

Intraspecific competition and subterranean herbivory: individual and interactive effects on bush lupine

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High mortality of plants growing in dense monospecific stands (i.e. self-thinning) usually results from intense intraspecific competition. However, inconspicuous below-ground insect herbivory might be a potent but overlooked source of mortality within dense stands of plants, particularly if crowding limits a plant's ability to compensate for herbivore damage. Here I ask how high conspecific density influences a plant's ability to cope with heavy below-ground insect herbivory.

I manipulated conspecific density and exposure to an abundant root-borer, the ghost moth (*Hepialus californicus*), and examined the impacts on the fecundity, growth, and survival of bush lupine (*Lupinus arboreus*), a fast-growing shrub that grows in dense monospecific stands in coastal grasslands. Both herbivory and intraspecific competition affected seed production, size, and mortality of bush lupine over the two years of the experiment. Plants consistently produced fewer seeds when growing at high versus low density and ghost moth herbivory also significantly reduced seed production. The negative effects of herbivory on plant fecundity were similar, regardless of plant density. In contrast, plant survival was affected by both competition, herbivory, and the interaction of these factors. In high density plots, plant survival was uniformly low (averaging 0.45–0.50); plants exposed to herbivores died from heavy herbivory, and plants protected from herbivores died due to intense intraspecific competition that compensated for losses due to herbivory. In low density plots, ghost moth herbivory similarly reduced lupine survival, from an average survival probability of 0.94 in plots protected from these herbivores to 0.55 in plots exposed to herbivory. Thus, results show that regardless of plant density, below-ground herbivory can be a potent source of mortality.

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Plants that recruit episodically, for example after fire or other large disturbances, often grow at very high density. Individuals within these dense stands can be subject to considerable self-thinning, and this thinning can have substantial effects on the overall demography and population dynamics of the species involved (Yoda et al. 1963, Schlesinger and Gill 1980, Keeley et al. 1989, Crawley 1992, Guo and Rundel 1998).

It is usually assumed that intense intraspecific competition between close neighbors drives the thinning process. However, thinning might also result from herbivory (Waloff and Richards 1977). Although this has seldom been considered, there are two reasons to expect

that herbivory might contribute to substantial mortality of plants growing at high density. First, dense plants may be more vulnerable to herbivore damage than plants at low density. Plants growing at high density can be water or nutrient stressed and therefore easily succumb to herbivores (Mattson and Haack 1987, Karban et al. 1989, Whitham et al. 1991). This has been shown in studies of interspecific competition and herbivory; plants competing for a limiting resource are less able to marshal the resources needed for compensatory growth following herbivory than are plants growing free from competitors (Louda et al. 1990, Steinger and Müller-Schärer 1992). As a result, plants stressed by

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crowding that are attacked by herbivores often suffer greater reductions in fecundity (Bentley et al. 1980, Lee and Bazzaz 1980, Maschinski and Whitham 1989) and survival (Parker and Salzman 1985) compared to plants damaged by herbivores growing with fewer competitors.

Second, high densities of plants can attract more insect herbivores and therefore might accrue more damage than plants growing at lower density (Root 1973). As well, plant defenses can be compromised when individuals grow at high density (Karban et al. 1989). This could provide another mechanism whereby plants could have greater herbivore-driven mortality at high versus low density.

Most studies that have simultaneously manipulated herbivory and interspecific competition have examined how herbivory alters competitive interactions. These studies have shown that tissue loss from herbivory can reduce above-ground growth, below-ground biomass, or overall stature, which in turn can lower the competitive ability of community dominants (Harper 1977). Reversals in competitive dominance due to selective herbivory have been shown for situations in which grasses compete with forbs (Cottam et al. 1986, McEvoy et al. 1993; but see Fowler and Rausher 1985), grasses compete with grasses (Watt and Hagger 1980), and when there is competition between forbs (Bentley and Whittaker 1979). By altering competitive hierarchies, herbivory can also alter the trajectory of secondary succession (McBrien et al. 1983, Brown 1990).

But just as herbivory can alter competitive interactions, competition can alter the ability of plants to respond to herbivory (Hjältén et al. 1993). And this sort of interaction between competition and herbivory might be difficult to detect observationally if the herbivore involved feeds below ground, on plant roots. Might subterranean consumers be “silent killers” of plants, inflicting considerable thinning within high density stands, yet having less impact on plant fitness at low density? Despite the fact that below-ground herbivores are common in many communities (Brown and Gange 1990) we understand very little about the conditions under which these herbivores influence plant fitness.

In coastal grasslands in California, bush lupine (*Lupinus arboreus*), a fast-growing evergreen shrub, is commonly attacked by an abundant subterranean herbivore, the ghost moth (*Hepialus californicus*) (Strong et al. 1995). Larvae of the ghost moth girdle the outside of plant roots when young, and then bore into the shoots and roots of plants where they create large feeding cavities. A large percentage of shrubs are often infested by ghost moth caterpillars, and it is not unusual for plants to contain upwards of 10–15 caterpillars in their trunk and roots (Strong et al. 1995, Maron 1998). Although plants are able to tolerate high levels of herbivory, occasionally entire stands die en masse

(Strong et al. 1995). These dramatic die-offs often occur when plants are growing at high density (Strong et al. 1995, Maron and Simms 1997).

In this paper, I ask whether the high mortality of lupines that often occurs within dense stands may result from an interaction between intraspecific density and herbivory. To address this question, I experimentally triggered lupine germination and subsequently factorially manipulated lupine density and below-ground herbivory within plots containing same-aged plants. Over two years I examined the individual and interactive effects of competition and herbivory on plant fecundity, size and mortality.

Study site and organisms

This study took place on the 147-ha Bodega Marine Reserve (BMR) in central coastal, California, USA. The site experiences a typical Mediterranean climate, with seasonal rains heaviest from November to March. BMR consists of coastal grassland and dune habitat. Grasslands are underlain with sandy soil formed from decomposing diorite granite of the Pacific Plate (see Barbour et al. 1973 for a detailed description of the area). Bush lupine is a dominant plant in grasslands and is scattered more sparsely throughout dunes. In grasslands, there is a large lupine seedbank, and germination out of this seedbank is episodic; seedling abundance can vary by several orders of magnitude between years (Maron and Simms 1997). Large pulses in germination lead to high seedling and juvenile shrub density and dense even-aged stands of adult plants (Davidson 1975, Strong et al. 1995, Maron and Simms 1997). Where shrubs are less dense, the interstitial spaces between shrubs is occupied by a variety of native and introduced grasses and forbs.

Lupine seedling germination occurs with the onset of the winter rainy season in early November, peaks in late January and early February, and ceases with the end of the rainy season in April. Seedlings grow quickly and become large shrubs with canopies over 1 m in diameter by the time they first flower, late in their second spring. Lupine seeds have a “hard” seed coat, and as in most legumes, dormancy is physically enforced by a testa that prevents seeds from imbibing water (Hyde 1954, Rolston 1978). Dormancy can be broken by soil disturbance, oscillations in soil temperature, or other factors that scarify or crack the seed coat (Quinlivan 1961, 1966).

Lupines are frequently fed upon by ghost moth larvae. Females broadcast eggs while flying over patches of lupine bushes during winter and spring nights (Wagner 1986, A. Whipple pers. comm.). Small first and second instar larvae develop in the soil and litter under lupines and feed on the exterior of the upper portions

of lupine roots. By mid- to late spring, caterpillars burrow into plants and create extensive feeding galleries inside the central shoot and upper tap root of plants. Shrubs can contain upwards of 15 caterpillars in their roots, and damage to plant tissue can be extensive (Opler 1968, Strong et al. 1995, Maron 1998, unpubl.). Despite this, plants often survive attack by ghost moth caterpillars. Plants that are killed usually die after they have set seed, in late summer or early fall when caterpillars are at their maximal size. Ghost moths are univoltine; pupae usually eclose in late fall.

Although other small arthropod larvae can also occasionally be found on the outside or inside of lupine roots, these other herbivores are rare, very small, and impose little damage relative to *H. californicus* (pers. obs.).

Methods

Competition and herbivory experiment

To determine whether intense intraspecific competition within dense monospecific stands of lupines may render bushes more vulnerable to below-ground herbivory, I conducted a factorial randomized block design experiment. I manipulated lupine density and the density of ghost moth caterpillars in plots containing one-year-old lupines and examined the effects of these treatments on plant fecundity, growth, and mortality over two years. To ensure enough plants for the experiment, I experimentally triggered a large pulse of seedling recruitment by covering a 15 m × 24 m site with black shade cloth. The black shade cloth increased the temperature of the soil in summer, which can break the hard lupine seed coat and trigger germination (Maron 1998, unpubl. data). From 15 May 1994 to 1 November 1994, I covered an area of grassland (referred to as Upper Draw by Strong et al. 1995 and Maron and Simms 1997) that previously supported a dense stand of lupine that died off in fall 1993. The wood remnants of dead lupine were removed so that the shade cloth could be laid flat on the soil surface. The soil contained a large lupine seedbank (Maron and Simms 1997).

Lupine seedling germination in the covered area, as well as in the surrounding grasslands, began in mid-November 1994. On 8 February 1995, I estimated seedling density in the entire plot, which averaged 21 seedlings/m². Between 14–21 January, 1996, I established six parallel 2 m × 15 m experimental blocks within the 15 m × 24 m site, with each block separated from one another by at least 2 m. Within each block, I established four 1.2 m × 1.2 m plots at haphazardly chosen locations; plots were separated from each other by at least 2 m. A minimum plot size of 1.2 m × 1.2 m was needed to ensure that there were 13 one-year-old plants in each plot. I randomly assigned a different

density (high or low) and herbivory (suppression or control) treatment to plots within blocks. Young lupine bushes were thinned in low density plots to attain a density of 3 plants/plot (2.1 plants m⁻²) and high density plots were thinned to attain a density of 13 plants/plot (9 plants m⁻²). These densities represent the mid to upper portions of the range of densities at which one-year-old plants can usually be found (Maron unpubl.). In low density plots, plants were thinned so that the remaining lupines were widely spaced within each plot. In high density plots, plants universally grew towards the outer edges of the plot, which resulted in all plants having one side on which they were free from competition with any neighbor. All plants in each plot were marked with wire stake flags.

To manipulate ghost moth abundance in the herbivore suppression plots, starting on 23 February 1996 I sprayed all lupine trunks and the soil at the base of plants with the insecticide Dursban (DowElanco Corp., Midland, MI), at a concentration of 0.5 ml active ingredient/L water (application rate = 40 mL insecticide/water mixture per plot). Insecticide was applied on calm days; this combined with the fact that insecticide was applied to the base of shrubs rather than to their foliage minimized any potential for insecticide drifting between plots. Dursban has been extensively and successfully used in studies of below-ground herbivory (Brown and Gange 1989a, b), including studies of ghost moth herbivory on bush lupine (Maron 1998). The active ingredient in Dursban is chlorpyrifos [0,0-diethyl-0-(3,5,6-trichloro-2-pyridinyl) phosphorothioate], an organophosphate that contains one atom of phosphorus. The active ingredient has no toxic effects on nitrogen-fixing *Bradyrhizobium* bacteria, nitrifying and denitrifying bacteria, fungal populations (Pozo et al. 1995) and earthworms (Clements et al. 1986). Nor does it affect nodule number or size (Revellin et al. 1992). Monthly applications of Dursban effectively kills ghost moth caterpillars on or in lupine roots and suppresses colonization of roots by ghost moth larvae. Short-term experiments have shown that Dursban has no positive or negative effects on lupine growth (Maron 1998).

In 1996 and 1997 I sprayed all plants in insect removal plots with Dursban every 3–4 weeks from March to June, the period during which early instar ghost moth larvae are developing in the soil around lupine roots. Control plants were sprayed with water on the same schedule as above. I censused all plants in each treatment plot every three months, beginning in March 1996. I used dial calipers to measure the stem diameter at ground level of all lupines in each plot at the beginning of the experiment, and in July 1996 and 1997. Some plants had multiple trunks that were unconnected above ground but connected underground; on these plants I measured each trunk at ground level. I used stem diameter measurements to calculate a total basal stem area for each plant.

In July 1996 and July 1997, I counted the total number of seed pods on each plant in each plot. I also haphazardly chose and harvested 20 dried pods per plant and counted the total number of intact, filled seeds per pod. In some cases, plants produced fewer than 20 pods total, and for these plants I counted seeds in all available pods. Pods were sampled just before dehiscence, when all seeds had fully developed. I used pod and seed data to calculate the mean total seed output (total seed output = number of pods \times mean number of seeds per pod) of all plants in each treatment plot in 1996–1997.

To confirm that plants that died were in fact killed by ghost moth herbivory, in fall 1997, toward the end of the experiment, I dissected the central shoot and tap root and counted the number of ghost moth larvae in nine lupine bushes immediately after they had died. All bushes were from plots exposed to ghost moth herbivory (five were from high density plots and four were from low density plots.)

Data analysis

Systat 8.0 for Windows (SYSTAT 1998) was used to perform statistical analyses. For each of the two years, I calculated mean fecundity, size, and mortality of lupines in each treatment plot. I also calculated mean annual growth rate (in trunk diameter) of plants in different treatment plots between July 1996 and July 1997. I performed a three-way repeated measures analysis of variance (rmANOVA) to test the effects of block, density and herbivore exclusion on mean per capita seed production and plant size per plot. Each of the two years of data were the repeated measure; fecundity values were log-transformed to ensure homogeneity of variance between treatments. Interactions of block with density and herbivore suppression were never significant so they were dropped from the model.

In addition to examining the effects of density and herbivory on seed production across years, I performed a three-way ANOVA to determine the effects of block, density and herbivore exclusion on plant growth and mean cumulative per capita seed production across the entire experiment. Cumulative fecundity was calculated by summing the number of seeds produced by each plant across both years of the experiment, and then using these values to calculate mean cumulative per capita seed production on a per plot basis. Cumulative seed yield per plot was calculated as the sum of the cumulative per capita seed production in a plot. Analyses were performed on log-transformed data.

To determine the effects of density and herbivory on mean plant mortality per plot, I performed a three-way repeated-measures ANOVA on each year's log transformed data (where the transformation was $\log(1 + \% \text{ mortality})$). Data were log transformed to insure that

the interaction of density \times herbivory would be multiplicative rather than additive. An additive interaction term for mortality data is not appropriate since values can sum to greater than 1.0. By the start of year two, initial densities of plants in plots had changed. I therefore calculated percent mortality from year 1–2 based on the number of individuals in plots that were alive at the start of year 2 (rather than the number alive at the start of the experiment). In one low density herbivore suppression plot, all three plants were killed by gophers (*Thomomys bottae*). The source of mortality was obvious from the mounds of fresh dirt and severed roots that remained where there were earlier healthy plants. Since these were the only plants to die from gopher herbivory, I excluded this plot from calculations of mean per plot plant mortality.

Results

In both years of the experiment, plants growing at high density produced significantly fewer seeds than did plants growing at low density (Table 1, Fig. 1). A 4.3-fold increase in plant density (from 3 to 13 plants per plot) resulted in between a 43% and 66% decrease in mean per capita seed production, depending on year. Cumulatively across both years of the experiment, plants in high density plots produced, on average, 52% fewer seeds than did plants in low density plots, a significant difference (ANOVA, $F_{1,14} = 11.6$, $P = 0.004$).

Heavy below-ground insect herbivory also significantly reduced mean per capita seed production (Table 1, Fig. 1). Careful inspection of plant shoots and the upper portions of plant roots in the summer of 1996 and 1997 revealed that in both years all plants in control plots were infested with ghost moth caterpillars. The number of caterpillars per plant could not be ascertained without destructively harvesting plants, but the signs of infestation were diagnostic. Plants had one and often multiple bore holes into their trunks and upper roots and sawdust-like frass of ghost moth larvae exuded from these holes. In contrast, plants that had been treated with insecticide lacked these signs of *H. californicus* infestation. Cumulatively over both years of

Table 1. Results of three-way repeated measures ANOVA (years 1 and 2 are the repeated measures) testing the impacts of block, density (high vs low) and herbivory (ghost moth suppression vs control) on total seed production.

	df	MS	F	P
Block	5	0.71	1.4	0.30
Density	1	5.4	10.4	0.006
Herbivory	1	4.1	8.0	0.02
Density \times Herbivory	1	0.16	0.31	0.59
Error	14	0.51		

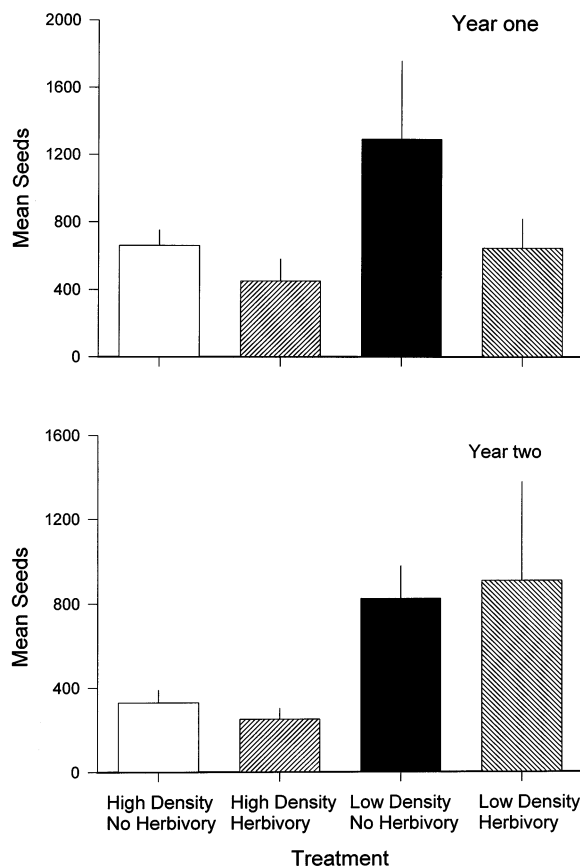


Fig. 1. Mean (+1 SEM) number of seeds produced by plants within different treatment plots in the first (top panel) and second (bottom panel) year of the experiment ($N = 6$ plots per treatment, except for low density, no herbivory treatment where $N = 5$ in year two).

the experiment, plants exposed to ghost moth herbivory produced 31% fewer seeds than did plants protected from herbivory, a significant decrease (ANOVA, $F_{1,14} = 6.6$, $P = 0.022$). There were no interactive effects of density and herbivory on plant fecundity in either year of the experiment (Table 1).

Plant mortality was also dramatically altered by both density and ghost moth herbivory (Fig. 2). In both years of the experiment, plants in high density plots experienced greater mortality than plants in low density plots (rmANOVA, $F_{1,14} = 20.4$, $P < 0.0005$). There was no difference between years in the magnitude of density-dependent mortality ($F_{1,14} = 0.29$, $P < 0.59$). In the first year of the experiment, average mortality of plants in high density plots was more than three times higher than in low density plots (18% mortality in high density plots vs 5% mortality in low density plots). In year two, average mortality was 17% greater in high versus low density plots.

In both years, plants in plots exposed to ghost moth herbivory had higher mortality than plants in herbi-

vore-free plots (rmANOVA, $F_{1,14} = 22.6$, $P < 0.0003$). In year one, plants exposed to root herbivory suffered double the mortality (16% vs 8%) of plants protected from herbivory. There was no significant interaction between density and herbivory on plant mortality during year one of the experiment. During year two, ghost moth herbivory again substantially affected plant mortality, but the effects were dependent on plant density (as indicated by a significant herbivore suppression by density interaction in the rmANOVA, $F_{1,14} = 9.9$, $P < 0.008$). In high density plots, plant mortality was universally high (overall mean = $0.46 \pm \text{SEM } 0.05$); survivorship was only 9% higher for plants protected from root herbivory compared to control plants. In contrast, in low density plots, plant mortality was low, but only in plots protected from herbivory (mean = $0.07 \pm \text{SEM } 0.07$). Plants in low density plots that were exposed to ambient levels of herbivory suffered high mortality (mean = $0.52 \pm \text{SEM } 0.07$). Cumulative mortality across the entire two years of the experiment was significantly influenced by both initial density, herbivory, and the interaction of these factors (Table 2, Fig. 2). Many plants initially growing at high density died, regardless of herbivory. An average of between 50–65% of plants in high density plots died, depending on exposure to herbivory. In contrast, exposure to root herbivores increased plant mortality in low density plots from 6–55%, on average.

Plants that died in the fall of 1997 contained an average of 10.8 ($\pm \text{SEM } 1.77$) larvae per bush. There was no difference in the number of caterpillars in plants from low and high density plots (t -test, $t = 0.5$, $P = 0.63$).

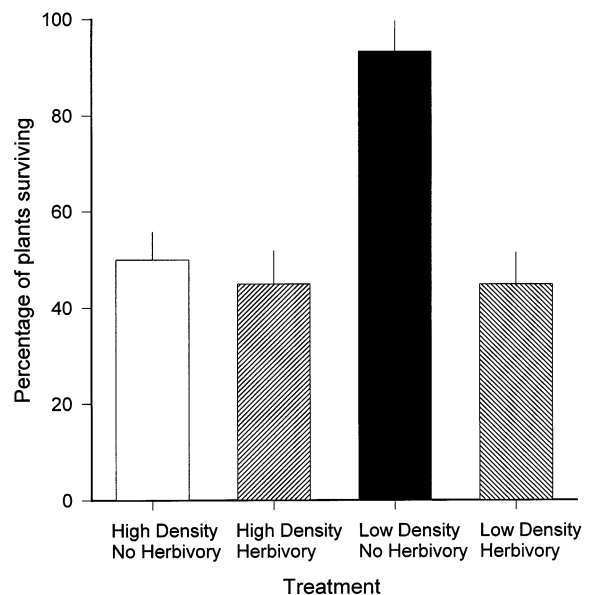


Fig. 2. Mean (+1 SEM) percentage of plants surviving throughout the study in different treatment plots. Sample sizes as in Fig. 1.

Table 2. Results of three-way ANOVA on log-transformed data testing the impacts of block, density (high vs low) and herbivory (ghost moth suppression vs control) on cumulative mean plant mortality per plot across the entire two years of the experiment.

	Cumulative mortality, yr 0–2			
	df	MS	F	P
Block	5	0.013	0.97	0.47
Density	1	0.26	18.9	0.007
Herbivory	1	0.34	25.0	0.002
Density × Herbivory	1	0.13	9.3	0.009
Error	14	0.04		

Because ghost moth herbivory both reduced plant survival as well as fecundity, herbivore suppression effectively increased the total cumulative amount of seeds that were added to plots as a whole (ANOVA, $F_{1,14} = 5.0$, $P < 0.04$). Plots in which ghost moths were suppressed received 51% more seeds across the entire experiment than did plots containing plants attacked by ghost moths. Total cumulative seed yield (on a per plot basis) was also significantly affected by the initial density of plants in plots (ANOVA, $F_{1,14} = 8.7$, $P < 0.01$). High density plots received 90% more seeds over the course of the experiment than did low density plots, despite the fact that plant density had negative effects on per capita seed production (Fig. 3).

Shrub size

Across both years of the experiment, there were significant differences in mean plant size between density treatments (Fig. 4). Plants in low density plots had significantly larger trunks than plants in high density

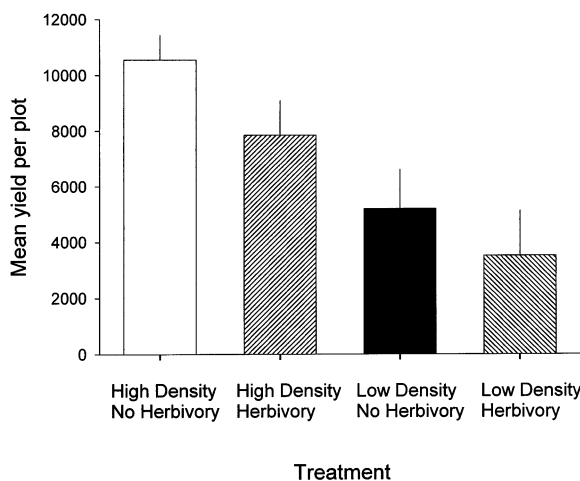


Fig. 3. Mean (+ 1 SEM) total seed yield in different treatment plots. Seed yield is the sum of all seed production per plot across both years of the experiment. Samples sizes as in Fig. 1.

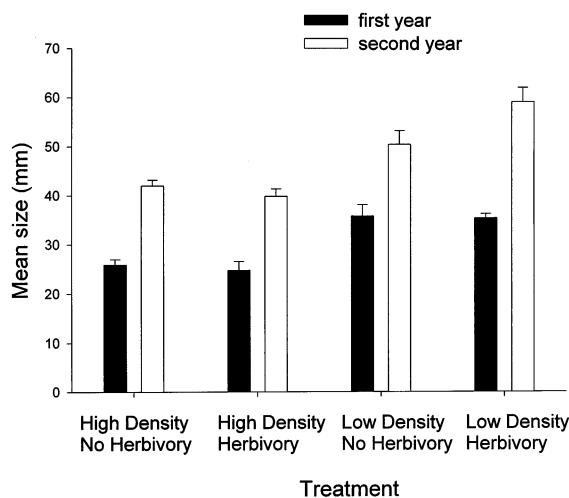


Fig. 4. Mean (+ 1 SEM) trunk diameter of lupines in different treatment plots during the first (black bars) and second (clear bars) year of the experiment. Measurements taken in July of each year, sample sizes as in Fig. 1.

plots (rmANOVA, $F_{1,15} = 32.8$, $P < 0.0001$). Plants in low density plots also exhibited greater growth between years than did plants in high density plots (two-way ANOVA, $F_{1,19} = 13.7$, $P = 0.02$). In contrast, the overall impact of herbivory on plant growth was not significant (rmANOVA, $F_{1,15} = 2.3$, $P = 0.15$). However, the effects of herbivory on growth differed between years, as evidenced by a significant year by herbivory interaction (rmANOVA, $F_{1,15} = 15.4$, $P < 0.002$). In year two, plants exposed to below-ground herbivores were larger compared to plants protected from below-ground herbivory (Fig. 4). This effect was not due to any positive impacts of herbivory on plant growth (two-way ANOVA, $F_{1,19} = 1.4$, $P = 0.25$); rather, small plants were killed by herbivores, leaving a population of larger plants than those in low density plots exposed to herbivory.

Discussion

Bush lupines in coastal grasslands recruit episodically and often grow in dense monospecific stands. Results from this study indicate that both high conspecific density and heavy below-ground insect herbivory contribute to the reduced performance of plants in these stands. Plants growing at high density consistently produced fewer seeds than did plants growing at low density. Ghost moth herbivory also substantially depressed plant fecundity, in year one and cumulatively across both years of the experiment. The magnitude of the cumulative reduction in plant fecundity resulting from herbivory was similar to the reduction in cumulative fecundity due to plants growing at high density. Average cumulative seed production was reduced from

1589 seeds per plant to 1045 seeds per plant as a result of exposure to herbivory and average cumulative seed production was reduced from 1804 seeds per plant to 1254 seeds per plant as a result of plants growing at high density.

Intraspecific competition between shrubs had little influence on the fraction of plants that were killed by herbivores. At both high and low density, plants suffered similar levels of herbivore-driven mortality. Mean mortality from herbivory was only 5% greater for plants in high versus low density plots (Fig. 2). Root boring was clearly the cause of mortality of plants not sprayed with insecticide. Regardless of plant density, plants in plots exposed to herbivores had extensive damage to their shoots and roots and died in late summer and fall, when plants normally die from ghost moth herbivory (Strong et al. 1995, Maron 1998). At least on the small scale of this experiment, it did not appear that plants in high density plots attracted more ghost moth caterpillars than did plants in low density plots.

At high density, plants protected and exposed to herbivory had a similar probability of dying. In contrast, at low density plants protected from herbivory had very low mortality rates. Therefore, competition appeared to compensate for mortality due to herbivory, eliminating any difference in mean mortality between high density plots exposed to and protected from herbivores. In low density plots where density-dependent mortality was minimal, plant mortality was high only in plots where plants were exposed to ghost moths.

A critical issue in plant-herbivore studies is whether herbivore-driven reductions in seed production, of the type observed in this study, affect future plant abundance and dynamics (Crawley 1989, 1992, Louda 1989, 1994, Jermy 1993, Louda and Potvin 1995). It is often argued that any enhanced recruitment that results from gains in seed production brought about by protecting plants from herbivores are negated by compensatory density-dependent mortality of the next generation of plants that recruit at high density (Crawley 1992). Results from this study shed light on this issue, since we can ask whether two years of density-dependent mortality compensated for the initial difference in plant density that was experimentally imposed. Results indicate that cumulative density-dependent mortality in high density plots was only partially compensatory. That is, the differential mortality between plants in high versus low density plots was not of sufficient magnitude to ultimately equalize plant density between the treatment plots. Differences in the initial density of plants were still apparent two years later. At the end of the experiment, mean plant density in high density plots protected from herbivores was 6.5 (SD = 2.1) compared to a mean plant density of 2.8 in low density plots protected from herbivores (SD = 0.44). Moreover, despite high mortality of plants in high density plots, total seed yield on a per plot basis was much greater for high compared to low density plots.

The interactive effects of competition and herbivory on bush lupine population dynamics are likely to be complex, because the dynamics of many bush lupine stands in grasslands are oscillatory. Although plant mortality is high, lupines continually recolonize areas from germination out of a large seedbank. Thus, competition and herbivory can each influence the number of individuals alive at any given time, but they can also potentially influence seedbank dynamics and the amplitude of recruitment events out of the seedbank.

These results indicate that insect herbivores and intraspecific competition can cause equally high plant mortality. Whether this is generally true for other species that recruit at high density is mostly unknown, as there has been little experimental work that explicitly examines how the magnitude of plant mortality resulting from intraspecific competition and herbivory differs (but see Rausher and Feeny 1980). Adult plant mortality resulting directly from insect herbivory is often considered small (Crawley and Pacala 1991), and in many cases insect herbivores are thought to have their biggest impact by increasing the probability of plants dying from competition rather than by directly killing plants (Crawley 1997). This view of the relative importance of competition and insect herbivory has been shaped, in part, by research that has primarily involved above-ground herbivores on annual plants. However, a growing literature documents important individual and population-level impacts of below-ground herbivores on plants (Brown and Gange 1989a, b, 1990, Steinger and Müller-Schärer 1992, Moron-Rios et al. 1997, Notzold et al. 1998, Maron 1998). Where both above- and below-ground herbivores attack the same plant, below-ground herbivores appear to have greater negative impacts on plant performance than do above-ground herbivores (Ingham and Detling 1986, Moron-Rios et al. 1997). As evidence mounts, and the nuances of these cryptic interactions become better known, we may discover that subterranean herbivores have greater direct effects on plant populations than heretofore considered.

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