

Effects of Shade and Clipping on Coast Live and Blue Oak Seedling Mortality and Growth in California Annual Grasslands¹

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Abstract: Responses of oak seedlings to shade and clipping treatments were studied in unirrigated, unweeded exclosures at Hastings Reservation, Monterey County, California from 1988 through 1991. Locally collected acorns were planted (December 1988) and a greater number of coast live than blue oak seedlings emerged (84 versus 54 percent), but fewer survived (by Year 3, 10 versus 40 percent). Blue oak benefited from but did not require shade for survival, in contrast with coast live oak. Clipping treatments resulted in greater coast live oak mortality but possibly benefited blue oak. Ultimately, both species established seedlings in annual grasslands during a prolonged drought.

Livestock ranching is the primary use of many oak habitats in California (Bolsinger 1988). Ranchers and land managers might have greater assurance about management strategies likely to promote oak recruitment if they had more information on the specific effects of biomass removal on oak survival and growth.

Anecdotal evidence abounds on the deleterious effects of livestock grazing on oak regeneration. However, for a variety of political and logistical reasons, there has been little research and therefore a paucity of data about specific effects of livestock grazing and wildlife browsing upon oak seedling establishment, growth, and survival (Allen-Diaz and Bartolome 1992, George and Hall 1991).

Our experiment sought to understand how coast live oak (*Quercus agrifolia* Nee) and blue oak (*Q. douglasii* Hook & Arn.) seedling growth and survival are influenced by herbivory and canopy. Coast live and blue oak dominate almost half of the oak woodlands in the state and offer several interesting points of comparison. Coast live oak is an evergreen species and blue oak deciduous, although as seedlings both often maintain leaves throughout the year. The seedlings are reputed to differ in their ability to survive under tree canopy. Field observations have suggested that tree canopy had an important effect on sapling survival (Muick and Bartolome 1987), and I wanted to investigate its effects on seedlings. Simultaneously, I investigated how different kinds and seasons of herbivory (biomass removal as a first-level proxy for grazing effects) would affect oak seedlings.

The study investigated three hypotheses: (1) Do seedling emergence, growth, and survival in response to shade treatments differ between coast live oak and blue oak in annual grasslands? (2) Do seedling survival and growth in response to clipping treatments differ between coast live oak and blue oak in annual grasslands? and (3) Are there interactions among these treatments and species affecting survival and growth? The results of the first two hypotheses are presented and discussed in this paper (for a full discussion see Muick 1995).

Methods

Research took place at University of California's Hastings Reservation, Monterey County, California, from 1989 to 1991 on three sites within old fields near blue or coast live oak stands. A comparison of the three sites (North Field, Robinson

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Saddle, and Tire Flat) is presented in *table 1*. At each site an enclosure was constructed, fenced above and below ground, to exclude all vertebrate herbivores. The enclosures were rested for one year after fencing, and remaining rodents were live-trapped and removed.

Table 1—Comparison of site and soil characteristics of the three Hastings sites including data from soils analysis by UC Davis, DANR Soils Laboratory

Characteristic	North Field	Robinson Saddle	Tire Flat
Elevation (ft)	1800	1840	1760
Slope (pct)	0-5	0-5	0-5
Depth to clay pan (ft)	4	5	6
SO ₄ -S	20	21	21
N (total N; Kjeldahl method)	0.066	0.040	0.063
P (carbonate; Olsen test)	6.4	3.6	4.8
CEC	18.0	9.0	16.5
Percent sand	77	87	76
Percent silt	13	8	14
Percent clay	10	5	10
Hastings sample number	901	902	903

Concerns about effects of fence edge and soil compaction were addressed. To minimize edge effects associated with fences, a 1-m boundary strip was established between the fence and the planting area. Since soil compaction is thought to inhibit oak seedling establishment, the planting areas were protected from treading and mechanical disturbance during trenching and fence construction. Foot traffic was restricted to well-defined paths which were used during all phases of the study.

Each enclosure measured approximately 6 by 8 m and was divided into quarter-plots. Each quarter-plot was further subdivided into 16 cells measuring 30 cm on a side. Cells were separated and positioned to equalize interactions (*fig. 1*). Fifteen cells were planted with acorns, and one was used for herbaceous vegetation observations. Each cell was planted with 16 acorns from a single source, either from one blue oak parent or one coast live oak population.

The experiment was a multifactorial design, and species and treatments were assigned randomly to cells. The resulting design was evaluated for adequate dispersion within the quarter-plot and balanced within each shade treatment and site.

A total of 2880 acorns was planted in this experiment. Acorns were planted on December 18, 1988, at a depth of approximately 5 cm. After planting, the cell received about 200 to 250 ml of water to prevent the acorns, some of which had emerging roots, from drying out before the next rain. This was the only additional water used in the experiment.

Herbaceous vegetation, consisting of annual grasses and forbs, was not modified beyond the disturbance associated with acorn planting. No fertilizer or irrigation was applied to the acorns or seedlings, and no pre-existing oak seedlings were observed.

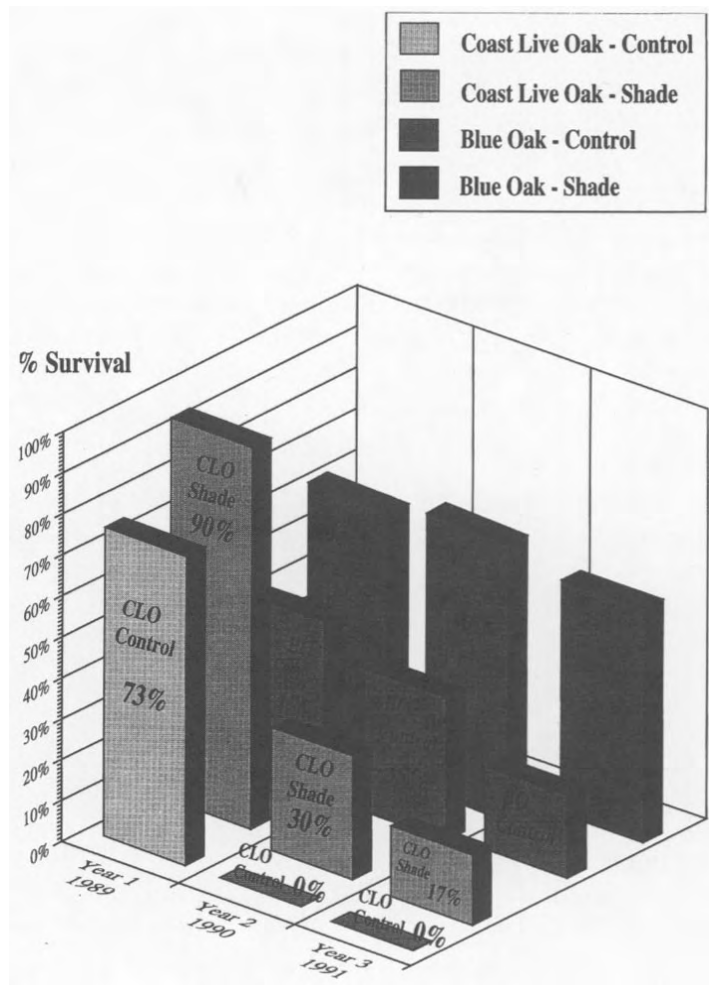


Figure 1—Seedling survival by species and shade treatment across three years of study, 1989 to 1991.

Experimental Treatments

Two intensities of clipping were used to simulate herbivory plus a control: (1) a moderate clipping treatment which removed all leaves, (2) a heavy clipping treatment which removed all stems and leaves at 0.5–1.0 cm above ground level, and (3) a control, no clipping. Seedlings were clipped on May 1, 1989.

Moderate clipping represented defoliation by insects, particularly grasshoppers. Heavy clipping represented browsing by deer, rabbits, woodrats, sheep, and cattle.

Although originally two seasons of clipping, early and late, were planned to investigate seasonality of seedling responses, the drought altered this plan. By July of Year 1, leaves and shoots of many unclipped seedlings of both species were dried and brown. Since there were few green leaves or shoots, it appeared unlikely that they would have been grazed; therefore the late season clipping was eliminated from the plan and clipping was limited to one season.

The shade treatment consisted of shaded and unshaded quarter-plots. One of the four quarter-plots on each site, and the one diagonal to it, were randomly assigned to the shade treatment. The two remaining quarter-plots were unshaded. Shade was produced by a 50 percent shade cloth tarp of WeathashadeTM suspended horizontally over a quarter-plot approximately 1 to 1.25 m above the ground.

Data Collection

Observations were made monthly from March 1989 and ended in July 1991. Each month I recorded, by cell, the number of seedlings and leaves, heights of seedlings, and annual vegetation. Annual biomass production was collected in the spring of 1989 and 1990 from a control cell within each quarter-plot.

Seedling emergence was defined as the presence of a shoot or stem with leaves in the spring of 1989. Survival was defined as the presence of a stem with green leaves or a living stem during any of the observation dates in Year 2 or 3. Dieback was defined as the unseasonal presence of brown and dried leaves, shoots or parts of shoots, and was common for both species at all sites. The maximum number of seedlings with green leaves and/or stems observed for a species at a site was used to represent survival for that time interval.

Data Analysis

Data were entered into a database using ExcelTM spreadsheet software and were summarized monthly by site, quarter-plots, and treatments over the course of the experiment. SYSTATTM and ExcelTM were used to produce frequencies and other descriptive statistics. The SASTM general linear model (GLM) for split plot designs was used to evaluate the seedling responses to treatments. Seedling number was square root transformed to increase consistency with the assumptions of the GLM.

Results

Even during the most extreme drought of the century, coast live and blue oak seedlings survived in ungrazed annual grasslands, although patterns of growth and survival would probably have been different under wetter conditions.

Observations are summarized by species for three periods. Year 1 was the first growth period—March through September 1989. Year 2 was the second growth period—October 1989 through September 1990. Year 3 was the final growth period of the study—October 1990 through July 1991.

General Linear Model (GLM) Analysis

The GLM analysis testing of the first hypothesis (*table 2*) demonstrated that the species differed significantly in emergence and survival ($P \geq 0.001$). By Year 2 the shade treatment effects were also highly significant in explaining survival ($P \geq 0.001$).

The second hypothesis “Do seedling survival and growth in response to clipping treatments differ between coast live oak and blue oak in annual grasslands?” was rejected for Year 1, although the clipping treatment resulted in greater mortality among coast live oak than among blue oak seedlings. However,

Table 2—Summary of the general linear model (GLM) analysis of the three hypotheses (Type III model).

	Seedling survival year 2 April 1990				Seedling survival year 3 June 1991			
	Site	Spp	Shade	Clip	Site	Spp	Shade	Clip
Overall Model F	21.30	20.43	20.40	1.21	11.26	21.94	12.20	5.12
P	0.0001	0.0001	0.0001	0.3069	0.0001	0.0001	0.0009	0.0089
Interactions (omitted for brevity)								

by Year 3 the clipping treatment began to explain the differences in seedling survival ($P \geq 0.0089$).

Coast Live Oak

Emergence, responses to shade treatment and site—In Year 1, 1215 coast live oak seedlings, 84 percent of 1440 acorns planted, emerged in 4 months. Whereas shaded quarter-plots in North Field and Robinson Saddle were more favorable for seedling emergence than unshaded quarter-plots, an equal number of seedlings emerged on shaded and unshaded treatments at the more mesic Tire Flat. The driest site, Robinson Saddle, exhibited the greatest differences between shade treatments in seedling emergence. There, 90 percent of the acorns planted under shade produced seedlings whereas only 60 percent of the acorns emerged when not shaded. Robinson Saddle also exhibited earlier seedling dieback than North Field and Tire Flat. In Year 1, species was highly significant in explaining the differences in seedling emergence. A summary of coast live oak response by site and treatment is presented in *table 3*.

Table 3—Results of GLM of seedling height in April 1991, Year 3 (Type III model)

	Mean square	F	P
Main effects			
Site	264.24	39.59	0.0001
Spp	223.81	33.53	0.0001
Shade	339.42	50.84	0.0001
Clip	38.07	5.70	0.0041
Interaction (omitted for brevity)			
Error	6.67		

In Year 2, the population of coast live oak seedlings decreased dramatically, and most survivors were located under shade. Only 17 percent (202) of the original seedlings survived across all three sites, and only one of these grew on an unshaded quarter-plot. In Year 2, shade also became significant in explaining the differences in seedling survival.

By Year 3, 74 percent of the previous year's seedlings survived. However, this represented only 10 percent of the original seedling population established in 1989. Tire Flat, the most mesic site, had four times as many seedlings as North Field. No unshaded coast live oak seedlings survived the third year.

Responses to clipping treatments—Clipping treatments increased seedling mortality. In Year 2, 45 percent of unclipped seedlings survived compared to 16 percent of moderately clipped seedlings and 12 percent of heavily clipped seedlings. By Year 3, only 8 percent of clipped seedlings (both treatments) survived under shade versus 23 percent of unclipped seedlings. Although the hypotheses that clipping has different effects on seedling survival by species was rejected in Year 2, its significance increased in Year 3.

Blue Oak

Emergence, responses to shade treatment and site—By June 1989 in Year 1, 773 blue oak seedlings, or 54 percent of the 1440 acorns planted, emerged (*table 4*). On unshaded quarter-plots, 47 percent of the acorns produced seedlings, with maximum numbers appearing in March and April before dieback and/or dormancy ensued. On shaded quarter-plots, 60 percent of the acorns emerged; most seedlings emerged in April and June, about a month **after** peak numbers on unshaded quarter-plots.

Table 4—Blue oak seedling emergence and survival by shade and clipping treatments and site for April 1989, April 1990, and June 1991
**** no surviving seedlings**

Site	Blue oak unshaded				Blue oak shaded			
	Acorns	89 Seedlings	90 Seedlings	91 Seedlings	Acorns	89 Seedlings	90 Seedlings	91 Seedlings
Unclipped								
North Field	144	82	51	25	160	92	86	84
Robinson Saddle	160	45	**	**	112	65	3	4
Tire Flat	128	63	18	16	144	81	66	66
Subtotal	432	190	69	41	416	238	155	154
Moderate clipping								
North Field	48	20	11	11	48	29	31	24
Robinson Saddle	48	17	**	**	32	20	**	**
Tire Flat	32	28	11	8	64	26	20	22
Subtotal	128	65	22	19	144	75	51	46
Heavy clipping								
North Field	48	23	9	1	32	28	29	27
Robinson Saddle	32	**	**	**	96	60	2	1
Tire Flat	80	46	14	4	32	14	7	9
Subtotal	160	69	23	5	160	102	38	37
Total	720	324	114	65	720	415	244	237

In the spring of Year 2, the relationship between seedling survival and shade treatment was more pronounced. Shaded seedling populations remained relatively stable after Year 1. Shaded seedling survival was higher (58 percent), although some unshaded seedlings did survive (28 percent). In Year 2 species and shade were both significant in explaining the differences in seedling emergence (*table 2*). Almost all the shaded seedlings that emerged in Year 1 survived into Year 3, whereas the numbers of unshaded seedlings declined. Species and shade treatments continued to be significant in explaining differences in seedling survival (*table 5*).

Responses to clipping treatments—The interactions between survival and clipping treatment were most pronounced on the dry Robinson Saddle site where all unshaded blue oak seedlings died. There, in Year 3, only five shaded blue oak seedlings remained alive.

On unshaded North Field and Tire Flat quarter-plots, only moderately clipped blue oak seedlings survived. Unclipped and heavily clipped seedlings continued to die. Shaded blue oak seedlings in North Field appeared to be little affected by clipping. On Tire Flat, mortality of shaded seedlings increased in direct relation to clipping intensity the first 2 years but stabilized after Year 2.

Herbaceous Vegetation

Annual vegetation was measured on each cell, and shaded vegetation was taller (*table 6*). The average height of shaded annual vegetation averaged 24 versus 16 centimeters when unshaded, a pattern that persisted in Years 2 and 3. Annual vegetation was at least twice the height of the average coast live or blue oak seedling during the spring and early summer. There was no apparent difference in vegetation heights on control cells and those with either oak species.

Discussion and Conclusions

Rainfall at Hastings was below average for the year preceding the experiment and the 3 years reported here. Average precipitation for 1987-88 through 1990-91 was 37.3 cm. In contrast, the average precipitation from 1970-71 through 1986-87

*Table 5—Coast live oak seedling establishment and survival by shade and clipping treatments and site for April 1989, April 1990, and June 1991. ** no surviving seedlings*

Site	Coast live oak unshaded			Coast live oak shaded			
	Acorns	89 Seedlings	90 & 91 Seedlings	Acorns	89 Seedlings	90 Seedlings	91 Seedlings
Unclipped							
North Field	192	178	**	128	126	70	21
Robinson Saddle	112	48	**	144	131	1	1
Tire Flat	160	131	**	128	108	85	62
Subtotal	464	357		400	365	156	84
Moderate Clipping							
North Field	16	16	**	64	60	4	**
Robinson Saddle	80	35	**	48	41	**	**
Tire Flat	32	31	**	48	39	18	12
Subtotal	128	82		160	140	22	12
Heavy Clipping							
North Field	32	29	**	48	46	1	1
Robinson Saddle	48	18	**	48	44	**	**
Tire Flat	48	39	**	64	54	16	11
Subtotal	128	86		160	144	17	12
Total	720	525		720	649	195	108

was 57 cm. At the outset of the study, I decided not to irrigate the oak seedlings regardless of precipitation. My primary objective was to obtain results applicable to landscape and ecosystem levels of management; irrigation is not a practical technique at those scales.

Although patterns of growth and survival would probably have been different under wetter conditions, without a comparable study in wetter years, the extent to which results were influenced by drought is unknown.

Comparison of Species' Responses to Treatments

Coast live oak and blue oak seedlings were similar in their positive response to the shade treatment. The two species differed in the number of seedlings established, timing of emergence, percent survival, and the extent of the positive responses to shade and clipping treatments.

Coast live and blue oak seedlings responded favorably to shade and both experienced higher mortality without it. Both coast live and blue oak had more and taller seedlings when shaded. On the driest site, Robinson Saddle, neither

Table 6—Heights of herbaceous vegetation (cm) at the three sites.

	Apr-89	Apr-90		Jun-91	
	Annual vegetation*	Grasses	Forbs	Grasses	Forbs
Unshaded					
North Field	19.57	36.18	18.82	47.77	12.26
Robinson Saddle	10.11	20.13	20.24	21.01	9.98
Tire Flat	16.55	25.90	22.35	19.8	12.33
Mean height	15.41	27.40	20.47	29.53	11.52
Shaded					
North Field	30.14	50.40	22.56	56.27	9.51
Robinson Saddle	15.49	29.65	22.64	52.73	15.39
Tire Flat	22.86	40.13	25.96	28.89	13.45
Mean height	22.83	40.06	23.72	45.96	12.78

* In 1989 measurements were averaged between grasses and forbs, then separated in 1990 and 1991.

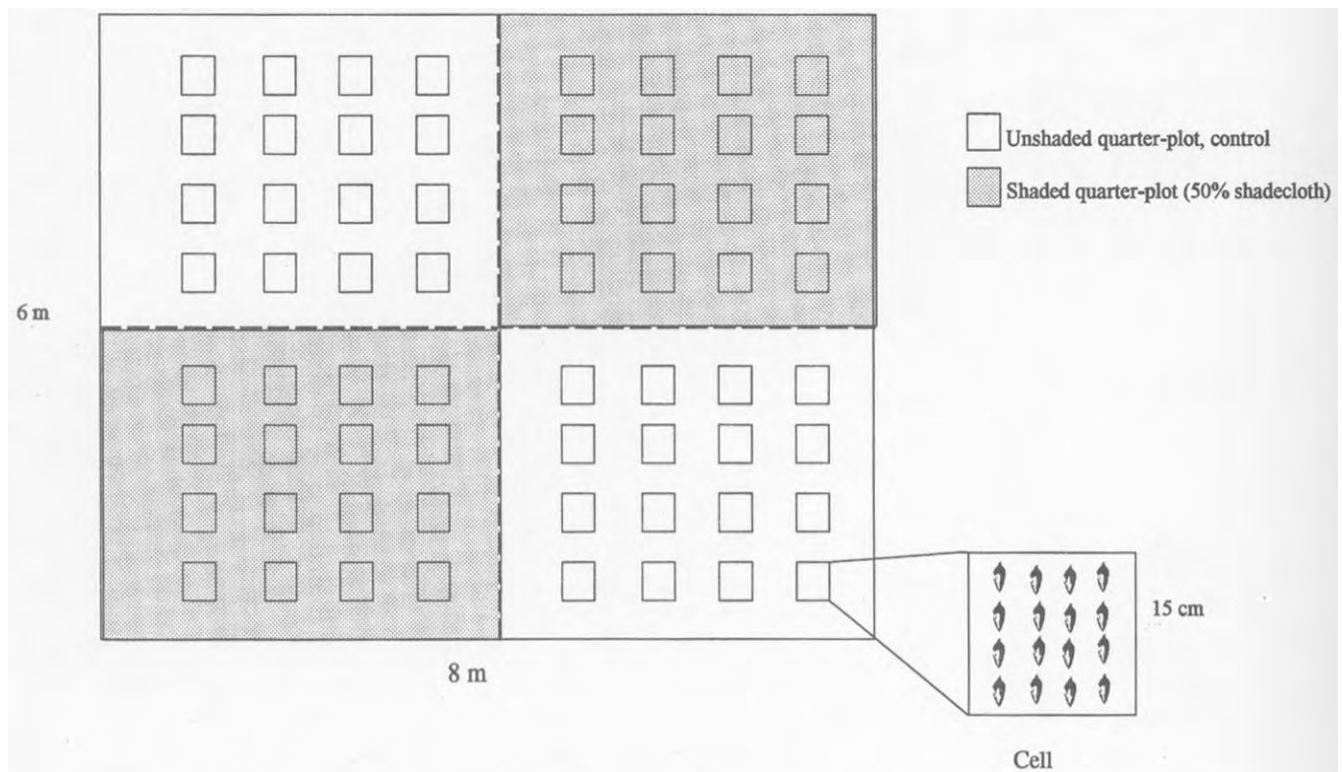


Figure 2—Planting diagram for one site containing four quarter-plots and sixteen cells per quarter plot.

species was able to survive without shade. Even then, only one coast live oak and five blue oak seedlings survived under shade after the first year. A comparison of species' survival in response to shade treatments is summarized in *figure 2*.

Seedling establishment—Despite identical handling, storage, planting, and allocation among sites and treatments, 84 percent of coast live oak acorns established seedlings in comparison with only 54 percent of blue oak acorns. At the time of planting, many blue oak acorns had emerging radicles (an uncontrolled variable), and this may have influenced establishment and survival. Since no laboratory germination tests were undertaken, it is not known if acorn viability was the same for both species. No other causes of acorn mortality or germination inhibition were determined.

Timing of shoot emergence—Blue oak exhibited delayed shoot emergence under some conditions. Although coast live oak is known to germinate late and blue oak is known to germinate early (Griffin 1971, Matsuda and McBride 1989), and blue oak hypocotyls are often visible emerging from the split tips of acorns still on the tree, the relative timing of shoot emergence has not been noted previously.

Seedling Survival and Mortality

Dieback and clipping treatments—Coast live oak experienced higher mortality than blue oak after dieback and clipping treatments. For coast live oak, seedling dieback often resulted in mortality (Griffin 1971, Jepson 1910, Snow 1973). A high proportion of seedling biomass is located in coast live oak's shoots and leaves, whereas more of blue oak's is located in roots (Matsuda and McBride 1989). When the aboveground portion of the coast live oak seedling dies or is removed, there are few reserves elsewhere for use in generating new shoots or leaves.

Despite the benefits of shade, by the final year, most of the surviving coast live oaks were those that had never been clipped. This lack of sprouting by seedling coast live oak contrasts with the documented vigorous sprouting of

saplings and tree-sized individuals. Sprouting is so predictable in coast live oak stands that they have been successfully managed as coppices (Pillsbury and others 1987).

If the rate of seedling mortality observed in this study is indicative of rates in wild populations, larger size classes of coast live oak play a greater role in regeneration and recruitment. The poor ability of year-old coast live oak seedlings to sprout and recover from clipping has not previously been noted, though drought effects must be considered.

More blue oak seedlings sprouted and survived across the range of sites and treatments. A small number of unshaded seedlings, 15 percent of moderately clipped and 3 percent of heavily clipped, survived through Year 3, in contrast with no survival among clipped coast live oak seedlings.

Effects of the drought—Although the difference in rates of species' survival was not anticipated, a possible explanation emerges when drought effects are considered. Blue oak's ability to survive unseasonal leaf drop and stem dieback and its vigorous sprouting and adaptive morphology (including waxy leaf coating and substantial biomass allocation to roots) undoubtedly enhanced its survival during the longest drought of the century. Because more of the unshaded, moderately clipped blue oak seedlings survived, this suggests that seedlings may even have benefited from leaf removal on unshaded treatments. However, other explanations may be possible.

Acorns were planted at a density of 16 per square foot. The effects of seedling competition for moisture within cells and quarter-plots cannot be eliminated and may have affected seedling establishment, growth, survival, and responses to treatments. Although no measurements of soil or plant moisture were taken, it is reasonable to assume that competition for soil moisture occurred both among oaks and between oaks and annual species. Since the larger, longer, and fleshier tap roots of blue oak seedlings appear better able to obtain and store soil moisture than the thinner, shorter, and wiry roots of coast live oak seedlings, this may have afforded blue oak an advantage during the drought.

It is unlikely that seedling competition with annual herbaceous vegetation was as deleterious as exposure to full sun since shaded quarter-plots had taller annual vegetation and more and taller oak seedlings than unshaded quarter-plots.

Shade—For both species, shade was highly significant in explaining seedling height and survival ($P > 0.001$), despite the fact that coast live oak is considered shade-tolerant and blue oak is considered shade-intolerant (Sudworth 1908). The shade treatment may have ameliorated the effects of low soil moisture since shadecloth typically reduces soil temperatures which can result in higher soil moisture or reduced evapotranspiration. Perhaps the benefit of shadecloth on blue oak survival is more pronounced during drought years, although seems unlikely given the results of a greenhouse study using the same seed stock (Muick⁴; see also Muick 1995).

⁴ Unpublished data on file at 2660 Gulf Drive, Fairfield, CA 94533.

For both species, seedlings experienced massive dieback and/or mortality between June and August in 1989 and June and July, in 1990 on all unshaded quarter-plots and on two-thirds of the shaded quarter-plots. For example, on North Field, 143 coast live oak seedlings had green shoots or leaves in July and none were visible in August. On Robinson Saddle, 89 blue oak seedlings were alive in June, and only one seedling had leaves in July. For both species, critical sprouting periods were between March and April in 1990, and March and June in 1991.

The greatest mortality of coast live oak seedlings probably occurred in July of the first year when only about a fifth of the seedlings survived. Clipping treatments increased the mortality rates to such a degree that, by the final year, only one-third of the clipped seedlings survived in comparison with two-thirds of the unclipped seedlings.

The greatest mortality of blue oak was observed during the acorn to seedling stage when less than half of the blue oak acorns grew into seedlings. Blue oak seedlings usually emerged later and were shorter than coast live oak. However, once established, blue oak seedlings demonstrated remarkable persistence (perhaps enhanced by lower density) and became the dominant species on each quarter-plot and treatment by the end of the study.

Deer Browsing and Livestock Grazing

One study directly examining the effects of livestock grazing on blue oak seedling survival concluded that seasonal grazing was compatible with oak regeneration (George and Hall 1991). However, the study, which used container-grown seedlings, lasted only one year. The results of this study support findings of compatibility between blue oak seedling survival and grazing by demonstrating the ability of blue oak seedlings to sprout after clipping.

Findings and Recommendations

Coast Live Oak

Findings

Both shade and protection from herbivory enhanced coast live oak seedling establishment, growth, and survival.

The greatest mortality of coast live oak seedlings resulted from dieback, desiccation, and clipping treatments during the first year.

Unlike older seedlings, 1- to 3-year-old coast live oak seedlings are not vigorous sprouters and appear to be vulnerable to both desiccation and herbivory.

Recommendations

- For habitat restoration projects coast live oak seedlings should be shaded and protected from herbivory.
- For ranchers, land managers and researchers, established seedling populations should be protected from herbivory to facilitate growth and survival.

Blue Oak

Findings

The greatest mortality of blue oak was observed at the acorn-to-seedling stage when less than half of the blue oak acorns produced seedlings, even though many of the blue oak acorns planted had emerging radicles.

Shade and protection from herbivory were of positive benefit to blue oak seedling establishment, growth, and survival, but neither was completely limiting.

First-year blue oak seedlings sprouted new stems and leaves in response to clipping—simulated herbivory—more vigorously than first-year coast live oak seedlings.

Blue oak seedlings emerged later than coast live oak seedlings on most sites under both shaded and unshaded conditions.

Both unclipped and clipped blue oak seedlings were shorter than comparably treated coast live oak seedlings, indicating slower aboveground growth.

Once established, blue oak seedlings demonstrated remarkable persistence, both in relation to shade treatments and site.

Recommendations

- For habitat restoration projects blue oak seedlings should be shaded and protected from herbivory.
- For ranchers and researchers, established seedling populations should be protected from herbivory to facilitate growth and survival. This study supports the possibility that, under certain conditions, blue oaks may be able to tolerate some types of herbivory.

Both Coast Live and Blue Oak

First-year dieback is common to both species. Seedlings typically responded to precipitation within 2 weeks with new shoots, leaves, or basal sprouts. Based on these observations, I offer the following cautionary advice. In dry years and at dry locations, seedling surveys conducted after June are likely to under-represent populations of 1- to 3-year-old seedlings since leaves and stems may have died back and are not visible.

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