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RESTORATION STRATEGIES FOR OVERCOMING LIMITATIONS TO SCRUB OAK REGENERATION ON CATALINA ISLAND

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Abstract—When the removal of feral pigs and goats from Catalina Island by 2002 did not produce a flush of island scrub oak seedlings, and observations of patches of dying mature oaks increased, a study was initiated to identify possible limiting factors to scrub oak regeneration. The study addressed two current potential island-wide factors: herbivory by non-native deer and bison, and competition from non-native annuals, primarily grasses. Also addressed were soil-mediated differences among potential restoration sites (eroded slopes, oak-dieback areas, and healthy oak stands), microsite characteristics related to proximity to oak canopy, and the potential value of tree-tubes to oak seedling growth and survival. After three years, data indicate that microsite characteristics related to seedling proximity to oak canopy cover and the use of tree-tubes have more significant impacts on growth and survivorship than protection from ungulate herbivory with fences, annual grass control, or soil-mediated site differences. Soil nutrients, moisture, and texture as well as pathogen loads were monitored but their impacts on oak seedlings were not consistent.

INTRODUCTION

On Catalina Island, the lack of saplings and limited number of seedlings of island scrub oak (*Quercus pacifica*) have been attributed to non-native ungulates. During the last two centuries, bison (*Bison bison*), pigs (*Sus scrofa*), goats (*Capra hircus*), and deer (*Odocoileus hemionus*) were introduced to the island. They proliferated, contributing to acorn, seedling, and basal sprout herbivory (Griffin 1971; Peart et al. 1994; Sweitzer and Van Vuren 2002; Manuwal and Sweitzer 2006). By 2002, 99% of the feral pigs and 100% of the goats were removed from Santa Catalina Island (Schuyler et al. 2002a, b). However, oak regeneration did not increase as dramatically as expected, and, at the same time, patches of dying mature oaks (hereafter referred to as "dieback" areas) were noted on the channel side of the island. A more recent examination of historical aerial photographs suggests that patches of scrub oaks have been slowly dying over the past 80 years with no indication of regeneration (Knapp, in press).

Dieback may be attributed to site-specific characteristics that may have decreased the vigor of trees and made them vulnerable to soil-borne pathogens. However, it may also be indicative of forest senescence, since the lack of regeneration coincides with high rates of goat and pig herbivory on the island, leaving only mature trees. Senescence is a greater concern for the long-term persistence of oak woodland than localized "dieback" because it suggests a much wider-scale loss of mature, acorn-bearing oaks. Without identifying and mitigating the limiting factors to natural scrub oak regeneration, Catalina Island stands to lose the scrub oak woodland ecosystem that covers 33% of the island. The observed lack of seedling regeneration and dieback raises concern that a permanent habitat transformation from oak woodland to annual grassland could occur, leading to the establishment of a less diverse and non-native dominated alternative stable state (George et al. 1992; Suding et al. 2004; Acacio et al. 2007).

The numerous studies in California on limitations to oak regeneration implicate multiple factors. Oaks do not form a persistent seed bank, and regeneration has been shown to be limited by herbivory of acorns and seedlings (Menke and Fry 1980; Adams et al. 1992; Groot Bruinderrink and Hazebrock 1996). Although pigs and goats have been removed from Catalina Island, deer and bison remain and continue to be a potential threat to young oaks. Acorn predation by rodents, such as ground squirrels (*Spermophilus beecheyi nesioticus*) or mice (*Peromyscus maniculatus catalinae*), may also contribute to reduced regeneration (Linsdale 1946). Competition from established annual grasses is a second factor thought to limit oak regeneration. Studies have implicated non-native annual grasses such as *Bromus diandrus*, common on Catalina Island, as one of the primary factors responsible for reducing soil moisture (Knoop and Walker 1985; Zutter et al. 1986; Gordon and Rice 2000), and inadequate soil moisture has been shown to limit regeneration of oaks (Gordon and Rice 1993; Swiecki et al. 1997; Gordon and Rice 2000; Davis et al. 1991). Finally, oak regeneration and growth may be sensitive to soil characteristics that vary among potential restoration sites, as well as microsite conditions that are related to proximity of the parent canopy (Tyler et al. 2002). Potential restoration sites include large gaps in scrub oak woodlands caused by localized dieback or by loss of tree cover and erosion due to past impacts of feral ungulates. In these patch types, soil-mediated characteristics such as reduced water-holding capacity (e.g., sandy, eroded soils) or soil pathogens (e.g., dieback areas) are potential limiting factors. Studies have also shown that partial shade increases survivorship of another drought tolerant oak species, *Quercus douglasii* (Callaway 1992), because of reduced water stress (Muick and Bartolome 1987). Furthermore, proximity to conspecific parents may allow beneficial mycorrhizal symbionts to colonize seedlings more readily and facilitate nutrient uptake (Dickie et al. 2002). Therefore, seedlings growing under the canopy edge might experience benefits from ready mycorrhizal colonization, relief from evaporative demand provided by the partial shade, and fog drip from the canopy drip line, while seedlings in the open may benefit from full sun and reduced competition from mature trees and impacts from associated soil pathogens.

This study compared the effects of herbivory, competition from annual grasses, oak canopy shade, and soil condition as potential factors limiting scrub oak regeneration. Additionally, I evaluated the effectiveness of two methods (tree-tubes vs. fences) for limiting ungulate impacts, and examined the influence of different restoration patch types (eroded, dieback, and healthy) on oak recruitment. This design allows us to identify key limiting factors to island scrub oak regeneration, while concurrently evaluating the success of potential restoration strategies needed to mitigate these factors.

MATERIALS AND METHODS

A field experiment was conducted on Catalina Island to evaluate the success of various restoration strategies for reducing the impacts of potential limiting factors to scrub oak regeneration. Using a series of factorial designs, I evaluated herbivory with fencing and tree tubes; considered competition with annual grasses using herbicide treatments; considered microsite characteristics by planting in canopy and open field sites; and evaluated the impact of erosion and dieback on soils by planting in three different sorts of patch types: eroded, dieback, and healthy oak stands.

Herbivory

Herbivory was examined using fencing treatments in a factorial study with competition and microsite factors within healthy oak stands ("H" in Table 1). Within patches of healthy oak woodland, groups of planted acorns were exposed to combinations of three herbivory treatments (fenced, tree-tube, control), two competition treatments (weeded, unweeded), and two microsite treatments (open, edge). In each patch, 40 sites were planted for each of the 12 groups representing treatment combinations. This was replicated over five patches. However, one patch burned in a wildfire in 2007, and we only analyzed data for the remaining four patches.

The impacts of herbivory and possible ways to circumvent it were evaluated with three treatments: fencing, tree-tubes, and a control. Within each healthy patch, there were four treatment combinations (competition and microsite) each with 40 acorn planting sites for a total of 160 acorn planting locations ("sites") assigned to each herbivory treatment. Those in the "fenced" treatment were enclosed within a single fenced area that included trees and sufficient open space to accommodate the microsite and competition treatment combinations. The 2.4 m tall plastic deer fence was supported by 3 m t-stakes with a top wire. A large fenced area was used rather than many individual fences to simulate the wide-scale loss of herbivory and potential for increased grass cover and associated reduced soil moisture that may result if deer and bison are removed from the island. Outside the fenced area, acorns in the 160 "tree-tube" treatment sites, from the four microsite x

Table 1. Study design. (H) indicates treatment combinations used to examine effects of herbivory. (C/M) indicates treatment combinations used to examine effects of competition and microsite. (PT) indicates treatment combinations used to examine patch type. Within each patch replicate, there are 40 planting sites per treatment combination.

		HEALTHY (n = 4)		DIEBACK (n = 5)		ERODED (n = 5)	
		Edge	Open	Edge	Open	Edge	Open
FENCED	Weeded	H,C/M	H,C/M	C/M	C/M		
	Unweeded	H,C/M	H,C/M,PT	C/M	C/M,PT		PT
TREE-TUBES	Weeded	H,C/M	H,C/M	C/M	C/M		
	Unweeded	H,C/M	H,C/M,PT	C/M	C/M,PT		PT
CONTROL	Weeded	H	H				
	Unweeded	H	H				

competition treatment combinations, were planted in tree-tubes (Tubex™, Treessentials, St. Paul, MN). In the event that large herbivores cannot be removed from the island, tree-tubes have been shown to have success in previous oak restoration projects (Stratton 2005), and may be a feasible strategy for reducing herbivory on oaks. Tree-tubes have been shown to have minimal effect on solar insolation on oaks because of low photosynthetic rates, and to improve growing conditions by moderating the temperature and increasing CO$_2$ (Frearson and Weiss 1987). Tree-tubes may also protect planted acorns from rodent predation. In addition to fenced and tree-tube treatments, acorns were planted in 160 control sites that were located outside the fenced area, without the use of tree-tubes.

Competition and Microsite

To address the effects of weed competition, sites assigned to "weeded" treatments were treated with annual spring applications of herbicide (Round-up Pro$^{\text{TM}}$, St. Louis, MO) to kill grass and forbs within a 1-m diameter circle around the seedlings. McCreary and Tecklin (1997) demonstrated that this is an effective weed control technique for oaks. Herbicide was applied in 2005 and 2006, but not 2007 due to the low rainfall (79 mm versus 345 mm long-term average, unpublished data) and the early death of annual grasses. No herbicide was applied to "unweeded" sites.

Microsite characteristics related to proximity to the oak canopy were evaluated by locating planting sites either along the canopy edge ("edge") along the dripline or in open areas at least 2 m from tree canopies ("open").

To examine the effects of weed competition (C) and microsite (M) on oak regeneration, two weeding treatments (weeded, unweeded) and two microsite treatments (open, edge) were evaluated over two restoration patch types (healthy, dieback) and two herbivory treatments (fenced, tree-tubes; see "C/M" in Table 1). Competition and microsite were not evaluated in the eroded patch type, because these patches lacked both ground vegetation and canopy cover. The eight treatment combinations were replicated in four healthy patches and five dieback patches. Within each patch, 40 planting sites were assigned to each treatment combination. Soil moisture was monitored gravimetrically from the four fenced treatment combinations (2 weeding treatments x 2 microsite treatments) in each of the five healthy and five dieback patches at the end of the dry season in 2006. Volumetric soil moisture was also monitored with capacitance-type sensors that measure the dielectric constant or permittivity of soil (Decagon ECH20 Sensors, Pullman, WA) hourly from May 2005 though January 2006 with three replicate 4-sensor arrays in fenced healthy plots to compare microsite and competition factors.

Restoration Patch Types

The effect of planting sites on oak recruitment from acorns was examined by evaluating three potential restoration patch types: stands of healthy oaks (healthy patches), areas experiencing the unexplained dieback of mature oaks (dieback patches), and bare, eroded sites within oak groves where we might want to re-establish oaks to restore soil stability and continuity of the oak woodland (eroded patches). Five patches were selected to represent each restoration patch type. All 15 patches were located on the channel side of Catalina Island on northwest-facing slopes of less than 20% grade between Toyon Bay and Empire Landing. Three weather stations placed across the range of sites and a year of data showed no difference in environmental factors (Stratton, unpublished data). Soils ranged from dense sandy clay soils in the eroded sites to loamy, organic soils within oak stands. To characterize the soils for texture and nutrient values, composite soil collections were made from 0–10 and 10–20 cm depths from five replicates of each of the three patch types in edge and open positions (only "open" was sampled in the eroded patches). Soil texture and nutrients were quantified for each sample at San Diego State University Soils Lab. There were no differences by depth so the two depths were pooled when calculating the mean for each patch type.

Within each patch type, fenced and tree-tube treatments compared the relative success of these two techniques for limiting herbivory. Because eroded patches lacked both ground cover and oak canopy, interactions with weed competition or microsite could not be evaluated among all patch types. Therefore, all planting sites were located in open areas, and acorns in eroded patches were not subjected to a weeded treatment. In healthy and dieback patches, the open grown unweeded treatments were used for the comparison with the open grown seedlings from the eroded patch type (see "PT" in Table 1). In all replicates of the three patch types there were 40 planting sites associated with each open-planted, herbivory treatment (fencing, tree-tubes).

Planting and Data Collection

More than 35,000 acorns, without insect holes and moist enough to sink in water, were collected in fall 2004 from 68 sites between Bulrush Canyon and Empire Landing. All acorns were stored in flats in moist sand and peat in a cold storage facility for two months and then sorted evenly such that each treatment combination had a stratified mix of 320 acorns representing all collection sources. Eight acorns were planted in each of the 40 acorn planting sites per treatment combination, to ensure that initial germination results would not greatly limit the replication in the study design. All planting was conducted during the first week of December 2004 after a significant rainfall event. All planting locations were > 2 m apart, marked with painted rebar, and identified by unique numbers on metal tags.

In 2005, germination rate for each treatment was calculated as the percentage of planted acorns that germinated. Afterward, all but the tallest seedling in each location were clipped, leaving one seedling per site. Between 2005 and 2007, the growth (height) and survivorship of seedlings were monitored annually in June. In 2007, vigor was assessed for each seedling, and evidence of herbivore or insect damage was noted. High vigor seedlings had new growth and little damage, while low vigor seedlings were significantly dessicated and had lost leaves. The majority were rated intermediate so only the high and low vigor are reported here because they were in notably healthier or poorer condition. Within each patch, survivorship was calculated for each treatment combination as the percentage of the 40 sites whose seedlings had survived. Likewise, percent high/low vigor and percent herbivore/insect damage were calculated from the 40 sites per treatment combination within each patch.

Data Analysis

As aforementioned, one healthy patch burned in 2007, so data from this patch were not used in any of the seedling analyses. A three-way ANOVA (Minitab, Minitab Inc., State College, PA) was used to analyze data within the remaining four healthy patches. To assess the importance of herbivory, I compared the three levels of the herbivory treatment (fenced, tree-tube, control), using microsite location and weeding treatment as covariates. Each level of the fencing treatment was replicated at the level of each treatment combination group. Analyses were performed for the response variables germination, survivorship, height, percent low vigor seedlings, percent high vigor seedlings, percent herbivore damage, and percent insect damage. Because analyses were already sufficiently complex and because treatments such as herbicide were not equivalent among years, survivorship and height data for each year (2005–2007) were analyzed separately. Post-hoc two-sample t-tests followed by False Discovery Rate (FDR) analyses were performed where there were three factors in order to compare each pair separately and consider multiple comparisons.

To look at effects of competition and microsite on oak regeneration, I analyzed data from two levels of the weeding treatment (weeded, unweeded), two levels of the microsite treatment (canopy edge, open field), and used fencing treatment (fenced, tree-tubes) and two levels of patch type (healthy, dieback) as covariates. A general linear model was required rather than ANOVA, because the number of replicates was uneven among patch types. Response variables analyzed were germination, survivorship, height, percent low vigor, percent high vigor, percent herbivore damage, and percent insect damage. Where there were three factors, post-hoc two-sample t-tests followed by FDR analyses were performed. The general linear model was also used to compare mean gravimetric soil moisture readings between the weeded and unweeded, and edge and open groups within fenced treatments of healthy and dieback patches. A general linear model was also used to compare daily volumetric soil moisture averages over 187 days from three replicate 4-sensor arrays (competition and microsite treatment combinations) in healthy plots using array location as a factor in order to capture the power of the mean daily soil moisture averaged from hourly samples.

To evaluate the success of potential restoration strategies, I used a general linear model to compare oak regeneration in open, unweeded sites across three potential restoration patch types (healthy, dieback, eroded) and two herbivory treatments (fenced, tree-tube). In healthy and dieback patches, the data from unweeded open site treatments were compared with the eroded patches which were all open and unweeded. Response variables analyzed were germination, survivorship, height, percent low vigor, percent high vigor, percent herbivore damage, and percent insect damage. As with the other analyses, post-hoc two-sample t-tests followed by FDR analyses were performed where there were three factors.

RESULTS

Rainfall was significantly above the long-term average of 345 mm during 2005 (759 mm) when the acorns were germinating, but was below average in the ensuing two years of the study (269 mm and 79 mm). Tyler et al. (2002) found that acorn germination rates and initial survivorship are highly correlated with rainfall. Average acorn germination rates were 27%; however, because 8 acorns were planted at each of the 40 planting locations per treatment combination, the effective seedling establishment rate for the study averaged 80%.

Herbivory

Table 2 summarizes the results of ANOVA within healthy patches. In this table, interaction terms are not presented unless significant. Germination rates did not differ among the herbivory treatments, fenced ($\overline{x} = 28.3$), tree-tube ($\overline{x} = 26.1$), and control ($\overline{x} = 27.2$) (Table 2). Survivorship among herbivory treatments was not significantly different in the first two years (Table 2; Fig. 1). However, by the third year the tree-tube-protected seedlings (49%) began to survive at a significantly higher rate than seedlings in the fenced (28%; $p = 0.042$) or control sites (22%; $p = 0.0025$). Seedling growth (height) was significantly different among herbivory treatments in 2006 and 2007 (Table 2), with post-hoc tests indicating that mean heights of tree-tube protected seedlings were taller than those of fenced seedlings, which were taller than control ($p < 0.05$ for all comparisons; Fig. 1). The fenced and control groups had a very low mean percentage of seedlings rated high vigor (1% and 2% respectively), while on average, 11% of tree-tube groups had seedlings that were classified as high vigor (Tables 2, 3). Fenced and control groups also had a higher proportion of seedlings rated "low vigor" compared to those protected by tree-tubes, but these differences were not significant (Tables 2, 3). A higher percentage of the seedling damage in fenced and tree-tube treatments was attributed to insects rather than herbivores ($p < 5\%$; Table 3). There were no significant interaction effects within this analysis.

Annual Grass Competition

Table 4 summarizes the results of the general linear model analysis within healthy and dieback patches. The mean volumetric soil moisture percentage in weeded planting sites (11.5%) was significantly higher than unweeded sites (9.9%; Table 4). Acorn germination was higher in weeded

Table 2. ANOVA tests of effects for treatments within healthy patches. Results for interaction terms are not presented unless significant.

Response variable	Year	Source of variation	df	SS	MS	F	p
Germination	2005	Herbivory	2	45.5	22.7	0.17	0.847
		Competition	1	544	544	3.99	0.51
		Microsite	1	2305	2305	17.02	0.000
Survivorship	2005	Herbivory	2	28.4	14.2	0.03	0.967
		Competition	1	516.8	516.8	1.23	0.274
		Microsite	1	3631.4	3631.4	8.62	0.005
	2006	Herbivory	2	587.8	293.9	0.73	0.486
		Competition	1	1813	1813	4.53	0.039
		Microsite	1	12192	12192	30.47	0.000
	2007	Herbivory	2	6309	3154	12.15	0.000
		Competition	1	1752	1752	6.75	0.013
		Microsite	1	10208	10208	39.32	0.000
Height	2005	Herbivory	2	1.1147	0.5573	4.42	0.018
		Competition	1	0.4565	0.4565	3.62	0.064
		Microsite	1	0.1706	0.1706	1.35	0.251
	2006	Herbivory	2	8.6517	4.3259	13.79	0.000
		Competition	1	0.868	0.868	0.28	0.602
		Microsite	1	0.1382	0.1382	0.44	0.510
	2007	Herbivory	2	13.019	6.509	15.99	0.000
		Competition	1	0.1005	0.1005	0.25	0.622
		Microsite	1	0.0495	0.0495	0.12	0.729
%Low vigor	2007	Herbivory	2	24547	12274	2.63	0.084
		Competition	1	4750	4750	1.02	0.319
		Microsite	1	10730	10730	2.30	0.137
%High vigor	2007	Herbivory	2	934	467	9.40	0.000
		Competition	1	72.81	72.81	1.47	0.233
		Microsite	1	51.35	51.35	1.0	0.315
%Herbivore damage	2007	Herbivory	2	854	427	2.75	0.075
		Competition	1	74.2	74.2	0.48	0.493
		Microsite	1	440	440	2.84	0.099
%Insect damage	2007	Herbivory	2	5803	2901	5.05	0.011
		Competition	1	276	276	0.48	0.492
		Microsite	1	144	144	0.25	0.619

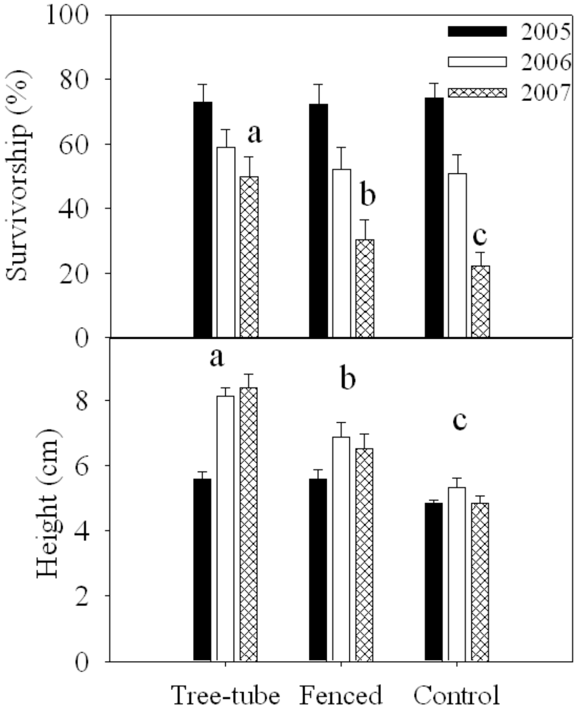

Figure 1. Mean survival and height of seedlings among three herbivory treatments within healthy patches for three years of study (*n* = 16 for each treatment). Letters (a,b,c) indicate treatments that are significantly different from each other at α =.05, as determined by post-hoc 2 sample t-tests.

plots ($\bar{x}$ = 31%) than unweeded plots ($\bar{x}$ = 24%) in both patch types and across fencing and microsite treatments (p = 0.0001; Table 4). For all years, seedlings in the weeded treatment had higher total survivorship than seedlings in the unweeded treatment (Table 4; Fig. 2). Weeded seedlings, however, were not significantly taller than unweeded seedlings (Table 4; Fig. 2). Weeded treatments had a significantly higher proportion of high vigor seedlings (Table 3); however, the weeding treatment had less effect on height or survivorship than other treatment comparisons.

Microsite

Within healthy and dieback patches in the fenced and tree-tube treatments, microsite characteristics related to canopy cover showed the largest effect on oak regeneration. Beginning with higher mean acorn germination in open sites ($\bar{x}$ = 35%) compared to canopy edge ($\bar{x}$ = 21%; Table 4), open field seedlings had higher survivorship across all patch types and herbivory (fencing type) treatments (Table 4; Fig. 3). The survivorship pattern is consistent across all three herbivory treatments: tree-tube seedlings had significantly higher survivorship overall and double the survivorship out in the open (63%) compared to in the canopy edge (31%). Fenced seedling survivorship, while lower overall, was also nearly three times higher in the open (38%) than in the canopy edge (13%). Within the healthy patches, seedlings in control treatments that were grown in the open had 31% survival compared to canopy edge at 12%. Seedlings in open treatments only showed slightly higher growth than seedlings in edge treatments (Table 4; Fig. 3) While soil nutrients were higher under the canopy edge (Table 5), soil moisture was slightly lower (8.5%) compared to 11% for open sites (Table 4).

Table 3. Vigor and damage assessments by treatment comparisons. Data reflect mean percentages of surviving seedlings/replicate in 2007 rated as high or low vigor; as damaged by herbivores (deer and bison combined) or insects. Significant differences to the p<0.05 level are noted with a/b notation, as determined by post-hoc t-tests. Means represent values only from those treatments common to the factors evaluated in each set of rows (divided by lines).

Treatment (n)	% High vigor	% Low vigor	% with herbivore damage	% with insect damage
Healthy (8)	4.6	28.2	0.62	70.2
Dieback (10)	19.3	22.5	5.89	56.9
Eroded (10)	19.6	32.5	0.18	62.1
Fenced (16)	1.5 a	82.9	5.2	79.9
Control (16)	2.4 a	50.1	11.6	54.5
Tree-tubes (16)	11.3 b	27.8	1.4	75.0
Weeded (36)	15.9 a	47.0	4.2	73.9
Unweeded (36)	7.8 b	31.9	5.5	66.4
Open (36)	17.9 a	27.9	3.8	66.2
Canopy edge (36)	5.8 b	51.0	5.9	74.0

Table 4 . General Linear Model tests of effects for treatments common to healthy and dieback patches. Results for interaction terms are not presented unless significant.

Response variable	Year	Source of variation	df	SS	MS	F	p
Germination	2005	Competition	1	998.7	998.7	12.32	0.001
		Microsite	1	4128	4128	50.93	0.000
		Herbivory	1	26.2	26.2	0.32	0.572
		Patch Type	1	44.3	44.3	0.55	0.462
Survivorship	2005	Competition	1	1088	1088	4.07	0.048
		Microsite	1	7708	7708	28.84	0.000
		Herbivory	1	58.7	58.7	0.22	0.641
		Patch Type	1	636.7	636.7	2.38	0.127
	2006	Competition	1	3368.8	3368.8	9.53	0.003
		Microsite	1	16577	16577	46.87	0.000
		Herbivory	1	4958	4958	14.02	0.000
		Patch Type	1	844.1	844.1	2.39	0.127
	2007	Competition	1	1927.2	1927.2	6.58	0.013
		Microsite	1	17189	17189	58.67	0.000
		Herbivory	1	10332	10332	35.26	0.000
		Patch Type	1	243	243	0.83	0.365
Height	2005	Competition	1	0.119	0.119	0.26	0.615
		Microsite	1	0.003	0.003	0.01	0.932
		Herbivory	1	0.007	0.007	0.01	0.906
		Patch Type	1	8.403	8.403	18.10	0.000
	2006	Competition	1	1.242	1.242	1.12	0.294
		Microsite	1	4.865	4.865	4.38	0.040
		Herbivory	1	17.236	17.236	15.54	0.000
		Patch Type	1	37.834	37.834	34.10	0.000
	2007	Competition	1	18.742	18.742	2.73	0.103
		Microsite	1	19.229	19.229	2.80	0.099
		Herbivory	1	111.38	111.38	16.23	0.000
		Patch Type	1	187.89	187.89	27.38	0.000
%Low vigor	2007	Competition	1	3250	3250	1.05	0.310
		Microsite	1	10244	10244	3.29	0.074
		Herbivory	1	22067	22067	7.10	0.01
		Patch Type	1	16482	16482	5.3	0.025
%High vigor	2007	Competition	1	1298	1298	10.16	0.002
		Microsite	1	2750	2750	21.52	0.000
		Herbivory	1	2494	2494	19.52	0.000
		Patch Type	1	1973	1973	15.44	0.000
%Herbivore damage	2007	Competition	1	28.4	28.4	0.16	0.69

Table 4 (continued). General Linear Model tests of effects for treatments common to healthy and dieback patches. Results for interaction terms are not presented unless significant.

Response variable	Year	Source of variation	df	SS	MS	F	p
		Microsite	1	86.5	86.5	0.49	0.486
		Herbivory	1	468	468	2.66	0.108
%Insect damage	2007	Patch Type	1	185	185	1.05	0.309
		Competition	1	986	986	2.66	0.108
		Microsite	1	1072	1072	2.89	0.094
		Herbivory	1	23.4	23.4	0.06	0.803
%Soil moisture	2006	Patch Type	1	3707	3707	9.99	0.002
		Competition	1	5.164	5.164	0.73	0.395
		Microsite	1	1.054	1.054	0.15	0.700
Soil moisture	2005	Patch Type	1	108.25	108.2	15.36	0.000
		Competition	1	0.261	0.261	60.13	0.000
		Microsite	1	0.479	0.479	110.5	0.000

Healthy, Dieback, Eroded Patches

Soil nitrate and total organic matter were significantly higher in the dieback sites than in the healthy or eroded sites (Table 5). Clay content was lower in dieback sites than in healthy sites while sand content was significantly higher in the eroded and dieback sites than in the healthy sites (Table 5). Soil moisture was assessed gravimetrically in fall 2006 and was significantly higher in the dieback sites (7.3%) than in the healthy sites (4.7%; $p < 0.001$; Table 4).

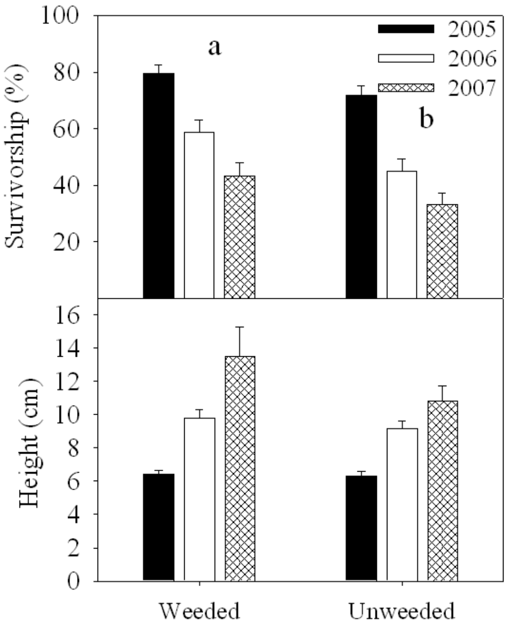

Figure 2. Mean survivorship and height for weeding (competition) treatments in healthy and dieback patches (n = 36). Differences in survivorship were significant for all years ($p < .05$), while height differences were not significant.

Results of the general linear model analyzing patch type and herbivory (fencing type) treatment are displayed in Table 6. There were no significant differences in acorn germination rates or total survivorship among the healthy, dieback and eroded patches (Table 6; Fig. 4). The combined dieback seedlings were significantly taller in all years ($p < 0.0001$, ANOVA, Table 6), and by 2007 were more than twice as tall (18 cm vs. 7 cm) as seedlings in healthy or eroded patches. Dieback ($\bar{x} = 19\%$) and eroded ($\bar{x} = 19\%$) sites were also assessed to have a greater percentage of high vigor seedlings compared to healthy ($\bar{x} = 4.6\%$) sites; however those differences were not significant (Tables 3, 6). Monitors also noted higher levels of insect damage in healthy sites ($\bar{x} = 70\%$) than in dieback ($\bar{x} = 56\%$) or eroded sites ($\bar{x} = 62\%$), however those differences were not statistically significant (Tables 3, 6). Survivorship of tree-tube seedlings was significantly higher than fenced seedlings only in 2007 and there were no interaction effects, although that effect was larger in dieback patches ($p = 0.007$, ANOVA). Similarly, tree-tube seedlings were

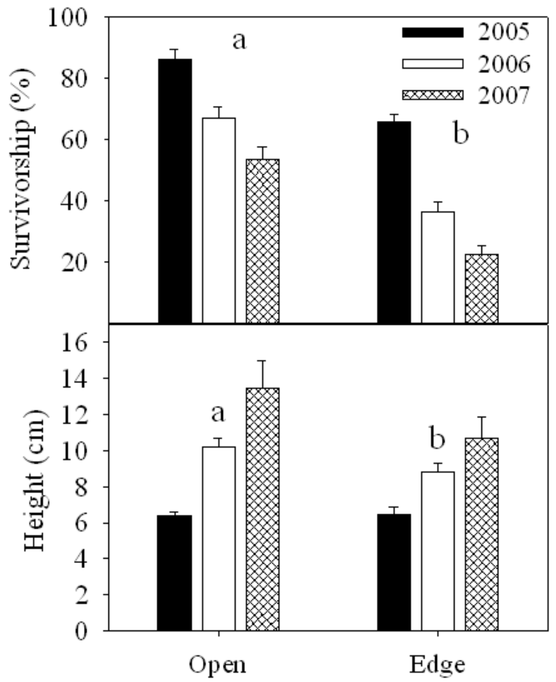

Figure 3. Mean survivorship and height of open grown and canopy edge seedlings from healthy and dieback patches (n = 36). Differences in total survivorship were significant all years (p < .001) and differences in height were only significant in 2006 (p < .05).

significantly taller than fenced seedlings in 2006 (p < 0.019) and 2007 (p < 0.012, ANOVA, Table 6).

DISCUSSION

Initially, herbivory, annual grass competition, and dieback were hypothesized to be the driving forces in the scrub oak ecosystem of Catalina Island. Our weeding and herbivory (fencing type) treatments were designed to evaluate the importance of these factors. Factors such as planting microsite (open field vs. canopy edge) and planting method (tree-tubes vs. fencing) were added to our research to supplement future restoration and management planning decisions. Results to date suggest that microclimate characteristics associated with open-grown and tree-tube protection have statistically and biologically more significant benefits to scrub oak seedling survivorship in their first three years than the fencing or the weeding treatment implemented in this study. Seedlings protected by tree-tubes had higher survivorship and growth in all relevant comparisons; and open-grown seedlings had at least twice the survivorship of canopy-edge seedlings in all relevant comparisons, even though height differences were insignificant.

Importance of Herbivory and Competition with Annual Grasses to Regeneration

Although numerous other studies have demonstrated significant enhancement of oak growth when seedlings were protected from deer browsing (Swiecki et al. 1997; Harvey 1989; Tyler et al. 2008), we found only minimal positive impacts of fencing out large herbivores. Indeed, herbivory by non-native deer and bison did not affect acorn germination or growth of small seedlings: we saw only a 6% increase in seedling survivorship between unfenced and fenced seedlings. Average seedling height among all seedlings, however, is just 5 cm, which means seedlings are still hidden within the annual grass canopy and less vulnerable to the impacts of

Table 5. Soil properties (nutrients and texture) compared between patch types (healthy, dieback, and eroded (for open field collected samples only)); and compared between open and edge sites across healthy and dieback plots. a/b notation used to signify significant differences; no letters indicate insignificant differences: p < 0.05.

	Organic %	P-P04 ug/g	N-NH4 ug/g	N-N03 ug/g	Clay %	Sand %	Silt %
Healthy (n=10)	1.27 a	4.19	2.26	1.67 a	18.14	40.6 a	41.2 a
Dieback (n=10)	2.02 b	3.16	2.05	14.3 b	7.6	50.6 ab	41.7 a
Eroded (n=10)	1.15 a	3.9	4.2	2.4 a	14.73	60.5 b	24.7 b
Open (n = 20)	1.65 a	3.67 a	2.16 a	7.99	12.9	45.7	41.5
Edge (n=20)	2.55 b	6.19 b	3.69 b	12.15	11.8	52.4	35.8

Table 6. General Linear Model tests of herbivory and patch type effects for open, unweeded treatment combinations in healthy, dieback, and eroded patches. Results for interaction terms are not presented unless significant.

Response variable	Year	Source of	df	SS	MS	F	p
Germination	2005	Herbivory	1	238.1	238.1	1.8	0.19
		Patch type	2	166.0	83.0	0.63	0.542
Survivorship	2005	Herbivory	1	65.8	65.8	0.17	0.688
		Patch type	2	707.8	353.9	0.89	0.426
	2006	Herbivory	1	1254	1254	2.11	0.161
		Patch type	2	802	401	0.67	0.520
	2007	Herbivory	1	4001	4001	8.91	0.007
		Patch type	2	501.6	250.8	0.56	0.580
Height	2005	Herbivory	1	0.117	0.117	0.67	0.421
		Patch type	2	5.86	2.93	16.92	0.000
	2006	Herbivory	1	4.51	4.51	6.44	0.019
		Patch type	2	25.59	12.79	18.29	0.000
	2007	Herbivory	1	18.64	18.64	7.67	0.012
		Patch type	2	71.10	35.55	14.62	0.000
%Low vigor	2007	Herbivory	1	2232	2232	5.76	0.026
		Patch type	2	573.2	286.6	0.74	0.490
%High vigor	2007	Herbivory	1	26.3	26.3	0.10	0.749
		Patch type	2	1240	620	2.47	0.106
%Herbivore damage	2007	Herbivory	1	72.2	72.2	1.04	0.318
		Patch type	2	191.5	95.7	1.38	0.272
%Insect damage	2007	Herbivory	1	1915	1915	3.15	0.090
		Patch type	2	794	397	0.65	0.530

browsing by large herbivores. Deer and/or bison browsing may play an important role as seedlings enter the sapling stage and are more visible to these herbivores. Indeed Tyler et al. (2008) showed that deer browsing of coast live oak seedlings in Santa Barbara County, California, increased in importance as seedlings aged.

Weeding treatments did not confer significant benefits to growth; however, weeded sites had higher acorn germination rates and consistently higher survivorship than unweeded sites. These results are more or less consistent with previous studies that have demonstrated competitive effects of annual grasses on seedling survivorship or growth in California oaks (Gordon and Rice 1993; Danielsen and Halvorson 1991). Although statistically significant, these differences were not as large as those between open and edge or tree-tube and unfenced treatment comparisons. Just 30% more weeded seedlings (43% versus 33%) were alive in 2007 than unweeded seedlings, while 100% to 200% more open-grown seedlings survived than their canopy-edge counterparts. The only significant differences in acorn germination results were associated with increased light levels: weeded treatments and open grown treatments which both had significantly higher acorn germination rates. These results suggest that annual grass effects may begin with reduced germination and continue with reduced survivorship. The effects of the weeding treatment on growth might have been stronger if there had been more frequent weeding through the spring.

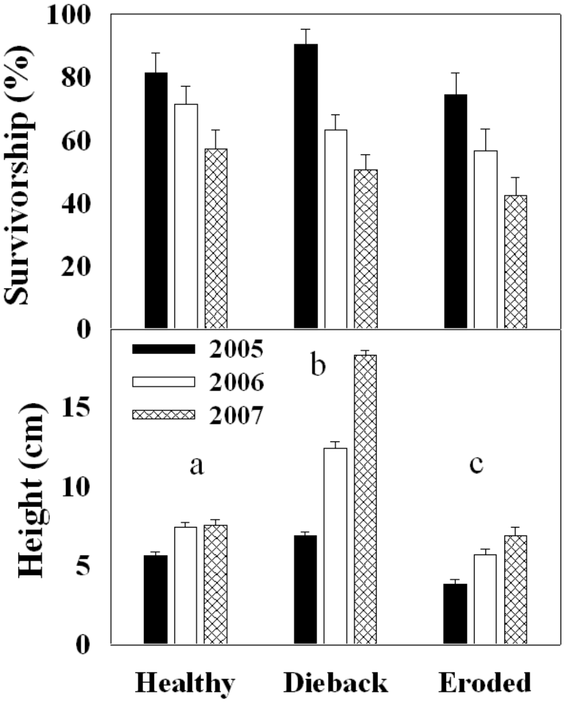

Figure 4. Mean survivorship and height by patch type for open grown, herbivore-protected (fenced or tree-tube) seedlings from unweeded treatments in healthy (*n* = 8 (1 block burned)), dieback (*n* = 10) and eroded (*n* = 10) patches. Differences in survivorship were not significiant. Differences in height were significant in all years ($p < 0.0001$).

Role of Microclimate and Patch Type

Survivorship of seedlings planted in the open was 120% higher (48% vs. 20%) than seedlings planted in edge locations (Fig. 3). This high survivorship was not due to nutrients because soil nutrients were higher in canopy-edge locations (likely due to increased woody debris) compared to open microsites. If light and water were limiting factors for canopy-edge seedlings, one might expect these seedlings to be shorter and possibly have lower vigor than their open-grown counterparts; however those differences were not apparent. An alternative explanation for significantly lower survivorship but equal heights between canopy-edge and open locations is that canopy-edge seedlings have disproportionately higher soil pathogen loads under conspecific canopies or by oak-specific insect herbivores; as found by Augspurger (1983) and Wada et al. (2000). We investigated this hypothesis by carefully unearthing dead seedlings from open and canopy-edge locations in both healthy and dieback patches in October 2007; the seedlings along with soil samples were sent to the soil pathogen laboratory at the University of California–Davis to test for colonization by soil pathogens or presence of soil-borne spores. Although slightly more identifiable soil pathogens (*Pythium* and *Mortierella*) were associated with dieback and canopy-edge seedlings, the results were inconclusive and unknown fungal hyphae were associated with all seedlings. Interestingly, no spores were found in any of the soil samples after baiting and incubation. Further tests of soil pathogen loads on seedlings should be pursued when the soils have been naturally wetted and fungi are active.

Interestingly, the patch type (dieback, healthy, eroded) did not significantly affect initial germination or survivorship although the seedlings growing in the dieback sites were significantly taller, particularly when grown in tree-tubes. These results demonstrate that factors other than soil pathogens or site-specific soil characteristics are causing the dieback phenomenon observed on Catalina Island. The results also indicate that restoration can occur in all patch types to re-establish oak trees in areas that are currently bare. Furthermore, these results suggest that dispersal of acorns to suitable germination sites out in the open may be a key limiting factor and an important, low-cost restoration strategy.

Why is Dieback Occurring?

The lack of difference in survivorship between the patch types (healthy, dieback, eroded) and lack of conclusive evidence about pathogens suggest the dieback phenomenon is more likely a result of senescence of old existing oak clones which have been unable to establish new basal sprouts due to browsing. The oaks may be more prone to death in areas where goats preferentially browsed on basal shoots over their 174-year tenure on the island (1827–2000). This repeated clipping of basal sprouts may have effectively drained the carbon stores in the underground storage rhizome (Langley et al. 2002; Canadell and Lopez-Soria 1998). According to growth ring counts from cores and cross sections, the maximum life span of an individual scrub oak stem is 100 to 115 years (de Gouvenain and Ansary, in press); however, as a multi-trunked organism, each scrub oak tree (or clone) may live longer as new basal branches replace senescing ones to form a "continuously regenerating canopy in the absence of herbivory" (Keeley 1992). The dieback patches are first detectable in early historical photos from the 1950s on the west end of the island and may reflect historical patterns of feral ungulate, primarily goat, activity. If the remaining trees can be protected from current deer browsing pressures, they may still have sufficient energy stores to regenerate new basal sprouts that could create vigorous canopies much faster than could new germinants.

A Strategy for Oak Restoration

Tree-tubes are known to increase apical stem growth and provide more consistent and longer growing conditions (Ponder 1994). Significantly more tree-tube seedlings were classified as having high vigor (11%) relative to fenced (2%) and unfenced (1%) seedlings. This effect is stronger where organic, nutrient-rich soils exist. All seedlings growing in the nutrient-rich soils of dieback patches were taller than those in healthy or eroded patches; however that benefit was most strongly seen in tree-tube seedlings. Tree-tubes could help seedlings grow out of the browse line and produce acorns sooner by stimulating apical growth, particularly in loamy, nutrient-rich soils. Given the high survivorship provided by the microclimate within tree-tubes and the overall suitability of all patch types and open areas, it would seem that the highest rate of return for planting effort would be to establish large patches of oaks from acorns planted in tree-tubes in open areas.

Although survival of 22% of the unfenced, unweeded control seedlings suggests that dispersal to suitable germination sites may be more limiting than herbivory; these seedlings are still shorter than surrounding annual grasses, and one cannot predict what percentage will make it to sapling or reproductive age (Manuwal and Sweitzer 2006). Although planting acorns without weed or browsing protection across the landscape (e.g., acting as a good disperser) might be significantly cheaper, investing in tree-tubes could produce a threefold increase in survivorship (63% vs. 22%). Also, the long-term prognosis for unprotected seedlings cannot be determined from three years of data. Clearly, however, fencing alone does not confer the kind of benefits offered by tree-tubes. Where a stand of oaks is desired quickly, tree-tubes may play an important role in helping seedlings grow above browse height.

If senescence caused by herbivore pressure on basal sprouting of adult plants is the cause of the dieback phenomenon, which recent examinations of historical photos suggest has been ongoing since the first aerial photographs in 1943, then the complete lack of saplings or regenerating basal sprouts is an alarm call for protection of this threatened scrub oak ecosystem. It portends an island-wide decline in mature oaks with depleted energy stores for regeneration and indicates an immediate need for animal removal or construction of exclosures around existing oaks to allow for basal regeneration of canopy stems before stand-level senescence becomes a broader, island-wide phenomenon.

The apparent lack of dispersal agents and the role that annual grasses may play in limiting availability of suitable germination sites for acorns that roll downslope or otherwise naturally disperse suggest that we cannot just wait for these disappearing stands to regenerate on their own. Human "dispersal" to canopy openings in good rain years and the use of tree-tubes may together expand this woodland to its original extent.

Future Research

Further research suggested by this study includes following this trial as the seedlings grow beyond the protection of the grass canopy to fully evaluate the effect of bison and deer on the growth of seedlings to saplings. This will have implications on the likelihood of stand expansion under current browsing pressures. A study correlating the relationship between the diameter of stems and their ability to bring photosynthate back to the underground storage tubers, as well as a study relating the diversity and size of the stems of trees and available energy and nutrient stores in underground storage tubers, would help us validate the hypothesis that the dieback phenomenon is a result of years of browsing pressure. A field study examining the range of sizes of stems in trees on the landscape will help assess the potential for ecosystem collapse under the current browsing regime.

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