

Indirect effects of deer herbivory on local nitrogen availability in a coastal dune ecosystem

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Herbivores can have indirect effects on local nutrient availability if their direct effects on plants lead to changes in the amount or chemical composition of litter reaching the soil surface. Using two enclosure experiments, we evaluated this possibility for black-tailed deer (*Odocoileus hemionus columbianus*) feeding on silver bush lupine (*Lupinus chamissonis*) in a coastal dune system in northern California. Our first experiment assessed the effects of deer herbivory on 360 lupines that were tracked from newly germinated seedlings in 1996 and 1997 until 2000, when most surviving individuals had reached reproductive age. Results from this experiment showed that browsing by deer significantly reduced growth rates and seed production of lupines and delayed the onset of reproductive maturity. Although deer had no effect on the density of litter accumulating underneath shrubs (g m^{-2}), browsing significantly decreased C:N ratios of leaf tissue, due primarily to increased nitrogen content of leaves. Deer browsing also caused significantly increased net nitrogen mineralization rates in the soil under shrubs, although pools of ammonium and nitrate were uninfluenced. The second experiment examined 72 established bush lupines from 1997 to 2000, and showed that deer browsing significantly decreased seed production but had no effect on shrub growth. We also detected trends for browsed shrubs to have reduced pools of ammonium and nitrate underneath their canopies, although no such patterns emerged for nitrogen mineralization rates. Collectively, these data suggest that changes in litter quality, more so than litter quantity, contributed to the indirect effects of deer herbivory on local nitrogen dynamics. We hypothesize that deer browsing induced chemical changes in lupine plant tissue, which increased the nitrogen content of litter reaching the soil surface and subsequently increased rates of nitrogen mineralization.

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Through both direct and indirect pathways, mammalian herbivores can have large effects on nutrient cycling at both local and regional scales (Huntly 1991, 1995). They can directly influence ecosystem properties through their activities as soil disturbance agents (Inouye et al. 1987, Tardiff and Stanford 1998) and producers of metabolic wastes (Ruess and McNaughton 1987, Day and Detling 1990, Steinauer and Collins 1995). Although less frequently considered, herbivores can also indirectly alter nutrient availability through their role as consumers of

plant biomass (McNaughton 1983, 1985, Pastor et al. 1988, Huntly 1991, 1995, McInnes et al. 1992, Hobbs 1996, Augustine and McNaughton 1998, Ritchie et al. 1998, Knops et al. 2000, Sirotiak and Huntly 2000). These indirect effects arise primarily from herbivore-mediated changes in the amount or chemical composition of plant litter reaching the soil surface.

Herbivore-mediated changes in litter quantity can occur via several pathways, each of which has implications for soil nutrient availability. First, herbivores may

reduce the number and/or size of individual plants and in turn reduce the amount of leaf litter that these hosts deposit underneath their canopies. Second, selective feeding by herbivores may alter the competitive dynamics between browsed and unbrowsed plant taxa and thereby lead to changes in community composition and/or litter production (Crawley 1983, Pastor et al. 1988, Bryant et al. 1991, Ritchie and Tilman 1995, Sirotiak and Huntly 2000). Herbivores may also reduce the fecundity of individual plants and, if the system is seed-limited, cause decreases in host abundance (Louda 1989, Louda and Potvin 1995) and litter deposition throughout the landscape. Under all of these scenarios, changes in litter quantity will affect the influx of nitrogen into the soil and possibly the rates at which it cycles (Pastor et al. 1988, 1993, Aber and Melillo 1991, Hobbie 1992, Chapin et al. 1995). Such changes may be especially influential when they involve nitrogen-fixing plants that can deposit substantial amounts of nitrogen to the soil via their leaf litter (Alpert and Mooney 1996, Maron and Jefferies 1999).

Herbivore-mediated changes in litter quality may also have important consequences for nutrient availability, but this possibility is less frequently considered (Choudhury 1988, Huntly 1991). Herbivores commonly change the chemical composition of their food plants, often by inducing the production of defensive compounds (Bryant et al. 1991, Karban and Baldwin 1997, Tollrian and Harvell 1999). If these changes persist, they may alter the C:N ratio of plant litter, which is a critical driver of decomposition and mineralization rates. In general, these rates increase as nitrogen content of litter increases and C:N ratios decrease (McNaughton 1985, DeAngelis et al. 1989, Ruess et al. 1989, Holland and Detling 1990, Holland et al. 1992, Pastor and Naiman 1992, Sterner 1994). Thus, it follows that herbivores which induce chemical changes in the tissue of their food plants may indirectly affect local nutrient availability (Choudhury 1988, Huntly 1991).

In this paper, we explore the influence of mammalian herbivores on a nitrogen-fixing shrub in a coastal dune ecosystem in northern California. Although we recognize that herbivores can have important direct effects on ecosystem processes, our focus here is primarily on their indirect effects that occur on a more local scale. Using multi-year exclosure experiments, we address three questions: 1) does herbivory by black-tailed deer (*Odocoileus hemionus columbianus*) directly affect the growth, tissue chemistry and reproductive success of silver bush lupine (*Lupinus chamissonis*)? 2) Does deer herbivory influence the quantity of litter accumulating on the soil surface underneath lupines? 3) Do deer indirectly alter nitrogen pools and mineralization rates underneath the canopy of lupine plants? We predict that black-tailed deer will indirectly influence local availability of soil nitrogen in two opposing ways. First, by decreasing the

size of nitrogen-fixing shrubs, we hypothesize that deer herbivory will decrease the quantity of nitrogen-rich leaf litter reaching the soil surface, and thereby lower nitrogen pools and mineralization rates. Second, we hypothesize that deer herbivory will induce increased nitrogen levels in the leaf tissue of silver bush lupine, which will persist in the leaf litter that reaches the soil surface and lead to increased nitrogen pools and mineralization rates. This latter hypothesis seems possible given that lupines are known to produce nitrogen-based defensive compounds (i.e. alkaloids; Wink 1983, 1984, 1987) that are inducible (Johnson and Bentley 1988, 1991), and increased nitrogen content in leaf litter is known to accelerate mineralization rates (Aber and Melillo 1991). In summary, by addressing these three research questions, we will explore the degree to which a dominant mammalian herbivore alters nitrogen availability, and the pathways by which such effects occur.

Study system

We have conducted our research on Bodega Head, a small peninsula in Sonoma County, California, USA. This coastal site is characterized by a Mediterranean-type climate and is located in the sand dunes of Sonoma Coast State Beaches, adjacent to the University of California's Bodega Marine Reserve. This site is characterized by highly seasonal rainfall, with over 90% of the annual precipitation falling between October and April. The soil is sandy, fast-draining, nitrogen-poor, and strongly alkaline (Barbour et al. 1973, J. H. Cushman, unpubl.). The site has a diverse assemblage of native and exotic plant species, with *Lupinus chamissonis* (silver bush lupine; Fabaceae) and *Ericameria ericoides* (false heather; Asteraceae) being the dominant shrubs. Both are low-growing evergreen taxa native to the coastal dunes of California.

Silver bush lupine is a nitrogen-fixing shrub that averages 15% cover at our Bodega dunes site. Plants produce inflorescences on new terminal shoots from March through May, starting when plants are a few years old (Warner and Cushman 2002, S. G. McNeil, pers. obs.). Plants that reach reproductive maturity generally survive 6–10 years (P. G. Connors, pers. comm.). Another bush lupine species, *Lupinus arboreus*, also occurs in the dunes and grasslands at Bodega Head (Barbour et al. 1973), but is not very abundant at our study site. The effects of insect and small mammal herbivores on this second lupine species have been studied extensively (Strong et al. 1995, Maron and Connors 1996, Maron 1997, 1998, Maron and Simms 1997, Maron and Jefferies 1999). However, only Warner and Cushman (2002) have examined previously the effects of herbivores on *L. chamissonis*.

There are numerous species of mammalian herbivores present in this system: black-tailed deer (*Odocoileus hemionus columbianus*), California hares (*Lepus californicus*), brush rabbits (*Sylvilagus bachmani*), meadow voles (*Microtus californica*), and deer mice (*Peromyscus maniculatus*). Our research focused exclusively on black-tailed deer because previous research at this dune site indicated that they were the primary mammalian herbivore of *L. chamissonis* (Warner and Cushman 2002).

Methods

Lupine growth, fecundity and tissue chemistry

We used two enclosure experiments to evaluate the effects of deer herbivory on long term growth, fecundity and tissue chemistry of *L. chamissonis*. The first experiment tracked two randomly selected lupine cohorts from newly germinated seedlings in January 1996 ($n=200$) and 1997 ($n=160$) until September 2000, when most surviving plants had reached reproductive age (we refer to this as the cohort experiment). For both cohorts, we randomly assigned all lupine seedlings to be either exposed to or protected from deer herbivory. Enclosures consisted of cylindrical poultry-mesh cages, 45 cm high \times 20 cm in diameter, anchored into the sand with steel U-shaped stakes. These enclosures allowed voles and deer mice to pass through and did not significantly alter ambient light levels, wind speed, air or soil temperatures (Warner and Cushman 2002).

We established a second experiment to assess the effects of deer herbivory on established bush lupines (the mature-shrub experiment). In February 1997, we selected and randomly assigned 72 mature lupines to be either exposed to or protected from deer herbivory. Enclosures consisted of 1 m high steel poultry-mesh fencing supported by bamboo stakes. We increased the size of all cages throughout the duration of the study to ensure that plants continued to be protected from deer.

We quantified shrub volume for all lupines used in the cohort and mature-shrub experiments. Volume is an excellent non-destructive measure of shrub size in our system, and previous research on *L. chamissonis* by Warner and Cushman (2002) found that lupine volume explained 95% of the variation in aboveground biomass. Throughout the growing season (January-June) from 1996–2000, we calculated volume by measuring the maximum height and three radii of each plant's canopy area, from plant center to perimeter, at 120-degree arcs around its circumference. We then averaged these four measurements to derive a mean radius, and used the formula for the volume of a hemisphere ($2/3\pi r^3$) to calculate plant volume.

We analyzed data on plant growth using similar statistical procedures as those used by Warner and

Cushman (2002). As they discussed, repeated-measure ANOVAs were not an option for these data because many lupines died during the multi-year field experiments. Instead, we calculated an index for each plant which equaled the difference in plant volume between two successive sample dates divided by the number of days elapsed between the 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 is days between measurements, and N is the number of time intervals used for a plant. This daily rate was then multiplied by 30 to generate a monthly rate.

We statistically analyzed our data using both JMP 3.1 and SAS 8.0 (SAS Institute; Cary, North Carolina, USA). Data were natural log-transformed when appropriate to equalize the variances for use in parametric statistics. We analyzed the effects of deer herbivory on lupines in the cohort experiment by using two-way ANOVAs, with herbivore treatment (deer present or absent) and cohort (1996 or 1997 seedlings) as grouping factors and average monthly growth rate as the response variable. We analyzed the effects of deer on lupines for the mature-shrub experiment using a one-way ANOVA, with herbivore treatment as the grouping factor and average growth rate as the response variable.

We determined the number of seeds produced per plant in both the cohort and mature-shrub experiments. To estimate seed production, we collected all ripe pods at three dates each summer for years 1999 (7/9, 7/29 and 9/3) and 2000 (6/1, 7/15 and 9/1). We summed the data obtained from the three sample dates for each year to obtain yearly estimates of seed production. We defined pods as ripe when they began to dehisce (but had not yet lost seeds) and when their stems began to senesce. This sampling procedure allowed us to collect the vast majority of fruits produced by focal plants without altering their patterns of resource allocation (deer do not browse lupine seed pods – J. H. Cushman, pers. obs.).

We analyzed the effects of deer herbivory on lupine fecundity in the cohort experiment using a repeated-measure ANOVA (type III sums of squares), with herbivore treatment and lupine cohort as the grouping factors and sample year (1999 or 2000) as the repeated measure. During the 2000 census year, we also randomly selected and weighed 10 seeds from each reproducing plant in the cohort experiment and calculated average seed weight per plant. To analyze these data, we used a two-way ANOVA, with herbivore treatment and cohort as the grouping factor and average seed weight as the response variable. Similarly, in the mature-shrub experiment, we analyzed fecundity with a repeated-measure ANOVA, with herbivore treatment as the grouping factor and sample year as the repeated measure. We also tested whether deer herbivory affected the age at

which lupines first reproduced. Here, we noted whether or not plants in the cohort experiment set seed in 1999, since this was the first time that any of these individuals were reproductively active. We then analyzed these data using a 2×2 contingency table, with herbivore treatment and cohort as grouping factors and seed production (yes or no) as the response variable.

To determine the effect of deer herbivory on tissue chemistry, we measured carbon-to-nitrogen (C:N) ratio of lupine leaf tissue in March 2000 for all surviving plants in the cohort experiment. We focused on leaflets still attached to shrubs rather than those that the plant had dropped to the ground because nutrients are rapidly leached from leaf litter on the soil surface (Aber and Melillo 1991). In addition, we used newly senesced leaflets on lupines rather than fresh, living material because many nutrients are re-absorbed prior to abscission (Clarkson and Hanson 1980). We collected approximately 50 newly senesced leaflets from the canopy of each plant, dried this material at 40°C for 48 h, and then ground it to a fine powder using a Wiley Mill grinder until the sample passed through a no. 60 mesh screen. Samples were then analyzed for nitrogen and carbon content at the University of California DANR Analytical Laboratory. These data were analyzed by using a two-way ANOVA, with herbivore treatment and cohort as grouping factors and C:N ratio of leaf tissue as the response variable.

Plant litter and soil nitrogen availability

To assess the impact of deer on litter accumulation, we collected all litter found underneath fenced and unfenced lupines used in the cohort experiment. Litter from under the canopy of each lupine was sieved to remove sand particles and dried for 72 h at 40°C. In February 1999, all litter, regardless of origin, was pooled, while in February 2000, lupine and non-lupine litter was assessed separately. Litter quantity was then divided by the area of the shrub from which it was collected to generate litter density (g m^{-2}). In both cases, we analyzed these data using two-way ANOVAs, with herbivore treatment and cohort as the grouping factors and litter density as the response variable.

To assess the indirect effect of deer herbivory on nitrogen pools and mineralization rates, we sampled the soil underneath each of the lupines used in our cohort and mature-shrub experiments. At a depth of 10 cm, we collected 40 g of soil sample from a randomly determined area underneath each shrub in December 1999, February 2000 and March 2000. These winter months received most of the annual precipitation and corresponded to the yearly peak in nitrogen mineralization at our site (J. H. Cushman, unpubl.). For each of these samples, we analyzed 20 g for ammonium (NH_4^+) and

nitrate (NO_3^-) content using standard KCl procedures (Binkley and Hart 1989, Binkley and Vitousek 1989, Cushman et al. 2004), and placed another 20 g of soil in a breathable polyethylene bag to incubate in the field underneath its respective plant for 30 days. The resulting extracts (initial and 1-month-old samples) were frozen and later analyzed for ammonium (NH_4^+) and (NO_3^-) content at University of California DANR Analytical Laboratory. Nitrogen content of the initial samples served as our estimates of pool sizes, whereas the difference in nitrogen between initial samples and those incubated for a month represented an estimate of net mineralization rates. We dried unextracted soil fractions in an oven at 60°C for 24 h, re-weighed samples to determine soil moisture content, and adjusted nitrogen values to control for differences in soil moisture.

For the cohort experiment, we analyzed these data using repeated-measure ANOVAs, with herbivore treatment and cohort as the grouping factors, sample period as the repeated measure, and NO_3^- and NH_4^+ pools and net nitrogen mineralization rate as response variables. We analyzed soil data for the mature-shrub experiment in a similar fashion, except that cohort was omitted as a factor in the model.

Results

Lupine growth, fecundity and tissue chemistry

The direct effect of deer herbivory on lupine growth rates varied greatly between our two experiments. In the cohort experiment, lupines protected from deer grew twice as fast as those exposed to deer (Fig. 1, $F_{1,116} = 3.94$, $P = 0.049$). The 1997 cohort responded more strongly to herbivory than the 1996 cohort, as indicated by the significant herbivore treatment \times cohort interaction term ($F_{1,116} = 4.09$, $P = 0.045$). In contrast, deer had no effect on the growth rate of lupines in the mature-shrub experiment ($F_{1,48} = 0.31$, $P = 0.577$).

Deer dramatically reduced the seed production of lupines in both experiments and delayed reproductive maturity in the cohort experiment. Plants protected from deer in the cohort experiment produced 10 times more seeds on average than plants exposed to deer herbivory (Fig. 2a, $F_{1,17} = 4.43$, $P = 0.05$). We detected no effects of deer on the average weight of individual seeds per plant ($F_{1,38} = 0.48$; $p = 0.70$). In addition, deer browsing altered the reproductive phenology of these lupines by decreasing the probability of a plant reproducing in 1999 (Fig. 3, $\chi^2 = 8.46$, $P = 0.0036$). In the mature-shrub experiment, protected plants produced three times more seeds than unprotected plants in both 1999 and 2000 (Fig. 2b, $F_{1,32} = 10.57$, $P = 0.003$). There was no difference in seed weight between herbivore treatment levels ($F_{1,27} = 0.00$, $P = 0.98$).

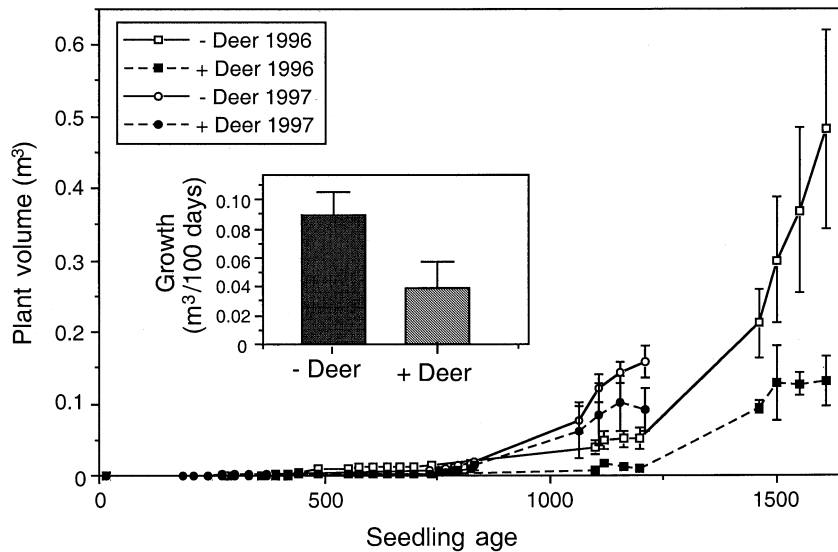


Fig. 1. Mean shrub volume (+1 SE) of juvenile bush lupine (*Lupinus chamissonis*) for two cohorts (1996 and 1997) through time as a function of the presence or absence of black-tailed deer.

In the cohort experiment, attached but newly senesced leaflets (i.e. those that were about to be abscised and become litter) from lupines exposed to deer herbivory had significantly lower C:N ratios than those protected from herbivory (Fig. 4, $F_{1,16}=8.37$, $P=0.016$). This decrease was due to increases in percent nitrogen of leaf tissue rather than percent carbon ($F_{1,16}=7.91$, $P=0.013$).

Plant litter and soil nitrogen availability

In the cohort experiment for both 1999 and 2000, we failed to detect an effect of deer herbivory on litter density (g m^{-2}) underneath lupine canopies (Table 1, 1999 total density - $F_{1,18}=0.739$, $P=0.395$; 2000 lupine density - $F_{1,18}=1.171$, $P=0.294$; 2000 total density - $F_{1,18}=0.742$, $P=0.4$). Because browsed plants in the cohort experiment were smaller in volume, they deposited less total leaf litter underneath their canopies than protected shrubs, but this effect vanished when the data were calculated as litter per unit area. We also failed to detect an effect of deer herbivory on pools of NH_4^+ and NO_3^- in the soil underneath their canopies compared to protected plants (Fig. 5a, NH_4^+ - $F_{1,20}=0.16$, $P=0.697$; NO_3^- - $F_{1,18}=0.20$, $P=0.658$). In contrast, we found that lupines exposed to deer herbivory in the cohort experiment had significantly greater rates of net nitrogen mineralization in soil underneath their canopies compared to protected plants (Fig. 6a, $F_{1,11}=17.76$, $P=0.015$). There was also a significant herbivore \times time interaction term ($F_{2,22}=6.63$, $P=0.006$), as the effect of deer on mineralization rates was strong in December 1999 and February 2000 and absent in March 2000.

For the mature-shrub experiment, we detected an insignificant trend in nitrogen pools between protected and unprotected lupines, with levels of NH_4^+ and NO_3^-

being somewhat greater underneath unbrowsed plants (Fig. 5b, NH_4^+ - $F_{1,31}=3.72$, $P=0.063$; NO_3^- - $F_{1,31}=2.27$, $P=0.142$). This pattern was most noticeable during December 1999, but the herbivore \times time interaction term was not significant for either NH_4^+ ($F_{2,62}=1.12$, $P=0.332$) or NO_3^- ($F_{2,62}=1.00$, $P=0.375$). No such differences between protected and unprotected lupines were found for net mineralization rates (Fig. 6b, $F_{1,24}=0.76$, $P=0.391$), nor was there a significant herbivore \times time interaction term ($F_{2,48}=1.46$, $P=0.243$).

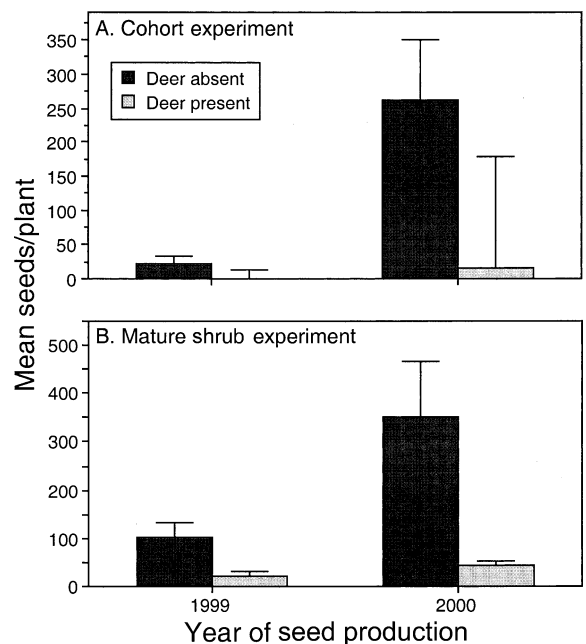


Fig. 2. Mean seed production (+1 SE) of juvenile (a) and established bush lupine (*Lupinus chamissonis*): b) in 1999 and 2000 as a function of the presence or absence of black-tailed deer.

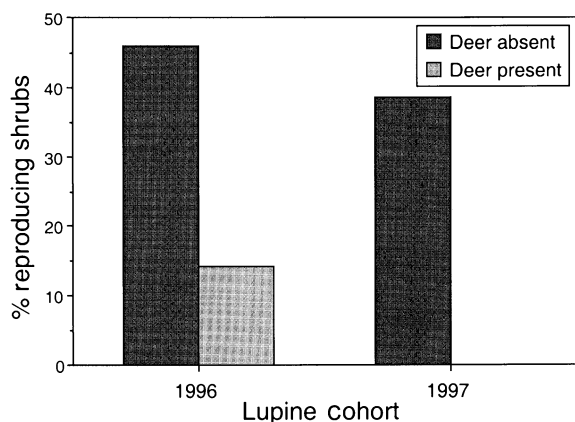


Fig. 3. Percent of juvenile bush lupine (*Lupinus chamissonis*) reproducing in 1999 as a function of presence or absence of black-tailed deer. 1999 was the first year in which any of these plants reached reproductive maturity.

Discussion

Herbivores can have indirect effects on local nitrogen availability if their direct effects on plants lead to changes in the quantity or quality of litter deposited on the soil surface. In this study, we have provided data from two enclosure experiments that explore the importance of black-tailed deer as mediators of litter deposition and nitrogen availability in a coastal dune ecosystem. Deer herbivory significantly reduced growth rates (Fig. 1), fecundity (Fig. 2), and C:N ratios of leaf tissue (Fig. 4) in silver bush lupine, and delayed the onset of reproductive maturity (Fig. 3). We also show that deer herbivory had strong indirect effects in this system, as deer browsing increased rates of nitrogen mineralization in the soil underneath lupine canopies (Fig. 6).

Numerous mechanisms could explain the accelerated mineralization rates that occur underneath the canopies of deer-browsed lupines. First, deer may have increased

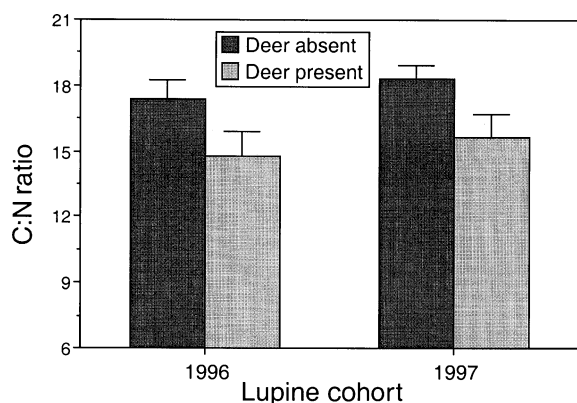


Fig. 4. Mean carbon-to-nitrogen ratios (+1 SE) of bush lupine (*Lupinus chamissonis*) leaves for two cohorts (1996 and 1997) as a function of presence or absence of black-tailed deer. Vertical lines correspond to 1 SE.

Table 1. Mean plant litter density (+1 SE; $g\ m^{-2}$) found underneath the canopies of silver bush lupines either exposed to or protected from herbivory by black-tailed deer. In 1999, data are presented for lupine and non-lupine litter combined, whereas in 2000, data are included for both total litter accumulation and lupine litter only.

Year	Litter type	Herbivore treatment	
		Deer present	Deer absent
1999	total litter	8.94 (0.11)	8.81 (0.09)
2000	total litter	8.82 (0.66)	9.36 (0.22)
2000	lupine only	5.90 (0.64)	6.66 (0.23)

nitrogen mineralization rates by depositing scat and urine beneath lupine canopies. Although large herbivores are known to accelerate nitrogen cycling through deposition of metabolic waste products (Ruess and McNaughton 1987, Day and Detling 1990, Steinauer and Collins 1995), this hypothesis is unlikely to explain our results given that we rarely found mammal scat underneath the lupine canopies. Although we lack data on patterns of urine deposition, we suspect that they were similar to those for scat. A second possibility is that deer disturbed the soil surface underneath shrubs with their hooves and thereby increased soil mixing and aeration, which in turn increased mineralization rates. However, we have not observed hoof prints underneath lupines and therefore doubt that soil disturbances played an important role. A third explanation is that deer herbivory may have opened up lupine canopies, increased light penetration and soil temperatures, and thereby elevated microbial activity and thus mineralization rates. At first glance, this hypothesis does not seem valid given that our observations, and those of Warner and Cushman (2002), indicate that deer herbivory caused greater branching and a more compact architecture. However, deer-browsed plants were smaller and more upright than unbrowsed ones, which may have increased the amount of sunlight hitting the soil surface underneath lupines, particularly during winter months when the sun was lower on the horizon. Thus, greater soil temperatures underneath browsed plants may have contributed to increased mineralization rates, although we doubt that they were sufficient to explain the magnitude of effects that we detected.

Deer-induced changes in litter quantity and quality are two additional factors that could potentially explain the increased nitrogen mineralization rates found underneath browsed plants. Increased litter quantities could lead to faster mineralization rates, but we found no evidence that deer had such effects on litter. Our data are more consistent with the litter-quality hypothesis, as the leaf tissue of deer-browsed lupines in the cohort experiment had significantly lower C:N ratios (Fig. 4) due to increases in nitrogen content rather than decreases in carbon. We suspect that these changes were caused by increases in nitrogen-based alkaloids, defensive com-

pounds found frequently in lupines (Wink 1983, 1984, 1987) and known to be inducible in lupines (Johnson and Bentley 1988, 1991). An alternative hypothesis is that herbivores induced increased photosynthetic rates in the remaining leaves, which involved increases in the amount of nitrogen-rich RUBISCO contained in these tissues. A review of herbivore impacts on photosynthetic rates provides support for this possibility. Welter (1989) reported that 62% of the studies considered found that leaf-chewing herbivores increased photosynthetic rates in the remaining, undamaged foliage (McNaughton 1979). Thus, it is possible that increased levels of RUBISCO, rather than alkaloids, were responsible for the increased nitrogen content found in leaves. In either case, if such herbivore-induced chemical changes in living leaf tissue were retained in abscised material, then there is abundant evidence in the literature to suggest that this litter would decompose more rapidly and lead to faster mineralization rates (Pastor et al. 1988, 1993, Aber and Melillo 1991, Hobbie 1992, Pastor and Naiman 1992, Sterner 1994). Numerous studies have shown that herbivores can increase or decrease the C:N ratios of their plants (Karban and Baldwin 1997), but we know of none that have linked these kinds of plant responses to mineralization rates (Choudhury 1988, Huntly 1991).

Deer browsing caused faster nitrogen mineralization in soil underneath lupines in the cohort experiment, but not in the mature-shrub experiment. This variability may be explained by the “legacy of herbivory past” and differences in experimental design. Plants in the cohort experiment were included in our study for all but the first few days of their lives, and we have hypothesized that they responded to herbivory by producing greater amounts of nitrogen-rich compounds, which decreased C:N ratios of plant tissues, and increased nitrogen mineralization rates. In contrast, in the mature-shrub experiment, lupines were undoubtedly subjected to deer herbivory for numerous years prior to their inclusion in our experiment. We hypothesize that they either had already experienced herbivore-induced changes in tissue chemistry or had undergone ontogenetic increases in nitrogen-containing defenses. Under either scenario, further exposure to or protection from herbivory would not influence tissue chemistry or soil nitrogen availability.

On a larger spatial scale, the effects of deer herbivory on nitrogen availability will depend on the importance and magnitude of two opposing effects. First, herbivory should increase overall availability of soil nitrogen by changing the chemical content of lupine tissue. For this to occur on a large scale, deer would need to browse – and induce persistent chemical changes in – a large fraction of the lupine plants that are distributed

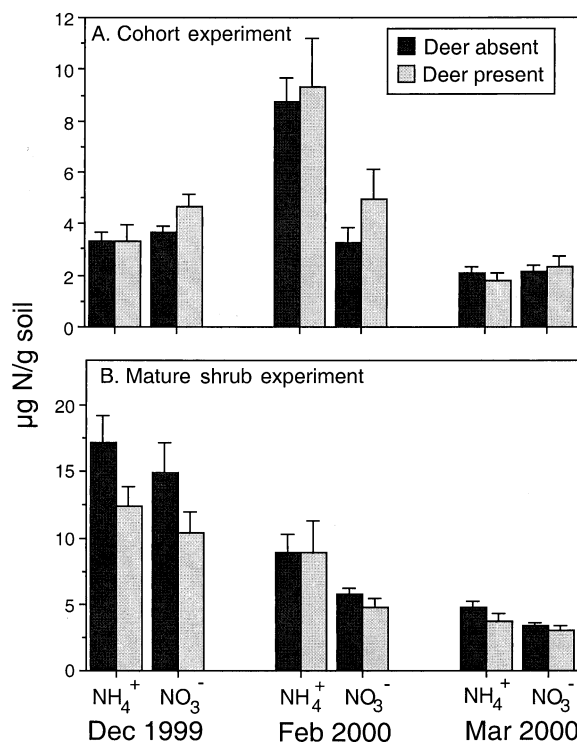


Fig. 5. Mean pools of plant-available nitrogen (+1 SE) in the soil underneath juvenile (a) and established bush lupine (*Lupinus chamissonis*: b) during three periods as a function of the presence or absence of black-tailed deer. Vertical lines correspond to 1 SE.

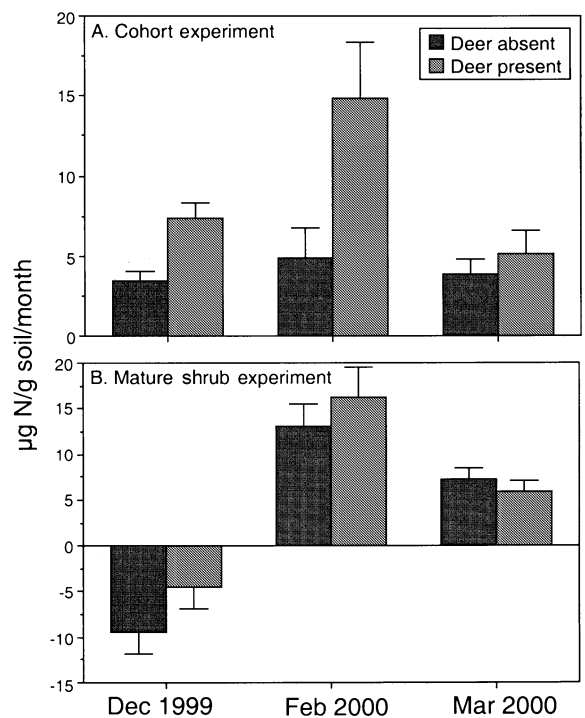


Fig. 6. Mean net nitrogen mineralization rates (+1 SE) in the soil underneath juvenile (a) and established bush lupine (*Lupinus chamissonis*: b) during three time periods as a function of presence or absence of black-tailed deer. Vertical lines correspond to 1 SE.

throughout the landscape. We suspect that such effects occur, given our results and extensive observations over the past 10 years indicating that well over 75% of the bush lupines at our study area are browsed regularly by deer (J. H. Cushman, pers. obs.). Second, deer herbivory may decrease overall nitrogen inputs in this dune ecosystem by reducing the abundance and biomass of bush lupines. This could occur due to herbivore-caused reductions in shrub size (Fig. 1) and lupine recruitment (Fig. 2, 3), as well as increased plant mortality (Warner and Cushman 2002). Partial support for this possibility comes from the mature-shrub experiment, which showed trends for browsed lupines to have smaller nitrogen pools underneath their canopies than protected shrubs.

The importance of this second pathway depends in part on whether or not deer-caused reductions in fecundity translate into decreased lupine recruitment. However, there continues to be considerable debate about whether recruitment in plant populations is limited by seed availability. Crawley (1997) has championed the view that most plant populations are not seed-limited, and argued that reductions in seed production caused by herbivory or post-dispersal granivory would usually have little effect on plant populations. However, Louda (1989) has shown that many systems are indeed seed-limited and that increased seed availability can increase plant population sizes (Louda and Potvin 1995). Furthermore, working in the same coastal dune ecosystem as this study, Maron and Simms (1997, 2001) found that recruitment was seed-limited for a closely related bush lupine species, *Lupinus arboreus* (Maron and Gardner 2000). If recruitment is also seed limited in *L. chamissonis*, then reductions in fecundity by deer could have large effects on the size of this plant population. We also suspect that herbivore-induced delays in reproductive maturity would further reduce overall seed production and recruitment because shrub mortality is so high in our system (Warner and Cushman 2002).

If herbivore-driven reductions in lupine recruitment occur, we hypothesize that there will be large and spatially widespread decreases in nitrogen inputs (i.e. litter quantity) that may outweigh the increases that occur via litter quality. This is because silver bush lupine is a nitrogen-fixing shrub that has large effects on this dune system – with soils underneath lupine canopies having significantly higher nitrogen pools and mineralization rates than those in adjacent open dunes (J. H. Cushman et al., unpubl.). This pattern has also been found for *Lupinus arboreus* in dune systems in northern California (Alpert and Mooney 1996, Maron and Connors 1996, Maron and Jefferies 1999). Thus, deer herbivory may reduce the number of nitrogen “hot-spots” distributed throughout this nitrogen-deficient dune landscape.

Herbivores will be especially likely to have effects at the ecosystem level if their feeding leads to changes in

the cover or abundance of nitrogen-fixing plants. A number of studies have explored this possibility for mammalian herbivores. For example, in riparian meadows of Yellowstone National Park, Sirotinak and Huntly (2000) found that vole herbivory caused significant reductions in the aboveground biomass of herbaceous legumes, which in turn decreased the nitrogen content of litter entering the system and the rates of nitrogen mineralization. In an oak savanna in Minnesota, Ritchie et al. (1998) and Knops et al. (2000) have also found that white-tailed deer reduced the abundance of an herbaceous legume and subsequently decreased primary productivity and soil nitrogen. These results, coupled with ours, underscore the importance of nitrogen-fixing plants in terrestrial ecosystems and the critical roles that mammalian herbivores can play in regulating their influences.

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