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Herbivory and an endagered plant, can a limited population handle the pressure?

Sandra Baron
San Jose State University

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HERBIVORY AND AN ENDANGERED PLANT,

CAN A LIMITED POPULATION HANDLE THE PRESSURE?

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APPROVED FOR THE DEPARTMENT OF BIOLOGY

Dr. Rodney G. Myatt

Dr. Shannon Bros

Dr. Rachel E. O'Malley

APPROVED FOR THE UNIVERSITY

ABSTRACT

An insect exclusion study to assess the effects of herbivory on a federally listed endangered annual spineflower: *Chorizanthe robusta* var. *robusta* (Polygonaceae) was conducted in a stable rear dune habitat at Sunset State Beach, CA. A microlepidopteran larva in the genus *Aroga* (Gelechiidae) was the primary insect herbivore. Excluding insects during the growing season resulted in an increase in seed output of 58% ($P = 0.008$). This increase was due to the larger size of pesticide treated plants ($P = 0.003$), since seed/flower ratios did not differ. Insect exclusion did not affect survivorship.

The relationship between patch size and herbivore attack was also examined. Rabbits removed seed heads from 11% of the study plants, and plants growing in small protected patches were more likely to be grazed by rabbits ($P < 0.001$), while plants in large patches were more likely to be infested with larvae ($P = 0.003$).

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INTRODUCTION

Numerous studies have shown that insect herbivores reduce survivorship, growth, and reproductive output of plants (Rausher & Feeny 1980; Louda 1982, 1984; Crawley 1983, 1989). In many cases plant fecundity is more dramatically affected by herbivory than is survivorship, and an increase in seed number is often found when herbivores are excluded (Crawley 1983; Kinsman & Platt 1984; Brown et al 1987; Root 1996; Wise and Sacchi 1996; Mauricio 1998; Maron 2001), even when herbivory is at very low levels (Root 1996; Parmesan 2000). Some studies have shown that a reduction in seed is likely to lead to a reduction in plant abundance (Louda 1982; Wise and Sacchi 1996; Maron 2001) (but see Crawley and Gillman 1989).

The question of how herbivores affect plant populations is still widely debated (Crawley 1983, 1989; Carson & Root 2000). Although there is a scarcity of research on wild plant populations, the primary reason that the relationship between herbivory and plant abundance remains unresolved is the difficulty of separating the multitude of confounding factors which operate in the wild. For example, herbivory can have less influence on populations in highly competitive environments where density-dependent seedling mortality negates the effect of a reduction in seed (Crawley and Gillman 1989; Parmesan 2000), as well as more effect early in succession where competition is less (Brown et al 1987). Resource availability and physical constraints on a plant can limit its ability to recover from herbivore damage (Louda et al 1990), but compensatory growth is not always possible, even when resources are plentiful (Wise & Sacchi 1996). Abiotic conditions can ultimately have the greatest influence on plant abundance even where herbivores reduce seed production dramatically (Crawley & Gillman 1989). Habitat patchiness is another attribute of natural systems which can increase or decrease the incidence of herbivory (Bach 1988), as can variations in the chemistry of the host plant population (Zangerl & Berenbaum 1993). In addition, results from insect exclusion studies can vary greatly by site or by year (Bevill et al 1999; Palmisano 1997). These factors make it extremely difficult to unravel the complex relationships between herbivores, plants, climate, and available resources in natural communities (Crawley 1989; Root 1996).

Endangered plants characteristically have populations that are limited in size and extent. Any factor which reduces survivorship or reproductive output can contribute to the possibility of extinction. Consequently, when working to protect and enhance endangered plant populations, an important first step is to try to identify factors which lead to population decreases (Pavlik et al 1993). A reduction in seed number due to herbivory is a factor which could have a great effect on a limited population. In addition, demographic information is needed to evaluate these populations and assist in the development of recovery plans, and this type of information is often more useful than genetic information (Schemske et al 1994). Because destructive manipulations of habitat parameters such as patch size is not an option when studying endangered plant populations, measurements taken in the wild, such as the correlation between patch size and herbivory, can be informative.

This study addresses two questions: 1) Do insect herbivores contribute to population decline in the endangered plant species: *Chorizanthe robusta* var. *robusta* by reducing survivorship and/or seed output? 2) Does habitat patchiness influence the likelihood or type of herbivory on an individual plant? Excluding herbivores from a subset of plants and comparing plant performance is the best way to assess the effects of herbivory in wild plant populations (Crawley 1989). In a preliminary study on this plant species, 60 plants were monitored and only 50% survived (personal observation). The primary herbivore was a small moth larva (Lepidoptera: Gelechiidae, J. Powell pers. comm.). Therefore, in the current study I focused on whether excluding insect herbivores resulted in an increase in plant survivorship, plant size, flower number, and seed number. Since insect herbivory can decrease seed output directly or indirectly by decreasing pollination rates (Mothershead & Marquis 2000), seed/flower ratios were analyzed. In addition, differences in plant density were examined for possible correlations with plant size and reproductive output.

The effect of habitat patchiness on herbivore distribution was investigated in two ways. First, by conducting a survey for infested *C. robusta* plants in an untreated area adjacent to the study site to better estimate a landscape level distribution of larval infestation; and secondly, by correlating patch size with herbivore attack within the experimental blocks. Although mammals were not excluded in this study, any plant that was grazed by rabbits was noted and the entire block was removed from the experimental analysis. However, these unanticipated disturbances were examined to reveal correlations with habitat parameters.

METHODS

Plant Species

Chorizanthe robusta var. *robusta* (C. Parry) (polygonaceae) is an annual spineflower which inhabits sandy soil sites in Santa Cruz County. Plants are low-growing and extremely variable in size, forming a single upright stem or multiple branching stems. *C. robusta* germinates in the winter and flowers from April through June (USFWS 2000). Each plant produces a number of small flowers which mature at different times during the flowering period, and each flower can produce one seed. This plant is federally listed as endangered and is known from only seven populations, some of which are very limited in size (USFWS 2000). There are some taxonomic uncertainties about *C. robusta* at Sunset Beach due to the proximity of a closely related species, *Chorizanthe pungens* Benth. (Ertter 1996). *Chorizanthe pungens* is thought to grow primarily on the fore dunes and *Chorizanthe robusta* primarily on the rear dunes, however no published studies have quantified the genetic structure of the species complex. The plants chosen for this study were on the rear dunes and morphologically similar to *C. robusta* plants at other sites.

Insect Herbivore

Although this study examines the effects of excluding all insects, the primary insect which I have observed feeding on *C. robusta* (at Sunset Beach and at one inland site) is a small moth larva, 3 - 10 mm long, with a brown body and large black head. These were identified from a reared moth as an undescribed species in the genus *Aroga* (Gelechiidae) (J. Powell personal communication). More work is needed to determine if this species is a specialist on *Chorizanthe* and endemic to the Monterey Bay Area. Gelechiidae is a large family, the species of which cannot be identified by the larval stage. Gelechiids are most often larval host plant specialists which specialize on a wide range of plant species. They are primarily univoltine (having one generation per year), generally have five or six instars, and development takes approximately six weeks (J. Powell personal communication). Microlepidoptera such as these are not well studied, and 50% to 90% of species with small adults collected in California remain undescribed (Powell 1999). Larvae observed in this study created shelters made of silken fibers with bits of sand and litter attached. These shelters were attached to the base of the *C. robusta* plant, and larvae stayed inside them when not feeding on the leaves. Pupation occurred in shelters on the soil surface, or buried in the sand, and moths emerged in July.

Study Site

Sunset State Beach was selected as the location for this study because the largest known population of *C. robusta* (many thousands of plants) occurs over a wide area on the rear dunes. Sunset State Beach is located in central California just west of the town of Watsonville (36° 52.89 N, 121° 49.69 W) (Figure 1). The study site was within a 300 square meter area on the top of a rear dune, with exposure to the north, south, east, and west. These rear dunes are stable and vegetated with coastal scrub species such as *Ericameria ericoides* (Less.) Jepson . The habitat is varied; small to large openings between shrubs contain open sand, moss, grasses, bracken fern, and forbs. Much of the study site is colonized by *Syntrichia princeps* (De Not.) Mitt [*Tortula princeps*], a low growing moss which forms mats in which *C. robusta* and other forbs grow. Almost all of this moss turned brown between March 6 and March 8, 2001, even though there was rain on March 6.

The central coast of California has a moderate Mediterranean climate. During the study period (October - April 2000/2001), average monthly temperatures ranged from 48 to 59 ° F. Average monthly rainfall of approximately 2.4 inches was less than normal for this period (by an average of 0.5 inch/month). The last measurable rainfall for the season was on or about April 18 (U.S. Dept. of Commerce 2002).

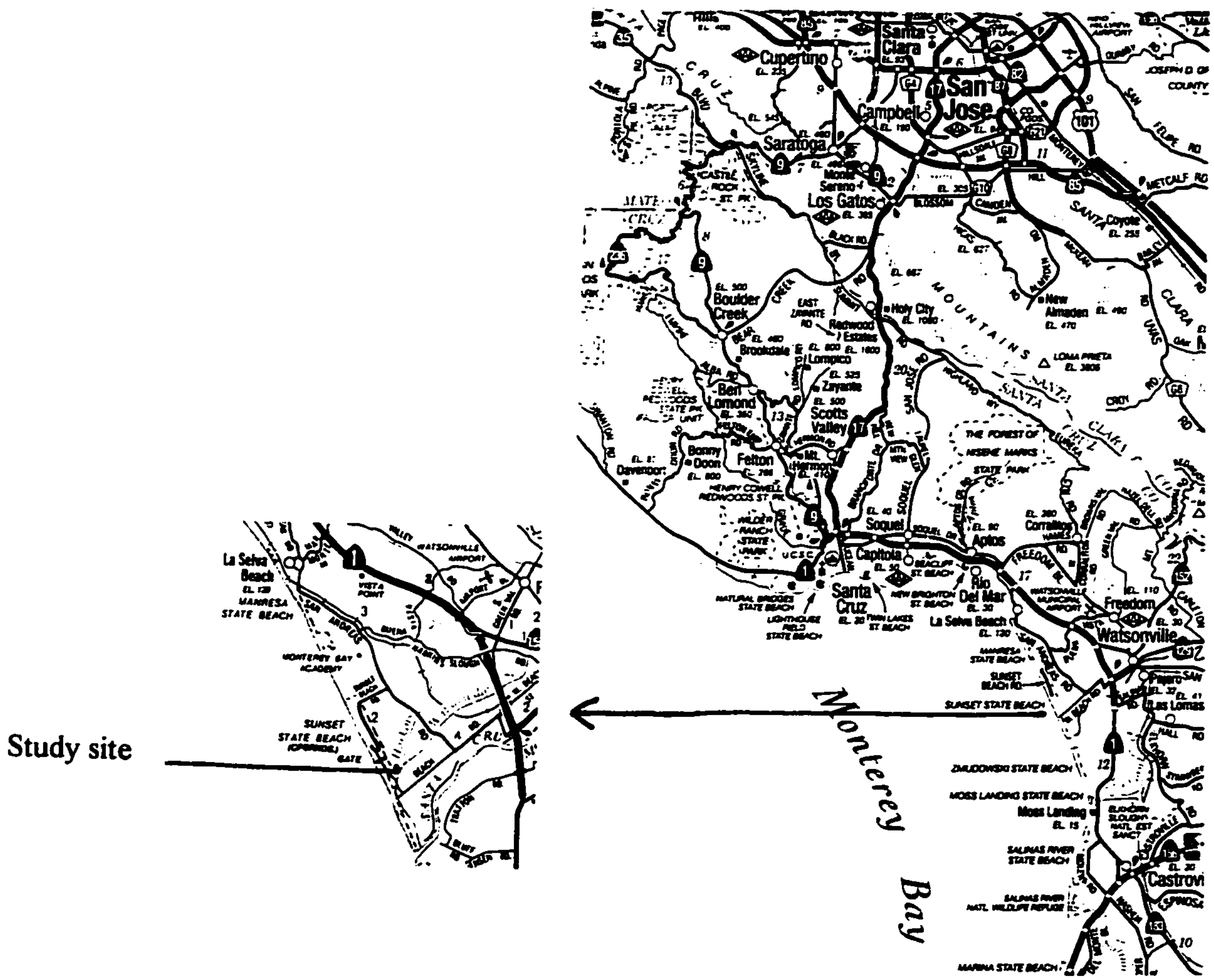

Figure 1. Monterey Bay area with an enlargement of Sunset Beach showing the location of the study site.

Experimental Design

The experimental design for this study had two parts: 1) an insect exclusion experiment was conducted in a randomized block design 2) demographic and habitat parameters were measured.

An insect exclusion experiment was used to determine the effect of herbivory on plant survivorship, size, and reproductive output. Three treatments were performed: 1) plants sprayed with an insecticide (exclusion of insect herbivores) 2) plants sprayed with water (control for spray effects) and 3) plants left untreated (control). A selective application of insecticide would provide an adequate method to exclude herbivory by small insects (Root 1996). A randomized block design was used to minimize effects potentially caused by microhabitat variation. Fifty blocks of three plants each were established in clearings between shrubs. Within these patches, three plants of similar size were chosen haphazardly and marked with a randomly selected flag that noted the treatment option. Insecticide and water treatments were applied every seven to ten days from March 17 to May 14, 2001, until plants were in flower and larval feeding was no longer observed. Plants were sprayed in the morning hours when winds were calm and temperatures low. The insecticide used was Carbaryl (1-naphthol *N*-methylcarbamate), a ready-mixed aqueous solution of a wide-spectrum carbamate insecticide, brand name Sevin (Rhone-Poulenc). Carbaryl kills chewing insects for three to ten days, it has a half life of seven days in aerobic soil, and is moderately toxic to mammals, birds, and aquatic organisms; and highly toxic to bees (PMEP 1993). Prior studies on this insecticide indicate that its effects on plant growth are minimal (Jones et al 1986; Gibson et al 1990).

The effect of herbivore exclusion on plant survivorship was assessed by monitoring the study plants throughout the treatment time. To determine the effect of herbivore exclusion on plant size and reproductive potential, study plants were collected and total stem length (stem and all branches) was measured, the number of flowers and seeds per plant were counted, and each plant's seed/flower ratio was calculated.

Seventeen of the fifty blocks had signs of larval infestation, so these blocks were used to evaluate the effect of larval exclusion. Survivorship, plant size, and reproductive output was analyzed using a Randomized Block ANOVA (SYSTAT 1999) GLM with treatment (herbivore removal, spray control, and no treatment) as the independent variable; survivorship, plant size, flower number, seed number, or seed/flower ratio as the dependent variable; and site (17 levels) as the block. Levine's test (SPSS 2000) for equality of variance showed that flower number and seed number in infested blocks did not meet the criteria for the ANOVA test, so these data were transformed using ranks. Two a priori comparisons were used to determine if treatment differed from controls: 1) herbivore removal vs. spray control and no treatment 2) spray control vs. no treatment.

Thirteen blocks without infestation were also measured and analyzed in the same way to determine the effects of the insecticide in the absence of gelechiid larvae. All of these data were normally distributed with equal variances.

A significance level of alpha < 0.025 was used to evaluate the results from the herbivore exclusion experiment. For evaluating research design elements, a significance level of alpha < 0.05 was used.

Demographic Measurements

Demographic and habitat parameters measured and analyzed were: 1) density of study plants 2) survey for infested plants outside the treatment area 3) patch size of study plants.

The density of each study plant was measured at the beginning and end of the study period by positioning the subject plant in the center of a ten cm square and counting all of the plants within the square. Pearson Product Moment Correlation (SYSTAT 1999) was used to determine if there were potential relationships between plant density and measurements of plant size, reproductive output, and patch size.

A survey was performed in a 14 square meter area adjacent to the study site. Within this area, all plants were counted and all infested plants were noted. A plant was considered infested if it had any sign of feeding shelters. Plants were counted using a 0.7 m. x 0.4 m. frame (quadrat) placed contiguously over the area being surveyed. A total of 56 quadrats were examined. These data were used to estimate the percentage of infested plants and the distribution of larvae outside the treatment area.

The area of the patch (opening in the shrubs) in which each study plant was growing was measured to assess whether there was a relationship between patch size and herbivore attack. Rabbit (*Sylvilagus bachmani* Grinnell and Storer) grazed plants were recognized by a clean slanted cut on the stem (Farrand 1996) and larval infested plants were identified by feeding shelters. Two-sample t-tests (SYSTAT 1999) were used to determine if herbivory differed for various sized patches.

RESULTS

Insecticide treatment had no real effect on survivorship of the plants. Only 2 of 150 marked plants were lost during the study (buried by gophers). However, late season grazing by rabbits completely removed seed heads from 11% of the study plants, and these blocks were removed from treatment analyses.

Exclusion of insect herbivores in blocks with larval infestation led to a significant increase in plant size (a priori comparison between herbivore exclusion and controls), and water had no effect (a priori comparison between the spray control and no treatment (RCB ANOVA Table 1, Figure 2). Variations in plant size were affected by microhabitat variations, therefore a block design was necessary (Table 1). In blocks without larval infestation, insecticide did not affect plant size but water did have an effect (Figure 3).

Because seed number and flower number were highly correlated (0.92) only seed number was used to analyze the effect of herbivory on reproductive output. Exclusion of insect herbivores within larval infested blocks led to a significant increase in seed number (a priori comparison between herbivore exclusion and controls), and water had no effect (a priori comparison between the spray control and no treatment) (RCB ANOVA Table 2, Figure 4). Microhabitat variations affected seed number as indicated by the significant block effect which suggests that a block design was necessary (Table 2). In blocks without larval infestation, herbivore exclusion did not increase seed number, but water did have an effect (Figure 5).

Insect exclusion did not have a significant effect on seed/flower ratios in blocks with larval infestation ($P = 0.16$) or in blocks without larval infestation ($P = 0.51$).

Table 1. Plant size. RCB ANOVA (and associated a priori comparisons) for examining effects of herbivore removal on plant size in blocks with larval infestation (N = 17).

	df	MS	F	P
Treatments	2	337	7.24	0.003
Insect exclusion vs controls	1	620	13.28	0.001
Spray control vs. no treatment	1	56	1.19	0.283
Block	16	125	2.68	0.009
Error	32	47		

Table 2. Seed number. RCB ANOVA (and associated a priori comparisons) for examining the effects of herbivore removal on seed number in blocks with larval infestation (N = 17).

	df	MS	F	P
Treatments	2	751	5.60	0.008
Insect exclusion vs. controls	1	1479	11.04	0.002
Spray control vs. no treatment	1	22	0.17	0.686
Block	16	328	2.45	0.015
Error	32	134		

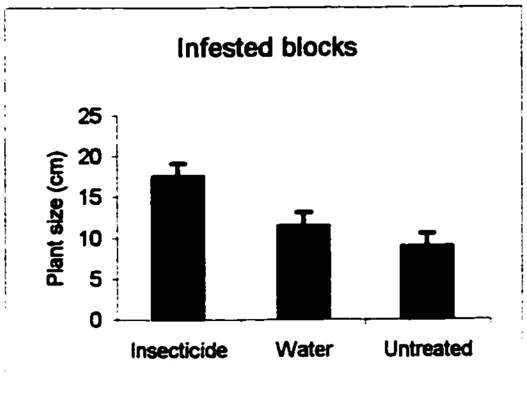

Figure 2. Mean (SE) plant size by treatment. A priori between insecticide and controls (P = 0.001), a priori between water and untreated (P = 0.28) (N = 17).

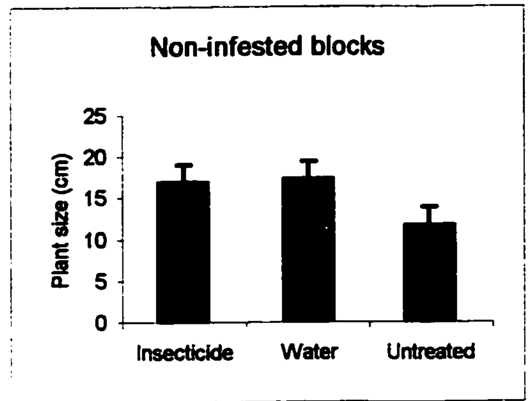

Figure 3. Mean (SE) plant size by treatment. A priori between insecticide and controls (P = 0.37), a priori between water and untreated (P = 0.08) (N = 13)

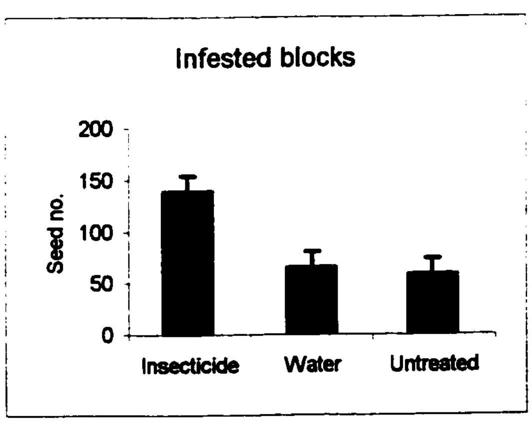

Figure 4. Mean (SE) seed number by treatment. A priori between insecticide and controls (P = 0.002), a priori between water and untreated (P = 0.69) (N = 17).

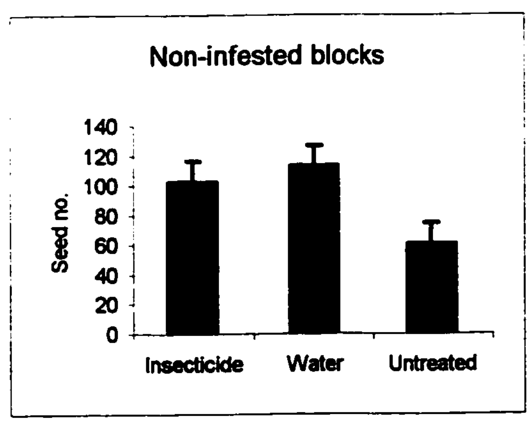

Figure 5. Mean (SE) seed number by treatment. A priori between insecticide and controls (P = 0.37), a priori between water and untreated (P = 0.014) (N = 13).

Density was not found to be correlated with plant size, flower number, seed number, or patch size in blocks with or without larval infestation, so it was removed from the analysis. However, growth parameters were all correlated with each other (Table 3).

Table 3. Density. Pearson Product Moment Correlation for examining effects of density on flower number, seed number, plant size, and patch size.

	Flower no.	Seed no.	Plant size	Beg. density	End. density	Patch size
Flower no.	1.00					
Seed no.	0.92	1.00				
Plant size	0.84	0.79	1.00			
Beg. density	0.04	0.04	0.21	1.00		
End. density	-0.45	-0.41	-0.36	0.43	1.00	
Patch size	0.29	0.21	0.23	0.16	0.03	1.00

The results of the survey for larvae outside the treatment area showed that although only 3% of the 4876 plants surveyed had signs of infestation, they were distributed in 61% of the 56 quadrats surveyed.

The results of the patch size analysis (two-sample t-tests) indicated that the average patch size of larval infested plants was larger than the average size of patches without larval infestation (Figure 6). The average patch size of rabbit grazed plants was smaller than the average patch size without evidence of rabbit grazing (Figure 7).

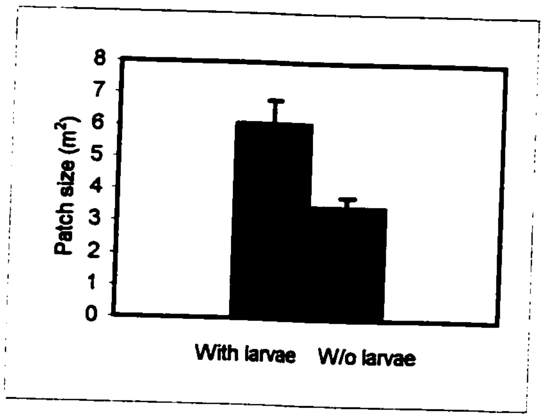

Figure 6. Mean (SE) patch size for larval infested plants vs. non-infested plants ($P = 0.003$) ($N = 145$).

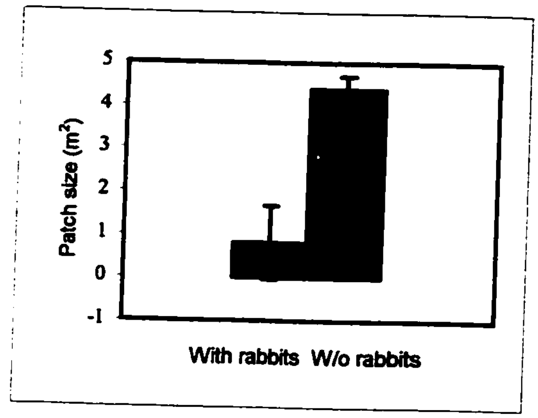

Figure 7. Mean (SE) patch size for rabbit grazed plants vs. non-grazed plants ($P < 0.001$) ($N = 145$).

DISCUSSION

Insect Exclusion Experiment

Insecticides can affect plant performance in various ways, and potential growth effects from insecticide use needs to be considered. Although the effect was not significant, insecticide treated plants in blocks without larval infestation had lower average plant size and seed numbers. In other studies, Carbaryl has been shown to have a negative or minimal effect on plant growth (Jones et al 1986; Sengupta 1989; Gibson et al 1990) so it is unlikely that carbaryl induced plant growth in the current study.

Insect exclusion had no effect on plant survivorship and this conforms to the results of other studies (Louda 1982; Kinsman and Platt 1984; Root 1996). Survivorship was 98% during the current study, but in 2000 I found survivorship to be 50%. Larval infestation levels were similar both years, with approximately 25% and 30% of the plants infested. Consequently, differences in survivorship are likely due to climatic conditions or other factors. During the winter of 2000, rainfall was extremely heavy in January (9.6 inches) and February (10 inches); this is above normal for these months by an average of 6 inches per month.

Despite unusually high plant survivorship, insect herbivores caused a considerable reduction in seed output in infested blocks. Seed to flower ratios were not significantly different for insecticide treated plants, and this is consistent with the findings of other researchers (Louda 1982; Kinsman and Platt 1984). Therefore insects reduced seed output by reducing plant size rather than by reducing pollination rates. Plant size has been correlated with seed output in numerous studies (Rausher & Feeny 1980; Wolfe

1983; Brown et al 1987; Stöcklin & Favre 1994) as well as in my earlier work on this plant species (Baron 1998). Since larvae remove leaves, they compromise the plants ability to garner resources (Louda 1984; Louda et al 1990). *Chorizanthe robusta* had little opportunity for compensatory growth because larvae were active until plants flowered.

Herbivory and Patch Effects

The effect of the patchy environment on herbivory was apparent in many ways. The significant block effects seen in the insecticide treatment analyses indicated that microhabitat variations affected plant growth and reproduction, and that a block design was essential for this system. In addition, there was a trend for larvae to be more common in large patches. This could indicate that moths select oviposition sites based on patch size, or that larvae have better survivorship in large patches. Certainly, large patches would decrease search time for the insect at both moth and larval stages. Doak (2000) points out that insect herbivores may not respond directly to patch size, but to differences in plant parameters such as size or density in different sized patches. However, no correlation between patch size and plant density or plant size was found in the current study. Solomon (1981) also found no relationship between infestation of a host specific moth (Gelechiidae) and plant density or relative abundance, and Rausher and Feeny (1980) found that differences in density were not correlated with the likelihood of oviposition.

In contrast to larval infestation, rabbit grazing was more prevalent in small patches surrounded by shrubs, and other studies have also shown that rabbits avoid large open areas and stay close to shrub cover (Swank & Oechel 1991; Palmisano & Fox 1997). Rabbits removed mature seed heads from 11% of the study plants, consequently, to truly assess the effects of herbivory on *C. robusta*, mammals as well as insects need to be excluded. In a study on chaparral herbs, rabbits were found to have a greater effect on survivorship than competition, but they rarely grazed *Chorizanthe* (Swank & Oechel 1991). Watkinson and Harper (1978) found substantial mortality of an annual grass in a sand dune habitat due to the removal of inflorescences by rabbits, and in a study on the effects of herbivory on a native thistle at Sunset Beach, Palmisano and Fox (1997) found that mammals (rabbits, gophers, and moles) accounted for more damage than insects.

The effects of these two herbivores on the plant population are potentially very different. Although the relative number of larval infested plants from the survey was less than that indicated by the number of infested plants within the blocks, both measures implied that larval infestation was well distributed over the study area, likely at varying density depending on patch structure. In contrast, rabbits were grazing in small patches, where plants may be closely related. If the whole patch is eaten in one season, this could decrease genetic variability in the population more dramatically than even a higher level of herbivory that is spread over a large area. However, this effect could be mitigated by rabbit facilitated dispersal of *C. robusta* seeds between patches.

Plant Population Dynamics

Moth larvae decreased seed output approximately 58% in approximately 30% of plants. Rabbits removed seeds completely from 11% of plants. Will this substantial reduction in seed production have an effect on the plant population? It is generally agreed that if a plant is not seed limited, herbivores could not have a great effect on its population dynamics (Crawley 1983, 1989; Louda 1982). If there are a shortage of "safe sites" for seed germination, reducing seed supply will not affect plant abundance, as was seen in a study by Crawley and Gillman (1989). However, in a review paper of seed augmentation studies, Turnbull et al (2000) found that 50% of the studies (27 studies with 90 species) showed evidence of seed limitation, and this was highest for annual plants in sand dune environments. Although *C. robusta* fits this profile, the population at the study site is large and concentrated, so it may be microsite limited. However, the patchy nature of the habitat makes this difficult to assess and according to Maron and Gardner (2000) "seed vs. safe" site limitations can vary over years and over the topography of a site.

A related consideration is density-dependent seedling survival, where a reduction in the number of seedlings can lead to increased survival of others (Maron & Gardner 2000). However, in a study on bush lupine, Maron (2001) found that density-dependent mortality in the second year was not enough to cancel out the effects of the reduction in seed caused by herbivory. Maron and Gardner (2000) used simulations to test the effects of seed reductions over a range of conditions with regard to seed limitation, density-dependent seedling survival, and seed banks. They found that herbivores can reduce plant populations even when density-dependent mortality is high, and the existence of a seed bank can amplify these effects. This differs from the widespread belief that seed banks can buffer a population against yearly fluctuations (Pavlik et al 1993). Maron and Gardner emphasize that field studies are needed to confirm the results of these simulations.

Chorizanthe robusta seeds are not dispersed from the flowers, and flowers examined from prior years have not contained viable seeds (personal observation). Studies on a closely related species (*Chorizanthe pungens* var. *hartwegiana*) have shown little evidence of a long term seed bank (J. McGraw personal communication). Consequently numerous attributes of *C. robusta* populations could cause them to be vulnerable to reductions in seed due to herbivory. They are short lived annual plants in sand dune environments, unlikely to have long term seed banks, and they are found in few widely scattered populations. Research has shown that small populations of endangered plants can be limited by low seed production (Pavlik et al 1993; Bevill et all 1999), and populations of *C. robusta* at inland sites are very small.

Evolutionary Relationships

The results from this and similar studies (Parmesan 2000) support the idea that herbivores can be an important force in shaping plant populations. Although Bernays and Graham (1988) and others maintain that insect density is generally too low to influence the relative abundance of plant genotypes, clearly there is the potential for huge effects when the seed supply is so greatly reduced. The highly variable nature of herbivory over the landscape and the potential for herbivores to select plants based on environmental conditions such as patch size, creates opportunities for "selection mosaics by environment" and increases the potential for genetic polymorphisms (J. Thompson personal communication).

It is unusual for an annual plant to have a specialist herbivore (Crawley 1983). Presumably it would be even more unlikely for an endangered plant with few, widely separated populations. However, most microlepidopterans (small moths) are specialists and they can survive in small habitat patches (Powell 1999). In a study of the range size of host plants for a variety of insect herbivores in England, Hopkins et al (2002) found a higher percentage of "micro moths" were associated with rare plants than any of the other taxa they studied. At Sunset Beach *C. robusta* grows in large monospecific patches which make monophagy advantageous (Crawley 1983). Larvae collected on *C. robusta* would readily eat both *C. robusta* and the closely related *C. pungens*, but not any of the other plants offered (personal observation). The question of whether this moth species is a specialist on this rare plant is more important with regard to the insect population than to the plant population. If it is found to be a specialist on *Chorizanthe*, it would certainly be in need of protective status as well.

Evolutionary relationships between species can evolve over small time scales, even decades, and changes in the distribution of metapopulations are one of the "normal processes of evolution" (Thompson 1998). *Chorizanthe robusta* appears to exhibit metapopulation behavior; plants will colonize along trails and in small openings over the landscape, and these small fugitive populations can persist for many years (personal observation). Consequently, an evolutionary relationship between this moth species and *Chorizanthe* is certainly possible, and if the moth is a specialist on *Chorizanthe* a co-evolutionary relationship may exist. This interesting association merits further study.

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