

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

Frank W. Davis Mark Borchert L.E. Harvey Joel C. Michaelsen²

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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²Assistant Professor of Geography, University of California, Santa Barbara; Forest Ecologist, Los Padres National Forest, Goleta, California; Postgraduate Researcher, Queen's University, Ontario, Canada; Assistant Professor of Geography, University of California, Santa Barbara.

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
		Buried				1140	0.36	
			+				540	0.30
	-						600	0.42
	1986				2220	0.50		
		Surface				1140	0.36	
			+				660	0.31
				-				480
		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
		Buried				1020	0.61	
						1632	0.18	
	1987					1056	0.12	
		Surface	+				528	0.07
				Buried	+			
		-				576	0.29	
		Surface	-				288	0.24
				Buried	-			

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:

$$100 \times \sin(\text{slope}) \times \cos(\text{azimuth}).$$

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 enclosure experiments. Treatments are listed by the predators that had access to the plots. Numbers refer to the number of replicates in each enclosure. Numbers in parentheses are for Agua Escondido (AE), when different from American Canyon (AC) (Borchert and others 1989).

Predator access	Enclosures			Description
	Deer	Cattle	Control	
No predators (NP)	2	2(3)	—	All predators were excluded using a 2.4 by 2.4 m subenclosure. 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 subenclosure.
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 subenclosures.
Birds (B)	6(5)	6(5)	—	Subenclosures were left uncovered in the cattle and deer enclosures.
B,M, Gophers (BMG)	6	—	—	Unprotected plots in the deer enclosure.
B,M,G, Deer (BMGD)	—	6	—	Unprotected plots in the cattle enclosure.
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 enclosure 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 G^2 (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
Buried	NP	120	0.12	0.04	0.03	0.02	0.02
			51	37	30	30	21
	BMGDC	180	0.43	0.31	0.25	0.25	0.17
			51	17	11	8	6
			0.28	0.09	0.06	0.04	0.03

¹NP = 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

¹NP = 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 enclosures 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.

Seedling origin ²	B/NP		Treatments ¹ BMG/BMGD		BMGDC	
	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)	—	—	—	—

¹B = birds; G = gophers; M = mice; NP = no predators.

²AC = American Canyon; AE = Agua Escondido.

³Values 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.

Treatment	AC ¹		AE ¹	
	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

¹Values in columns not followed by the same letter are significantly different at least at p5 0.05.

²AC = American Canyon; AE = Agua Escondido.

treatments at AC (table 8). The very high biomass production at AE was the result of rapid succession to riggut 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 G² reduction differs considerably between the two regression trees: 43.6 and 70 percent for the seedling survival and seedling recruitment trees, respectively. The lower G² 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 surveys³ 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.

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