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Herbivory and seedling establishment in post-fire southern California chaparral

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Summary. A caging experiment was conducted to determine the effects of herbivorous insects and small mammals on first-year establishment of *Ceanothus greggii* (ceanothus) and *Adenostoma fasciculatum* (chamise) seedlings in post-fire chaparral. Insect herbivory had no effect on either species. Observations of tagged seedlings revealed that nearly all herbivory was due to small mammals, and was preferentially greater for ceanothus. When seedlings were protected from herbivory chamise experienced higher mortality. Small-mammal herbivore pressure on ceanothus seedlings tipped the survivorship balance for unprotected seedlings in favor of chamise, allowing a relatively higher establishment of chamise seedlings during the first growing season after chaparral fire.

Introduction

Chaparral species are adapted to the water stress, nutrient deficiencies and frequent wildfires characteristic of Mediterranean-type ecosystems (Hellmers et al. 1955; Hanes 1977). The mature chaparral environment is thought to be particularly hostile to seedling establishment. Seedlings developing under a mature canopy must overcome shading, phytotoxins, the presence of nonwetting agents in the soil and intense herbivore pressure (Osborn et al. 1967; Christensen and Muller 1975b).

Fires have been postulated to facilitate seedling establishment in chaparral by: volatilizing allelochemics present in soil under mature chaparral; releasing nutrients bound in standing biomass; opening the canopy to allow light penetration; stimulating germination by seed scarification; and reducing the numbers of herbivores (McPherson and Muller 1969; Christensen and Muller 1975a, b; DeBano and Conrad 1978). Nevertheless, the post-fire environment is stressful for seedling growth. Several workers have documented high seedling losses in the first year or two after fire (Horton and Kraebel 1955; Gibbens and Schultz 1966; Hanes 1971) and attributed these losses to competition and drought stress (Schultz et al. 1955; Biswell and Gilman 1961; Gibbens and Schultz 1966; Hanes 1977).

The role of herbivory in seedling establishment is uncertain. Firstly, the literature contains conflicting accounts of the response of mammalian herbivores to chaparral fires. Biswell (1961) found that deer populations in chamise chaparral increased by a factor of four in the first year after fire and that jackrabbit populations increased by a factor of five to ten. Christensen and Muller (1975a) found a reduction in the numbers of small herbivorous mammals after fire. Secondly, of the several studies that have assessed the effect of herbivorous mammals on post-fire seedling success, most have de-emphasized the importance of herbivory (Biswell and Gilman 1961; Gibbens and Schultz 1966; Christensen and Muller 1975a).

Insects are capable of influencing species composition in Mediterranean-type vegetation (Fuentes et al. 1981; Louda 1982). In the Chilean matorral, insect herbivory decreases the competitive ability of some plant species and effectively excludes them from the matorral community (Fuentes et al. 1981). Almost no quantitative data on the effects of insect herbivores are available for the California chaparral (Force 1981 and 1982).

Thus, herbivorous mammals and insects have the potential to impact post-fire seedling establishment in chaparral. This study was designed to test the hypothesis that herbivory by small mammals and insects is an important factor for the first-year establishment of seedlings in chaparral dominated by *Ceanothus greggii* Gray (ceanothus) and *Adenostoma fasciculatum* H. and A. (chamise).

Materials and methods

Study area

All observations and experiments took place at San Diego State University's Sky Oaks Research Station, 16 km east of Oak Grove, in northern San Diego County. A prescribed burn was carried out on a 2.5-hectare plot in the Comb's Camp area of the station on 9 December 1981. The burned area is in 65-year-old undisturbed chamise chaparral, punctuated with clumps of *Adenostoma sparsifolium* Torr., and occasional individuals of *Ceanothus greggii* and *Quercus dumosa* Nutt. The site is at approximately 1600 m elevation on a west-facing slope of 0–20 degrees. By March, large numbers of chamise and ceanothus seedlings had appeared. Mean seedling densities on 6 March were similar for the two species (approximately 43 m^{-2}).

Caging experiment

On 1 May 1982, cage-type exclosures were set up to protect groups of seedlings from herbivores. Seven treatments were established:

Treatment	Replicates	
C	11	Full cage. Mammals excluded
C+I	21	Full cage, insecticide. Mammals excluded and insects reduced
C+W	10	Full cage, watered. Mammals excluded and water equal to that used in applying insecticide added
$^1/_2$C	11	Half cage. Herbivory permitted but cage effect simulated
$^1/_2$C+W	11	Half cage, watered. Herbivory permitted, cage effect simulated, water equal to that used in applying insecticide added
Co	21	Untreated control
Co+W	21	Control, watered. Water equal to that used in applying insecticide added

Treatments C, C+I, and C+W were covered with 40 x 40 x 32-cm-high cages of 1-cm mesh hardware cloth. In treatments $^1/_2$C and $^1/_2$C+W, "half cages" (open on two sides) allowed small-mammal herbivory while simulating "cage effect". Insecticide (Ortho Isotox, Chevron Chemical Company) was sprayed for treatment C+I using the recommended concentration of 30 ml l^{-1} water. Spraying at biweekly intervals was effective in eliminating most evidence of insect herbivory on treated seedlings. Treatments C+W, $^1/_2$C+W and Co+W were sprayed biweekly with an equal volume of water as a control for effects of adding water with the insecticide. Both insecticide and water were sprayed at a rate of 20 ml m^{-2}.

At monthly intervals, seedlings in all plots were counted and examined for evidence of insect or mammal herbivory.

Tagged seedling observations

To provide direct data concerning the fate of individual seedlings, 60 seedlings of each species were tagged on 16 April 1982. Adjacent pairs of seedlings (one of each species) were located and a small plastic nursery tag was placed into the ground about three cm from each. Fifteen pairs of seedlings were tagged along each of four transects. Height, health (recorded as "green", "browning", or "dead") and evidence of herbivory were monitored at monthly intervals. Herbivory was noted by describing damage and extent (e.g., "2 leaves 25% eaten" or "stem bitten off at 25 mm"). Because of high mortality in this first group of seedlings, an additional 80 seedlings were tagged on 20 August 1982 (ten of each species in each transect).

Statistical analysis

Results of the caging experiment (survival data collected on 11 December 1982) were tested for differences in means among treatments and among species. Since the raw data are proportions, arcsin transformation usually improved both normality and equality of variances. For these cases analysis of variance was performed after transformation. When neither transformed nor untransformed data met the assumptions for ANOVA, the Mann-Whitney U-test was used.

Results

Caging experiment

About one-half of the caged ceanothus seedlings survived the first growing season (mean survival = 53%; standard error = 4%; $n = 37$ cages) compared to only 9% of the half-caged and uncaged control seedlings (standard error = 2%; $n = 59$). A similar but less pronounced difference existed for chamise seedlings: 34% (standard error = 6%; $n = 28$) of caged seedlings survived vs 15% (standard error = 3%; $n = 46$) of half-caged and control seedlings. The increase in seedling mortality due to exposing ceanothus to herbivory was 44%, while the increase for chamise seedlings was only 19%.

The effect of added water was tested by three 1-way ANOVA's for each species (Table 1). Results were not significant (all P's > 0.25). The one-way ANOVA's for an effect of insect herbivory were also not significant for either species ($P \geqslant 0.25$, Table 1). The tests for "cage effect" showed that alteration of the microenvironment by the half-cage treatments did not significantly affect seedling survival ($P > 0.20$, Table 1). The lack of significance of these analyses made it possible to increase the power of tests for small-mammal effect by pooling the data from treatments C, C+W, and C+I as well as those from treatments Co, Co+W, $^1/_2$C, and $^1/_2$C+W. Tests for small-mammal effect on the pooled data were highly significant for ceanothus ($P \leqslant 0.001$) and chamise ($P < 0.01$, Table 1). The assumption of "no cage effect" may be questioned despite nonsignificant results. Therefore the test for significance of small-mammal herbivory was repeated omitting the Co and Co+W data (Table 1: A.4.b. and B.4.b.). The results remained highly significant for ceanothus ($P \leqslant 0.01$) but were not significant for chamise ($0.1 < P < 0.25$).

Protected ceanothus seedlings survived in greater proportions than chamise (53% vs 34%). When seedlings remained unprotected, however, chamise seedlings survived in greater proportions (15% vs 9%). Both differences were significant ($P < 0.05$) when tested by ANOVA on arcsin-transformed data.

Tagged seedling observations

Observations on tagged seedlings were made during two periods: spring/summer 1982 and fall 1982 (Table 2). Ceanothus seedlings sustained much higher mortality due to mammal herbivory during both periods, while greater numbers of chamise seedlings died from other causes. Mortality from mammal herbivory was much higher during the fall than in spring and summer. Ceanothus survival exceeded that of chamise during spring and summer, but was substantially less during fall.

All damaged seedlings showed a sharp, clean, angled slice through the stem. This browse effect is characteristic of rodents and lagomorphs. The stripping and tearing which is characteristic of deer browsing was not seen on any of the seedlings.

The mammalian herbivores

Tracks, fecal pellets, and sightings indicated that many brush rabbits (*Sylvilagus bachmani*) fed at the burn site. This became evident in late June 1982 and continued through December. Similar evidence indicated that one or

Table 1. Among-treatment comparisons for caging experiment. Columns are: comparison being made and test used; test statistic; degrees of freedom (*df*); result; and probability of type-I error. See Methods for descriptions of treatment categories. NS = not significant; SIG = significant

Test	Statistic	*df*	Result	Prob
A. Ceanothus				
1. Water effect: All 1-way ANOVA's; data transformed (arcsin)				
a) (C) vs (C + W)	F = 0.90	1.17	NS	$P > 0.25$
b) (${}^1/_2$C) vs (${}^1/_2$C + W)	F = 0.62	1.19	NS	$P > 0.25$
c) (Co) vs (Co + W)	F = 1.35	1.36	NS	$P > 0.25$
2. Cage effect: (Co) + (Co + W) vs (${}^1/_2$C) + (${}^1/_2$C + W) Mann-Whitney test	U = 392.5	$n_1 = 21$ $n_2 = 38$	NS	$P > 0.20$
3. Effect of insect herbivory: (C + I) vs (C) + (C + W) 1-way ANOVA	F = 0.029	1.35	NS	$P \gg 0.25$
4. Effect of small-mammal herbivores:				
a) (C) + (C + W) + (C + I) vs (${}^1/_2$C) + (${}^1/_2$C + W) + (Co) + (Co + W) Mann-Whitney test	U = 191.5	$n_1 = 37$ $n_2 = 59$	SIG	$P \ll 0.001$
b) (C) + (C + W) + (C + I) vs (${}^1/_2$C) + (${}^1/_2$C + W) 1-way ANOVA; data transformed (arcsin)	F = 38.30	1.56	SIG	$P \ll 0.001$
B. Chamise				
1. Water effect: All 1-way ANOVA's; data transformed (arcsin)				
a) (C) vs (C + W)	F = 0.45	1.10	NS	$P > 0.25$
b) (${}^1/_2$C) vs (${}^1/_2$C + W)	F = 0.03	1.13	NS	$P \gg 0.25$
c) (Co) vs (Co + W)	F = 0.08	1.29	NS	$P \gg 0.25$
2. Cage effect: (Co) + (Co + W) vs (${}^1/_2$C) + (${}^1/_2$C + W) 1-way ANOVA; data transformed (arcsin)	F = 0.698	1.44	NS	$P \gg 0.25$
3. Effect of insect herbivores: (C + I) vs (C) + (C + W) 1-way ANOVA	F = 0.008	1.26	NS	$P \gg 0.25$
4. Effect of small-mammal herbivores:				
a) (C) + (C + W) + (C + I) vs (${}^1/_2$C) + (${}^1/_2$C + W) + (Co) + (Co + W) Mann-Whitney test	U = 406	$n_1 = 28$ $n_2 = 46$	SIG	$P < 0.01$
b) (C) + (C + W) + (C + I) vs (${}^1/_2$C) + (${}^1/_2$C + W) 1-way ANOVA; data transformed (arcsin)	F = 2.80	1.41	NS	$0.25 > P > 0.1$

Table 2a, b. Survival of tagged seedlings in percent. **a** In late spring and summer (16 April–20 August), based on 60 seedlings of each species. **b** In fall (21 August–28 November), based on 56 chamise and 60 ceanothus seedlings

Period	Species	Killed by herbivores	Other deaths	Total mortality	Survival
a) Spring/Summer	Chamise	10	62	72	28
	Ceanothus	20	43	63	37
b) Fall	Chamise	25	02	27	73
	Ceanothus	43	00	43	57

a few mule deer (*Odocoileus hemionus*) were present during a brief period in June and July. Their browsing was restricted to *Quercus dumosa* stump sprouts. Surface heaps formed by pocket gophers (*Thomomys bottae*) were first noticed in early May. This burrowing activity was evident for a few months, but no fresh activity was noticed after August. Thus, seedling damage coincided most closely with visible rabbit activity.

Discussion

Results of the caging experiment, alone, strongly support the hypothesis that small-mammal herbivory influences the first-year establishment of ceanothus seedlings. The hypothesis of significant impact by insect herbivores is falsified for both ceanothus and chamise seedlings.

Caging experiment results which are most germane to the overall conclusions are as follows. The effect of small-mammal herbivores on chamise seedling mortality was considerably less than on ceanothus seedlings. In addition, protected chamise seedlings suffered significantly higher mortality than protected ceanothus seedlings. The combination of these results indicates that: (1) small-mammal herbivores prefer ceanothus to chamise seedlings; (2) herbivory is relatively less important in the survival of chamise seedlings, while death from other causes is relatively more important; (3) chamise seedlings predominate under conditions of heavy herbivory because of the preference of herbivores for ceanothus. However, exclusion of herbivores allows ceanothus seedling establishment to predominate.

One weakness of the caging experiment is the assumption that all of the difference in survival between protected and unprotected seedlings is due to small-mammal herbivory. The tagged seedling observations do not have this weakness and thus provide a test of the conclusions drawn from the caging experiment. Over the period of observation, nearly twice as many ceanothus seedlings as chamise seedlings were killed by small-mammal herbivores and a much greater number of chamise seedlings died from other causes (Table 2). Thus, the conclusions that small-mammal herbivores prefer ceanothus and that herbivory is a relatively less important factor for the survival of chamise are supported by a second independent field observation.

The third conclusion (that chamise predominates under conditions of heavy herbivory and ceanothus predominates when herbivores are excluded) is also supported by the tagged seedling data. If this conclusion is correct, one would expect the ratio of ceanothus survival to chamise survival to be greater than 1.0 during periods of low herbivore pressure, and less than 1.0 during periods of relatively high herbivore pressure. This was observed at the Sky Oaks study site. During a period of high physical stress (initial establishment and summer drought stress) and low herbivore pressure the ceanothus to chamise survival ratio was 1.68 (Table 2A). During a period of relatively low physical stress (seedlings are well established; drought has ended) but relatively high herbivore pressure, the ceanothus to chamise survival ratio was 0.78 (Table 2B).

First-year seedling establishment does not guarantee survival into the mature chaparral stand. Assuming an initial seedling density of 43 m^{-2} and an estimate of 0.5 plants m^{-2} in mature chaparral, nearly 99% mortality must occur if all plants in the mature stand develop from seedlings. However, the re-establishing stump sprouts of chamise (nearly 100% survival) will usurp much of the space that would otherwise be available for seedlings.

The point of this research is not the demonstration of a detrimental effect of herbivores on chaparral seedlings (they may very well be harvesting the excess already doomed) but the demonstration of a relatively greater effect of herbivores on one species. This herbivore preference has the potential to affect species composition at any stage of chaparral recovery. Moreover, the preferred species (ceanothus) is an obligate seeder, dependent upon seedling survival for re-establishment. Chamise is a strong stump sprouter and can maintain its numbers even with 100% seedling mortality.

In conclusion, a comparison of the effects of herbivore pressure on the first-year survival of two species of seedlings in post-fire chaparral has shown:

1. Insects have very little, if any, effect on survival.
2. In the absence of herbivory, chamise sustains higher mortality.
3. Ceanothus is preferred by small-mammal herbivores and consequently sustains higher herbivore-induced mortality.
4. This herbivore pressure on ceanothus seedlings is enough to tip the survivorship balance in favor of chamise, allowing a relatively higher establishment of chamise seedlings during the first growing season in post-fire chaparral.

Establishment and first year survival in an inimical environment are crucial hurdles in the development of chaparral plants. The importance of herbivory during this first year has been demonstrated. It remains to be shown (1) why chamise seedlings are less palatable to small-mammal herbivores than ceanothus, (2) if this advantage of chamise seedlings is true in other chaparral areas, (3) if this advantage is increased or carried through to later years as a factor responsible for the relatively low ratio of ceanothus to chamise individuals in mature chaparral, and (4) if small-mammal herbivory is an equally important factor in the post-fire establishment of other species from seedlings and in the re-establishment of crown-sprouting species.

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