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John L. Maron

University of Montana - Missoula, john.maron@mso.umt.edu

Robert L. Jefferies

University of Toronto

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BUSH LUPINE MORTALITY, ALTERED RESOURCE AVAILABILITY, AND ALTERNATIVE VEGETATION STATES

JOHN L. MARON¹ AND ROBERT L. JEFFERIES²

¹Botany Department, University of Washington, Box 355325, Seattle, Washington 98195 USA

²Department of Botany, University of Toronto, Toronto, Ontario, Canada M5S 3B2

Abstract. Nitrogen-fixing plants, by altering the availability of soil N, potentially facilitate plant invasion. Here we describe how herbivore-driven mortality of a native N-fixing shrub, bush lupine (*Lupinus arboreus*), increases soil N and light availability, which promotes invasion by introduced grasses to the detriment of a native plant community.

Soils under live and dead lupine stands contained large amounts of total N, averaging 3.14 mg N/g dry mass of soil (398 g/m²) and 3.45 mg N/g dry mass of soil (438 g/m²), respectively, over four years. In contrast, similar lupine-free soil was low in N and averaged only 1.66 mg N/g dry mass of soil (211 g/m²) over three years. The addition of N fertilizer to lupine-free soil produced an 81% increase in aboveground plant biomass compared to plots unamended with N. Mean rates of net N mineralization were higher under live lupine and where mass die-off of lupine had occurred compared to soils free of bush lupine. At all sites, only 2.5–4.2% of the total soil N pool was mineralized annually.

Soil enriched by lupine is not available to colonists while lupines are alive. The dense canopy of lupine shades soil under shrubs, reducing average photon-flux density in late spring from 1725 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (full sunlight) to 13 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (underneath shrubs). Stand die-off due to insect herbivory exposed this bare, enriched soil. In January, when annual plants are establishing, average photon-flux density under dead lupines killed by insect herbivores was 370 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, compared to the photon-flux density under live lupines of the same age, which averaged 83 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The availability of bare, N-rich patches of soil enabled nonnative annuals (primarily *Lolium multiflorum* and *Bromus diandrus*) to colonize sites, grow rapidly, and dominate the plant assemblage until lupines reestablished after several years. The N content of these grasses was significantly greater than the N content of the mostly native plants that occupied adjacent coastal prairie devoid of bush lupine. Between 57 and 70% of the net amount of N mineralized annually was taken up by introduced grasses and subsequently returned to the soil upon the death of these annuals. Even in the absence of further N inputs, we estimate that it would take at least 25 yr to reduce the soil N pool by 50%, indicating that the reestablishment of the native prairie flora is likely to be long term.

Key words: bush lupine; insect herbivory; plant assemblages; plant invasion; soil nitrogen mineralization and enrichment.

INTRODUCTION

Nitrogen-fixing plants have long been known to have important community- and ecosystem-level impacts. These effects have been traditionally studied within primary successional communities, where enrichment of N-poor soil by native N-fixers can facilitate successional change (Olson 1958, Lawrence et al. 1967, Connell and Slayter 1977, Walker and Chapin 1987, Morris and Wood 1989). Recently, however, with the increasing spread of nonnative N-fixing trees and shrubs, concern has focused on the role of exotic N-fixers in native plant communities (Vitousek et al. 1987, Witkowski 1991, D'Antonio and Vitousek 1992). Because soil N enrichment is thought to decrease species richness and to increase the susceptibility of communities to invasion (Hedde and Specht 1975, Heil

and Diemont 1983, Bobbink and Willems 1987, Tilman 1987, Aerts and Berendse 1988, Hobbs et al. 1988, Huenneke et al. 1990, Bobbink 1991, Hobbs and Huenneke 1992, Marrs 1993, Wedin and Tilman 1996), alien N-fixers potentially facilitate the spread of other exotic plants through their effects on soil N availability (Vitousek and Walker 1989, Witkowski 1991, Stock and Allsop 1992, Stock et al. 1995).

Studies of the effects of soil N enrichment on plant assemblages usually involve fertilizing plots and examining subsequent changes in species composition (Willis and Yemm 1961, Tilman 1987, Bobbink et al. 1988, Hobbs et al. 1988, Huenneke et al. 1990, Burke and Grime 1996, Wedin and Tilman 1996). More recently, atmospheric deposition of N has been linked to changes in plant composition (Press et al. 1986, Bobbink and Willems 1988, Morris 1991). But what of the effects of native N-fixing plants on soil N availability and invasion? We know surprisingly little about this

issue, despite the fact that many communities increasingly contain a suite of alien grasses and forbs that might benefit from high N soil created by native N-fixers.

Limited evidence suggests that any facilitating effect of N-fixing plants on invasion might not be realized until after the N-fixer dies. For example, in early successional communities on a recently erupted volcano, Mount St. Helens, *Lupinus lepidus* enriches N-poor soil and, in doing so, appears to facilitate colonization by other plants, principally the exotic, *Hypochaeris radicata*. However, sites enriched by *L. lepidus* only become colonized after *L. lepidus* dies (Del Moral and Bliss 1993). This raises the question of whether herbivores that kill N-fixing plants may modulate the impact of these plants on invasion. Although studies have shown that herbivory on dominant plants can alter community and ecosystem properties (McNaughton 1979, Jefferies 1988, Pastor et al. 1988, 1993, Whicker and Detling 1988, Jefferies et al. 1994, McNaughton et al. 1997), these effects have been little explored in systems where N-fixing plants are involved. Hence, while ecosystem changes initiated by N-fixing plants are well recognized (Vitousek and Walker 1989, Witkowski 1991), feedbacks between these plants, herbivory, altered ecosystem-level characteristics, and invasion are poorly documented. In this study, we examine how herbivore-driven changes in the abundance of a dominant N-fixing shrub alter ecosystem processes to the benefit of exotic plants.

Californian coastal prairie grasslands often are dominated by bush lupine (*Lupinus arboreus*), a large, native, N-fixing shrub that is capable of rapidly enriching soil (Gadgil 1971, Palaniappan et al. 1979, Baker et al. 1986, Bentley and Johnson 1991, 1994). At our study site, bushes are frequently attacked by a variety of insect herbivores, some of which kill plants (Strong et al. 1995, Maron 1998). On a fine spatial scale, mortality of isolated islands of lupines growing within mostly native coastal prairie promotes subsequent invasion into dead lupine patches by weedy introduced plants (Maron and Connors 1996). Invasion on this scale appears to be facilitated by the dual combination of soil enrichment and shrub death. Lupines enrich patches of soil; subsequent herbivore-driven lupine death exposes these enriched sites to light, making them available to weedy colonizers (Maron and Connors 1996).

Here we examine the ecosystem-level impacts of bush lupine in more detail, and we consider whether the same processes that promote invasion on a fine spatial scale, into individual dead lupine patches, might occur on larger spatial scales, after entire lupine stands are killed by herbivores. In particular, we ask how episodic recruitment and the establishment of dense lupine stands and subsequent death from insect herbivory alter the availability of soil N and light, and whether changes in the availability of these resources might be responsible for promoting changes in the prairie plant

assemblage. To address these questions, we determined whether prairie soils devoid of bush lupine are N-limited for plant growth. We then quantified the extent to which lupine occupancy and herbivore-driven mortality alter total soil N pools, rates of net N mineralization, and light availability beneath shrubs, which appears to be important in enabling N-rich patches created by lupine to be colonized. Finally, we measured the fraction of the total annual pool of mineralized N that is utilized by invasive annual plants that colonize enriched sites, and we estimated, in the absence of N inputs, the time required for the soil N pool to be depleted to a value comparable to that of soil free of lupine.

METHODS

Study area

This study took place on the 147-ha University of California Bodega Marine Reserve (BMR), situated on a coastal headland in Sonoma County, California, USA (Barbour et al. 1973). The site experiences a typical Mediterranean climate, with seasonal rains heaviest from November to March. Bush lupine, a perennial evergreen shrub, is abundant on BMR, where it forms dense stands within a coastal prairie plant community. Bushes can live at least 10 yr if they escape herbivory, but many shrubs die at younger ages (Davidson 1975; J. L. Maron, *personal observation*). The interstitial spaces between bush lupines primarily support the introduced annual grasses *Bromus diandrus* and *Lolium multiflorum*, along with a few native and introduced forbs, most of which are annuals. In the few grassland sites free of lupine, the prairie plant community is composed of several species of native perennial bunchgrasses and many small native annual forbs, including the annual lupine, *Lupinus nanus* (see Maron and Connors 1996 for a full description of this plant community). These remnants of mostly native coastal grassland vegetation are increasingly rare in California; most coastal grasslands in California are composed of introduced grasses and forbs (Heady et al. 1995).

To determine whether lupine occupancy and herbivore-driven die-off alters soil N relations, we compared soil N dynamics and plant community properties within three large (1–1.5 ha) contiguous sites (Fig. 1): a dense lupine stand (hereafter referred to as LL, for live lupine), a dead lupine stand composed of >40 000 dead plants that were killed by subterranean ghost moth (*Heplialus californicus*) caterpillars in the summer of 1992 (hereafter referred to as DL, for dead lupine), and an area mostly free from bush lupine (referred to as NL, for no lupine). The vegetative history of these sites is known from aerial photographs taken at various times over the last 40 years. At both DL and LL, dense stands of lupine have repeatedly died off, but subsequently regenerated from recruitment out of a dense seedbank (Strong et al. 1995, Maron and Simms 1997). In contrast, NL (and several smaller sites nearby) has his-

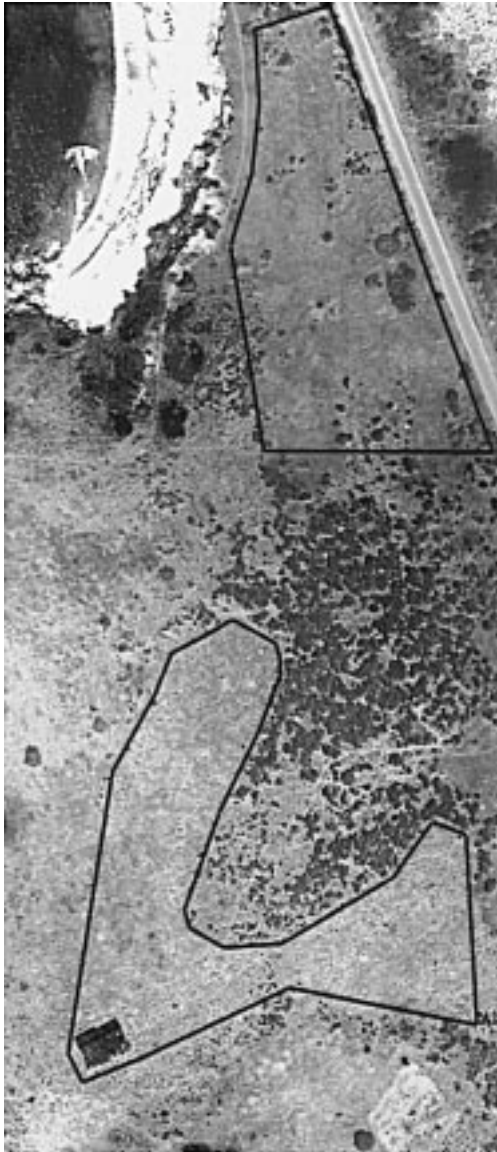


FIG. 1. Aerial photo showing NL (no lupine), LL (live lupine), and DL (dead lupine) sampling sites. NL (closest to the ocean at the top of the photo) and DL are outlined; LL is unmarked and lies between NL and DL. The photo was taken in August 1994.

torically lacked lupine, probably because prior agricultural activities on Bodega Head >35 yr ago kept plants out of these areas. Lupine colonization of these sites has been slow, because heavy lupine seeds do not disperse far from parent plants. As a result, these areas presently contain only isolated islands of bushes rather than dense stands, which dominate most of the grassland habitat at BMR. Although colonization of lupine-free sites has been slow, once established, the lupines flourish (J. L. Maron, *unpublished data*). Apart from differences in lupine density, there are no obvious differences in gross site characteristics between NL, DL,

and LL. However, in order to compare soil characteristics at the three primary sites, we took 50 g of soil at a depth of 5 cm, just below the surface layer of loose litter, at eight randomly chosen locations within each of the three areas. The samples were analyzed for pH; percentage of sand, silt, and clay; and cation-exchange capacity, using standard analytical procedures at the University of California at Davis soil laboratory. We used one-way ANOVAs to compare soil characteristics among sites. These and all other statistical analyses were performed using SYSTAT 5.0 for Windows (SYSTAT 1992).

An advantage of knowing the vegetative history of contiguous sites with similar soil characteristics is that it enabled us to determine how historical differences in lupine occupancy affect soil N relations and plant community characteristics. However, a drawback to this design is a lack of replicated sites with different known histories of lupine occupancy. Since there was only one stand of lupine that died en masse during most of this study (DL), as well as only one site about which we have unequivocal information (from >40-yr-old aerial photographs) of the lack of lupine (NL), it was not possible to replicate these large (>1.5 ha) sites. This lack of site replication hampers our ability to generalize beyond the sites we studied. However, we sampled total soil N and plant biomass at three additional smaller sites that have lacked lupine for at least 15 yr, as well as beneath live lupine bushes in several additional stands (as a replicate of the LL stand). In the case of the dead lupine stand, the only possibility for replication came from sampling the soils and plant assemblages in the interstitial spaces between lupines at three additional sites. Aerial photographs and the remains of dead wood in the soil show that these interstitial spaces represent places where lupines have died in the recent past. Additionally, we measured plant-available soil N under isolated dead lupines within NL, to compare with the majority of sites at NL that lacked lupine.

Nitrogen limitation in soil free from bush lupine

In order to determine whether N might be limiting in soils historically free from bush lupine, we established experimental blocks in eight randomly selected locations at NL. Each block contained two 1-m² plots that received either N or no amendment. Fertilization was randomly assigned to a plot within a block. Wire mesh, 75 cm in height, was erected around each 1-m² plot to exclude aboveground mammalian grazers. The plots were fertilized on 18 November 1994 with the addition 14.34 g of reagent grade ammonium nitrate (5.02 g N/m²). This amount of N was approximately equivalent to annual difference in amount of mineralized inorganic N found in areas with and without lupines (see *Total soil nitrogen and carbon*). On 17 February 1995, we again added N to plots (5.02 g N/m²) in an attempt to maintain high inorganic N concentrations in the upper levels of soil in the presence of extremely heavy rains (152 cm/yr, over twice the

annual average at our site; Bodega Marine Laboratory, unpublished data).

On 6 May 1995 at peak biomass for annual species, we subsampled total plant biomass within all plots by cutting and bagging aboveground vegetation within a 30 × 30 cm quadrat placed in the center of each plot. The vegetation was sorted into three categories—grass, forbs, and *L. nanus*—dried at 60°C for 36 h, and then weighed. We used a one-way ANOVA to test for differences in mean plant biomass between fertilized and nonfertilized plots.

Total soil nitrogen and carbon

In order to examine the influence of bush lupine on total soil N and carbon, we collected 50 g of soil at the rooting depth of most grasses and forbs in the community, between 5 and 10 cm below the soil surface, immediately below the loose litter layer. We collected samples at randomly selected locations within each of the three different primary study areas. Soil samples were collected at LL and DL sites in April 1993, at the NL site in July 1994, and at all three sites in both May and October 1994, in October 1995, and in May 1996 ($n = 3-6$ in each sampling period, except on 18 October 1994, where $n = 2$). In May 1996 we collected four soil samples at the three additional sites that lacked lupine, at one additional site under live lupine, and at three additional sites in the interstitial spaces between live lupines (where lupines had died in the recent past). In order to determine soil N levels at soil depths >5 cm, on 19 October 1995 we collected three additional soil samples at each of the primary areas at depths of 10 cm and 20 cm. All soils were dried at 50°C for 1 wk, and total soil N and C were measured with a LECO 600 carbon-hydrogen analyzer (St. Louis, Missouri, USA).

We compared concentrations of total soil N among sites by first averaging samples within sites and within year and then performing one-way ANOVAs on log-transformed data. Least square means post hoc comparisons (with Bonferroni adjustment) were made to examine differences between individual sites. Average C:N ratios of soils were compared among sites using a one-way ANOVA on arcsine-transformed data.

Exchangeable levels of inorganic soil nitrogen and net rates of nitrogen mineralization

To determine how soil N pools varied on a fine spatial scale between isolated dead lupine bushes (killed in September 1993) scattered throughout NL and surrounding prairie that lacked lupine, we measured exchangeable levels of NH_4^+ and NO_3^- in soil, monthly, from November 1993 to March 1995. We sampled soil under solitary dead lupines at NL and at sites several meters away. For comparison with fine-scale variation in N caused by lupine colonization at NL, we also sampled soil monthly at LL and at DL from April 1993 through April 1995. From May to August 1995 (in-

clusive), measurements were interrupted; further measurements were made at NL (away from dead lupines only), at LL, and at DL, from September 1995 to April 1996. Under isolated dead lupines at NL we took only one sample per month for determination of inorganic N. At all other sites, each month we took two 50-g samples between 5 and 10 cm below the soil surface. In each area we sampled soil at six randomly chosen locations separated by at least 20 m. One of the two soil samples was used for the determination of exchangeable levels of soil NH_4^+ and NO_3^- . The other sample was incubated in the field at 5 to 10 cm beneath the soil surface for one month to determine net rates of N mineralization. Samples to be incubated were placed in a polythene bag (Glad sandwich bag) porous to air exchange; each bag was enclosed in a wire cage to protect it from pocket gophers (*Thomomys bottae*). When soil was collected monthly for measurement of extractable N, we also collected the buried bags and replaced them with bags containing new soil sampled from randomly chosen locations.

Immediately after samples were collected, we measured percent soil moisture in 10–15 g subsamples. These subsamples were weighed, dried at 60°C for 2–7 d, and then reweighed. Moisture values were used to express rates of net N mineralization and levels of exchangeable ammonium and nitrate on a dry mass basis.

Ammonium and nitrate ions were extracted from 10 g of soil placed in a flask containing 50 mL of 1 mol/L KCl, which was kept at room temperature and shaken periodically. Twenty-four hours later, we filtered each sample through Whatman 40 ashless filter paper into vials and froze the filtrate. Some samples were analyzed for NH_4^+ and NO_3^- on a Carlson diffusion-conductivity analyzer (Carlson 1986); others were analyzed colorimetrically using a Technicon auto analyzer (Technicon Industrial Systems, Tarrytown, New York, USA). The phenol-hypochlorite method was used to detect NH_4^+ , while Marshall's reagent was used to detect NO_3^- (as NO_2^- , following cadmium reduction). The analytical error associated with the use of this equipment is <2%, and detection limits are similar between the two analyzers.

Net N mineralization rates were calculated monthly by determining ammonium and nitrate levels in soil within buried bags after incubation, and subtracting amounts of ammonium and nitrate found in unbagged samples at the beginning of the incubation. The values were summed for each site from May 1993 to April 1994. Mean net mineralization rates from mid-September to mid-April at each site were also calculated by summing monthly values. We used an ANOVA to compare mean annual and 7-mo mineralization rates between sites. We used least square means post hoc comparisons (with Bonferroni adjustment) to examine specific differences between individual sites. We also calculated total soil N and net N mineralization rates on a 1-m² basis by estimating the bulk density of a 1 ×

1 × 0.1 m block of soil 5–10 cm below the soil surface (127 kg). For comparisons of levels of total inorganic N, we determined the 4 mo when total net exchangeable inorganic N was highest at each site (November–February and October–January for 1993–1994 and 1994–1995, respectively). We then summed these 4-mo values for each replicate within each location and performed a two-way ANOVA (with year as a random factor and location as a fixed factor) on log-transformed data to compare the averages of these summed values between sites and across years. We used least square means post hoc comparisons (with Bonferroni adjustment) to compare means between sites.

Species composition

In February 1993 we established six 4 × 4 m permanent plots at randomly chosen locations at the DL site in order to characterize the plant community that established where lupine had died in the late summer of 1992. At this time the woody skeletons of lupines were intact, and the soil was bare of vegetation. In May of each year, from 1993 to 1996, we subsampled vegetation in two permanent 0.5 × 0.5 m subplots within each plot. Within the subplots, we recorded shoot frequency of all plant species within a grid of 25 × 10 × 10 cm squares and calculated average changes in frequency for each species each year within each of the six plots.

In order to determine the amount of N in the new plant biomass and to express it as a percentage of the soil N pool, we measured total plant biomass and tissue carbon and N. We sampled plant biomass in late April or early May (1993–1996 inclusive), when the standing crop was at or close to its peak. Outside the 4 × 4 m plots, we placed a 30 × 30 cm quadrat in three (1993) or four (1994–1996) randomly chosen sites dominated by *L. multiflorum*, *B. diandrus*, and the forbs *Claytonia perfoliata* and *Stellaria media*. We sampled the biomass of each of these two groups separately in 1993 ($n = 3$), but in subsequent years the vegetation was almost exclusively composed of annual grasses, and hence separate samples of biomass were not collected.

In May 1996, we sampled aboveground plant biomass in the interstitial spaces between live lupines, where individual lupines had died at the primary LL site, and within three additional live lupine stands. We further sampled vegetation under live lupines at the LL site. We took four samples of interstitial plant biomass from each site and under canopies at the LL site, as described above. Grasses and forbs were separated before drying.

Each May from 1993 to 1996, we sampled aboveground plant biomass within four 25 × 25 cm quadrats placed in randomly selected locations within the NL site, and in May 1996 at the three additional sites that were free from bush lupine. The samples collected in 1996 were separated into grasses and forbs and weighed. Vegetation sampled at all sites was dried at

50°C for at least 7 d, weighed, ground, and the C and N contents of tissues were determined with a LEECO 600 analyzer (LECO Corporation, St. Joseph, Missouri, USA).

In May 1996, we measured the root biomass and root : shoot ratio of 10 randomly selected plants of *B. diandrus* and *L. multiflorum*. Plants were excavated, gently washed in water to remove soil, and separated into shoots and roots, which were dried for 55 h at 60°C and weighed. The N and C contents of tissues were analyzed as described above.

Light measurements

To quantify the extent to which lupines decrease light availability, we used a LI-COR quantum sensor to measure photon-flux density (PFD) above and at ground level under the canopies of six randomly chosen 2-yr-old lupines. Measurements were made in full sunlight at midday solar time on 9 May 1996. To quantify how dead lupine skeletons affect light penetration to the soil surface during winter, when most annual grasses are establishing within areas where lupines have died, on 5 January 1998 we measured PFD at midday under and above the skeletons of eight randomly chosen 2-yr-old dead lupines and under and above eight randomly chosen live lupines of the same age. Dead lupines were within a large lupine stand that had died during fall 1997 (J. L. Maron and S. Harrison, *unpublished data*). We expressed light penetration as the percentage of PFD (measured without obstruction, above lupines) reaching the ground surface, and then compared the mean level of PFD penetrating through live and dead lupines using a *t* test.

RESULTS

Soils at each of the three primary sites were similar in mineral composition and pH (Table 1). Soil free from bush lupine at the NL site, however, contained significantly less organic material (ANOVA, $F_{2,21} = 13.0$, $P < 0.001$), which may explain its lower cation-exchange capacity ($F_{2,21} = 15.6$, $P < 0.001$) compared to sites with live and dead lupine.

Nitrogen limitation in soil free from lupine

Addition of fertilizer to plots at the NL site produced significant effects on total aboveground plant biomass ($F_{1,14} = 18.4$, $P < 0.001$). Biomass harvested from fertilized plots averaged 6563 g/m², an 81% increase over biomass in control plots, which was largely the result of an increase in the growth of grasses relative to that of forbs. On average, 80% of the total biomass sampled in fertilized plots was composed of grasses, whereas grasses only contributed an average of 58% of the biomass in control plots. Average forb biomass was similar in fertilized and control plots ($F_{1,14} = 0.011$, $P = 0.92$).

TABLE 1. Soil characteristics at live lupine (LL), dead lupine (DL), and lupine-free (NL) sites ($n = 8$ at each site). Data are means ± 1 SE.

Characteristic	LL	DL	NL
Organic matter (%)	5.1 \pm 0.31	5.6 \pm 0.54	2.9 \pm 0.13
Sand (%)	88.4 \pm 0.32	87.5 \pm 0.42	86.6 \pm 0.46
Silt (%)	6.9 \pm 0.48	6.25 \pm 0.31	7.0 \pm 0.78
Clay (%)	4.75 \pm 0.25	6.25 \pm 0.25	6.4 \pm 0.5
pH	5.6 \pm 0.1	5.5 \pm 0.08	6.0 \pm 0.04
Cation exchange capacity (mmol/100 g)	14.3 \pm 0.73	14.9 \pm 0.68	10.6 \pm 0.26

Total soil nitrogen and carbon

Concentrations of total soil N were significantly different between sites ($F_{2,21} = 10.3$ in 1994, $F_{2,6} = 34.8$ in 1995, $F_{2,15} = 29.2$ in 1996, $P < 0.001$ in all years). Soil from the primary live and dead lupine sites contained higher amounts of total N than that in the lupine-free site (least squared difference post hoc multiple comparison with Bonferroni correction, $P < 0.05$ in all years), although mean total soil N was not significantly different in any year between LL and DL (post hoc comparison $P > 0.05$). Depending on the year, soil from the lupine-free site contained between 36 and 55% less N than lupine-influenced soil (Table 2). Total soil N averaged 342–462 g/m² at the LL site, 394–521 g/m² at the DL site, and 190–254 g/m² at the NL site. At each of the three sites, soil N declined with soil depth (Table 3).

Despite differences among sites in total soil N, average C:N ratios were not statistically different in 1994 or 1995 ($F_{2,21} = 0.25$ in 1994, $F_{2,6} = 0.72$ in 1995, $P > 0.05$ in both years). In 1996, however, the average C:N ratio at the NL site was significantly lower than that at the DL site, although not significantly different from the C:N ratio at the LL site ($F_{2,15} = 3.86$, $P =$

TABLE 2. Mean (± 1 SE) soil N pool sizes, C:N ratios, and cumulative net N mineralization rates, at LL, DL, and NL. (See *Methods* for sampling dates and sample sizes used to calculate annual averages of total soil N and C:N ratios.) Annual (1993–1994) or 8-mo (1994–1995 and 1995–1996) net mineralization rates are sums of monthly averages from each site ($n = 6$ at each site).

Year	LL	DL	NL
Pool size, total soil N (mg N/g dry mass soil)			
1993	3.7 \pm 0.3	4.1 \pm 0.3	Not sampled
1994	3.1 \pm 0.2	3.3 \pm 0.3	2.0 \pm 0.1
1995	3.1 \pm 0.1	3.3 \pm 0.3	1.5 \pm 0.03
1996	2.7 \pm 0.1	3.1 \pm 0.2	1.5 \pm 0.1
C:N ratio			
1993	12.8 \pm 0.5	13.5 \pm 0.2	
1994	12.4 \pm 0.7	12.4 \pm 0.9	13.1 \pm 0.6
1995	13.7 \pm 0.4	13.1 \pm 0.6	13.1 \pm 0.04
1996	14.2 \pm 0.4	15.0 \pm 0.5	13.3 \pm 0.4
Net mineralization rate (μ g/g dry mass soil)			
1993–1994	107.9 \pm 12.6	82.4 \pm 9.4	51.4 \pm 9.2
1994–1995	78.9 \pm 17.1	92.8 \pm 12.8	36.3 \pm 3.9
1995–1996	86.2 \pm 26.4	80.2 \pm 13.9	30.5 \pm 2.7

0.044; post hoc least square means with Bonferroni adjustment = 0.042 between values from NL and DL sites).

Patterns of total soil N at additional replicate sites sampled in 1996 were similar to those at the primary sites. Total soil N was significantly lower at the three additional lupine-free sites (mean value for all three sites = 207 g N/m²), compared to total soil N under lupines (mean value = 305 g N/m²), or compared to that in interstitial areas between live lupines (mean value = 283 g N/m²; $F_{2,25} = 6.98$, $P < 0.005$). The mean value for the lupine-free sites was not significantly different from that at the primary NL site ($F_{3,14} = 0.619$, $P = 0.614$).

Exchangeable levels of inorganic soil nitrogen and net rates of nitrogen mineralization

Exchangeable NH₄⁺ and NO₃⁻ concentrations varied seasonally at all sites; peaks in NH₄⁺ and NO₃⁻ occurred from early to midwinter, with the onset of rain (Figs. 2 and 3). During peak periods in midwinter, total inorganic N was consistently different among sites and years ($F_{3,40} = 6.39$ and $F_{1,40} = 5.1$, $P < 0.01$ for site and year, respectively), with year-to-year differences varying by site (as indicated by a significant site-by-year interaction; $F_{3,40} = 3.4$, $P < 0.03$). In each year, soil under live lupine and dead lupine contained significantly higher inorganic N compared to soil from the lupine-free area (LSD post hoc comparisons with Bonferroni correction based on separate ANOVAs for each year, $P < 0.001$; Fig. 4).

Rates of net N mineralization were significantly different among sites (Table 4). In 1993–1994, greater amounts of N were mineralized annually in soils from LL than in NL (post hoc comparison, $P < 0.02$), but there was no significant difference in net mineralization rates between LL and DL or DL and NL (post hoc

TABLE 3. Mean (\pm SE) values for total soil N at different depths at LL, DL, and NL sites.

Soil depth (cm)	Total soil N (mg N/g dry mass soil)		
	LL	DL	NL
5	3.1 \pm 0.1	3.3 \pm 0.3	1.5 \pm 0.03
10	2.3 \pm 0.5	2.1 \pm 0.2	1.1 \pm 0.1
20	1.5 \pm 0.1	2.1 \pm 0.2	1.1 \pm 0.2

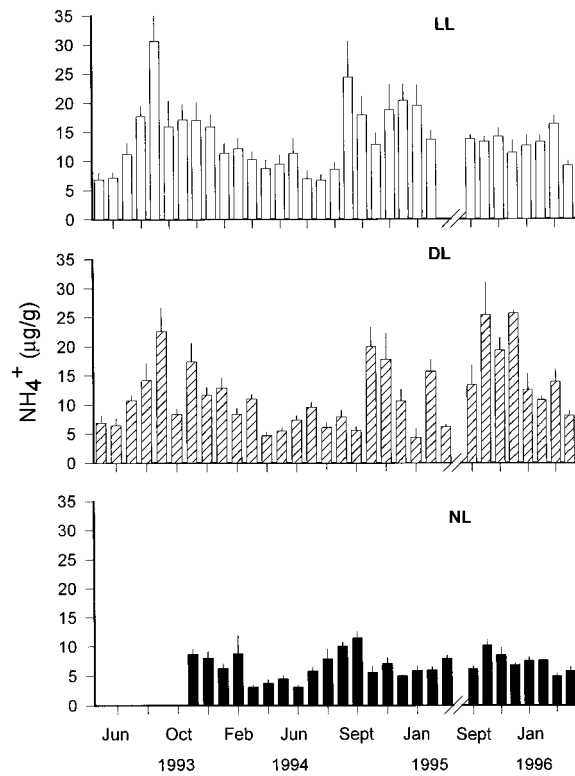


FIG. 2. Ammonium (NH_4^+) concentrations (mean + 1 SE) from within a live lupine stand (LL), a dead lupine stand (DL), and an area mostly free from lupine (NL); $n = 6$ at each site. Samples were taken every 28–32 d.

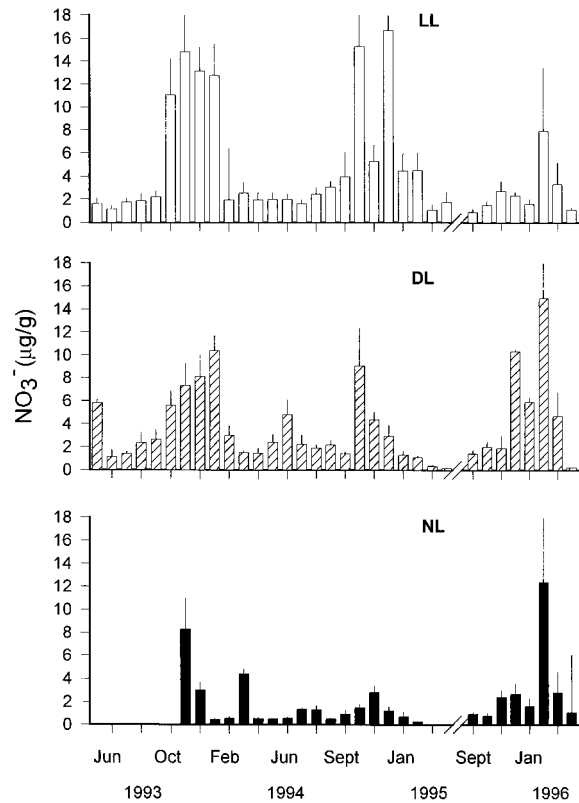


FIG. 3. Nitrate (NO_3^-) concentrations (mean + 1 SE) from within a live lupine stand (LL), a dead lupine stand (DL), and an area mostly free from lupine (NL); $n = 6$ at each site. Samples were taken every 28–32 d.

comparison, $P > 0.05$). From mid September to mid April 1994–1995 and 1995–1996, mineralization was significantly higher in soils from both the live and dead lupine stands than in soils from the NL site (Table 2; post hoc comparison, $P < 0.05$ for both LL vs. NL and DL vs. NL). Net N mineralization rates also showed seasonal patterns in both 1993–1994 and 1994–1995, with mineralization rates being highest at all sites in mid winter (Fig. 5).

Only a small fraction of the total pool of soil N in the different sites became available as net mineralized N each year. For both 1993–1994 and 1994–1995, this percentage (2.5–4%) was not substantially different among sites.

Species composition, plant biomass, and plant nitrogen content

In the first spring after stand die-off, the plant assemblage that established in the bare soil within the dead lupine stand was composed primarily of the native forb *C. perfoliata*, the introduced forb *S. media*, and the exotic grasses *B. diandrus* and *L. multiflorum* (Fig. 6). Growth of these colonists was rapid, and the concentration of foliar N was high (Table 5). *B. diandrus*/*Lolium multiflorum* contained an average of 1.52% N. The comparable value for the combined forb biomass

was 1.42% N. In 1995 and 1996, the DL plant community was dominated by *L. multiflorum* and *B. diandrus* (Fig. 6). The combined biomass of these species contained an average of 1.3% and 0.96% N in 1995 and 1996, respectively. In 1996, belowground biomass of the grasses averaged $11.7 \pm 1.26\%$ (mean ± 1 SD) of the aboveground biomass. Nitrogen concentration was 88% of that of the aboveground biomass. In contrast to the DL site, plant biomass was low in the lupine-free NL site. Mean values for plant biomass were 295, 288.8, and 324 g dry mass/m² in 1993, 1995, and 1996, respectively. These values were all significantly lower than corresponding values for the DL site (for each year, $P < 0.02$). At the NL site, forbs contributed an average of 22% of the aboveground biomass, whereas, at the DL site, over 99% of the biomass was composed of introduced grasses in 1996.

In 1995 in the NL site an average of 4.2 g N/m² was present in aboveground vegetation, compared to 9.7 g N/m² in vegetation at the DL site. A similar pattern was found in 1996, when the vegetation at the NL site contained, on average, 4.7 g N/m² (forbs = 1.33 g N/m², grasses = 3.34 g N/m²), again a smaller amount of N than that present in aboveground biomass at the DL site, which averaged 7.4 g N/m².

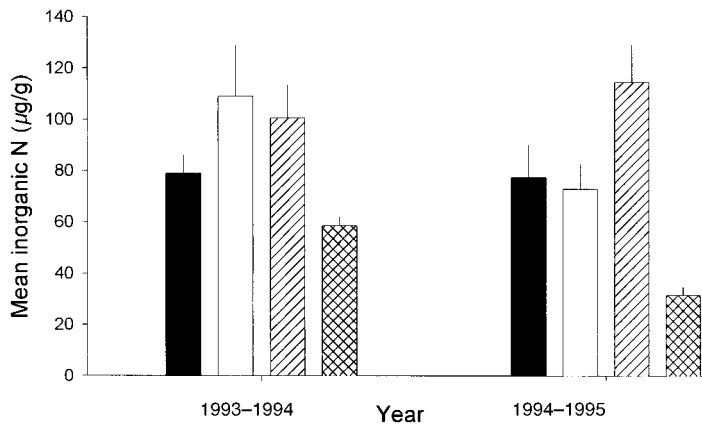


FIG. 4. Total inorganic N (mean + 1 SE) under isolated dead lupine at NL (black bar), within a dead lupine stand at DL (open bar), under a live lupine stand at LL (hatched bar), or at NL away from isolated dead lupines (cross-hatched bar). The figure presents means from six values at each site, with each value being the sum of measurements taken monthly across a 4-mo period when levels of exchangeable N were highest.

Amounts of aboveground biomass at the additional sites sampled in 1996 were similar to those of the primary sites. The three sites sampled (in addition to NL) that were lupine-free supported total aboveground biomass that averaged 289, 166.5, and 241 g dry mass/m², respectively (compared to 324 g/m² at NL and 771 g/m² at DL in 1996). Forbs contributed an average of $18.3 \pm 1.89\%$, $29.5 \pm 3.73\%$, and $24.9 \pm 1.5\%$ to the biomass at the three additional sites, respectively. In addition, average biomass at these sites was significantly lower than that sampled from the interstitial spaces between lupines at the three additional sites ($F_{1,18} = 37.36$, $P < 0.0005$), where mean values for aboveground biomass were 513.9, 479.5, and 623.8 g dry mass/m², respectively. The interstitial plant community growing between lupines was composed almost entirely of grasses at all sites (99% of the total biomass). Amounts of plant biomass at the three additional sites within each habitat type (LL, DL, NL) were not significantly different from corresponding values for the primary sites ($P = 0.33$; ANOVA with site nested within habitat).

Measurements of photon-flux density

The average PFD above the lupine canopies in the full sunlight in May 1996 was $1725 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$,

whereas under the lupine canopy, at ground level, the average value fell to $13 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ($n = 6$), <1% of the PFD in full sunlight. In January 1998, when lupine canopies are less dense than in spring, the average PFD under live lupine canopies was $83 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, which was 8% of the average PFD in full sunlight ($1040 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Significantly more sunlight penetrated through dead lupine skeletons (mean PFD = $370 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) than through the can-

TABLE 4. ANOVA testing for differences in mean net N mineralization rates across 12 mo (1993-1994) or 7 mo (1994-1995 and 1995-1996) between LL, DL, and NL sites.

Source	df	MS	F	P
1993-1994				
Site	2	4800	7.3	0.006
Error	15	660		
1994-1995				
Site	2	5202	5.5	0.016
Error	15	945		
1995-1996				
Site	2	3.1	1.5	0.01
Error	15	0.24		

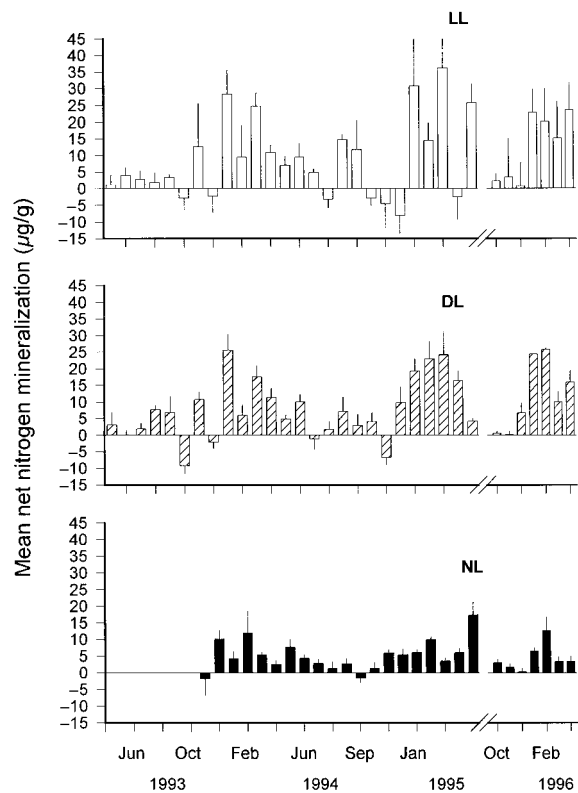


FIG. 5. Monthly rates of net N mineralization (mean + 1 SE) within a live lupine stand (LL), a dead lupine stand (DL), and an area free from lupine (NL); $n = 6$ at each site. Samples were taken every 28-32 d.

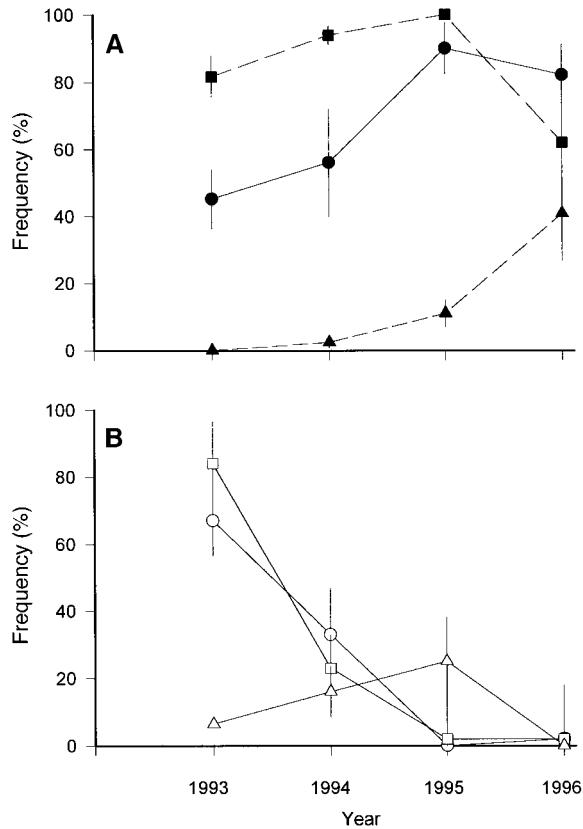


FIG. 6. Mean (± 1 SE) frequency (%) of (A) grasses (solid squares, *L. multiflorum*; solid circles, *B. diandrus*) and bush lupine (solid triangles, *L. arboreus*), and (B) forbs (open squares, *S. media*; open circles, *C. perfoliata*; open triangles, *Lasthenia* spp.) in permanent plots at the DL site ($n = 6$). Only plants that occurred at a frequency $>5\%$ in two of the four years were plotted. The next most common species in plots included the introduced grasses *Aira caryophylla* and *Vulpia bromoides*, the introduced forbs *Cerastium glomeratum*, *Galium aparine*, and *Rumex acetosella*, and the native forbs *Achillea millefolium* and *Trifolium gracilentum*.

opy of live lupine (t test with separate variance, $t = 2.88$, $P < 0.025$).

DISCUSSION

Continual lupine occupancy and turnover has resulted in N enrichment of sandy soils on BMR, some of which rival highly managed agricultural soil in their fertility (Sprent 1987). In contrast to the lupine-influenced soil, which contained over a three-year period an average of 414 g N/m² at 5–10 cm immediately below the loose litter, soil at contiguous lupine-free sites contained over the same period an average of 221 g N/m² (Table 2). Organic N content of soils under live lupines was high, and C:N ratios were low. These conditions favor microbial decomposition and high rates of N mineralization. Our results on the effects of lupine on soil N relations are similar to those found for bush lupine at locations where the plant has been introduced

TABLE 5. Mean standing crop and N content of grasses and forbs in DL ($n = 4$ for both grasses and forbs in all years except 1993, where $n = 3$). The final row shows percentage of annual amount of mineralized N (estimated for 0–10 soil depth; mineralization rates calculated from May to April for both 1993–1994 and 1994–1995) that is sequestered in grasses at the end of the growing season in May. Ellipses indicate absence of forbs from samples in 1994–1996.

Parameters	1993	1994	1995	1996
Standing crop grasses (g dry mass/m ²)	898	568	767	771
Standing crop forbs (g dry mass/m ²)	525
N content of standing grass crop (g/m ²)	13.6	6.0	10.0	7.32
N content of standing forb crop (g/m ²)	7.2
Percentage of annual pool of net mineralized N that is cycled through plant biomass		56	72	

(Gadgil 1971, Palaniappan et al. 1979, Baker et al. 1986).

Lupine occupancy leads to the continual creation of patches of N-rich soil, which significantly boosts plant biomass, and presumably leads to the increased dominance of exotic grasses, to the detriment of slower growing native species. Yet, while lupines are alive, enriched soil is unavailable for colonists, because light availability beneath the dense lupine canopy is reduced by 98–99%. Insect herbivory and subsequent lupine stand mortality, however, open these enriched sites to light, which then makes them available to invasive fast-growing colonists. Thus, unlike vertebrate herbivores and defoliating insects, which can alter rates of N cycling or change pool sizes of N (Bocock 1963, Chew 1974, McNaughton 1979, Ohmart et al. 1983, Schowalter 1981, Swank et al. 1981, Hollinger 1986, Jefferies 1988, Whicker and Detling 1988, Pastor et al. 1993, Lovett and Ruesink 1995, McNaughton et al. 1997), insect herbivory on lupine acts to increase light availability, which makes N-rich sites available to weedy colonists. A similar result was found for leaf beetles (*Trihabda canadensis*) that fed on goldenrod (*Solidago missouriensis*). Herbivory on goldenrod monocultures led to invasion by other plants; changes in resource (light and N) availability initiated the process that facilitated invasion (Brown 1994).

Neither enrichment nor change in light availability, alone, appears sufficient to promote invasion. For example, fertilization of lupine-free sites does not immediately result in the increased dominance of invasive plants (J. L. Maron and R. L. Jefferies, unpublished data). This may be because fertilized sites do not have a legacy of light limitation, which limits existing species. As well, although plant biomass responds immediately to fertilization, it usually takes several years for plant species composition to change in response to fertilization. By the same token, creation of bare soil alone does not result in invasion. Introduced species

are no more common in disturbed patches in sites free from lupine than they are in undisturbed patches in these same areas (Maron and Connors 1996). Thus, both soil enrichment and lupine death, as dual processes, appear essential in facilitating invasion.

At BMR, sites previously occupied by lupine are invaded primarily by *B. diandrus* and *L. multiflorum* and to a lesser extent by *Vulpia bromoides*. These grasses germinate in early winter, when mineralized soil N is high, and take up between 57 and 70% of the annual mineralized N in the DL site. Plant biomass at this site and in the interstitial spaces between lupines in LL stands is significantly greater than the biomass of the more species-rich (mostly native) plant assemblages growing in lupine-free sites.

Once sites become enriched, we predict that it will take years for the N status of these soils to decline to levels present in soils free from lupine, even in the absence of further inputs of N. At the DL site, where bush lupines were absent for 3–4 yr, N levels remained high. Only a small fraction of the total soil N is mineralized annually, and much of this N appears to be recycled in the litter of annual plants. Calculations based on net N mineralization rates and on N sequestered in annual plants indicate that, in the absence of new N inputs, it would take ~25 yr to reduce the amount of soil N by 50%. Such calculations are based on the rate of turnover of the highly labile fraction of N. Rapid depletion of this fraction within a few years (in the absence of reinvasion of lupine) may result in lower rates of N release in the soil, in spite of the persistent, large soil N pool, as increasingly recalcitrant fractions dominate turnover dynamics. However, the estimate of 25 yr is similar to long-term results from land that has been left fallow, where it has taken >41 yr for the initial pool of soil N to decline by half in the absence of N inputs (Addiscott 1988). Prior N fertilization of sites can affect N mineralization years after fertilization has ceased (Vinton and Burke 1995), and even in unfertilized grasslands, total soil N content declines slowly (Olff et al. 1994).

The amount of N mineralized varied between 2.5 and 4.2% of the total N pool in the three areas, values that are similar to those obtained in other studies of temperate or subarctic soils (Nadelhoffer et al. 1983, Pastor et al. 1984, Hart and Gunther 1989, Wedin and Pastor 1993). Similarities among sites in the percentage of the total soil N pool that is mineralized reflects, in part, the fact that C:N ratios of soil are similar among the three sites. As well, the relative sizes of the most highly labile fraction of the total N pool are comparable in the LL, DL, and NL sites. Values of the annual net amount of N mineralized in the three areas varied between 6.6 g/m² at the NL site to 16.6 g/m² in soils at the LL site, values that are similar to those from soils of old fields where plots were fertilized with N (Pastor et al. 1987). As found in other studies, seasonal variation in net rates of N mineralization was high (Davy

and Taylor 1974, Taylor et al. 1982, Morecroft et al. 1992), with large pulses of mineralization in the late fall and early winter of 1994, 1995, and 1996.

Although annual grasses dominate sites after lupine mortality, germination from a long-lived seed bank allows lupines ultimately to reestablish in these sites (Maron and Simms 1997). Over periods of 4–10 yr, this produces a cyclical change in the plant community, characterized by stand development, herbivory, stand death, colonization by introduced grasses and forbs, and then reestablishment of dense lupine stands. We have documented one such cycle of change in the DL site, but historical photographs indicate that similar oscillations in the plant assemblages have taken place in the past, both at the DL site and other locations on BMR (Strong et al. 1995). In fact, at the end of this study, we witnessed another large lupine die-off that killed ~95% of the bushes within LL, as well as bushes in nearby areas. Plants died as a result of both heavy defoliation by an unusually dense outbreak of tussock moth (*Orgyia vetusta*) caterpillars and subsequent flooding during an extremely wet winter.

Within Californian coastal prairies, shrub species such as *L. arboreus*, *Ulex europaeus* (another N-fixer), and *Baccharis pilularis* frequently colonize formerly heavily grazed pasture (McBride and Heady 1968, Heady et al. 1995). Although prairie grasses may reestablish at these sites where shrubs do not invade, it is evident from the present study that if N enrichment occurs, it may preclude the establishment of most native species. Active management will be necessary to lower total soil N, especially the size of the highly labile pool. Common practices include cropping of vegetation, removal of surface soil and shrubs, and burning of aboveground vegetation and litter in order to maintain prairie plant assemblages (Marrs 1993). These practices alone, however, may be insufficient to reestablish native flora if poor dispersal limits native plant recruitment into these sites.

Results from this study and those from a companion study (Maron and Connors 1996) suggest that bush lupines and the phytophagous insect herbivores that kill them together influence community and ecosystem processes. The combination of N-fixation and rapid growth, community dominance, and susceptibility to insect herbivory make bush lupine particularly influential at our site in determining coastal prairie plant assemblages.

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