting. Previous research on the relationship between season of harvest and sprouting has been mixed, with both positive (Buell 1940; Roth and Hepting 1943), and neutral (Johnson 1977) results reported. For blue oak, the only previous study found a seasonal pattern of sprouting with more sprouting of trees harvested during the winter months (Longhurst 1956), although seasonal effects on sprouting tended to decrease over time.

Our finding that tree diameter was inversely related to degree of sprouting has been reported by others. Johnson (1977) found that the probability of sprouting decreased with increasing stump diameter, and Roth and Hepting (1943) reported that very large stumps would not sprout at all. That blue oak DBH is correlated with the number and length of sprouts is similar to

Johnson's (1975) finding for northern red oak that DBH was positively correlated with the percent of stumps with long sprouts.

While the overall level of sprouting varied considerably among sites, we found no correlations between sprouting and obvious site factors, including annual rainfall. In fact, the site with the highest percentage of sprouting was San Luis Obispo which had average rainfall (55 cm per year). We suspect hybridization between blue oak and desert scrub oak (*Quercus turbinella* Greene subsp. *californica* Tucker) at this site may have contributed to the high degree of sprouting. Hybrids of these two species are known to occur in the general area (Benson and others 1967) and would likely demonstrate a greater tendency to sprout. While the plot trees appeared to have predominantly blue oak traits, a preliminary analysis of trichomes on the undersides of some sample leaves indicated that some hybridization was occurring.

Another factor which varied greatly by site was the degree of browsing. Trees outside fences were subject to some browsing at all sites, but at Hopland browsing was so severe that sprouts on all unprotected stumps were chewed back almost completely. This intense browsing pressure at Hopland was attributed primarily to a high resident black-tailed deer (*Odocoileus hemiomus*) population, and secondarily to sheep. Where such high populations of browsing animals are present, sprouts apparently need protection in order to produce new trees. Even at the sites where browsing pressures are less, it appears that the differences between protected and unprotected sprouts are increasing with time.

Our results also indicate that blue oak sprouts generally grow much more rapidly than seedlings. After two years, average length of the longest sprout per stump was over 64 cm, even though half of the stumps were repeatedly browsed. This growth is far greater than would normally be expected from natural seedlings or even from artificial plantings, unless intensive planting and maintenance procedures were followed. In addition, many of the fastest growing sprouts originated high on the 90-cm stumps which means that after two years they were well on their way out of the browse zone. Such rapid growth has important implications for regeneration programs. Much of the land where blue oak grows is in private ownership where the principal use of the land is livestock grazing. If landowners choose to cut some trees for firewood, or to thin dense stands to produce increased forage, encouraging and protecting sprouts would likely lead to new trees more rapidly than the planting of seedlings.

As indicated in this discussion, while there were marked differences in sprouting due to different treatments, for the study as a whole the level of sprouting was high and the growth of sprouts vigorous. This is somewhat surprising since blue oak is often labeled a poor sprouter or non- sprouter. Clearly this is not the case at many sites in California. It must be recognized, however, that results from a two-year trial do not translate into long-term management options. Long-term monitoring is required to determine if stump sprouts will survive to become mature trees. The results from this study are also not applicable to other native oak species in California which vary greatly in their sprouting abilities.

CONCLUSIONS

Contrary to common belief, blue oak sprouts well after harvesting. Of 960 trees cut at five separate sites, over 60 percent had living sprouts at the end of two years and average length of the longest sprout was over 64 cm. Stump height had the greatest influence on sprouting, with approximately twice the sprouting for 90-cm stumps compared to ground-cut stumps. Season of cutting, on the other hand, had little influence, suggesting trees can be harvested at any time of the year and still sprout. Larger diameter trees were less likely to sprout than small ones, but DBH and sprout growth were positively correlated. Unprotected sprouts were damaged by browsing. Damage was especially great where there were large populations of browsing animals present. Where sprouts were protected, however, they grew quite rapidly. These results suggest that stump sprouting can help offset losses from tree harvesting by replacing a sizeable percent of the trees which are removed.

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Factors Limiting the Establishment of a Chaparral Oak, *Quercus durata* Jeps., in Grassland[1]

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Abstract: We studied factors that restrict colonization of grassland by *Quercus durata* Jeps., an oak commonly found in chaparral on serpentine soils. The study site contained a chaparral/grassland border that had been stable for at least 50 years. Monitoring of acorns planted in the chaparral understory and grassland revealed that, although initial seedling emergence was similar in the different sites, seedling survival was much higher in the chaparral. No seedling in the open grassland survived beyond the third year of the study, while 25 percent in the chaparral understory were still alive at the end of 6 years. The differences in survival could not be explained by differences in animal activity and herbivory. Rather, the high solar radiation load on seedlings in the grassland appeared to play a major role in mortality. Experimental shading of seedlings in the grassland with light shade cloth increased seedling survival.

Little successful oak seedling establishment has been observed in California grasslands and savannas in recent decades (Griffin 1977, White 1966). Over historical time, oak cover has been reduced and oak woodland has been converted to grassland in many areas (Holmes 1990). Because of this, concern has focused on the ability of oaks to establish in grasslands. Studies addressing this problem have identified several bottlenecks to seedling establishment. Acorns suffer high levels of predation by a wide variety of mammals, rodents and birds (Griffin 1980, Borchert and others 1989, McCreary 1989). In addition, germination of acorns may be reduced by heating and drying, conditions often encountered at the soil surface after acorn drop (Griffin 1971, Keeley 1987, McCreary 1989). Despite these pre-germination obstacles, seedlings often emerge (Griffin 1971). Seedlings rarely survive, however, and browsing of seedlings (above- and belowground) has been identified as a major factor preventing oak establishment (Griffin 1976).

In addition to animal damage, physical characteristics of the grassland environment may be hostile to oak seedling survival. In the mediterranean-type climate of California, high radiation loads, high soil surface temperatures and drought coincide in grasslands during the summer. While the grassland annuals escape these conditions by dying, the oak seedlings must survive them. There are some indications that mesic sites, such as those Provided by tree cover and north-facing aspects, are more conducive to oak seedling survival in some areas of California (Griffin 1971, Muick and Bartolome 1987). This study was implemented to determine whether simple shading could increase oak seedling survival in a grassland setting.

We studied the survival of seedlings of *Quercus durata* Jeps. at Stanford University's Jasper Ridge Biological Preserve, San Mateo County, California. *Quercus durata is* a shrubby oak, commonly occurring in stands of chaparral on serpentine soil. Our site had serpentine soil with a stand of chaparral adjacent to an area of grassland. Aerial photographs revealed that the chaparral/grassland boundary had not moved in at least 50 years (Davis and Mooney 1985). Cattle grazing, which may have prevented invasion of the grassland by oak, was removed from the site in 1960. Acorns reach the grassland and germinate, as evidenced by small scattered *Quercus durata* seedlings found several meters from the edge of the chaparral during the course of this study. The stability of the chaparral/grassland boundary suggests, however, that survival of these seedlings is nil. We planted acorns across this boundary and compared the survival of seedlings in the chaparral understory, in the bare zone adjacent to the chaparral, in the grassland, and in the grassland with artificial shading.

METHODS

Acorns were collected from *Quercus durata* shrubs at our site in October of 1984, during the time of natural seed dispersal, and planted in plots along four transects: one through the chaparral understory, one along the bare zone and two parallel to the bare zone in the grassland. Acorns were planted approximately 2-3 cm deep and at least 25 cm apart (234-240 acorns per transect). During the summer months, 40-percent shade cloth was erected over half of each grassland transect.

Planting locations (located with a grid) were examined every 2-4 weeks. Initial emergence of a shoot from the soil surface was noted and the presence or absence of a live shoot was subsequently monitored. Condition of the shoot (browning leaves, herbivory) was also noted. A live shoot was defined as one having some green leaf area. After the first summer, it became obvious that oak seedlings did not resprout during the summer drought. Therefore, only plants with previously live shoots were monitored during the summer. Seedlings were monitored for six years (1985-1990). Because the seedlings often resprouted following shoot loss, a seedling was only

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considered dead if it did not resprout the following year. Differences among treatments and sites in the fraction of acorns producing aboveground shoots (percent emergence) and in the fraction of seedlings surviving six years were compared using G-tests.

Because of the patchiness of shade within the chaparral understory, planting locations were scored for degree of shadiness. At four times during one sunny day in July of 1986, planting locations were visually scored to estimate their daily interception of direct sunlight. A score of 1 to 4 was assigned depending on whether direct sunlight impinged on >95, 50-95, 5-50, or <5 percent of the soil surface. Summation of these scores over the day yielded an arbitrary ranking of shadiness for the locations in which acorns were planted. The association of plant survival with shade was examined by using a Mann-Whitney two sample test to compare the shade score distribu-tions of sites in which seedlings emerged and sites in which they survived.

To compare the degree of shading imposed by the shade cloth with that produced by other, natural sources of shade, daily courses of photosynthetically active radiation (PAR) were measured (1) in full sun, (2) under shade cloth, (3) under the edge of the chaparral canopy, and (4) under small, isolated shrubs in the grassland at Jasper Ridge. Measurements were collected on a clear midsummer day (4 July 1990) using gallium-arsenide sensors (PH 201 A, NEC, Tokyo, Japan) monitored by Campbell 21x data loggers (Campbell Scientific, Logan, UT).

RESULTS

Plant emergence (the percent of acorns producing aboveground shoots) ranged from 65 percent in the unshaded grassland to 76 percent in the bare zone. While emergence was statistically higher in the shaded grassland and bare zone than in the unshaded grassland, high numbers of seedlings emerged in all sites.

Site	Percent emergence[1]
Grassland	65[a]
Shaded grassland	73 [b]
Bare zone	76[b]
Chaparral	69 [ab]

[1] Values superscripted by the same letter are not significantly different, G-test, $p<0.05$.

Experimental shading increased the survival of oak seedlings in the grassland (fig. 1). In the natural, unshaded grassland, no seedling survived past the third year. Six percent of the seedlings in both the bare zone and shaded grassland were alive at the end of six years. Seedlings in the chaparral understory had the highest survival at the end of six years (25 percent). Survival in the chaparral understory was significantly higher than that in any other treatment (G-test, $p<0.01$). Survival in shaded grassland was significantly higher than that in natural, unshaded grassland (G-test, $p<0.01$).

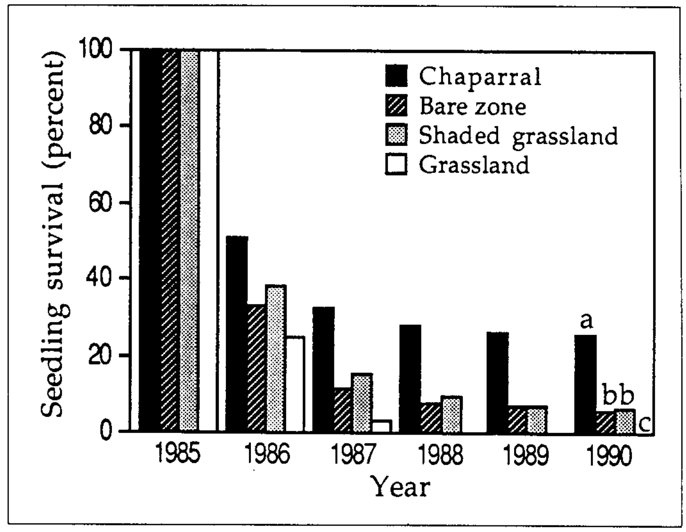

Figure 1—Seedlings alive each year in different treatments and sites. Numbers are percentages of those seedlings alive the first year: 133 in the open grassland, 158 in the shaded grassland, 161 in the bare zone and 143 in the chaparral understory. (Because some seedlings were destructively harvested the first year, these numbers are lower than the number of seedlings that emerged.) Letters indicate statistical differences among treatments and sites for final (1990) survival. Values superscripted by the same letter are not significantly different, G-test, $p<0.05$.

The shade provided by the shade cloth in the grassland was much less than that cast by either the chaparral canopy or small isolated shrubs in the grassland. The shade cloth transmitted approximately 55 percent of the photosynthetically active radiation (fig. 2). The scatter in the data was due to the small sensors detecting shadows cast by the weave of the shade cloth. Light levels under a small, 40 cm tall poison oak in the grassland (fig. 2) were only 5-6 percent of full sunlight during much of the day. The light regime in the chaparral understory was extremely

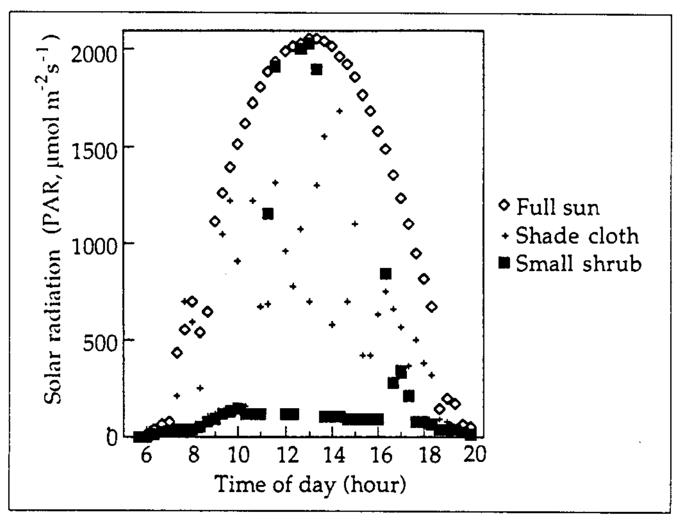

Figure 2—Photosynthetically active radiation (µmol $m^{-2}s^{-1}$) in full sun, under the shade cloth and under a small shrub in the grassland.

variable. Light levels in full shade (no direct sunlight) were also approximately 6 percent of full sun (data not shown).

Within the chaparral understory, seedling survival was higher in the shadier microsites (fig. 3). Comparing the distribution of shade among sites in which seedlings emerged and sites in which they survived revealed that survival was higher in the shadier sites (Mann-Whitney two sample test, $p<0.01$).

The higher seedling survival in the chaparral did not appear to be related to a lower incidence of animal damage. On the contrary, levels of animal damage appeared higher in the chaparral than in other sites and treatments. A greater proportion of the plants that died in the chaparral died with evidence of severe animal damage (severe browsing or evidence of gopher damage), compared to plants that died in any other site (G-test, $p<0.01$) (fig. 4). Root damage to seedlings was difficult to assess, but gopher disturbance was observed in all sites (grassland, bare zone and chaparral understory).

DISCUSSION

Artificial shading of seedlings in the grassland increased survival, but final survival (at the end of six years) was still low. It is uncertain how many of these seedlings will ultimately survive to adulthood. At the end of six years, the tallest seedling in any site was only 15 cm tall. The fact that seedling mortality was very low for the past three years, however, suggests that the remaining seedlings may be well established and have a high probability of continued survival.

The association of high seedling survival with shady microsites within the chaparral understory is consistent with the hypothesis that shade increases seedling survivorship, but is not conclusive. The canopies of the adult shrubs may coincide with some feature of the underlying rock and soil that actually controls shrub distribution. However, such possible associations were not factors in the grassland shading experiment, and shading increased seedling survivorship in both grassland transects.

The mechanism by which shading increased seedling survival is not clear. Shading may reduce leaf temperatures of the seedlings or improve their water status by reducing the transpiration rate of both the oak seedlings and the competing grassland annuals. Additionally, some interaction of high light, high temperature and water stress, all of which may be reduced by shading, may have a negative impact on seedling metabolism. Some evidence exists that water stress in some California grasslands contributes to poor performance of oak seedlings. Gordon and others (1989) showed that competition from grassland annuals for soil moisture reduced emergence and growth rates of blue oak seedlings (*Quercus douglasii* Hook. & Arn.). Griffin (1971, 1980) found that clearing competing grassland vegetation decreased rates of mortality in seedlings of several oak species, but a study on *Quercus lobata* Née (Griffin 1976) showed little effect of grass interference on seedling survival. Snow (1973) observed that, while seedlings of *Quercus agrifolia* Née experienced lower water potentials when competing with herbaceous vegetation, visible injury (browning of leaves) was associated with whether or not the seedling was shaded rather than its degree of water stress. Thus, while alleviation of water stress may improve oak seedling performance, other factors associated with shading may interact with seedling water status to affect survival.

The difference in seedling survival between the bare zone and the grassland in this study may have resulted partly from improved soil water status in the bare zone and partly from shading by the adjacent chaparral. The soil moisture regimes in the grassland, bare zone and chaparral at our study site are quite different. Davis and Mooney (1985) showed that, below approximately 60 cm, soil was driest in the chaparral during the summer. At shallower depths soil dried most rapidly in the grassland, presumably due to water depletion by the grassland

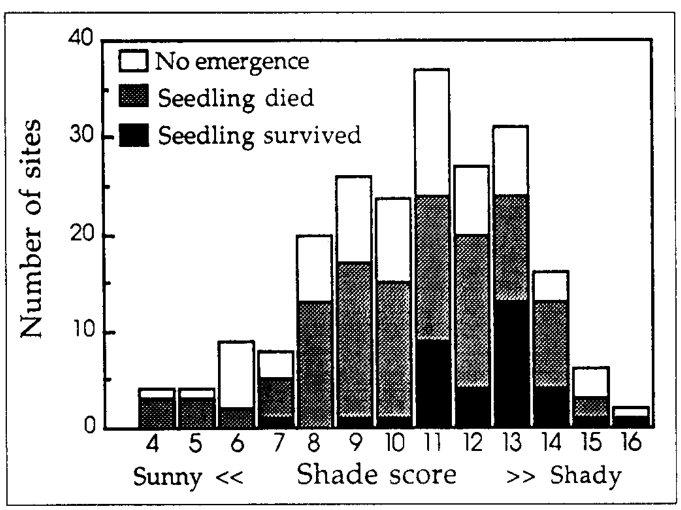

Figure 3—Distribution of shade among planting sites in the chaparral understory. Graph indicates sites in which seedling emergence occurred and sites in which seedlings survived six years.

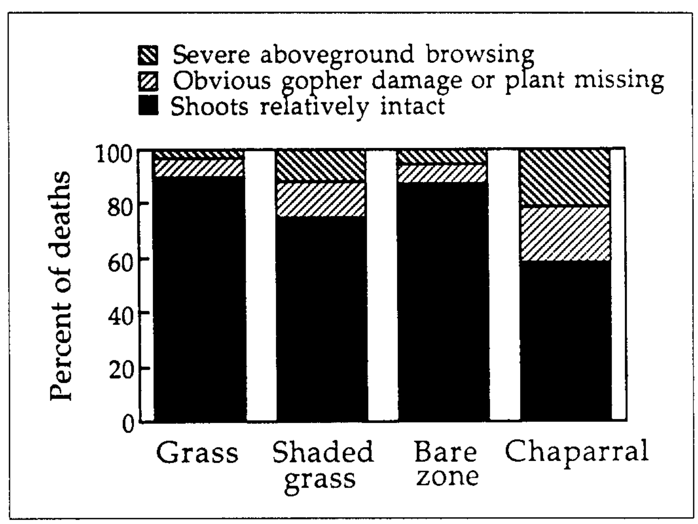

Figure 4—Final symptoms or fates of plants that died in the different sites and treatments.

annuals. Soil water potential in the bare zone was higher than that in the grassland during a large part of the summer drought. The higher soil water potentials in the bare zone, as well as partial afternoon shading of some seedlings by adjacent chaparral, may have increased seedling survival in the bare zone over that in the grassland.

Our main conclusion is that high summer radiation loads in the grassland contribute to the lack of oak seedling survival there. The shade provided by the mature chaparral canopy increases seedling survival in the chaparral. Other factors may vary between the chaparral and grassland, contributing to the difference in seedling survival between habitats. These factors, however, are not obvious. The soil in the grassland was similar to that in the chaparral (Davis and Mooney 1985) and evidence of animal damage to seedlings (this study) actually indicated a higher incidence of animal damage in the chaparral. Despite the possible existence of other factors restricting the establishment of oak seedlings in the grassland, artificial shading in the grassland did increase seedling survival. Furthermore, the artificial shading imposed was unnaturally light. The numbers of seedlings surviving under the shade cloth may have increased with a heavier shade treatment that more realistically imitated the shade cast by the chaparral canopy or by isolated shrubs in the grassland.

The results of this study are consistent with the observations of other investigators, noting increased seedling survival in shade for various California oak species (Griffin 1980, Griggs 1987, Muick and Bartolome 1987, Snow 1973). Increased survival of oak seedlings has been associated with shade, not only in California, but also in the central Rocky Mountain region, where seedlings of *Quercus gambelii* Nutt. were shown to survive much better under canopy protection (Neilson and Wullstein 1983). Observations such as this, combined with the results of this study, suggest that, in and open habitats, shading can improve oak seedling survival. Although artificial shading may be unrealistic as a large-scale management practice, the use of nurse plants to provide shade in grassland settings for fostering oak seedling establishment may prove profitable.

ACKNOWLEDGMENTS

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Artificial Regeneration of Blue and Coast Live Oaks in the Central Coast[1]

Tim R. Plumb Bennie Hannah[2]

Abstract: The primary goal of this study was to find economical and effective planting techniques that will ensure the establishment and early survival of coast live oak (*Quercus agrifolia* Née) and blue oak (*Q. douglasii* H. and A.) in the Central Coast region of California. Eight treatments were evaluated ranging from unprotected seed spots to those protected by 1/4-inch hardware cloth exclosures. Planting was repeated for two years. Seedling establishment varied significantly among study sites and between planting years. Poor germination and survival was attributed to below normal rainfall before and during the study. Seedling survival was enhanced with the use of animal exclosures and somewhat by shade. Blue oak establishment was somewhat better than that for coast live oak.

Lack of adequate regeneration of several woodland oak species is a major hardwood problem in California (Bartolome and others 1987; Bolsinger 1988; Griffen 1976; Johnson 1985). Many factors either individually or together impact acorns and the seedlings that develop from them. Acorns are a primary food for many animals including cattle, deer, turkeys, pigs, and assorted rodents. Birds and insects are extremely important factors in acorn utilization and seedling mortality (Griffin 1980; Brown 1980). Grazing by domestic livestock has been identified as the most persistent pressure on oak reproduction since the introduction of livestock by the Spanish in the late 18th century (Rossi 1980). However, excluding livestock from an area has not guaranteed seedling establishment (Griffin 1980). Where cattle and deer are excluded, small rodents, especially gophers, mice, and ground squirrels seem to be the major cause of seedling mortality (Griffen 1976; Borchert and others 1989; Adams and others 1987). The increase in small mammal populations is likely due to an abundance of annual grass seeds and roots and a reduction of predators.

Competition from annual grasses and herbaceous weeds for moisture, light, and nutrients also affects the survival of oak seedlings (Adams and others 1987; McCreary 1989). Moisture stress is believed to be an extremely important cause of seedling death, especially on marginal sites and during years of low rainfall. Blue oak (*Quercus douglasii* H. and A.) establishment has been found to be positively associated with increasing canopy cover and more mesic sites (Borchert and others 1989). On north-facing sites or partial shade, seedlings are able to survive in a grass cover even in dry years (Griffin 1980). Weed control in late winter or spring will decrease soil moisture loss due to transpiration. Weed control will also reduce the impact of pocket gophers and insects by removing their food source near the planting sites.

The overall objective of this study was to determine practical and economical methods of successfully establishing blue oak and coast live oak (*Q. agrifolia* Née) regeneration. Factors evaluated include three types of animal exclosures, light exposure (open versus canopy shade), and weed control to reduce moisture stress. The study was carried out on four planting sites in the Central Coast of California for two consecutive years to account for climatic variation.

STUDY AREAS

Blythe Ranch

The Blythe Ranch site is about 8 miles northwest of Paso Robles; descriptive characteristics are listed in table 1. The predominant vegetation is a woodland mixture of individual trees and small stands of coast live oak and blue oak with an occasional valley oak (*Q. lobata* Née) and it is interspersed with small areas of chaparral and open grassland. The soil under the two oak species is distinctly different even when the trees are in close proximity of each other with the coast live oak soil being decidedly more sandy than the blue oak soil.

A resident herd of about 20 cattle grazed the site continuously during the study. Wildlife typical of the coastal area is abundant including mule deer (*Odocoileus hemionus*), pocket gopher (*Thromomys bottae*), ground squirrels (*Spermophilus beecheyi*), and several flocks of wild turkeys (*Meleagris gallopavo*).

U.C. Hastings Reservation

The vegetation at Hastings Reservation is similar to that at Blythe Ranch with individual trees and small stands of coast live oak and blue oak, but with a greater component of valley oak. Wildlife species are abundant; there were no cattle or other livestock on this area.

[1]Presented at the Symposium on Oak Woodlands and Hardwood Rangeland Management, October 31-November 2, 1990, Davis, California.

[2]Professor and Graduate Student, Natural Resources Management Department, California Polytechnic State University, San Luis Obispo, Calif.

Table 1—***Name, location, and physical characteristics of the four oak regeneration planting sites***

Name	Location	Elevation (ft.)	Soil	Rainfall (in.)[1]	Species	Cattle	Aspect and Slope
Blythe Ranch	8 miles NW of Paso Robles	725	Sandy loam (CLO) to Clay loam (BO)	24 (10-34)	Coast live Blue oak	Yes oak	SE 10-40%
U.C. Hastings Reservation	26 miles SE of Carmel	2,200	Sandy loam with clay hardpan	20 (12-40)	Coast live oak	No	SE 10-40%
Agua Escondido (USFS)	20 miles SE of San Luis Obispo	2,490	Clay loam	— (11-16)	Blue oak	Yes	SE 15-20%
Benedict Ranch	10 miles W of Buellton	820	Santa Lucia series mixed with small rocks	14 (9-16)	Coastal live oak	Yes	N 10-15%

[1] Rainfall data collected locally at the Blythe Ranch and U.C. Hastings Reservation; data for other sites taken from nearest official weather station. First number is long-time average; numbers in parenthesis are for 1985-1989.

Agua Escondido

Agua Escondido is the most xeric of the test sites. Blue oak is the dominant tree species forming a small wooded savanna in a sea of chamise chaparral. Various Mediterranean herbaceous plants form a continuous ground cover. The area was grazed in 1987-88 by a herd of Brahman cattle.

Benedict Ranch

Coast live oak is the predominant tree species intermixed with small areas of grass and coastal sage. Over forty head of cattle grazed the area for a few months during the 1988 growing season, and a few horses had been pastured in the area during most of the study.

METHODS

Treatments

The eight planting treatments compared in this study (table 2) fall into the following three general categories: unprotected seed spots (Treatments 1-3), weed control-mulch (Treatment 4), and three types of animal exclosures (Treatments 5-8). All of the treatments were established in full sunlight at all sites or in the shade as noted in table 2.

Treatment 1 is a basic "control" planting without site preparation or weed control, and it simulates natural seedling establishment. Treatments 2 and 3 are the controls for the different levels of site preparation used in Treatments 5 to 8. Weed control was obtained either by scalping (scraping away herbaceous vegetation) or with black, 2-foot-square woven plastic sheets pinned in place with U-clips.

Three levels of predator exclusion were evaluated. In Treatment 5, only cattle were excluded from 40-foot-square barbed wire exclosures. Treatment 6 involved the use of 3-foot-high by 2-foot-diameter hog wire exclosures that were designed to keep out all large mammals. Treatments 7 and 8 involved the use of 1/4-inch hardware cloth exclosures that were 4 inches in

Table 2—***Study design and number of seed spots per treatment by test site and exposure for a single species***

	Test Area[2]				Total
	---------- I ---------		---II,III, IV-----		Seed
Treatment[1]	Open	Shade	Open	Shade	Spots[3]
1. Unprotected control, not predug or scalped	25	25	25	25	200
2. Unprotected, not scalped	25	25	25	25	200
3. Unprotected	100	100	25	25	350
4. Weed mats, unprotected	25	25	25	—	125
5. Cattle excluded	100	100	—	—	200
6. Large mammals excluded	25	25	25	—	125
7. Small and large mammals excluded	25	25	25	—	125
8. Small and large mammals excluded, mechanical clipping	25	25	25	—	125
Total seed spots:	350	350	175	75	1450

[1] Unless otherwise noted, all treatments include predigging and scalping.
[2] Test Area I = Blythe Ranch; Area II = Hastings Natural History Reservation; Area III = Benedict Ranch (coast live oak); Area IV = USFS site at Agua Escondido (blue oak).
[3] There were 1,450 see spots/species/year for a grand total of 5,800 for the study.

diameter and extended 12 inches above and 12 inches below the ground level. All animals are excluded except small insects. Mechanical clipping, Treatment 8, is a technique that is used to simulate animal browsing when there is no way to control the wildlife population. The above ground part of a seedling was cut back to ground level in late spring.

Planting Technique

The location of each seed spot was preselected and marked with a 2-foot-long 1/4-inch iron rebar stake. Except for Treatment 1, each seed spot was predug with a 4-inch power auger to a depth of 18 inches. Where required, a hardware cloth exclosure was installed and the soil refilled. Three acorns were planted at each seed spot between December, 1987, and January 1989. For the first year's planting, the acorns were placed straight down, point first, with the basal one-third of the acorn exposed. The second year, the acorns were pregerminated (Schettler and Smith 1980) and planted sideways 1 to 2 inches below ground.

Seed Collection and Storage

Acorns were collected directly from trees in October and November as close to each planting site as possible. An ample supply of blue oak acorns was available on each test site each year of planting. However, almost no coast live oak acorns were available at the Blythe and Hastings sites in 1987 and 1988.

The acorns collected in 1987 and 1988 were air-dried for several days and were then stored in plastic bags at about 38°F. Excess acorns were refrigerated until May, 1990, when a germination test was run to determine if the acorns were still viable.

Design and Analysis

An overall picture of the study design can be obtained from table 2 which lists the number of seed spots per treatment for each test site. Five 40-foot-square cattle exclosures were built on the north side of an individual tree with two-thirds of the exclosure in the open and one-third under the canopy. All the treatments for both planting dates were then randomly assigned to pre-selected seed spots. Logistic linear regression analysis was used to evaluate test results. Planting success was rated on the basis of at least one live seedling per seed spot. Sampling was done during late spring, after the first year's planting and again in late summer, 1988, and again in 1989. Germination for the second year's planting was evaluated in late summer, 1989.

Treatment Cost

An estimate of the cost for construction and setup of the animal exclosures and time required to predig a seed spot are listed in table 3. A fairly wide range in labor requirements is provided. Time for a specific job varied considerably depending on site conditions (e.g., loose versus hard soil), equipment availability, worker experience, etc. These figures should give a "ball-park" estimate of labor requirements and material cost.

Table 3—***Approximate labor requirements and material costs needed to fabricate and install the various items listed. The times and cost do not include site selection, supervision, travel time, etc.***

Item	Labor Requirements	Material Costs per unit[1]
Cattle exclosure 5-strand barbed wire 40 foot-square	[2]10-13 hours	$148.68
Large mammal exclosure hog wire	8-15 minutes	$2.07
Small mammal exclosure 1/4" hardware cloth	8-17 minutes	$0.87
Weed mats	1.5-2.5 minutes	$0.48
Pre-digging seed spots.	0.5-2.0 minutes	none

[1] Does not include the cost of equipment to manufacture or set up an item.
[2] Involved two workers plus an operator and tractor fitted with a 9-inch auger.

RESULTS AND DISCUSSION

Test Location

There was a considerable amount of variation in seedling survival among the four planting locations (figures 1-5) with the year of planting a confounding factor. Seedling establishment ranged up to 100 percent at Blythe in 1987-88 to less than 20 percent for both years of planting at the Benedict location.

Blythe Ranch

By far, the best initial seedling establishment obtained with the first year's planting was at Blythe. Percent seedling survival in May, about 5 months after planting, ranged from 52 to 96 percent for blue oak and from 48 to 100 percent for coast live oak (figure 1). Seedling survival dropped dramatically by the end of the first summer, especially for the coast live oak seed spots in the open where survival ranged from 0 to about 32 percent, except for the small mammal exclosures where over 80 percent of the seedlings were still alive. Overall, blue oak had less decline in survival over the summer than coast live oak, and the best establishment was obtained with the small mammal exclosures.

One explanation for the higher seedling survival at Blythe, compared to the other study locations, is that it was planted

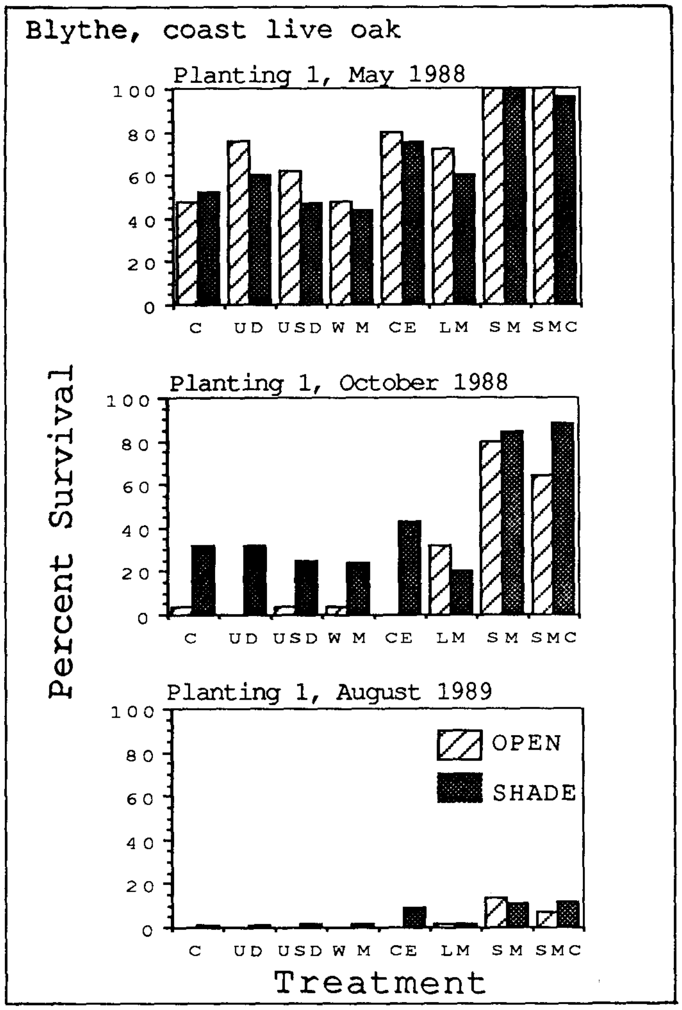

Figure 1—Percent survival of coast live oak seedlings over a 2-year period at the Blythe test site near Paso Robles. Planting 1 was done in December 1987. Treatments are as follows:

C .... Control, not scalped or predug
UD .... Unprotected, not scalped
USD ...... Unprotected
WM .... Weedmats
CE .... Cattle excluded
LM .... Large mammals excluded
SM .... Small mammals excluded
SMC ...... SM and clipped

Note: unless other wise stated, all treatments were predug and scalped.

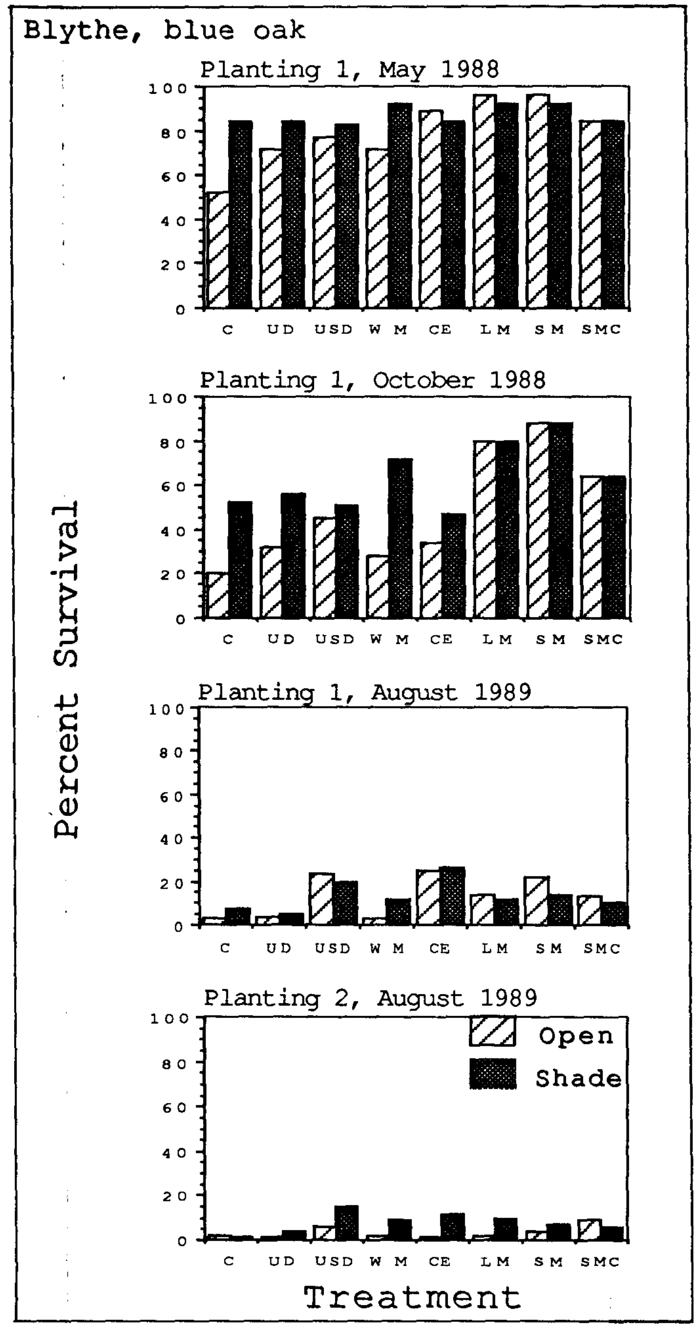

Figure 2—Percent survival of blue oak seedlings over a 1- or 2-year period at the Blythe test site near Paso Robles. Planting 1 was done in December 1987 and Planting 2 in January 1989. See Figure 1 for treatment description.

almost a month earlier. Early germination and root development would better prepare these seedlings for the dry months that followed than the acorns that were planted a month later and had less time to become established.

Results of the second year's planting at Blythe were very disappointing. Almost no coast live oak became established and blue oak establishment was not much better (figures 1 and 2). As in the previous 2 years, less than normal rain fell after December. Acorn predation began within a couple of weeks after planting. Several of the unprotected coast live oak seed spots were partially excavated to a depth of 1 to 2 inches. However, no predation of blue oak seed spots was observed at any time. The fact that almost no coast live oak acorns had developed at the study site during the first 3 years of this test may account for its selective predation. Within 4 weeks after planting, all of the remaining unprotected coast live oak acorns were removed by a flock of resident wild turkeys. The few seedlings that were established that year were mostly those protected by small mammal exclosures.

U.C. Hastings Reservation

Initial establishment of coast live oak seedlings at Hastings was fairly high for the protected seed spots with almost 55-65

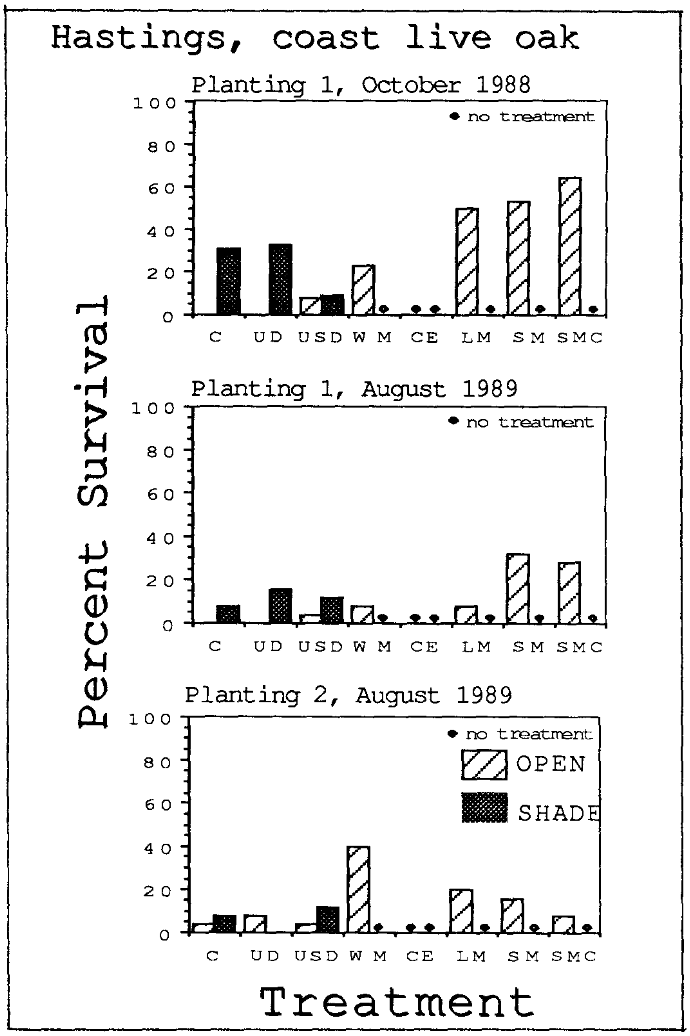

Figure 3—Percent survival of coast live oak seedlings over a 1- or 2-year period at the Hastings test site. Planting 1 was done in December 1987 and Planting 2 in January 1989. See Figure 1 for treatment description.

percent of the plants still alive after the first summer (figure 3). By the end of the second summer, 30 percent of the seedlings protected by the small mammal exclosures were still alive, a slightly higher percentage of seedling survival than at Blythe, but not significantly higher. On the contrary, coast live oak germination for the second year's planting was low, apparently the victim of the continuing drought. The best survival was obtained with weed mats; they had little or no positive effect on the first year's planting survival.

Blue oak seedling establishment with the first year's planting was extremely low with only a few percent of the acorns germinating (figure 4). It was not apparent why it was less successful than coast live oak in getting established the first year. Blue oak survival was considerably better with the second planting, especially with weed mats which resulted in over 85 percent survival (figure 4).

Agua Escondido

Seedling establishment at Agua Escondido was low the first year except for seedlings protected by small mammal exclosures (up to 50 percent survival at the end of the first summer, figure 5). However, seedling survival with the second year's planting was much higher for all treatments, ranging from 35 to 65 percent. There were no obvious reasons for the higher germination and survival the second year. Planting the first year was in December followed by 8.6 inches of rain between January and June. Planting the second year was in January with only 3.9 inches of rain until June. Based on just the amount of rainfall after planting, seedling establishment should have been extremely low instead of better.

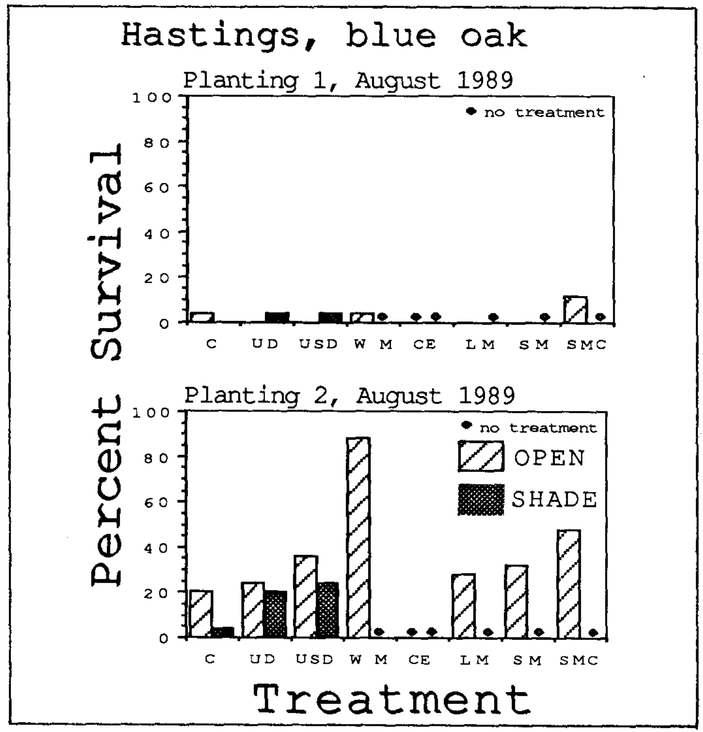

Figure 4—Percent survival of blue oak seedlings over a 1- or 2-year period at the Hastings test site. Planting 1 was done in December 1987 and Planting 2 in January 1989. See Figure 1 for treatment description.

Benedict Ranch

Coast live oak establishment for both years at the Benedict site was extremely low, less than 10 percent for both years of planting. Many of the acorns did not even germinate. The rocky soil, with its large air spaces, was not a favorable environment for satisfactory germination and development, especially when rainfall was below normal.

Species

Blue oak survival was significantly higher than coast live oak's for both years of planting and at all sampling dates with the exception at Hastings when only a few blue oak became established from the first year of planting, regardless of treatment (figure 4).

Because blue oak grows on more xeric sites and it better adapted to drought conditions than coast live oak (Matsuda and

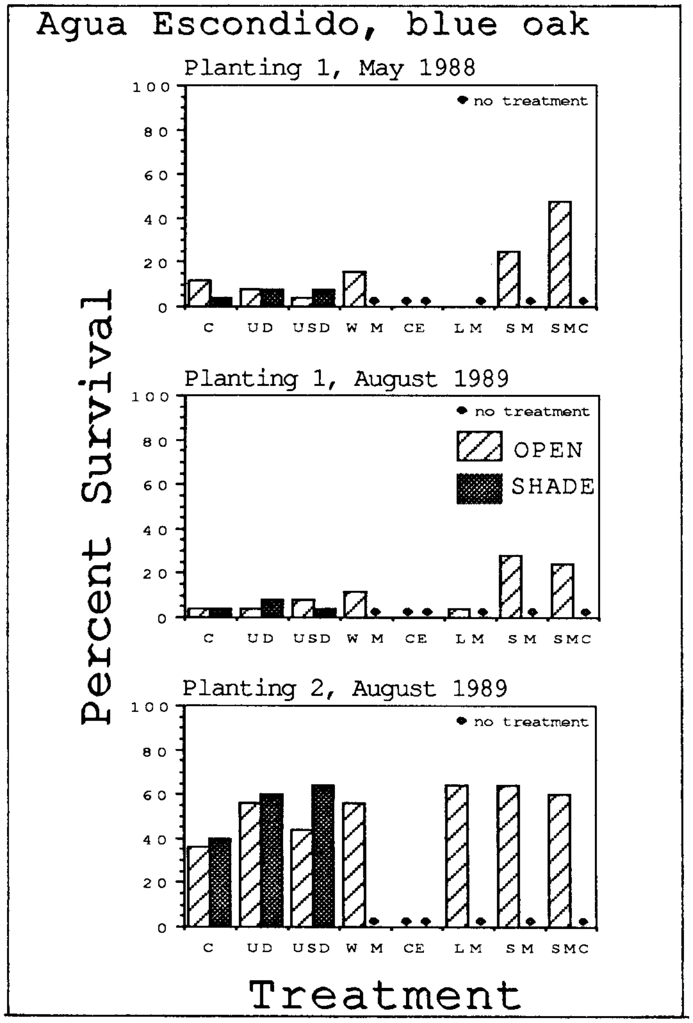

Figure 5—Percent survival of blue oak seedlings over a 1- or 2-year period at the Agua Escondido test site. Planting 1 was done in December 1987 and Planting 2 in January 1989. See Figure 1 for treatment description.

McBride 1986), it might be expected to have a higher survival rate than coast live oak during low rainfall years. The data from this study appear to substantiate this. However, even though blue oak performed better than coast live oak in this study, both numerically and statistically, its percent survival one year after planting was not high enough for the planting operation to be considered successful.

Light Exposure

In general, shade improved the odds for survival at the end of the summer for both years of planting. These results confirm other reports that oak regeneration is usually greater under tree canopy than it is in the open (Griffin 1971, Griggs 1987). More specifically, Bartolome and others (1987) indicate that it was more common to find oak saplings at the canopy edges than under the canopy or in the open. However, by the end of the second summer after planting (figures 1-2), seedling survival had dropped to such a low value that canopy effect was no longer of practical importance.

Treatments

Unprotected Controls (Treatments 1-3)

There was no significant difference in seedling establishment and survival among the three treatments involving unprotected seed spots. Compared to Treatment 1, which had no site preparation and amounted to simply planting acorns directly into the ground, there was no apparent advantage gained by predigging the seed spots or scalping the soil around a seed spot. Consequently, these cultural activities should not have had any effect on the other treatments.

Weed Mats (Treatment 4)

The weed mats effectively kept weeds away from the seed spots, but there appeared to be little positive effect on seedling survival for the first year of planting. In fact, they actually seemed to have a negative effect. This was unexpected because of the drought conditions during the study. Any treatment that reduced moisture stress should have been somewhat beneficial. The black mats may have caused elevated soil temperatures that were detrimental to the seedlings. At any rate, the weed mats had a strong positive effect on seedling survival at Hastings with the second year of blue oak planting (figure 4) and to a lesser extent with coast live oak (figure 3). There was no obvious reason for such a positive effect the second year and only at one location.

Animal Exclosures (Treatments 5-8)

Cattle alone had no significant impact on seedling survival, but where both cattle and deer were excluded (Treatment 5, large mammal exclosures), survival was significantly increased. Although this suggests that deer alone or in combination with cattle were responsible for seedling losses, there was no obvious field evidence for this conclusion.

The small mammal exclosures significantly improved the odds of seedling survival, at least until the first fall season after planting. However, percent seedling survival a year later had dropped from about 80 percent to only about 10 percent at Blythe (figures 1 and 2). This decline in survival was most likely due to the effect of moisture stress and points out the need to wait at least two years after planting to realistically evaluate seedling survival.

Live seedlings in the small mammal exclosures (Treatment 8) were clipped off at ground level by hand in the spring of 1988 to simulate animal browsing. Clipping appeared to have little effect on seedling survival and was not carried out with the second planting.

The 1/4-inch hardware cloth exclosures may be too durable for practical field use. If left in the ground, there is concern that they will severely restrict root growth as a seedling gets older. Removing an enclosure after a seedling is well established is not practical because almost the whole enclosure has to be dug up to get it out of the ground. This would be time consuming and a bit traumatic for the seedling. Also, at a cost of at least $1.00 per seed spot, including materials, construction, and installation, the hardware cloth exclosures would be too expensive for large field plantings.

Acorn Storage

There has been considerable debate about how long acorns can be stored and remain viable. White oak acorns are reported to be less durable than black oak acorns (Bonner 1979). Plumb and McDonald (1981) reported that scrub oak acorns, if air dried prior to cold storage, would remain viable for at least 15 months.

Results of a germination test, involving acorns collected for this regeneration study and acorns of other species stored during the same period, indicate that both white and black oak acorns will remain viable for at least 30 months. Percent germination for coast live oak and blue oak stored since October, 1987, were 30 and 46 percent, respectively. Coast live oak stored since October, 1988 and 1989, germinated at a rate of 40 and 100 percent, respectively. California black oak (*Q. kelloggii* Newb.) and canyon live oak (*Q. chrysolepis* Lieb.) were also viable after 2 years of storage (41 and 35 percent, respectively).

CONCLUSIONS

The results of this oak regeneration study varied from location to location and year to year at the same location, making it difficult to draw clearcut conclusions about the regeneration methods tested. There is little doubt that below normal rainfall during the 4 years of this study had an extremely negative effect on both acorn germination and subsequent seedling survival.

Even though some of the treatments resulted in statistically higher survival than obtained with the controls, the numerical results in terms of seedling survival were too low to have practical significance.

In summary, blue oak had a higher rate of survival than coast live oak. Planting in shaded sites increased the odds of seedling survival over planting in the open. Weed mats gave erratic results, but significantly increased seedling survival at a couple of sites in 1988. They need further testing. There was a clearcut advantage in using small, wire mesh cages to protect acorns and seedlings from animal depredation. Finally, cattle were not found to have any singular detrimental impact on oak survival.

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Factors Affecting Seedling Survivorship of Blue, Oak (*Quercus douglasii* H.& A.) in Central California[1]

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Abstract: Blue oak seedling mortality was studied in relation to vertebrate predators, initial acorn planting position, slope and aspect, and oak canopy cover at two sites in the Central Coast Ranges of California. Seedling survival rates (Psd) were related to treatment variables using logistic regression analysis. Analysis of 2842 seedlings for 3 years following establishment indicated that site, rodents and acorn planting position were important variables explaining seedling losses. Seedling mortality was six times higher in the savanna site than the north-slope forest apparently because of unusually heavy competition between oak seedlings and annual grasses. Rodents were significant mortality agents at both sites. Overall, mortality was high during the first 3 years after seedling establishment with most losses occurring in the first year. Height growth of seedlings at both sites was very low. High seedling mortality coupled with slow growth rates and concomitant browsing apparently make the transition from seedling to small tree a rare event in this region.

In a previous paper we reported on acorn germination and seedling recruitment of blue oak in relation to postdispersal predators, planting depth, oak canopy cover, slope angle and aspect, and herb layer at two sites in the Central Coast Ranges of California (Borchert and others 1989). In the first phase of this multi-year study we sowed over 8000 acorns in a series of large and small predator exclosures to measure the significance of individual mortality factors affecting blue oak acorn germination and seedling recruitment. Results indicated that year, site, acorn planting position and rodents interacted strongly to affect seedling recruitment from acorns (table 1).

Although mortality was high in the seedling recruitment stage, several thousand seedlings managed to establish in the two stands (Borchert and others 1989). Several researchers (Griffin 1971, McClaran 1986) have suggested that mortality after establishment rather than limited seed and seedling production is responsible for the widespread absence of regeneration in blue oak. Nevertheless, few studies (Griffin 1971, Griffin 1980) have documented losses of seedlings and saplings for more than a few years. In this paper we examine the causes of blue oak seedling mortality over the first 3 years after establishment and compare them to mortality agents affecting seedling recruitment.

METHODS

Site Description

We studied seedling mortality in blue oak forest at American Canyon (AC) and in blue oak savanna at Agua Escondido (AE), in the Coast Ranges of San Luis Obispo County, California (table 2). A more detailed description of each site is provided in Borchert and others (1989). AC was grazed by cattle continuously during the study, but AE was grazed only in 1986.

Average annual precipitation at Pozo, 9.5 km west of AC, is 527 mm. Precipitation in 1986 was 709 mm, well above the average. In 1987, 1988, and 1989, however, precipitation was 269, 453 and 328 mm, respectively, well below the average.

Exclosure Experiment

Beginning in 1984 at AC and 1985 at AE, we sowed acorns for 2 years in 38 each 2.4 by 2.4 m plots distributed over a 1.65 ha area that was divided into three adjacent 0.55 ha subareas: a cattle exclosure, a cattle/deer exclosure and an unfenced area. Six plots were distributed across the unfenced control area, half of the plots under oaks and the other half in the open. The remaining 32 plots were divided evenly between cattle and deer exclosures.

In each exclosure, 10 randomly selected plots received additional protection to prevent access by birds, mice and gophers, by birds and gophers, or by mice and gophers (table 3). These subexclosures were evenly distributed within each exclosure, with five plots placed under oaks and the other five placed in open areas. The remaining six plots in each exclosure received no additional protection and were located within 5 m of randomly selected subexclosures.

At AC, 30 surface and 30 buried acorns were sown in each plot in 1984 and 1985, and at AE in 1985. Because of a shortage of acorns at AE in 1986,28 surface and buried acorns were sown in the exclosures. A total of 8172 acorns were analyzed for seedling recruitment patterns (table 1). The sowing configuration is detailed in Borchert and others 1989. After establishment, seedling survival was monitored at both sites for an additional 4 years. In this paper we report on the survival of 2842 seedlings monitored from 1986 to 1988 at AC and 1987 to 1989 at AE.

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Site	Year	Planting Position	Mice	Gophers	Sample Size	P_s
Both sites					8172	0.36
American Canyon					4500	0.38
	1985				2280	0.27
		Surface			1140	0.17
			+		660	0.11
			-		480	0.26
		Buried			1140	0.36
				+	540	0.30
				-	600	0.42
	1986				2220	0.50
		Surface			1140	0.36
			+		660	0.31
			-		480	0.50
		Buried			1080	0.62
				+	510	0.50
				-	570	0.73
Agua Escondido					3672	0.33
	1986				2040	0.45
		Surface			1020	0.30
				+	540	0.17
				-	480	0.44
		Buried			1020	0.61
	1987				1632	0.18
			+		1056	0.12
		Surface	+		528	0.07
		Buried	+		528	0.18
			-		576	0.29
		Surface	-		288	0.24
		Buried	-		288	0.34

Table 1—*Hierarchical classification of factors affecting seedling recruitment from acorns sown at American Canyon and Agua Escondido experimental sites, based on hierarchical logistic regression analysis. See Borchert et al. (1989) for details of data analysis. Sample* size is *the number of acorns sown in each treatment. P is the proportion of acorns that produced first year seedlings. For example, 38 percent of 2280 acorns* sown *at American Canyon produced seedlings (row 2); 11 percent of 660 acorns sown at American Canyon in 1985, on the surface, and accessible to mice produced seedlings (row* 5).

Table 2—*Description of study sites.*

	American Canyon	Agua Escondido
Location	35°16'N, 120°16' W	35°11' N, 123°13'W
Elevation (m)	540	798
Slope	5-15°	11°
Soil depth (cm)	122-167	61-76
Soil texture	clay loam	coarse sandy loam
Oak density (tree/ha)	316	104
Oak crown cover (pct)	65	15

Measurement of Other Variables

For each plot a northness index was calculated as:

100 x sin(slope) x cos(azimuth).

Oak canopy cover was measured with a concave gridded mirror (spherical densiometer).

In May 1990 herbaceous biomass and litter were measured at each site by harvesting all the material from 15 each 20 by 20 cm quadrats taken at random from subexclosures, exclosures and controls. Harvested material was separated into litter and herb biomass, dried at 38° C for 48 hours and weighed.

Table 3—*Description of protection treatments used in the exclosure experiments. Treatments are listed by the predators that had access to the plots. Numbers refer to the number of replicates in each exclosure. Numbers in parentheses are for Agua Escondido (AE), when different from American Canyon (AC) (Borchert and others 1989).*

Predator access	Exclosures Deer	Cattle	Control	Description
No predators (NP)	2	2(3)	—	All predators were excluded using a 2.4 by 2.4 m subexclosure. Sides were 0.5-cm mesh hardware cloth buried to bedrock, 1 m high with a 25-cm border of galvanized flashing around the upper margin. 2.5-cm poultry netting was used to cover the top of the subexclosure.
Mice (M)	2(3)	2(1)	—	To allow mice to enter, 2.5-cm holes were placed at ground level around the perimeter of the subexclosures.
Birds (B)	6(5)	6(5)	—	Subexclosures were left uncovered in the cattle and deer exclosures.
B,M, Gophers (BMG)	6	—	—	Unprotected plots in the deer exclosure.
B,M,G, Deer (BMGD)	—	6	—	Unprotected plots in the cattle exclosure.
B,M,G,D, Cattle (BMGDC)	—	—	6	Unprotected plots in the control area.

In addition to counts, seedling heights were recorded for a random number of individuals in each plot for each year. We analyzed the heights of 4-year seedlings and pooled samples from B with the NP treatment and those from the BMG with the BMGD treatment to increase sample sizes (see table 3 for treatment codes). Seedling numbers from surface and buried acorns in the BMG and BMGD and BMGDC treatments at AE were too small for height analysis.

Data Analysis

Results from the exclosure studies were expressed as the seedling survival rate (Psd), i.e., probability of a seedling surviving from one year to the next for particular treatments. The dependence of Psd on predator treatments and environmental variables (site, planting position, northness and canopy cover) was estimated by fitting logistic regression models. Separate logistic models for nested subsets of the data were fitted using a dichotomous divisive classifier (Michaelsen and others 1987).

The choice of a variable for splitting the data at a branch of the hierarchical model and selection of variables to include in the logistic regression equations were based on the reduction in G2 (Sokal and Rohlf 1981), a measure of the strength of association between variables. Useful improvements in the model at each branch were tested by cross-validation which operates by dividing the data into groups, omitting each group in turn, estimating the model on the remaining groups, and testing it on the omitted group.

At each step, variables that produced the largest reduction in cross-validated G^2 were included in the logistic equations. The decision to stop splitting hierarchically was based on the small reduction in overall G^2 that resulted from further subdividing the data after the first three divisions.

One-way ANOVA and Sheffe's test were used to compare biomass and litter weights and seedling heights among the treatments. Mann-Whitney U test was used when sample sizes were <10.

Table 4—*Seedling survival at American Canyon. Data are given as absolute number of seedlings surviving after each year (above), and as the proportion of the total number of acorns sown (below).*

Planting position	Predator treatment[1]	Acorns sown in 1984 1984	1985	1986	1987	1988	1989
Surface	NP	120	34	10	8	7	5
			0.28	0.08	0.07	0.06	0.04
	BMGDC	180	22	7	5	4	4
			0.12	0.04	0.03	0.02	0.02
Buried	NP	120	51	37	30	30	21
			0.43	0.31	0.25	0.25	0.17
	BMGDC	180	51	17	11	8	6
			0.28	0.09	0.06	0.04	0.03

[1]*NP = no predators; BMGDC = birds, mice, gophers, deer, cattle.*

Table 5—***Seedling survival at Agua Escondido. Data are given as absolute number of seedlings surviving after each year (above), and as the proportion of the total number of acorns sown (below).***

Planting position	Predator treatment[1]	Acorns sown in 1985				
		1985	1986	1987	1988	1989
Surface	NP	120	62	18	7	4
			0.52	0.15	0.06	0.02
	BMGDC	180	28	3	1	1
			0.16	0.02	0.01	0.01
Buried	NP	120	75	33	4	4
			0.62	0.28	0.03	0.03
	BMGDC	180	107	35	12	11
			0.59	0.19	0.07	0.06

[1]*NP = no predators; BMGDC = birds, mice, gophers, deer, cattle.*

RESULTS

At AC, survival of seedlings from surface acorns after 5 years was similar (<5 percent) for the NP and BMGDC treatments (table 4). For seedlings from buried acorns, on the other hand, survival at the end of 5 years was five times higher in the NP than the BMGDC treatment.

At AE losses in the same two predator treatments were high regardless of planting position (table 5) with <5 percent of the seedlings still alive at the end of 5 years. At both sites seedling mortality was highest in the first year after establishment.

The hierarchical logistic regression tree for seedling survival (table 6) resulted in a 43.6 percent reduction of the total G^2 by division into 6 classes. An additional 1 percent reduction occurred by the fourth stratum but was not considered significant enough to include in the regression tree.

The first division of the data by site accounted for the largest GI reduction (29.5 percent). Psd was slightly more than six times higher at AC than at AE (table 6), a difference clearly reflected in the seedling survivorship (tables 4, 5).

At AC pocket gophers (*Thomomys bottae*) were the most important seedling predators; Psd was twice as high for protected seedlings (table 6). At AE, in contrast, mice (western harvest mouse, *Reithrodontomys megalotis,* and California pocket mouse, *Perognathus californicus*) were the most important seedling predators, although Psd was quite low (0.10) even in the absence of mice.

After gophers, Psd at AC was most influenced by planting position of the acorn. Seedlings from buried acorns had higher survival rates whether or not gophers were present. Still, the difference in Psd between surface and buried acorns was much greater in the presence of gophers (table 6).

Overall, seedlings were quite small at both sites, after 4 years averaging only 7 centimeters. Seedlings that originated from surface and buried acorns in the B/NP treatments did not differ in height between the two sites (table 7). At AC seedlings from buried acorns in the B/NP were significantly taller than those in the BMG/BMGD ($p<0.05$) or BMGDC ($p<0.001$) treatments, but seedling heights in the latter two treatments did not differ significantly. Surface-acorn seedlings did not differ in height between the B/NP and BMG/BMGD treatments at AC.

Herbaceous biomass of annuals at AE was significantly higher (4.5 times) in the exclosures than the control and was significantly higher (5.2 to 11.7 times) than biomass in all three

Site	Mice	Gophers	Planting Position	Sample Size	P_{sd}
Both sites				2842	0.24
American Canyon				1610	0.37
		+		543	0.22
			Surface	136	0.09
			Buried	407	0.27
		-		1067	0.44
			Surface	404	0.30
			Buried	663	0.53
Agua Escondido				1232	0.06
	+			669	0.03
	-			563	0.10

Table 6—***Hierarchical classification of factors affecting seedling establishment at American Canyon and Agua Escondido experimental sites, based on hierarchical logistic regression analysis. Sample size is the number of seedlings in the first year. P_{sd} is the proportion of seedlings that survived three years. Format is identical to that used in Table 1.***

Table 7—***Heights (cm) of 4 -year seedlings originating from surface and buried acorns in the BMG/BMGD, and BMGDC treatments at each site. Values are means and standard deviations with sample sizes in parentheses.***

	Treatments[1]					
	B/NP		BMG/BMGD		BMGDC	
Seedling origin[2]	Surface	Buried	Surface	Buried	Surface	Buried
Site						
AC	8.8±2.5a[3] (32)	9.3±2.5a (50)	8.0±1.9b (6)	6.8±2.6b (16)	—	5.4± 1.7b (28)
AE	7.7± 2.7a (8)	8.9± 3.3a (17)	—	—	—	—

[1]B = birds; G = gophers; M = mice; NP = no predators.
[2]AC = American Canyon; AE = Agua Escondido.
[3]Values in rows and columns not followed by the same letter are significantly different at least at p5 0.05.

Table 8—***Herbaceous biomass and litter weight (in grams) in the subexclosure, exclosure and control predator treatments at each site. Values are means and standard deviations for fifteen 20 by 20 cm plots.***

	AC[1]		AE[1]	
Treatment	Herbaceous biomass	Litter	Herbaceous biomass	Litter
Subexclosures	6.3±3.8a[2]	11.8±8.0a	75.0±33.9a	21.2±14.6a
Exclosures	14.2±14.1b	30.2±12.5b	73.7±16.5a	20.0±14.6a
Control	12.9±13.1b	18.6±10.5c	16.0±12.0b	12.9±9.2b

[1]Values in columns not followed by the same letter are significantly different at least at p5 0.05.
[2]AC = American Canyon; AE = Agua Escondido.

treatments at AC (table 8). The very high biomass production at AE was the result of rapid succession to ripgut brome (*Bromus diandrus)* after exclosure construction.

At AC, litter weight was significantly different among all the treatments (table 8). At AE litter weight was significantly higher in the subexclosures and exclosures than the control ($p<0.05$).

DISCUSSION

Compared to the seedling recruitment regression tree (table 1), the seedling survival regression tree is much less complex (table 6): it has fewer variables and strata, and there are fewer branches in the lower strata. In addition, the total G^2 reduction differs considerably between the two regression trees: 43.6 and 70 percent for the seedling survival and seedling recruitment trees, respectively. The lower G^2 reduction of the seedling survival tree suggests that variables useful for predicting seedling recruitment were less useful for predicting seedling survival. Unmeasured variables that may have played a role in seedling mortality include insect herbivory, drought, competition and soil microsite conditions (Griffin 1980).

Site was the most influential variable affecting both Ps and Psd. Compared to AC, Psd was much lower at AE even though initial rates of seedling recruitment were very similar (0.33 vs 0.38, table 1). We attribute these marked site differences in Psd to unusually heavy competition between *B. diandrus* and oak seedlings at AE. Gordon and others (1989) found that high densities of *B. diandrus* suppressed blue oak seedling emergence and root growth by reducing local water availability. They speculated that competition with annuals in combination with shoot suppression in drought years may result in a reduction in growth and ultimately the ability to resprout. Griffin (1971) also observed higher mortality of blue oak seedlings growing with annuals than those in cleared plots. At AE numerous seedlings were unable to resprout through the dense grass litter and thatch and those that did were tall and often etiolated. Many more never penetrated the thatch, and ultimately most died.

Rodents were the most important predators of both acorns and seedlings, but they were relatively more important as seedling predators. At AC gophers were the primary source of seedling losses. Griffin (1980) also noted heavy losses of valley oak (*Quercus lobata*) seedlings to gophers. Mice did, however, continue to consume seedlings at AC. Seedlings near runways were often dug up and the roots eaten but the stems left intact. At AE mouse herbivory was the most important mortality factor because dense grass at this site probably supported elevated densities of rodents. We noted, for example, that in some years mice stripped bark from previously browsed, low-growing oak saplings in the deer exclosure.

The year of acorn planting, an important variable in seedling recruitment, did not appear in the seedling survival tree. Acorn planting position, another significant variable in the recruitment stage, appeared only in the seedling survival tree at

AC, suggesting that seedlings from buried acorns may have developed more extensive root systems than seedlings from surface-sown acorns. Other variables that did not enter the model include northness, canopy cover, birds, deer and cattle.

Seedlings at both sites grew slowly during the first 5 years although growth almost certainly was reduced by successive years of below-average precipitation. If growth rates observed here are representative of blue oak seedlings in the study area, seedlings are likely exposed to an extended period of browsing before they can make the transition to larger size classes. Extensive stand surveys[3] indicate that shrubby, suppressed individuals <1 m are common in the region. These only rarely make the transition from shrubs to small trees (Harvey 1989). Combined high acorn and seedling mortality coupled with low growth rates and browsing severely limit the number of new trees recruited into these stands.

[3]Data on file at the supervisor's Office of Los Padres National Forest.

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Oak Tree Planting Project[1]

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Abstract: An Oak Tree Planting Project was conducted during 1989/90 in San Luis Obispo County by the Integrated Hardwood Range Management Program (IHRMP)/Central Coast. The local media and an IHRMP workshop were used to publicize the Planting Project and give information on the status of oaks (*Quercus* spp.) in California and oak planting techniques. Outreach efforts resulted in participation in the Oak Tree Planting Project by homeowners and ranchers as well as by 4-H, environmental, school, community, and homeowner-association groups: over 3,500 acorns were planted at about 1,200 sites (three acorns per site). The Oak Tree Planting Project provided a good opportunity for community awareness and involvement in helping ensure that oak trees will be around for future Californians to enjoy.

California has lost about one million acres of oak woodlands during the past 45 years to development and other causes of removal (Bolsinger 1988). In addition to this, several species of oaks are not regenerating well (Griffin 1971, 1976, Muick and Bartolome 1986). In response to these concerns the IHRMP was developed in 1986 to maintain and where possible increase the acreage of California's oak rangeland resource to provide wildlife habitat, recreational opportunities, wood and livestock products, high quality water supply, and aesthetic value. The IHRMP realizes the importance of involving and educating the public and that restoration of the oak woodlands can be accomplished in part through the use of educational programs and planting projects.

The Oak Tree Planting Project was an educational program conducted in San Luis Obispo County by the IHRMP/Central Coast. It was designed to use public participation to increase awareness of the importance of oak woodlands. It was felt that a hands-on experience would leave a valuable impression on the individuals participating in the project, as well as increase declining oak populations.

PROJECT DESCRIPTION AND IMPLEMENTATION

The objectives of the Oak Tree Planting Project were to (1) inform the people of San Luis Obispo county of the importance of having oak trees on and surrounding their property, (2) replace oak trees in some places where they were no longer growing, and (3) monitor growth and survival of the planted trees. The Oak Tree Planting Project was broken into four phases.

Phase One.—A workshop was held in September 1989 to generate interest in the project and to discuss the importance of oaks in our environment. This workshop provided information on the value of oaks, oak identification, collection and storage of acorns, oak planting and protection techniques, weed control, irrigation, and an example of a successful planting project on the central coast.

Phase Two.—The IHRMP/Central Coast collected acorns from the three common tree-sized oaks that occur in San Luis Obispo County: valley oak (*Quercus lobata*), blue oak (*Q. douglasii*), and coast live oak (*Q. agrifolia*). The acorns were stored for later planting by IHRMP and to give to homeowners, ranchers, and groups that needed acorns for planting.

Phase Three.—At the start of the oak-planting season in December 1989, a publicity campaign was launched (local newspapers, radio, and IHRMP newsletter) (fig. 1) to inform local residents of the Oak Planting Project and the availability of acorns and planting directions from the IHRMP. Also, a follow-up letter was sent to workshop participants to determine what assistance they might need for planting.

Phase Four.—Beginning in December 1989, acorns were planted. The IHRMP established two demonstration sites in San Luis Obispo County. Each demonstration site consisted of 40 planting sites, each cleared of weeds and protected with a wire exclosure. The IHRMP also coordinated planting activities of individuals and groups by providing acorns and helping to connect acorn planters with planting sites and available planting sites with planters.

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Figure 1—The Oak Tree Planting Project and the availability of information on oak planting was advertised by newspaper, radio, and newsletter.

PROJECT RESULTS

About 70 people attended the workshop of which 15 signed up to participate in planting. The greatest response was generated from radio and newspaper publicity at the start of the planting season. Many individuals and several agencies and community groups participated in planting activities (fig. 2).

The California Conservation Corps (CCC) assisted with the demonstration sites. They dug holes, planted acorns, constructed and installed aluminum screen protection cages, and cleared competing weeds from around each planting site. Several San Luis Obispo County 4-H groups volunteered their time to individuals and community groups with large areas to plant (fig. 3). For example, the 4-H groups helped the San Luis Obispo County Recreation and Parks Department plant a site at the Lopez Lake Recreation Area, and assisted the Toucan Terrace

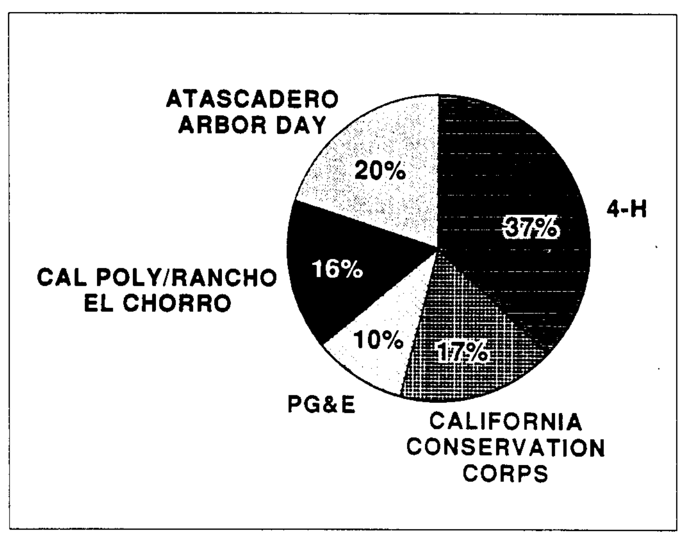

Figure 2—Newspapers, radio, and workshop publicity resulted in participation in the IHRMP Oak Tree Planting Project by individuals, several agencies, and community groups.

Figure 3—UCCE 4-H assisted community groups with planting.

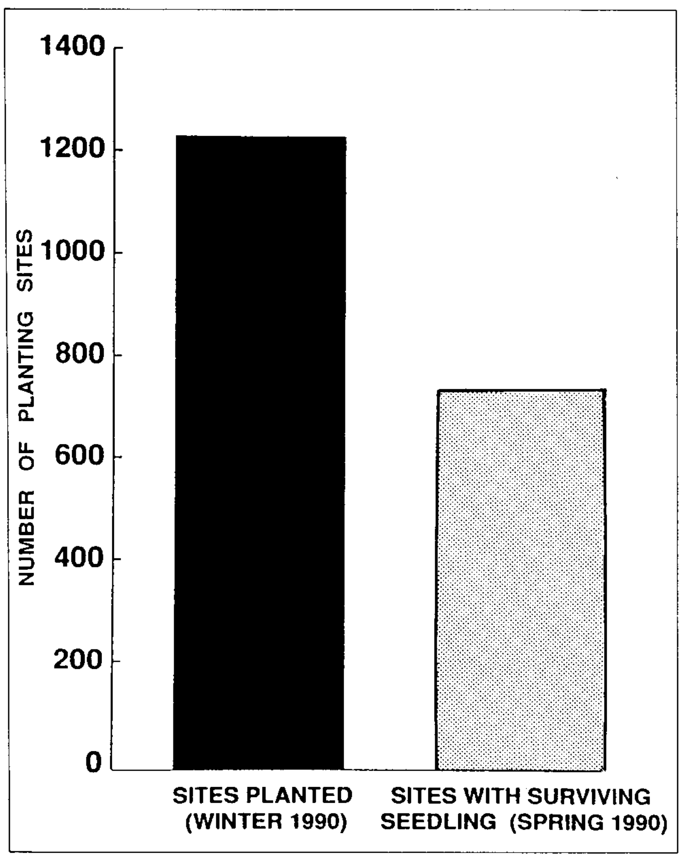

Figure 4—The participants in the Oak Tree Planting Project, planted and protected over 3,500 acorns at about 1,200 planting sites (three acorns per site) in winter 1989/90. Most plantings produced a healthy oak seedling.

Homeowners Association plant and protect 50 live oaks on 27 acres of "green space" along Highway 101 in Pismo Beach, California. PG&E sponsored a day of tree planting on the Santa Margarita Ranch just north of San Luis Obispo; approximately 10 volunteers planted 100 valley and blue oaks.

Several spin-offs were generated by the Oak Tree Planting Project. For example, Natural Resource Management (NRM) students from California Polytechnic State University, San Luis Obispo, explained the values of oaks and planting techniques to a class of 6th-grade students in San Luis Obispo County. The following week, the 6th graders and NRM students met at Rancho El Chorro Environmental Education Center in San Luis Obispo County and planted 80 coast live oaks. The 6th graders will help care for the seedlings and monitor survival and growth. The NRM students hope this becomes a long-term, on-going project between Cal Poly and Rancho El Chorro, with more planting and research.

In all, the IHRMP gave away over 3,500 acorns and about 1,200 sites (three acorns per site) were planted and protected (fig. 4). Of those sites planted, response to a mail questionnaire indicated that over half germinated and were doing well in June 1990.

FUTURE CONSIDERATIONS AND RECOMMENDATIONS

Our efforts in the Oak Tree Planting Project were very well rewarded. This type of project is an ideal opportunity for community awareness and involvement, as well as a method to increase oak populations. It was apparent that best results were achieved when careful instructions and on-site demonstrations of acorn planting and protection techniques were provided to participants. Furthermore, a long-term commitment to the protection and maintenance of the planting sites seems necessary for long-term survival of the planted oak trees.

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Oak Woodland Artificial Regeneration Correlating Soil Moisture to Seedling Survival[1]

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Abstract: Broadleaf P4, an hydrogel soil amendment, was tested under field and greenhouse conditions to determine if it would increase the survival and growth of coast live oak (*Quercus agrifolia*) and blue oak (*Q. douglasii*) seedlings during periods of moisture stress. Broadleaf P4 had little positive effect on seedling survival in the field, and it actually appeared to reduce survival of blue oak. Low survival was not surprising, however, because of the unfavorable growing conditions during the late winter and spring 1989. Under greenhouse conditions, coast live oak grew twice as tall as blue oak. This growth differential was expected, and it is well documented in the literature. P4 enhanced coast live oak seedling height growth with biweekly and triweekly watering, but it inhibited blue oak at all levels.

A number of oak regeneration problems have been identified in California. Poor regeneration is attributed to factors ranging from poor acorn crops and unsatisfactory fall and winter weather conditions to predation by all sizes and types of wildlife and domestic animals, to summer drought (Griffin 1971; Plumb 1980; Plumb and McDonald 198 1). Poor oak seedling establishment and survival the last 4 years (1986-1990) can partly be attributed to inadequate rainfall.

Water-absorbing polymers, used as soil amendments, have been proposed to be an aid to plant growth under conditions of moisture stress (Johnson 1984; Johnson and Veltkamp 1985). Synthetic chemicals such as Broadleaf P4,[3] that can function as super absorbers, include polyvinylalcohols, starch co-polymers, and polyacrylamide compounds (Johnson 1984). Broadleaf P4 is a hydrogel soil amendment composed of polyacrylamide polymers. These gels have the capacity to absorb 200-400 times their weight in water (figure 1), and they can last 5-10 years in the soil. As the soil dries, the gel releases over 95 percent of the water back to the soil (Piper 1989). As the polymers absorb and release water, they expand and contract which improves soil structure and increases air spaces in the soil favoring root development, especially in fine-textured soils. Irrigation can be reduced, and a soil's increased water-holding capacity should help overcome periods of drought, especially with sandy soils that have low moisture-holding capacity.

The objective of this study was to enhance the survival and growth of coast live oak (*Quercus agrifolia*) and blue oak (*Q. douglasii*) by improving soil moisture conditions. Three concentrations of the soil amendment Broadleaf P4 were tested under field and greenhouse conditions. Increased seedling survival would be an important advance in the successful regeneration and survival of oaks on harsh sites or during dry years.

METHODS

Greenhouse Test

This test was conducted in the Natural Resources Management Greenhouse at Cal Poly, San Luis Obispo, California, in winter, 1989. Soil treatments included untreated controls and soils containing at the rates of 3.2, 4.0, and 5.8 g of P4 per 0.52 cubic foot of soil. The soils were collected from under coast live oak or blue oak trees on the Blythe Ranch near Paso Robles (Plumb and Hannah 1991). The soil-P4 mix was placed in 4 x 14-inch PVC pipes and seeded with pre-germinated coast live oak or blue oak acorns. Each P4 concentration was repeated forty-five times for a total of 360 plants. The plants were mist-watered until germination. After germination, 1/3 of the seedlings were watered weekly, 1/3 biweekly, and 1/3 triweekly. Seedling survival and height growth were monitored for several months. A small soil moisture trial was also run to determine how much water would remain in the different P4 soil mixes

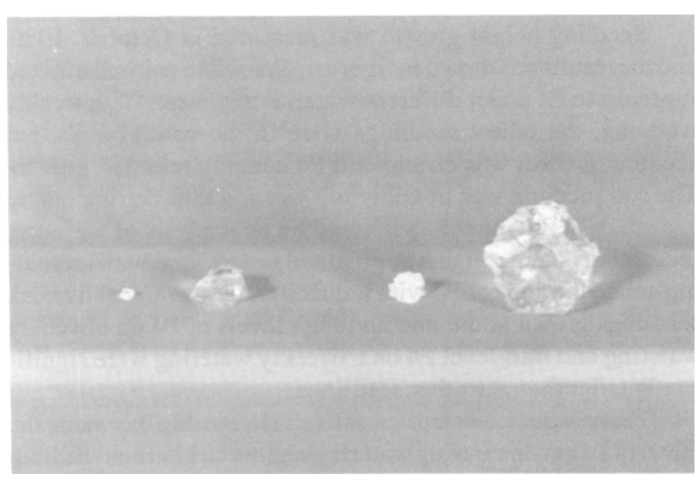

Figure 1—The massive water absorbing capacity of P4 is illustrated above with large and small granules of hydrated and unhydrated P4.

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[3]Broadleaf P4 is a trade name for polyacrylamide co-polymer. Its name is mentioned for information and does not imply endorsement by the authors.

when no plants were present. Two to three planting tubes of coast live oak and blue oak soils containing the three concentrations of P4 were watered to saturation and then sampled at weekly intervals.

Field Study

The same concentrations of P4 were evaluated at the Blythe Ranch. The soil from each seed spot was removed with a 4-inch power auger, mixed with P4, and returned to the planting hole. Two acorns were planted horizontally below the soil surface at each seed spot during the period from February to March, 1989. The seed spots were protected with a 4-inch diameter small mammal exclosure made of 1/4-inch hardware cloth. The seed spots were then watered with a quart of water to ensure that the P-4 was hydrated. The seed spots were located both in the open and under the canopy of five coast live oak and five blue oak trees. The P4 treatments were replicated four times and randomly assigned to seed spots in a 4 by 4 grid for a total of 160 spots per species.

RESULTS AND DISCUSSION

Greenhouse Test

Several of the oak seedlings were excavated to determine the distribution of roots and P4 in the soil medium. Figure 2 illustrates a coast live oak seedling grown in the high concentration of P4. Both large and small roots readily grow through the globules of hydrated P4. The effect of P4 on soil moisture after three weeks of drying (figure 3) graphically illustrates the increased level of potentially available water with the increasing concentrations of P4. The coast live oak soils were sandier than those associated with blue oak and, therefore, had lower moisture holding capacity and should benefit the most from P4 water enhancement.

Seedling height growth was measured in October, 1989, and the results are shown in figure 4. Coast live oak had a mixed response to P4 under different watering regimes. With weekly watering, the tallest seedlings were in the control soils, but seedling growth was erratic and P4 actually retarded growth. The soil medium was possibly too wet and thus detrimental to growth. On the other hand, based on an analysis of variance, increasing plant growth was positively correlated with increasing concentrations of P4 with reduced watering. Coast live oak seedlings grown at the mid and high levels of P4 on biweekly watering and mid-level P4 on triweekly watering were significantly taller than the other seedlings.

There was a clearcut negative relationship between the effect of P4 and increasing watering regime on blue oak seedling growth. Because blue oak is generally believed to grow on more xeric sites than coast live oak (Matsuda and McBride 1986), it is possible that the P4 soils were too moist for satisfactory blue oak growth.

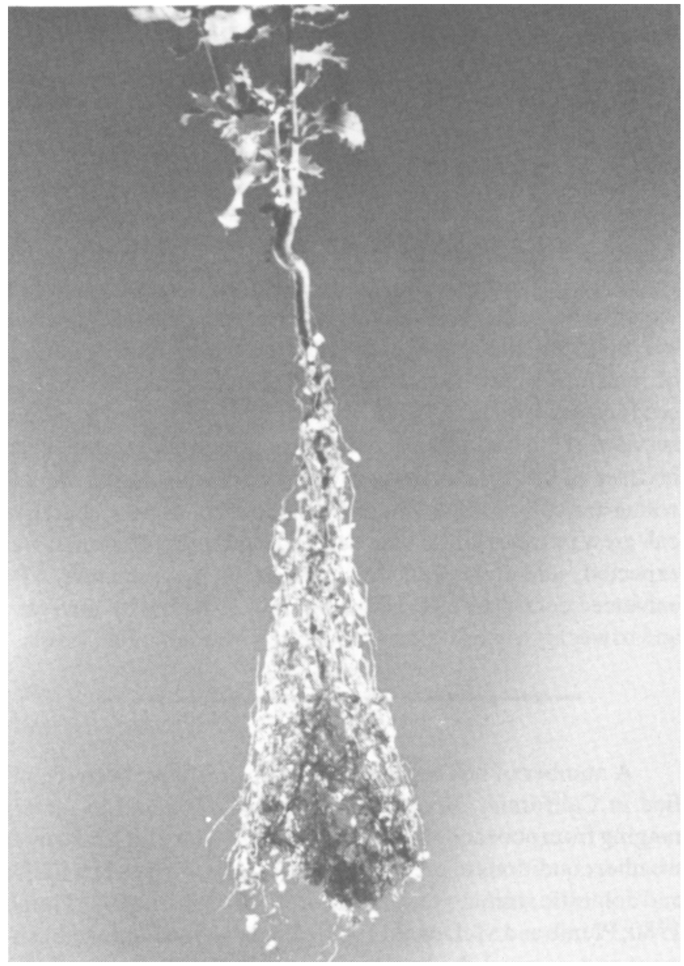

Figure 2—Both large and small roots readily grow through the globules of hydrated P4. This is illustrated here where the soil has been removed and only the gelatin-like P4 and roots remain.

Field Study

The results of P4 on seedling survival are shown in figure 5. There was no significant difference in seedling survival for any of the treatment variables including species, P4 concentration, and light exposure. If anything, P4 had somewhat of an inhibiting effect on survival. These results do not match the positive response that others have obtained. Also, they do not support the positive results obtained with coast live oak in the greenhouse test.

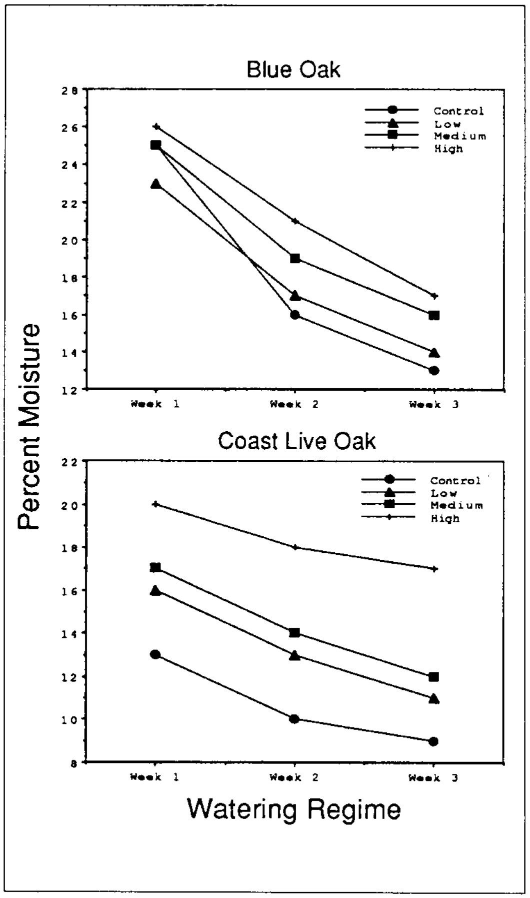

Figure 3—These graphs represent changes in percent soil moisture over a three week drying period for blue oak and coast live oak soils for different P4 concentrations.

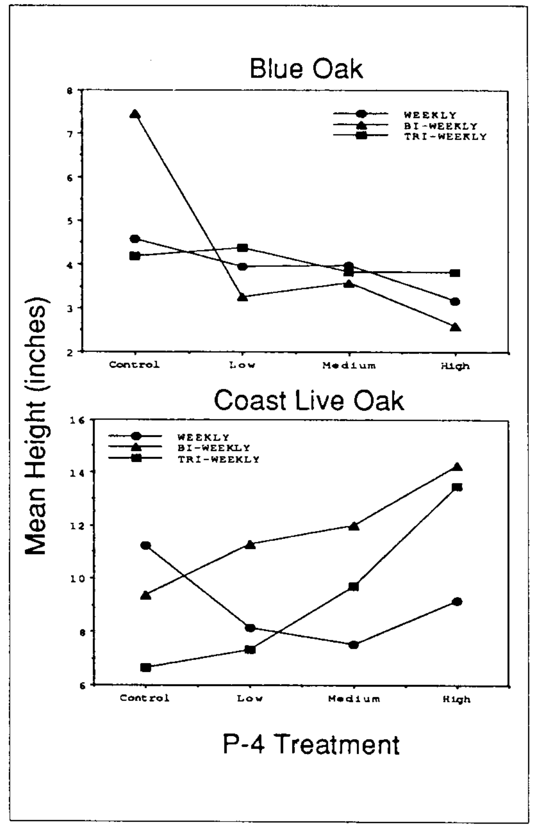

Figure 4—The effect of different concentrations of P4 on coast live oak and blue oak seedling height growth under three watering regimes are illustrated above. Coast live oak, but not blue oak, responses were significantly different, from the control treatment.

CONCLUSION

Although coast live oak responded favorably to P4 under greenhouse conditions, this positive effect did not carry over to the field study. The drought conditions in 1989 may have been too severe to have allowed any advantage of P4 to be demonstrated. More field testing should be done with coast live oak to further explore the effects of P4 on seedling survival. Some of the results of this work indicate that P4 may have kept the soil too moist for good blue oak growth; but this is contradicted by other results in this study where the available soil moisture was low, and there was still no positive effect of P4 on blue oak survival.

Finally, P4 shows enough promise that further testing should be done to determine if it can be used to enhance seedling survival.

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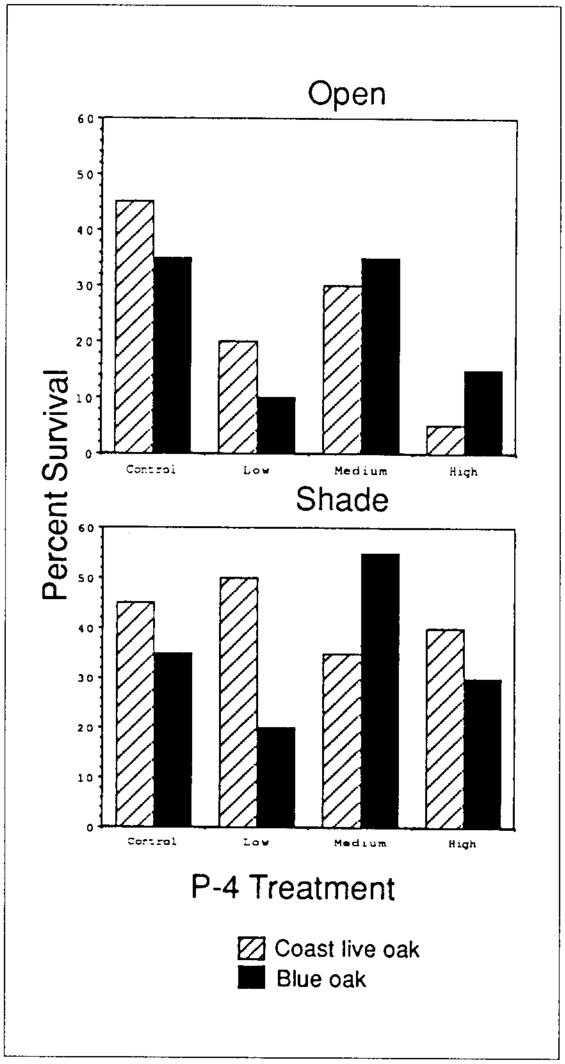

Figure 5—Blue oak and coast live oak pre-germinated acorns were planted in the ground in shaded and open areas. Seedling survival was determined for the first growing season. These graphs represent percent seedling survival for each Broadleaf P4 treatment in shaded and open exposures.

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