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## Influence of herbivores on a perennial plant: variation with life history stage and herbivore species

Received: 25 June 2001 / Accepted: 9 April 2002 / Published online: 25 May 2002  
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**Abstract** Herbivores have diverse impacts on their host plants, potentially altering survival, growth, fecundity, and other aspects of plant performance. Especially for longer-lived plant species, the effects of a single herbivore species can vary markedly throughout the life of the host plant. In addition, the effects of herbivory during any given life history stage of a host plant may also vary considerably with different types of herbivores. To investigate the effects of herbivory by black-tailed deer (*Odocoileus hemionus columbianus*) and snails (*Helminthoglypta arrosa* and *Helix aspersa*) on a nitrogen-fixing shrub, *Lupinus chamissonis*, we established three exclosure experiments in a sand dune system on the coast of northern California. These experiments documented that deer browsing significantly reduced the volume and growth rate of lupines in the seedling and juvenile life stages. Since plant volume was strongly correlated with aboveground dry biomass for lupines, such herbivore-induced reductions in volume should translate into losses of aboveground biomass. Deer browsing also significantly altered the likelihood of attack by and density of a leaf-galling cecidomyid fly (*Dasineura lupinorum*), suggesting that a vertebrate herbivore indirectly affected an invertebrate herbivore in this system. Although deer did not significantly affect the survival of lupine seedlings and juveniles, individuals protected from deer had consistently greater survival in the two separate experiments. Our results revealed that snails did not have a significant effect on the survival or growth of juvenile plants, despite being common on and around lupines. An exclosure experiment

revealed that herbivory by deer significantly reduced the shoot lengths of mature shrubs, but led only to a minimal reduction in growth rates. In addition, we found that browsed shrubs had significantly greater inflorescence production, but also produced individual seeds with significantly reduced mass. Collectively, these data indicate that deer and snails have widely differing effects on their shared host plant; browsing by deer indirectly affects insect herbivores, and the impacts of deer change markedly with the life history stage of their host plant.

**Keywords** Age-specific effects of herbivory · Coastal dunes · Deer and snail herbivory · Gall-forming cecidomyids · indirect effects · *Lupinus chamissonis*

### Introduction

The susceptibility and responses of plants to herbivory often change markedly during their lifetimes. Seedlings are generally regarded as the life history stage most vulnerable to mortality caused by herbivores (Crawley 1989; Hanley et al. 1995; Hanley 1996; but see Weltzin et al. 1998). Although usually less apparent to herbivores than more established plants (Feeny 1976; Rhoades and Cates 1976; Crawley 1983), seedlings are often less defended against (and/or more palatable to) herbivores and have lower proportions of carbohydrate resources available for recovery from herbivory (Crawley 1983; sensu Bryant and Julkunen-Tiitto 1995; Fenner et al. 1999). As plants mature, the impacts of herbivores typically shift from outright mortality to reductions in plant growth and fecundity (Crawley 1983, 1989; Ehrlén 1995). However, these generalizations have not been well substantiated by field studies that evaluate the effects of a single herbivore species on multiple life history stages of the same host plant (although see Louda and Potvin 1995). Such studies are critical for assessing the ecological and selective importance of herbivory for perennial plant species (Crawley 1985; Doak 1991, 1992; Whitham et al. 1991).

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The effects of herbivory during any given life history stage of a host plant may also vary with different types of herbivores (Crawley 1989; Strauss 1991; Hulme 1994). For example, vertebrate and invertebrate herbivores differ substantially in size, metabolic rate, feeding pattern, mobility, and dietary preference (Crawley 1989; Lindroth 1989). The effects of these two herbivore groups on their host plants should be profoundly influenced by such differences. Further, the relative importance of vertebrate and invertebrate herbivores may shift appreciably from one life history stage of a host plant to another. While seedlings and young plants are especially vulnerable to damage by invertebrates and smaller vertebrates (Crawley 1983, 1989; Hulme 1994; Hanley et al. 1995; Hanley 1996), mature plants, particularly longer-lived perennials, may be more likely to sustain damage from larger vertebrates (Crawley 1983).

Through its direct effects on a host plant, one herbivore species can indirectly alter the success of other herbivorous species using the same host (Faeth 1986; Strauss 1991). For example, numerous studies have shown that secondary plant metabolites, produced in response to feeding damage at one point in time, can function as induced defenses that reduce host-plant quality for subsequent herbivores (Bryant et al. 1985; Karban and Baldwin 1997; Agrawal 1999; Tollrian and Harvell 1999). While most studies of plant-mediated indirect effects have focused on interactions between temporally separated insect herbivores, a handful of studies consider interactions between more distantly related taxa, such as mammals and invertebrates (Strauss 1991; Roininen et al. 1997; Suominen et al. 1999a, b). These studies have reported widely differing results: Roininen et al. (1997) found that herbivory by moose indirectly benefited two hymenopteran herbivore species, whereas Strauss (1991) found that previous herbivory by two beetle species decreased the likelihood of future browsing by white-tailed deer. These results underscore the point that multiple herbivores using the same host at different times and plant life history stages can interact indirectly with each other in significant and often variables ways.

In this paper, we report on results from a study designed to assess the effects of vertebrate and invertebrate herbivores on seedlings, juveniles, and reproductive-age individuals of a nitrogen-fixing shrub, *Lupinus chamissonis*, in a sand dune ecosystem. Using three enclosure experiments, we have addressed the following questions: (1) Do vertebrate and invertebrate herbivores affect the survival or growth of *Lupinus* seedlings and juveniles? (2) Do the effects of vertebrate herbivores on the growth and fecundity of *Lupinus* individuals vary with life history stage of this species? and (3) Do vertebrate herbivores indirectly affect the abundance of invertebrate herbivores on their shared host plant species?

#### Study sites and organisms

We conducted this study in a coastal hind dune system on Bodega Head, California (38° 19' N, 123° 3' W). This

region has a Mediterranean-type climate, with 90% of the annual precipitation falling from October through April (Barbour et al. 1973). The sandy soils of this area are fast-draining, nitrogen-poor, and strongly alkaline (Barbour et al. 1973; J. H. Cushman, unpublished data). Unlike many dune systems in California, this site is not dominated by *Ammophila arenaria* (Poaceae; European beachgrass), and still has a relatively diverse native flora. It supports a population of the nitrogen-fixing shrub *Lupinus chamissonis* (silver bush lupine; Fabaceae), which averages 15% cover in the area. Seedlings of *Lupinus* are abundant following substantial winter rains and subsequent warming of dune soils. However, seedling mortality during the first several months of each growing season is high. The growth of surviving individuals of this evergreen, woody, perennial species typically corresponds to seasonal pulses of soil moisture, with shoot and leaf development being greatest from late winter through spring. Although flower production in this population is highly variable from year to year, inflorescences are produced on new terminal shoots from March through May, starting when plants are 1 year to a few years old (P.J. Warner and J.H. Cushman, personal observation). Fruit set follows soon after flowering, with seeds expelled as pods dry. Plants that reach reproductive maturity usually survive from 6 to 10 years (P.G. Connors, personal communication). Another bush lupine species, *Lupinus arboreus*, also occurs in the dunes at Bodega Head (Barbour et al. 1973; Maron and Simms 1997), but is not very abundant at our study site. Various annual and perennial forbs (herbaceous dicotyledons) and grasses also grow at this site, with the interstices among shrubs generally dominated by the exotic annual grass, *Vulpia bromoides* (Poaceae).

Numerous vertebrate herbivores are found on Bodega Head (Barbour et al. 1973), and black-tailed deer (*Odocoileus hemionus columbianus*) and California hares (or black-tailed jackrabbits, *Lepus californicus*) are especially common. Black-tailed deer feed on a variety of forbs and shrubs, whereas hares graze primarily on grasses and forbs (J.H. Cushman and P.J. Warner, personal observation). Other mammalian consumers in this system include brush rabbits (*Sylvilagus bachmani*), meadow voles (*Microtus californicus*), and deer mice (*Peromyscus maniculatus*). The dunes also feature at least two abundant mollusc species: the native snail *Helminthoglypta arrosa* and the non-native snail *Helix aspersa*. Both species are active primarily during the rainy season, feeding on a variety of perennial and annual plants.

In addition to mammals and molluscs, silver bush lupine hosts a number of insect herbivores, including root borers, miners of shoot tips, inflorescences and seeds, folivores, and stem- and leaflet-gallers, such as the galling midge *Dasineura lupinorum* (Diptera: Cecidomyiidae).

## Methods

### Seedling experiments

In late January 1996, we initiated a seedling experiment designed to assess the impacts of mammalian herbivores on the survival and growth of *Lupinus chamissonis* juveniles. We selected 200 naturally occurring lupine seedlings from throughout our dune site (approximately 300×200 m in size). Each seedling was less than 1 month old, with two healthy cotyledons and no more than two true leaves. We randomly assigned them to either exposure to or protection from vertebrate herbivores. Enclosures consisted of cylindrical poultry-mesh cages, 45 cm high×20 cm in diameter, anchored into the sand with steel U-shaped stakes. Periodically, we increased the sizes of cages to allow for increased plant size. These enclosures did not significantly alter ambient light levels, wind speed, air or soil temperatures (P.J. Warner, unpublished data).

Every 2–5 weeks, from 15 February 1996 through 15 January 1998, we collected data on seedling survival. At the outset of this experiment (1 February 1996), we also measured the height of each seedling and the length (base to tip) of either the longer leaflet or cotyledon on each plant (whichever was uppermost and fully developed). We then averaged these two measurements in order to derive a seedling radius, and estimated seedling volume using the formula for the volume of a hemisphere ( $V=2/3 r^3$ ). We then resumed estimating volume, for the duration of the experiment, approximately once a month starting in November 1996. We accomplished this by measuring the maximum height and three radii of each plant's canopy area, from plant center to perimeter, at 120° arcs around its circumference. We then averaged these four measurements to derive a mean radius, and used this result to calculate plant volume using the formula for the volume of a hemisphere. In April 1997, we haphazardly selected five compound leaves on each surviving lupine seedling, and measured the lengths of the three longest leaflets of each leaf. We then pooled the leaflet lengths on each plant (15 leaflet lengths) to generate a mean leaflet length per seedling.

In January 1997, we established a second seedling experiment to assess the joint effects of mammalian and molluscan (*Helminthoglypta* and *Helix*) herbivores on lupines. This experiment consisted of a two-way factorial design, with mammals (present or absent) and molluscs (present or absent) as the grouping factors. We grouped 160 newly germinated seedlings into 40 blocks of four, with seedlings within blocks matched for physical proximity and microhabitat. We randomly assigned each plant to one of four possible treatments: mammalian herbivores excluded, molluscan herbivores excluded, both herbivores excluded, and both herbivores present. As in the 1996 study, we excluded vertebrate herbivores with cylindrical poultry-mesh cages (snails were not deterred by these cages; P.J. Warner, unpublished data). To exclude snails, but allow access by all other herbivores, we placed Snail Barr copper cylinders, 5 cm high×12 cm diameter, around seedlings. When the mucous membranes of molluscs come into contact with the copper, an electrical current is generated that repels them. Terrarium trials substantiated the effectiveness of this material as a mollusc deterrent (P.J. Warner, unpublished data). From February 1997 through January 1998, we recorded survival of seedlings every 2–4 weeks. We measured plant heights and radii at the outset of the experiment (1 February) in the same manner as for the 1996 seedlings, and resumed calculating volume monthly, also as described above, beginning in August 1997, for the duration of the 1997 experiment.

A persistent issue in ecology has been the statistical problems associated with repeated measurements of the same sampled units (Underwood 1997). One approach has been to analyze such data using repeated-measure ANOVAs, which take into account the non-independence of multiple measurements over time for the same units. However, problems with these analyses arise when individuals die during the course of a study. When this occurs, one must choose between two unsatisfactory options: either exclude all data collected for dead individuals or enter zeroes after deaths

and contend with data that no longer conform to the assumptions of ANOVA. This situation occurred in both seedling enclosure experiments (and the mature shrub experiment discussed below), as many lupines died during the study period. To address this issue, we developed response variables that measured the effects of our treatment variable (presence or absence of mammalian herbivores) on average lupine growth over time. This method enabled us to use all plants initially included in the experiments without entering zeros for plants after they died. For each plant, we calculated an index which equaled the difference in plant volume between two successive sample dates divided by the number of days elapsed between these dates, summed over the entire experiment, and divided by the number of time intervals a plant lived. Thus, for each plant, the index equaled  $[(V_2-V_1)/t_1+(V_3-V_2)/t_2+(V_4-V_3)/t_3+\dots+(V_{n+1}-V_n)/t_n]/N$ , where  $V$  is plant volume,  $t$  corresponds to days between measurements, and  $N$  refers to the number of time intervals used for a plant. This daily rate was then multiplied by 30 to generate a monthly rate.

We analyzed most data from these experiments using either one- or two-way ANOVAs in the JMP 3.1 statistical program (SAS Institute). The grouping factor for the first seedling experiment was mammalian herbivores (present or absent), whereas molluscs (present or absent) and mammals (present or absent) were grouping factors for the second experiment. For both experiments, monthly growth rates were the response variable. Data on leaflet length were also included for the 1996 experiment. We log-transformed growth rate data to correct for heterogeneity of variances. Loss of degrees of freedom due to seedling mortality precluded us from using block as a grouping factor for these analyses in the second experiment.

We used survival analysis in the JMP 3.1 program to assess the effects of herbivores on lupine survival in the 1996 and 1997 seedling experiments. Specifically, we used Cox's Proportional Hazard Model, which is a semiparametric regression model that evaluates the effects of grouping factors on survival times. We used one factor (presence/absence of mammalian herbivores) in the 1996 experiment and two factors in the 1997 experiment (presence/absence of mammalian and molluscan herbivores).

### Mature shrub experiment

In April 1996, we established a third enclosure experiment involving reproductively mature *Lupinus* shrubs. This experiment consisted of a two-way factorial design, with mammalian herbivores (present or absent) and block as the grouping factors. We grouped 72 plants into 18 blocks of four, based on size similarity and physical proximity of plants. In each block, we assigned two shrubs to herbivore enclosures, with the other two plants unmanipulated to serve as controls. Enclosures consisted of 1 m-high steel poultry-mesh fencing supported by wooden stakes. As needed, we increased the size of enclosures to allow for shrub growth.

To assess the effects of mammals on the growth of individual shoots, we haphazardly selected branches in each of four canopy quarter-sections of every shrub. These branches had a minimum length of 1 cm, and were approximately 10, 60, and 110 cm from the center of a shrub, and at the shrub perimeter. Smaller shrubs had at least eight marked shoots, and the larger shrubs a maximum of 16.

Every 6 months from May 1996 through January 1998, we calculated plant volume, as in the seedling experiments (maximum height and three radii of the canopy of each shrub, averaged to calculate a mean radius to use in the formula for the volume of a hemisphere), and measured the length of marked branches. Beginning with the first appearance of flowers in March 1997, we counted the total number of inflorescences on each of these plants approximately every 2 weeks for 10 weeks. In June 1997, we collected and dried (at 60°C for 48 h) up to 30 fruits harvested from each plant and determined mean seed weight (mg) per plant.

We analyzed data from the mature shrub experiment using two-way ANOVAs, with mammalian herbivores (present or absent) and block (1–18) as the grouping factors. Shrub volume,

shoot length, number of inflorescences, and seed weight were the response variables, with both volume and shoot length estimated using the index described previously. One block was omitted from the seed weight analysis because the plants within it did not produce seed. We log-transformed both shrub volume and shoot length data to correct for heterogeneity of variances.

#### Biomass assessments

Although biomass can be an excellent predictor of reproductive success in plants (Crawley 1983), sampling biomass is destructive and prevents further data collection. Since we were interested in the long-term response of lupines to herbivory, we evaluated whether plant volume was a valid and non-destructive predictor of biomass. To determine the relationship between plant volume and aboveground biomass, we selected 25 lupine plants of various sizes from the dune population in June 1998. For each plant, we determined plant volume as outlined previously, then cut the primary stem of each plant at ground level. We removed accumulated sand and detritus from lower branches, dried the plants at 60°C for 72 h, and weighed them. We used linear regression analysis to evaluate the relationship between shrub volume and aboveground dry biomass, and log-transformed data to correct for heterogeneity of variances.

#### Abundance of leaflet galls

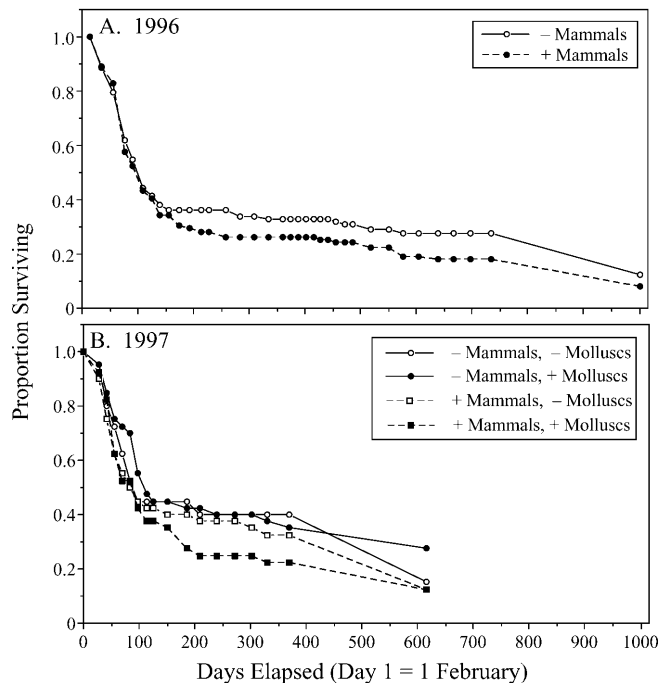
In April 1997, we determined the abundance of *Dasineura lupinorum*, a common leaflet galler of silver bush lupine, to evaluate the effect of mammalian herbivores on this insect. We counted the total number of galls on each juvenile plant surviving from the 1996 seedling experiment, and analyzed these data in two ways. First, using a 2×2 contingency table, we considered whether the likelihood of being galled by *Dasineura* was independent of herbivore treatment level (herbivores present or absent). Second, for those plants that had any level of galling, we used a one-way ANOVA to determine whether gall density (galls/shrub volume) differed significantly between herbivore treatment levels (herbivores present or absent). To correct for heterogeneity of variances, we square-root transformed data on gall density prior to statistical analysis.

## Results

### Seedling experiments

In both the 1996 and 1997 experiments, neither mammalian nor molluscan herbivores had significant effects on seedling/juvenile survival time through the second growing season (Fig. 1; Table 1 a). There was a trend for plants protected from mammals to survive longer than unprotected individuals, and this difference was consistent for both experiments.

Mammalian herbivores had a significantly negative effect on growth rates of juvenile lupines in both the 1996 and 1997 experiments (Fig. 2; Table 1 b). After 2 years of growth, the 1996 seedlings protected from mammalian herbivores were, on average, over five times larger in volume than those exposed to mammals. In the 1997 seedling experiment, we observed a similar pattern, with protected juveniles more than four times larger than their uncaged counterparts after 1 year. Molluscs did not have a significant impact on seedling/juvenile volume in 1997, nor was the interaction between molluscs and mammals significant (Table 1 b). Mammals also had a significantly negative effect on mean leaflet size in the



**Fig. 1** Proportion of *Lupinus chamissonis* seedlings surviving through time as a function of the presence or absence of mammalian herbivores (A) and the presence or absence of both mammalian and molluscan herbivores (B)

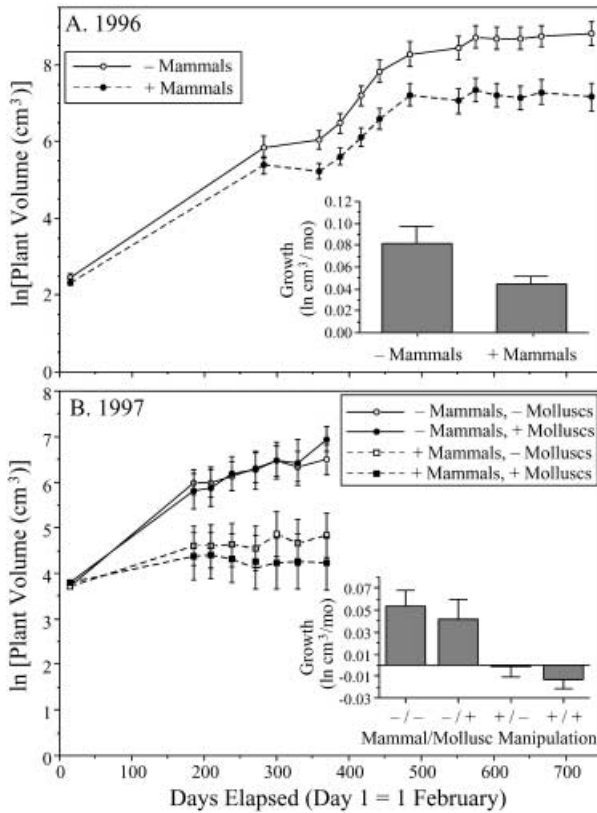
**Table 1** Results from statistical analyses evaluating the influence of mammalian and molluscan herbivores (present, absent) on the survival and growth rate of *Lupinus chamissonis* seedlings/juveniles in two experiments (1996 and 1997). Likelihood-Ratio Tests ( $\chi^2$ ) are presented for survival analyses whereas ANOVAs are shown for growth rates

Variable/ year	Source	df	MS	$\chi^2/F$	P
Survival					
A. 1996	Mammals	1	–	0.81	0.368
1997	Mammals	1	–	2.04	0.153
	Molluscs	1	–	0.05	0.828
	Mammals×Molluscs	1	–	0.47	0.494
B. Growth rate					
1996	Mammals	1	0.072	3.95	0.052
	Error	57	0.018		
1997	Mammals	1	0.289	21.43	<0.001
	Molluscs	1	0.017	1.29	0.262
	Mammals×Molluscs	1	0.002	0.17	0.685
	Error	54	0.014		

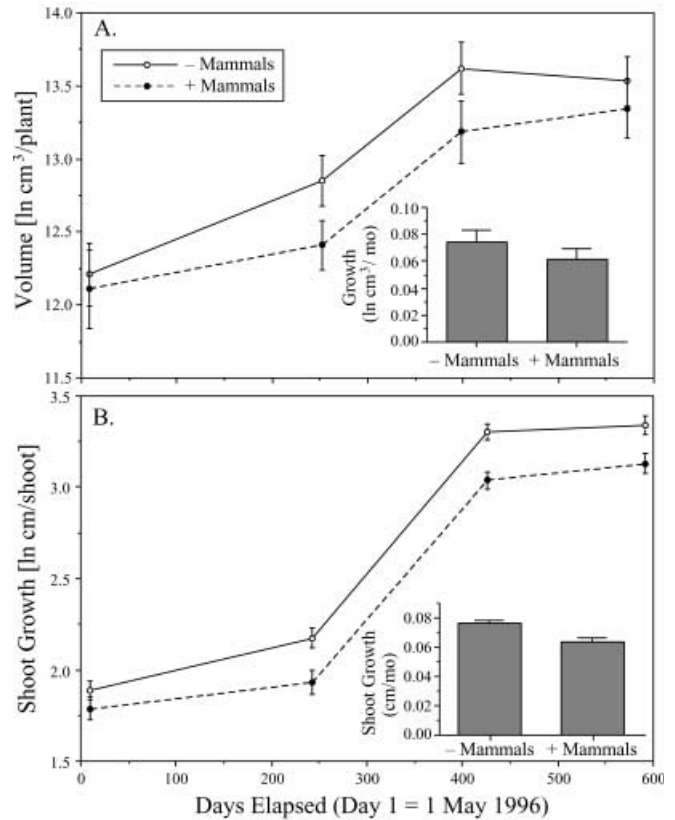
1996 seedlings/juveniles, as measured in April 1997, when the plants were approximately 15 months old ( $16.8 \pm 0.7$  mm vs  $19.4 \pm 0.7$  mm;  $F_{1,56} = 6.36$ ,  $P = 0.015$ ).

### Mature shrub experiment

Results from our herbivore-exclosure experiment with mature shrubs were more ambiguous than those obtained for lupine seedlings and juveniles (Figs. 3, 4; Table 2).



**Fig. 2** Volume of juvenile *Lupinus chamissonis* plants through time and lupine growth rates per month as a function of the presence or absence of mammalian herbivores (A) and the presence or absence of both mammalian and molluscan herbivores (B). Data were log-transformed to correct for heterogeneity of variances. Vertical lines correspond to  $\pm 1$  SE



**Fig. 3** Plant volume (A) and mean shoot length (B) through time in mature *Lupinus chamissonis* shrubs and lupine growth rates per month as a function of the presence or absence of mammalian herbivores. Data were log-transformed to correct for heterogeneity of variances. Vertical lines correspond to  $\pm 1$  SE

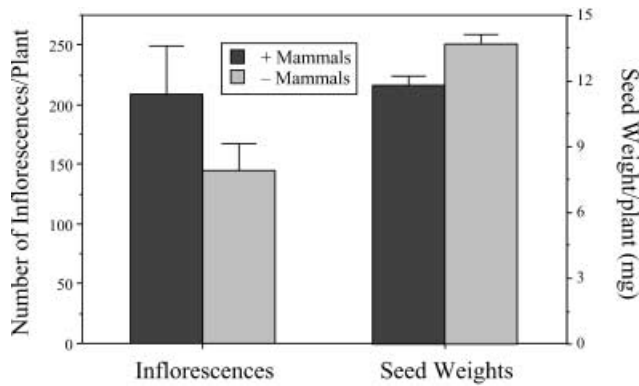
**Table 2** Results from two-way ANOVAs evaluating the effects of mammalian herbivores (present, absent) and block (1–18) on the growth rate, shoot length, inflorescence number, and seed weight of mature *Lupinus chamissonis* shrubs

Variable	Source	df	MS	F	P
A. Growth rate	Mammals	1	0.003	3.68	0.063
	Block	17	0.009	11.16	<0.001
	Mammals×Block	17	0.001	1.38	0.202
	Error	36	0.001		
B. Shoot length (cm)	Mammals	1	0.024	11.12	<0.001
	Block	17	0.008	3.75	<0.001
	Mammals×Block	17	0.002	0.92	0.549
	Error	36	0.002		
C. Inflorescence abundance	Mammals	1	72517.0	8.64	0.006
	Block	17	111,333.3	13.27	<0.001
	Mammals×Block	17	8003.9	0.95	0.532
	Error	36	8392.0		
D. Seed weight (mg)	Mammals	1	68.031	6.98	0.012
	Block	16	5.489	0.56	0.889
	Mammals×Block	16	8.830	0.91	0.569
	Error	34	9.744		

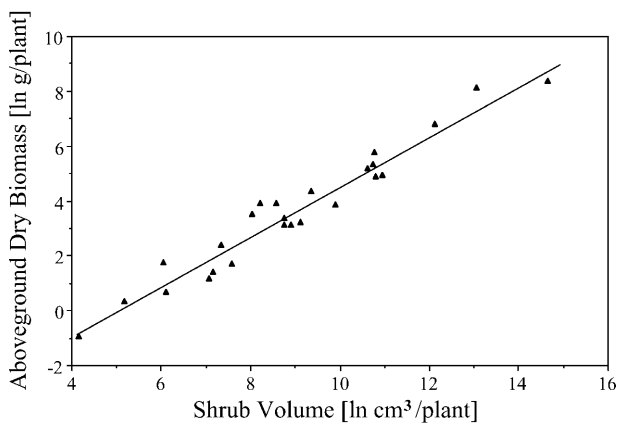
Mammals had no effect on shrub survival (Likelihood Ratio  $\chi^2=0.57$ ,  $df=1$ ,  $P=0.45$ ) and reduced growth rates of mature shrubs, although this was significant at the 0.063 level (Fig. 3A, Table 2 a). From May 1996 through December 1997, shrubs protected from mammalian herbivores increased an average of 184% in volume, while

unprotected plants increased by 152%. Although the blocking factor alone was significant, the mammal×block interaction term was not significant.

During the same time period, mammals had a significantly negative effect on the lengths of individual shoots on the same shrubs (Fig. 3b, Table 2 b). Plants protected



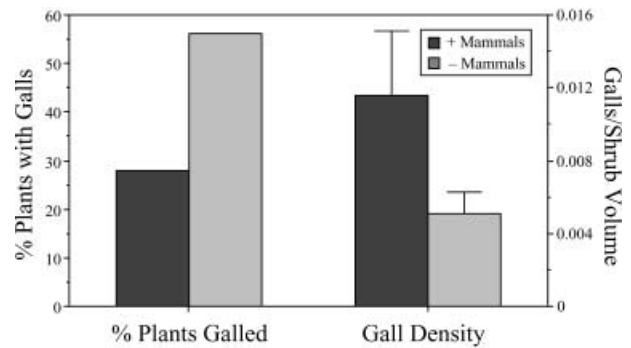
**Fig. 4** Fecundity of mature *Lupinus chamissonis* shrubs as a function of the presence or absence of mammalian herbivores. The mean number of inflorescences per plant (A) and the mean dry seed weight per plant (B). Vertical lines correspond to  $\pm 1$  SE



**Fig. 5** Relationship between aboveground dry biomass and shrub volume for *Lupinus chamissonis*. Both variables were log-transformed to correct for heterogeneity of variances

from mammalian herbivores had longer shoots than those left exposed to mammals: shoots on protected plants increased in mean length by 442%, while shoots on unprotected shrubs increased by 383%. Again, the block effect was significant, but the mammal $\times$ block term was not (Table 2 b).

After 1 year of manipulation, our experiment revealed that mammalian browsing significantly increased the numbers of inflorescences produced by shrubs (Fig. 4, Table 2 c). Plants exposed to herbivores had 1.5 times more inflorescences on average than protected shrubs. In contrast, our data indicated that mammalian herbivory significantly reduced mean seed weight per shrub (Fig. 4, Table 2 d). As with other parameters in this experiment, seed weight varied significantly among blocks. However, the mammals $\times$ block interaction term was not significant.



**Fig. 6** Influence of mammalian herbivores on the percent of *Lupinus chamissonis* shrubs galled by *Dasineura lupinorum* and the number of galls per plant corrected for shrub volume. Vertical lines correspond to  $\pm 1$  SE

### Biomass assessment

As shown in Fig. 5, linear regression analysis revealed that aboveground dry biomass of silver bush lupine increased significantly with increasing plant volume ( $y = -4.59 + 0.92x$ ;  $R^2 = 0.95$ ;  $F_{1, 23} = 414.06$ ;  $P < 0.0001$ ). Since plant volume predicted 95% of the variation in plant biomass, non-destructive measurements of plant volume were an accurate substitute for destructive sampling of aboveground biomass.

### Abundance of leaflet galls

As shown in Fig. 6, plants exposed to mammalian herbivores were significantly less likely to have *Dasineura* galls on their leaflets than protected plants (Likelihood Ratio  $\chi^2 = 4.65$ ,  $df = 1$ ,  $P = 0.031$ ). However, in contrast, for those plants attacked by this insect, there was a strong trend for gall density (galls/plant volume) to be greater for lupines exposed to mammalian herbivores compared to controls (Fig. 6;  $F_{1, 23} = 3.53$ ,  $P = 0.073$ ).

## Discussion

Our data indicate that herbivores have variable influences on a perennial plant in a coastal dune ecosystem. Field experiments demonstrated that mammalian herbivores significantly reduced growth rates of younger plants, as well as influenced the use of lupines by an insect herbivore. In contrast, these same herbivores had less clear-cut effects on mature shrubs: they had minimal effects on plant growth, increased inflorescence production, and decreased seed mass. In addition, herbivorous snails did not have a significant effect on survival or growth of juvenile lupines. These results suggest that the effects of herbivores on lupines in our system are strongly species- and stage-specific.

The effects of herbivores on lupines could have been caused by a number of mammalian species in our system, either individually or collectively. The possible

candidates are black-tailed deer (*Odocoileus*), California hares (*Lepus*), brush rabbits (*Sylvilagus*), meadow voles (*Microtus*), and deer mice (*Peromyscus*). The small size of both *Microtus* and *Peromyscus* eliminates them from consideration, as they could easily pass through the enclosure fencing used in this study (J.H. Cushman, unpublished data). However, the enclosure cages were capable of excluding the three remaining herbivore species. Based on extensive observations and physical evidence, we hypothesize that deer, rather than hares or rabbits, are the herbivores responsible for the observed impacts on *Lupinus*. Three lines of evidence support this view. First, scat produced by hares and rabbits was almost entirely comprised of graminoid fragments at our site, whereas this was not the case for deer (J.H. Cushman, personal observation). Second, much of the browsing damage sustained by lupine shrubs was on shoots well above the reach of hares and rabbits. Third, on multiple occasions, we observed deer feeding on lupines and often found their hoof prints around recently browsed plants.

Deer had a dramatically negative impact on the volume and growth rates of juvenile lupines (Fig. 2). Because volume and aboveground biomass were so strongly correlated (Fig. 5), the decreases in plant volume shown experimentally can be readily translated into reductions in aboveground biomass. Deer also had a significantly negative effect on leaflet size, a result that should further contribute to overall biomass loss. Reductions in biomass have often been shown to negatively influence reproduction, through delayed or decreased flowering (Crawley 1983; Mulder and Harmsen 1995), decreased vegetative reproduction (Bonser and Reader 1995), and reduced fruit and seed production (Crawley 1983; Hendrix 1988; Bonser and Reader 1995; Ehrlén 1995; Louda and Potvin 1995). Herbivore damage to shoots can also delay or alter sexual expression (Whitham and Mopper 1985; Juenger and Bergelson 1997).

The seedling stage is a vulnerable period for most plants, and herbivores commonly reduce seedling survival (Harper 1977; Crawley 1983; Hulme 1994; Ehrlén 1995; Hanley et al. 1995; Hanley 1996; Crawley 1997). However, neither of our seedling experiments (1996 or 1997) demonstrated that protected lupine seedlings survived in significantly greater numbers than their unprotected counterparts (Fig. 1). Nevertheless, in both experiments, we observed a trend of increased mortality in unprotected juvenile plants, which appeared approximately 150 days after germination. These results suggest that the effects of mammalian herbivory on juvenile plants may be age- or size-dependent. This view is supported by additional data showing that the effects of deer browsing on lupine growth did not appear until 200–275 days after germination (Fig. 2). Two potential explanations may be responsible for these results. First, lupines may become more palatable to herbivores as they age. Although some support for this view comes from studies showing that young plants are more heavily defended than older ones (Coley 1986; Roininen et al. 1993; Spiegel and Price 1993), these data come from tree

species and focus on comparisons between juvenile and older trees rather than seedlings and established plants. This explanation also is not supported by the findings of Fenner et al. (1999), who found that seedlings were generally more palatable to herbivores than adults (based on a study of 29 herbaceous species). Second, juvenile lupines may become more apparent to deer as they age and increase in size. We suspect that this latter explanation is more plausible for our system, as other studies have shown that plant size is a crucial factor that triggers the onset of browsing (Harper 1977; Hulme 1994; Hanley et al. 1995; Hanley 1996).

Snails and slugs have decidedly negative impacts on seedling survival for many plant species (Hulme 1994; Ehrlén 1995; Hanley et al. 1995; Hanley 1996; Crawley 1997). Although snails commonly feed on lupines and are abundant in our dune study system during moist, cool periods of the year (generally November–March), neither seedling mortality nor growth was significantly affected by mollusc herbivory in our experiment. Late winter and the entire spring of 1997 was a relatively dry period, with only 18.5 cm of rain falling from February 1 through June 30, compared with 50.8 cm for the same period in 1996 (Bodega Marine Laboratory, unpublished data). Snails were much less abundant in spring 1997 compared with the previous year (P.J. Warner, personal observation), and drought may have been a critical factor in reducing mollusc activity. Due to the low precipitation levels in 1997, an evaluation of the importance of snail herbivory in this lupine system is difficult. They may be extremely important in wet years, but were not influential in a dry one.

The effects of mammalian herbivores on mature lupines were quite different from those for seedling and juvenile plants. Whereas the deer have a significantly negative effect on growth rates of juvenile lupines (Fig. 2), we did not detect as strong an effect on older, reproductive-age individuals (Fig. 3a). Such age-specific results could be explained by three hypotheses: (1) our methods for estimating shrub volume were too coarse for detecting herbivore effects in older/larger plants; (2) deer did not browse older shrubs, or did so less intensively than juvenile plants; or (3) older plants were better able to compensate for tissue loss than were juvenile lupines. The first hypothesis is unlikely, given the strong relationship between shrub volume and aboveground dry biomass ( $R^2=0.95$ ) for shrubs of all sizes (Fig. 5). With respect to the second hypothesis, deer clearly browsed older plants at least occasionally (Fig. 3b), but perhaps less intensively than juveniles, due to age-related reductions in palatability or other factors. Older lupines should also have a greater ability to replace lost biomass than juveniles, given that most tissue losses will constitute a smaller fraction of total biomass and that larger plants generally have increased access to resources needed for tissue replacement.

Our results indicate that the effects of herbivory on lupine fecundity are complex. First, browsed shrubs produced significantly greater numbers of inflorescences

than unbrowsed individuals (Fig. 4), which is consistent with the hypothesis that lupines overcompensate in response to herbivory (see Paige and Whitham 1987; Maschinski and Whitham 1989; Whitham et al. 1991; Paige 1992). This result suggests that deer browsing on new shoots enhanced flowering through the removal of apical meristems and subsequent growth of new shoots from lateral meristems. However, other lines of evidence may refute or complicate the possibility of overcompensation. Despite greater inflorescence production in browsed plants, we also found that unbrowsed plants produced seeds that on average had greater mass. This suggests that lupines may exhibit an allocation trade-off, with greater inflorescence production – and potentially greater seed production – coming at the expense of reduced seed weight. In addition, the short-term effects of herbivory on inflorescence production may not persist in subsequent years, or may result in a cost of reproduction if survivorship in later years decreases as a result of initial increases in fecundity. This is especially true for longer-lived perennials, in which the impacts of herbivory on overall plant fitness may take several years to appear (Sacchi and Connor 1999).

An unexpected result of this study is that two distantly related taxa – deer and a cecidomyid fly – interact with each other on their shared host plant. As shown in Fig. 6, we found that juvenile lupines browsed by deer were less likely to be galled by *Dasineura* flies than plants protected from herbivory. In contrast, for those plants attacked by this cecidomyid, browsed lupines had greater gall density (galls/plant volume) compared to unbrowsed controls (although significance was at the 0.073 level). We believe that such apparently contradictory results may be explained as follows. First, browsed plants were significantly smaller than unbrowsed individuals (Fig. 2) and we hypothesize that female flies preferentially oviposited on larger, perhaps more apparent plants. At the same time we hypothesize that deer herbivory caused chemical changes in the leaf tissue of lupines, which in turn led to increased gall density on browsed plants. This latter hypothesis is supported by results from McNeil and Cushman (unpublished data), who conducted a field experiment at our site showing that browsed *L. chamissonis* had significantly higher nitrogen content in their leaf tissue than unbrowsed individuals. Insect herbivores are known to prefer high-nitrogen host plants (Crawley 1983; Price 1997), and this may explain the higher gall density on browsed lupines. At first glance, this hypothesis might appear suspect, given that lupines are known to employ alkaloids as a defense against herbivores (see Johnson and Bentley 1988; Harborne 1997; Price 1997), and that the increased nitrogen content of browsed plants would likely arise from an increase in these nitrogen-rich compounds. Such deer-induced changes in lupine might deter generalist insect herbivores, but as its name suggests, *Dasineura lupinorum* is a specialist on lupines (D.R. Strong, personal communication) and may have evolved the capacity to detoxify alkaloids thereby reaping the benefits of increased nitrogen available in deer-browsed plants.

In conclusion, for one of two herbivore species examined, our results support the generalization that impacts of herbivory shift from having strong negative effects on plant growth of early life cycle stages to having weaker effects on reproductive-age individuals. However, at best, we found only weak support for this generalization for plant survival. In addition, we detected ambiguous results for fecundity, as deer browsing caused increased inflorescence production but also decreased seed mass. Another factor complicating our assessment of this generalization is that we used experiments to evaluate the effects of herbivores on plants during two windows in their life cycle – the first few years of a plant's life and a year-long period of an adult plant's life. Due to logistical constraints, such approaches are often necessary when studying longer-lived perennial plants, but can lead to misleading conclusions about the net effect of herbivores on plant lifetime fitness. Studies of a plant's first few years of life are limited because they ignore the critically important reproductive phase. Alternatively, studies of reproductive-age plants for a given period are problematic because the past history of herbivory may affect (and bias) the outcome of experiments in unknown ways. The only way to resolve this dilemma is to redouble efforts to conduct long-term studies that truly capture the natural lifespan of host plants and to conduct matrix simulation models (sensu Doak 1992) based on field data to integrate the effects of herbivory over a plant's lifetime.

**Acknowledgements** We are grateful to Joy Diaz, Jon-Paul Harries, Derek Hoak, Sean McNeil, Jennifer Michaud, Emily Raab, Corrie Robb, Anna Sears, Mark Smith, and Simone Watts for assistance in the field. Anurag Agrawal, Caroline Christian, Nathan Rank and Sean McNeil provided invaluable statistical advice. Svata Louda and Phyllis Coley offered helpful suggestions regarding the herbivory literature. The following individuals provided useful suggestions at various stages of this project: Valerie Brown, Sharon Collinge, Peter Connors, Carla D'Antonio, Rodolfo Dirzo, and Pam Kittelson. We are especially grateful to John Maron for encouraging us to initiate this project and for offering many insightful comments. Drafts of this manuscript have benefited from comments by Anurag Agrawal, Caroline Christian, Elizabeth Dahlhoff, Sean McNeil, John Maron, Mary Price, Nathan Rank, Vanessa Rashbrook and an anonymous reviewer. Our research was supported by funds from the Bodega Field Conference, California Native Plant Society, National Geographic Society, Sonoma State University and the National Science Foundation (DEB-9981663 to J.H.C.).

## References

- Agrawal AA (1999) Induced responses to herbivory in wild radish: effects on several herbivores and plant fitness. *Ecology* 80:1713–1723
- Barbour MJ, Craig RB, Drysdale FR, Ghiselin MT (1973) Coastal Ecology. University of California Press, Berkeley, Calif.
- Bonsler SP, Reader RJ (1995) Plant competition and herbivory in relation to vegetation biomass. *Ecology* 76:2176–2183
- Bryant JP, Julkunen-Tiitto R (1995) Ontogenic development of chemical defense by seedling resin birch: energy cost of defense production. *Chem Ecol* 21:883–896
- Bryant JP, Wieland GD, Clausen T, Kuropat P (1985) Interactions of snowshoe hare (*Lepus americanus*) and fettleaf willow (*Salix alaxensis*) in Alaska. *Ecology* 66:1564–1573



- Coley PD (1986) Costs and benefits of defense by tannins in a neotropical tree. *Oecologia* 70:238–241
- Crawley MJ (1983) *Herbivory: dynamics of plant-animal interactions*. University of California Press, Berkeley, Calif.
- Crawley MJ (1985) Reductions in oak fecundity by low-density herbivores. *Nature* 314:163–164
- Crawley MJ (1989) The relative importance of vertebrate and invertebrate herbivores in plant population dynamics. In: Bernays EA (ed) *Insect-plant interactions*. CRC, Boca Raton, Fla. pp 47–71
- Crawley MJ (1997) *Plant ecology*. Blackwell, Oxford
- Doak DF (1991) The consequences of herbivory for dwarf fireweed: different time scales, different morphological scales. *Ecology* 72:1397–1407
- Doak DF (1992) Lifetime impacts of herbivory for a perennial plant. *Ecology* 73:2086–2099
- Ehrlén J (1995) Demography of the perennial herb *Lathyrus vernus*. I. Herbivory and individual performance. *J Ecol* 83:287–295
- Faeth SH (1986) Indirect interactions between temporally separated herbivores mediated by the host plant. *Ecology* 67:479–494
- Feeny P (1976) Plant apparency and chemical defense. *Recent Adv Phytochem* 10:1–40
- Fenner M, Hanley ME, Lawrence R (1999) Comparison of seedling and adult palatability in annual and perennial plants. *Funct Ecol* 13: 546–551
- Hanley ME (1996) The effect of mollusc grazing on seedling recruitment in artificially created grassland gaps. *Oecologia* 106:240–246
- Hanley ME, Fenner M, Edwards PJ (1995) The effect of seedling age on the likelihood of herbivory by the slug *Deroceras reticulatum*. *Funct Ecol* 9:754–759
- Harborne JB (1997) Plant secondary metabolism. In: Crawley MJ (ed) *Plant ecology*. Blackwell, Oxford, pp 132–155
- Harper JL (1977) *Population biology of plants*. Academic Press, London
- Hendrix SD (1988) Herbivory and its impact on plant reproduction. In: Doust JL, Doust LL (eds) *Plant reproductive ecology*. Oxford University Press, Oxford, pp 246–263
- Hulme PE (1994) Seedling herbivory in grassland: relative impact of vertebrate and invertebrate herbivores. *J Ecol* 82:873–880
- Johnson ND, Bentley BL (1988) The effects of dietary protein and lupine alkaloids on the growth and survivorship of *Spodoptera eridania*. *J Chem Ecol* 14:1391–1403
- Juenger T, Bergelson J (1997) Pollen and resource limitation of compensation to herbivory in scarlet gilia, *Ipomopsis aggregata*. *Ecology* 78:1684–1695
- Karban R, Baldwin IT (1997) *Induced responses to herbivory*. University of Chicago Press, Chicago, Ill.
- Lindroth RL (1989) Mammalian herbivore-plant interactions. In: Abrahamson WB (ed) *Plant-animal interactions*. McGraw-Hill, New York, pp 163–206
- Louda SM, Potvin MA (1995) Effect of inflorescence-feeding insects on the demography and lifetime fitness of a native plant. *Ecology* 76:229–245
- Maron JL, Simms EL (1997) Effects of seed predation on seed bank size and seedling recruitment of bush lupine (*Lupinus arboreus*). *Oecologia* 111:76–83
- Maschinski J, Whitham TG (1989) The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. *Am Nat* 134:1–19
- Mulder CPH, Harmsen R (1995) The effect of musk ox herbivory on growth and reproduction in an Arctic legume. *Arct Alp Res* 27: 44–53
- Paige KN (1992) Overcompensation in response to mammalian herbivory: from mutualistic to antagonistic interactions. *Ecology* 73:2076–2085
- Paige KN, Whitham TG (1987) Overcompensation in response to mammalian herbivory: the advantage of being eaten. *Am Nat* 129:407–416
- Price PW (1997) *Insect ecology*. Wiley, New York
- Rhoades DF, Cates RG (1976) Toward a general theory of plant antiherbivore chemistry. *Recent Adv Phytochem* 19:168–213
- Roininen H, Price PW, Tahvanainen J (1993) Colonization and extinction in a population of the shoot-galling sawfly, *Euura amerinae*. *Oikos* 68:448–454
- Roininen H, Price PW, Bryant JP (1997) Response of galling insects to natural browsing by mammals in Alaska. *Oikos* 80:481–486
- Sacchi DF, Connor EF (1999) Changes in reproduction and architecture in flowering dogwood, *Cornus florida*, after attack by the dogwood club gall, *Resseliella clavula*. *Oikos* 86:138–146
- Spiegel LH, Price PW (1996) Plant aging and the distribution of *Rhyacionia neomexicana* (Lepidoptera: Tortricidae). *Environ Entomol* 25:359–365
- Strauss SY (1991) Direct, indirect, and cumulative effects of three native herbivores on a shared host plant. *Ecology* 72:543–558
- Suominen O, Danell K, Bergstrom R (1999a) Moose, trees, and ground-living invertebrates: indirect interactions in Swedish pine forests. *Oikos* 84:215–226
- Suominen O, Danell K, Bryant JP (1999b) Indirect effects of mammalian browsers on vegetation and ground-dwelling insects in an Alaskan floodplain. *Ecoscience* 6:505–510
- Tollrian R, Harvell CD (1999) *The Ecology and evolution of inducible defenses*. Princeton University Press, Princeton, N.J.
- Underwood AJ (1997) *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press, Cambridge
- Weltzin JF, Archer SR, Heitschmidt RK (1998) Defoliation and woody plant (*Prosopis glandulosa*) seedling regeneration: potential vs. realized herbivory tolerance. *Plant Ecol* 138:127–135
- Whitham TG, Mopper S (1985) Chronic herbivory: impacts on architecture and sex expression of pinyon pine. *Science* 228:1089–1091
- Whitham TG, Maschinski J, Larson KC, Paige KN (1991) Plant responses to herbivory: the continuum from negative to positive and underlying physiological mechanisms. In: Price PW, Lewinsohn TW, Fernandes GW, Benson WW (eds) *Plant-animal interactions: evolutionary ecology in tropical and temperate regions*. Wiley, New York, pp 227–256