

John L. Maron

Interspecific competition and insect herbivory reduce bush lupine (*Lupinus arboreus*) seedling survival

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Abstract Seedlings suffer high mortality in most plant populations, with both competition and herbivory proposed as being important mechanisms causing seedling death. The relative strength of these factors, however, is often unknown. Here I ask how interspecific competition for light and insect herbivory jointly affect seedling survival of bush lupine (*Lupinus arboreus*), a native shrub common to coastal California. Bush lupine seedlings germinate in grasslands during winter, and throughout spring potentially compete for light with surrounding fast-growing annual grasses. By early summer, after grasses have died, seedlings can be defoliated by a locally abundant caterpillar, the western tussock moth (*Orgyia vetusta*). I examined the relative importance of competition and insect herbivory on seedling survival in two separate experiments. First, I compared seedling mortality in plots either exposed to or protected from tussock moth larvae. Plants were protected from herbivory by the judicious use of insecticide; control plants were sprayed with water. Tussock moth herbivory resulted in significantly greater (31%) seedling mortality. To determine the effects of interspecific competition for light on seedling survival, I manipulated the density of grass surrounding lupine seedlings. I removed all vegetation surrounding some individuals, and left intact vegetation surrounding others. Reducing competition resulted in a 32% increase in seedling survival from February to June, as well as changes in seedling growth. To determine whether there are interactive effects of competition and herbivory on seedling survival, I enclosed tussock moth larvae on half of all surviving seedlings within each of the two prior competition treatments, comparing growth and survival of defoliated and undefoliated seedlings. Defoliation in June led to an additional 50% mortality for individuals

that had grown with competitors through spring, and a 53% additional mortality for seedlings that grew without competitors through spring. Thus, although competition and herbivory both caused substantial seedling mortality, there was no statistical interaction between these factors. Competition-free plants were not less vulnerable to herbivory than plants that previously grew with competitors. Taken together, these experiments indicate that competition and herbivory are both important sources of mortality for bush lupine seedlings.

Key words Insect herbivory · Competition · Seedling · Survival · *Lupinus arboreus*

Introduction

Seedlings incur considerably higher mortality than juveniles or adults in most plant populations that are not increasing rapidly (Harper and White 1974; Harper 1977; Cook 1979), yet the sources of this mortality are poorly known. For example, insect herbivory on adult plants had received much attention (reviewed by Crawley 1983, 1989; Marquis 1992), but the impacts of insect herbivory on seedlings are less well resolved. Seedling mortality due to invertebrate herbivory most often involves slugs and snails (Cates 1975; Dirzo and Harper 1982; Fenner 1987; Hulme 1994; Hanley et al. 1995); these organisms are more obvious than small and ephemeral insects. While cases of insects killing seedlings are known (Clark and Clark 1985; Parker and Salzman 1985; Schmitt and Antonovics 1986) it is surprising how few studies examine how insect herbivores affect plant populations through their effects on seedling survival (Louda et al. 1990).

In contrast to insect herbivory, interspecific competition has received substantial attention. Competitive effects that limit seedling recruitment are thought to be important in determining species composition in many plant communities (Harper 1977; Grace and Tilman 1990). Despite an increasing number of studies that ex-

J. L. Maron
University of California, Bodega Marine Laboratory,
Box 247, Bodega Bay, CA 94923, USA
fax: 707-875-2089; e-mail: JLMARON@UCDAVIS.EDU

amine the joint effects of competition and insect herbivory (Whittaker 1979; Lee and Bazzaz 1980; Fowler and Rausher 1985; Parker and Salzman 1985; Cottam et al. 1986; Muller-Scharer 1991; Burger and Louda 1994), few examine the relative strength of these factors for seedling survival. Competition and herbivory may interact in non-obvious ways to affect plant survival, with seedlings more likely than adults to suffer this negative interaction (Crawley and Pacala 1991).

At my study site in coastal California, bush lupine (*Lupinus arboreus*) is the dominant native shrub, often growing in stands composed of hundreds of bushes. Lupine seedlings establish from late November to March within the interstitial plant community between adult lupines. This interstitial community is primarily composed of the fast-growing annual exotic grasses, *Bromus diandrus* and *Lolium multiflorum*. These grasses germinate with the onset of winter rains and often form dense swards by late spring. Lupines surviving their first summer rapidly grow into large shrubs, which allows them to effectively shade out the vegetation beneath them (Maron and Jefferies, unpublished work). Young seedlings, however, must compete with surrounding annual grasses during their first spring, and can be easily overtopped and shaded.

Observation suggests that competition threatens lupine seedlings during spring, and defoliation by insects can harm seedlings surviving into summer. Abundant western tussock moth (*Orgyia vetusta*) larvae annually defoliate adult bush lupines within a 1- to 2-ha area called Mussel Point (MP), where this study took place (Harrison 1994; Harrison and Maron 1995). Caterpillars hatch from late April to early June and then grow through five or six instars (for males or females, respectively) before pupating in late July. Individuals dispersing from defoliated adult lupines can defoliate lupine seedlings and seedlings may be particularly vulnerable to defoliation (Harper 1977).

In this paper, I report results of two experiments designed to assess the extent to which insect herbivory and interspecific competition contribute to high mortality for bush lupine seedlings. In 1993 I planted lupine seedlings in experimental plots to determine the fraction of seedlings that succumb to defoliation by tussock moth larvae. In 1995 I manipulated both interspecific competition for light and herbivory on natural seedlings, asking how these factors jointly affect lupine seedling survival.

Methods

This study took place on the University of California's Bodega Marine Reserve (BMR), Sonoma County, California.

Effects of tussock moth herbivory on lupine seedling survival

To determine whether herbivory by *O. vetusta* influences lupine seedling survival, I protected some seedlings from herbivory and

exposed others to ambient levels of defoliation. In January 1993 I germinated lupine seedlings from a bulk pool of seed collected in summer, 1992, from hundreds of lupine bushes. I grew seedlings in a green house for three months and then planted them in the field on 6 March 1993. I cleared vegetation from 24 plots, each of area 1.3 m², and planted a hexagonal array of six lupine seedlings within each plot. Twelve plots, randomly assigned, were planted at high density (0.50 m between seedlings) and twelve plots were planted at low density (0.18 m between seedlings). Two weeks after planting seedlings, I randomly selected six plots within each of the two density treatments and protected seedlings in these plots from defoliation by spraying them every 2 weeks with the insecticide malathion (Ortho, Chevron Corp.), at a concentration of 2.5 ml active ingredient/l water. Seedlings in control plots were sprayed on the same schedule with water unless there was a heavy fog drip on the day seedlings were scheduled to be sprayed. During the peak of tussock moth abundance, caterpillars colonized and defoliated seedlings continually and spraying seedlings every 2 weeks proved to be ineffective protection. To alleviate this problem, beginning in June, I removed caterpillars from seedlings by hand every 1–2 days.

Every 2 weeks from 25 March–31 August 1993, I measured the height of seedlings and recorded the presence of insects or insect damage to plants and the identity of seedlings that had died during the previous 2 weeks. I terminated the experiment at the end of August, approximately 1 month after all tussock moth larvae had pupated or died.

Natural seedling survival and growth

To compare the fate of natural seedlings with experimental seedlings, I followed the growth and survival of seedlings growing near my experimental plots at MP. These seedlings grew within undisturbed surrounding vegetation, unlike experimental seedlings that were placed in weeded plots. Thus, following the fate of these seedlings provided insight into the importance of competition that can affect seedling mortality in spring, before the onset of insect herbivory. In March 1993, I randomly selected and marked with a numbered wire flag 172 seedlings. Every 2–3 weeks I censused marked seedlings and noted individuals that had died during the previous 2- to 3-week interval. For 52 randomly chosen individuals from the total marked pool, I also measured seedling height and average height of the grasses surrounding that seedling.

I repeated these measurements on a new cohort of lupine seedlings in 1994. Within the same area, on 26 February 1994, I randomly selected and marked 83 seedlings. I censused this marked seedling population every 1–3 weeks, and measured the height of each seedling and the average height of grass surrounding each seedling.

Joint effects of competition and herbivory on seedling survival and growth

Interspecific competition for light from surrounding annual grasses is most likely to occur in spring, when grasses are growing rapidly. After grasses senesce in June, lupine seedlings face little threat of being overgrown. Seedling defoliation occurs later, during May and June, when third- and fourth-instar *O. vetusta* larvae that have hatched from overwintering egg masses on lupines abandon defoliated adult lupines, and encounter seedlings. To determine the joint contribution of competition and herbivory on lupine seedling mortality, I established a crossed factorial experiment. Starting in February 1995, I first manipulated the level of interspecific competition around seedlings. Then, in late May, after grasses had senesced, I manipulated levels of herbivory on surviving seedlings that had grown under different competitive regimes.

For the competition experiment, on February 15 1995, I haphazardly selected and marked 238 recently germinated seedlings at MP. I randomly selected 119 of these to receive a competition reduction treatment. This treatment consisted of cutting at ground

level all vegetation growing within a 15-cm radius of each lupine seedling. Control seedlings grew within undisturbed vegetation. Every two weeks from 15 February to 22 June I censused all seedlings, and clipped vegetation that had regrown from the previous clipping. I measured seedling height and height of surrounding grasses (for those seedlings for which the surrounding grass had not been clipped), and noted whether seedlings had died during the previous 2-week period.

Observations in previous years indicated that lupine seedlings that grew surrounded by dense vegetation were taller and thinner than seedlings growing in openings within vegetation. To determine if gains in above-ground stature came at the expense of root biomass, I initiated a separate experiment to determine if reducing levels of interspecific competition might affect lupine seedling shoot:root ratio. I randomly selected 38 seedlings (19 from each of the two competition treatments) from the marked seedling pool to sample destructively. On 17 March I harvested nine seedlings from each of the two competition treatments. Using a hand trowel, I carefully exposed the roots of each plant and removed the plant from the ground, ensuring that the root was not damaged in the process. This was easily accomplished because the soil was moist and sandy. I harvested again on 13 April, this time taking ten seedlings from each of the two treatments. Additional seedling harvests after April were not possible, as lupine roots become too long to remove from the ground undamaged. After each harvest, I dried the plants for 24 h at 60°C, and then determined the dry weight of above and below ground portions of each seedling.

For the defoliation experiment, on 23 May I enclosed eight third- and fourth-instar *O. vetusta* larvae on seedlings previously grown under the two competition regimes. I chose this number of caterpillars based on field results from 1993. Caterpillars were enclosed in 45-cm-tall cylindrical cages (20 cm diameter) that were placed over each lupine seedling and staked to the ground. Defoliation control plants (within each of the two competition treatments) received a cage but no caterpillars. Cages were constructed of chicken wire (mesh size = 3.8 cm) covered with "Tufbell" (Kanebo Corp., Japan) fabric, which allows 92–94% light penetration with a mesh size small enough to keep *O. vetusta* larvae from escaping. I kept caterpillars on plants until plants were completely defoliated, which for most individuals occurred within 3 days. I then monitored the survival of caged seedlings through summer and fall, the period of highest seedling mortality (J. Maron, unpublished work).

Data analysis, effects of tussock moth herbivory on lupine seedling survival

Many seedlings died throughout the experiment for reasons other than insect defoliation. By the time tussock moth larvae were most numerous on experimental seedlings in mid-June, 26% of experimental seedlings had already perished (32% from low density plots, 24% from high density plots). By far the most potent source of mortality for experimental lupine seedlings was the pocket gopher, *Thomomys bottae*. Seedling mortality due to pocket gopher herbivory or gopher tunneling was unambiguous, with seedlings either vanishing down gopher holes or remaining desiccated above ground, with their roots completely severed. By the end of the experiment, an average of 30% of seedlings were killed by pocket gophers, with 63% of the 24 plots having at least one of the six seedlings eaten by a gopher, and 42% of the plots having at least two seedlings eaten by gophers. Since seedling densities in plots diverged in such a way that same-density plots had very different spacing at the time of defoliation, I dropped density as a factor in subsequent analyses. Excluding those seedlings that had died from other sources (i.e. pocket gopher herbivory) before tussock moth larvae colonized plants, I used a Mann-Whitney rank sum test on arcsine-transformed percentages to test whether mean seedling mortality per plot was significantly greater for plants exposed to tussock moth herbivory compared to plants protected from herbivores. Arcsine transformation of percentages equalized variances,

although the distributions were non-normal. The influence of insect herbivory on seedling growth was analyzed using a *t*-test on final seedling heights, pooling all seedlings in each plot and then comparing mean heights of seedlings per plot in control versus treatment plots.

Data analysis, joint effects of competition and herbivory on seedling survival and growth

A chi-square test (with Yate's correction) was used to compare mortality of seedlings receiving different levels of competition and herbivory. Log-linear ANOVA was used to test for an interaction between competition and herbivory on seedling survival. A *t*-test was used to compare mean ratio of length of shoots versus roots of plants that had received different competition treatments. To normalize variances, *t*-tests were performed on log shoot length/log root length.

Results

Effects of tussock moth herbivory on lupine seedling survival

Herbivory on experimental seedlings by tussock moth larvae resulted in significant seedling mortality (Fig. 1). In 1993, tussock moth density was very high (Harrison and Maron 1995) and many of the larvae that colonized seedlings came from nearby mature bushes that had been defoliated. I first saw extremely small second-instar larvae on experimental seedlings on 22 April, with an average of 0.91 larvae per seedling in the unsprayed plots. *O. vetusta* numbers peaked in mid-June, when I counted as many as 20 third- or fourth-instar larvae on

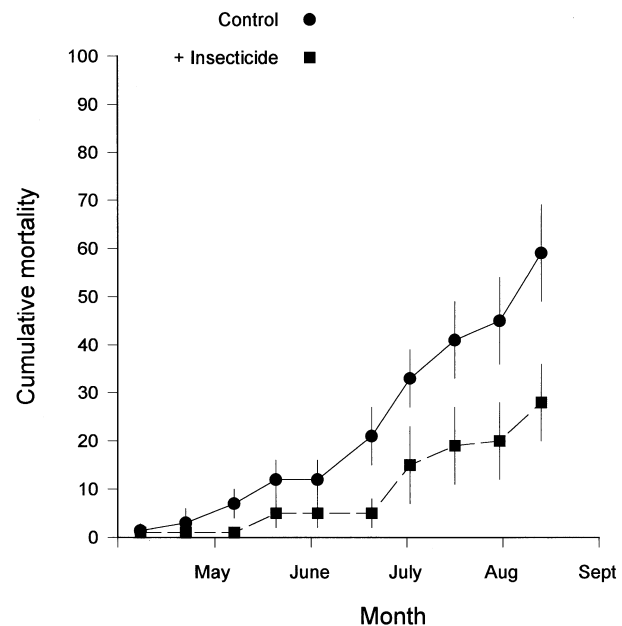


Fig. 1 Mean (\pm SE) cumulative mortality per plot of experimental lupine seedlings exposed to (circles) and protected from (squares) tussock moth herbivory (excluding seedling mortality due to pocket gopher herbivory)

some seedlings, with seedlings in unsprayed plots having an average of $2.7 (\pm \text{SE } 1.1)$ caterpillars on them. Seedlings in herbicide-sprayed plots that had been cleaned of *O. vetusta* larvae were consistently re-invaded by these caterpillars within 1 day, and seedlings in control plots were completely stripped of their leaves in 2 weeks or less. Once plants were denuded of their leaves, caterpillars usually departed to find another host plant; the defoliated seedlings usually died. By the end of the experiment, (excluding those seedlings killed by gophers and root boring insects), an average of 59% of seedlings in control plots had died, whereas an average of 28% of seedlings in sprayed plots had died, a significant difference (Mann-Whitney $U = 193$, $n = 12$, $P = 0.01$). The relatively high mortality of sprayed seedlings was partially a result of the inability of Malathion to completely exclude all *O. vetusta* larvae. On average 7% of control plants were defoliated and died.

Plants eaten but not killed by *O. vetusta* were shorter than seedlings protected from herbivory. On 30 June, seedlings in sprayed plots were significantly taller (mean height = 34.5 cm, $n = 12$ plots) than in control plots (mean height = 22.4 cm, $n = 10$ plots) (t -test on mean heights per plot: $t = -3.14$; $df = 20$; $P = 0.005$), despite the fact that the initial heights of seedlings at the time of planting were indistinguishable (t -test on mean heights per plot: $t = -1.04$; $df = 22$; $P = 0.3$).

Natural seedling survival and growth

Although tussock moth herbivory killed seedlings during early summer 1993, in both 1993 and 1994 many seedlings died in spring, before *O. vetusta* larvae had their greatest impact on survival of experimental seedlings (Fig. 2). During 1993, the heaviest period of mortality for natural seedlings occurred in May; in both years many plants were completely overtopped and lost to view by dense, tall stands of grasses, primarily the introduced annuals *Lolium multiflorum* and *Bromus diandrus*. A substantial number of overgrown plants died. By the end of April 1993, and the end of May 1994, most of the annual grasses had flowered and were just starting to senesce. At these times, the height of grass immediately surrounding marked lupine seedlings was significantly taller than lupine seedling heights (t -test; $df = 90$; $t = 5.3$, $P < 0.0001$ for 1993, t -test; $df = 96$; $t = -7.46$, $P < 0.001$ for 1994). Those seedlings that survived this period eventually grew to a height almost equaling the height of the surrounding vegetation (Fig. 3).

Joint effects of competition and herbivory on seedling survival and growth

Removing shoots of surrounding plants led to higher lupine survivorship (Fig. 4). Only 12% of lupine seedlings that received the grass removal treatment died by the end of May, when most of the grasses had senesced,

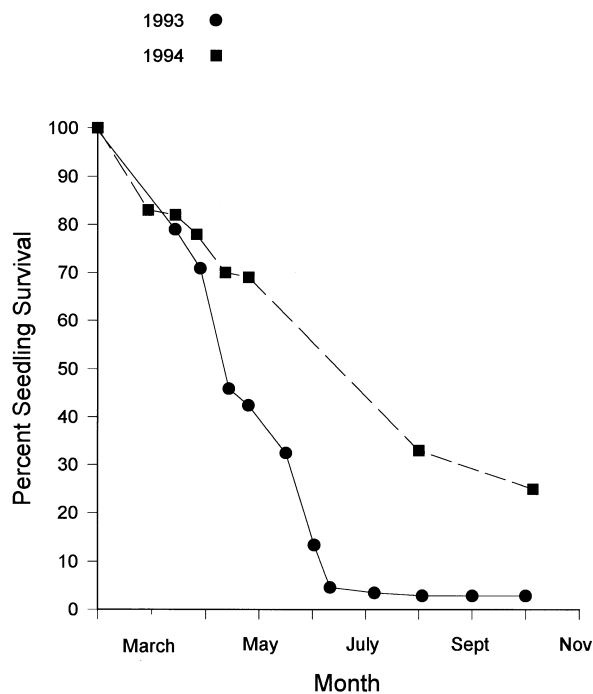


Fig. 2 Lupine seedling survival in 1993 (circles) and 1994 (squares)

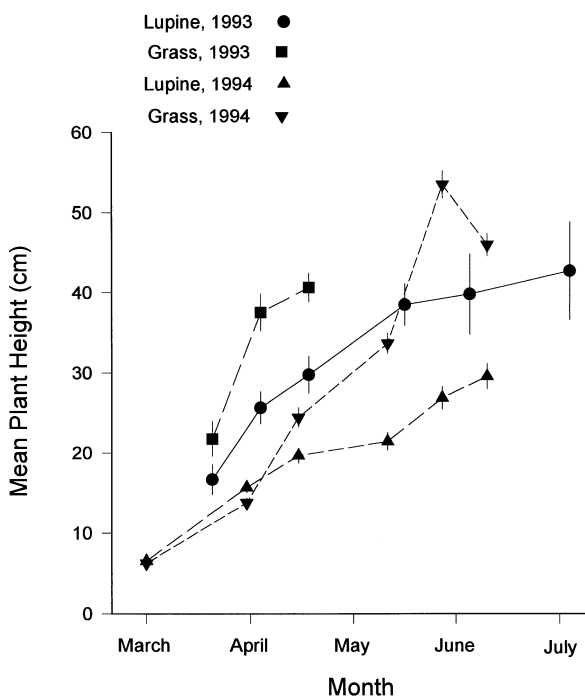


Fig. 3 Mean (\pm SE) height of lupine seedlings and surrounding grasses in 1993 and 1994

compared to 44% mortality for seedlings surrounded by grasses, a significant difference ($\chi^2 = 23.8$, $P < 0.005$).

Lupine seedlings surrounded by vegetation were taller than those growing free from competition (Fig. 5). However, by April, taller seedlings growing with competitors had significantly smaller roots than shorter

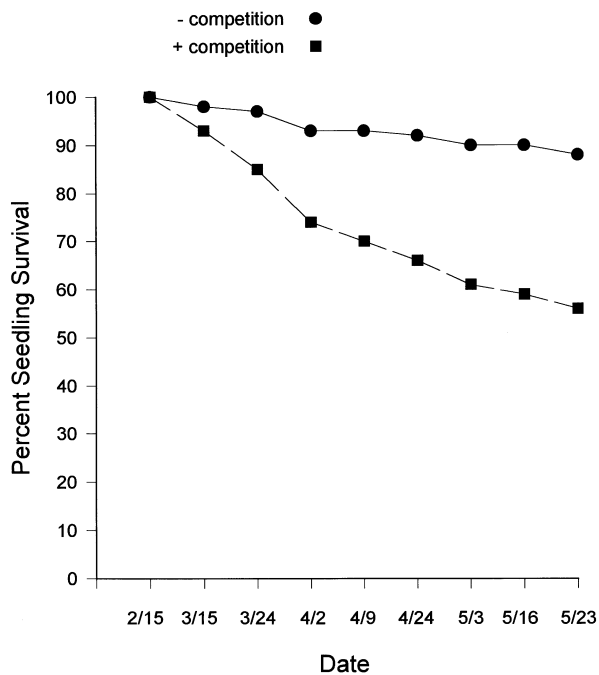


Fig. 4 Survival of lupine seedlings that grew surrounded by (squares) or free from (circles) above-ground competition

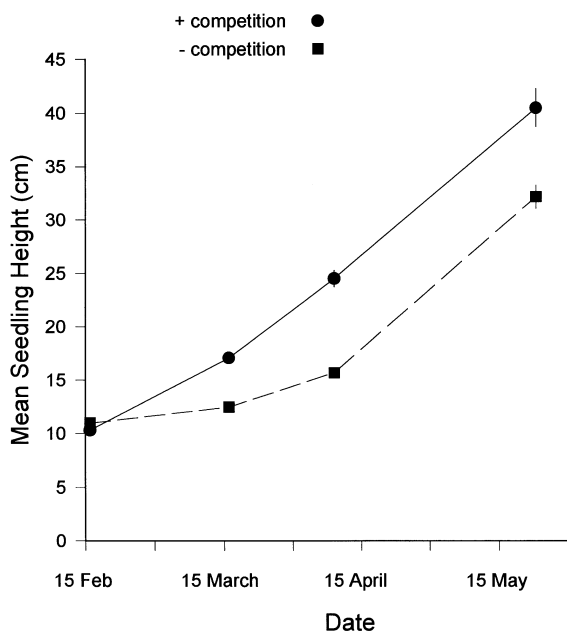


Fig. 5 Mean (\pm SE) height of lupine seedlings that grew surrounded by (circles) or free from (squares) above-ground competition

seedlings growing absent competition (t -test; $df = 16$, $P = 0.001$). Moreover, in both March and April, average shoot:root ratio of harvested plants was significantly greater for seedlings growing surrounded by vegetation compared to seedlings growing free from competition (t -test; $df = 16$, $P = 0.002$ for March, t -test; $df = 18$, $t = -3.33$, $P = 0.004$ for April).

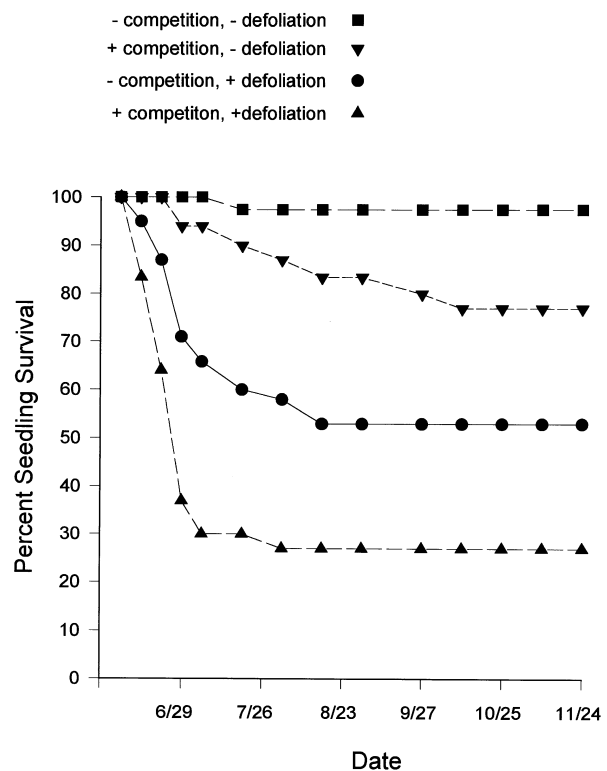


Fig. 6 Effect of previous competitive history and tussock moth defoliation on lupine seedling survival

As in 1993, defoliation by *O. vetusta* had large impacts on lupine seedling survival. Within each of the competition treatments, defoliation led to significantly greater seedling mortality compared to undefoliated individuals (Fig. 6). Moreover, the effects of defoliation on seedling mortality were similar regardless of previous competitive history; there was no statistically significant competition by herbivory interaction (log-linear ANOVA, maximum likelihood $\chi^2 = 1.14$, $P = 0.28$). For seedlings that had previously grown free from surrounding vegetation, defoliation reduced seedling survival by 53% compared to undefoliated seedlings, a significant decrease ($\chi^2 = 17.96$, $P < 0.005$). For seedlings that had previously grown surrounded by vegetation, defoliation reduced seedling survival by 50% compared to undefoliated seedlings, again a significant difference ($\chi^2 = 13.08$, $P < 0.05$; Fig. 6).

In 1995, herbivory appeared to have larger effects on seedling survival than did interspecific competition. Whereas competition reduced seedling survival by 32% during spring, defoliation reduced seedling survival by an even greater percentage – 50% – through summer and fall. Defoliation had large effects on seedling survival, despite the fact that seedlings were robust and tall before they were defoliated. Mean seedling height at the time of defoliation was 40.3 and 32.5 mm, respectively, for plants that had previously grown either surrounded by competitors or without competition.

Discussion

This study indicates that both interspecific competition and insect herbivory contribute to high mortality of bush lupine seedlings. Both natural and experimental defoliation of lupine seedlings by tussock moth caterpillars led to significantly greater seedling mortality compared to control plants protected from herbivores. In 1993, experimental seedlings that ultimately died were completely stripped of their leaves and were unable to re-leaf, even after the caterpillars had pupated. In a majority of years, defoliation of adult bush lupines by tussock moth larvae is both conspicuous and dramatic. This massive defoliation occasionally results in adult plant death, but much more frequently adult lupines re-leaf and live on (Harrison and Maron 1995). Lupine seedlings, however, are extremely vulnerable to defoliation, and inconspicuous herbivory by just a few late-instar larvae can kill individuals. When experimentally defoliated in 1995, lupine seedlings were only exposed to caterpillars for a few days, but this was enough to significantly increase seedling mortality compared to undefoliated plants. In many plant populations, insect herbivory on seedlings can be subtle and short-lived. This type of herbivory may occur routinely, but is probably overlooked in many systems. To fully understand the potential impacts of insect herbivores on plant populations, more experimental tests of the role of herbivory in plant establishment are needed (Louda et al. 1990).

Data from monitoring natural seedlings illustrate that the link between seedling distribution and abundance and herbivore activity is complex. Many natural seedlings in both 1993 and 1994 died before tussock moth larvae took their toll on experimental seedlings. Results from experimentally removing competitors showed that through spring, lupines compete with surrounding vegetation, and that shading and overgrowth by exotic grasses can also result in significant seedling mortality. Within 1 year, defoliation killed a slightly greater percentage of seedlings (17%) than competition. However, since the strength of these factors undoubtedly change from year to year depending on competitor and herbivore density, longer study is required to more fully assess the relative importance of these factors on seedling survival.

Seedlings surrounded by grasses were often tall and thin, and had significantly reduced root biomass compared to lupine seedlings that grew free from competition. Since plants with smaller roots might have fewer reserves to fuel re-leafing after herbivory, it seemed reasonable to expect that defoliation would have more severe effects on plants previously exposed to competition compared to competition-free plants. However, competitive history had little impact on the net effect of defoliation (Fig. 6); effects of competition and herbivory on seedling survival were additive. Unlike other systems where herbivory alters plant height (or growth), which then alters competitive ability (Louda et al. 1990), in this

system competition occurs first, with seedlings surviving into summer then having to contend with herbivory.

Lupines fix nitrogen and grow rapidly (Gadgil 1971; Sprent and Silvester 1973; Bentley and Johnson 1991). Via their leaf litter, they add significant amounts of nitrogen to the sandy soils (Alpert and Mooney 1996; Maron and Connors 1996; Maron and Jefferies unpublished work). Soils that have historically been occupied by bush lupine have more nitrogen and support greater grass biomass than soils in adjacent grasslands free of bush lupine, where nitrogen is limiting to plant growth (Maron and Connors 1996; Maron and Jefferies unpublished work). Due to this nitrogen enrichment, and the subsequent effects on grass biomass, lupines can alter the competitive environment, to the detriment of their own seedling survival.

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