

Selective herbivory on a nitrogen fixing legume (*Lathyrus venosus*) influences productivity and ecosystem nitrogen pools in an oak savanna¹

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Abstract: Herbivory is known to change the structure of vegetation, but the possible effects of herbivory on ecosystem nitrogen pools are not well documented. Here we report that 13 years of deer exclusion significantly influenced ecosystem nitrogen pools and caused ecosystem productivity to more than double in a regularly burned Minnesota oak savanna. Herbivore exclusion greatly increased the abundance of *Lathyrus venosus*, a native nitrogen fixing legume. Primary productivity also increased through time, as did total soil nitrogen. This increase in productivity did not occur in unfenced plots, where there was a loss of total soil nitrogen, probably because fire-induced nitrogen losses exceeded gains. This study documents that herbivores, through "top-down" effects on foodwebs, can strongly influence nitrogen pools in terrestrial ecosystems, and that legumes can play a critical role in replacing fire-induced nitrogen losses in Midwestern oak savannas.

Keywords: herbivory, legumes, nitrogen fixation, nitrogen cycling, oak savanna, exclosures.

Résumé : On sait que l'herbivorie peut modifier la structure de la végétation mais ses effets possibles sur le pool d'azote demeurent peu connus. Nous rapportons, ici, que 13 années d'exclusion du cerf de Virginie ont influencé significativement les pools d'azote de l'écosystème (une savane arborée de chêne fréquemment brûlée) et ont entraîné une augmentation de plus du double de la productivité. L'exclusion du cerf a permis une augmentation marquée de *Lathyrus venosus*, une légumineuse indigène fixant l'azote. La production primaire s'est aussi accrue avec le temps après l'exclusion, tout comme l'azote du sol. L'accroissement de la productivité ne s'est pas produit dans les parcelles témoins non clôturées où il y a eu une perte de l'azote total du sol, parce que les pertes d'azote attribuables au feu dépassaient probablement les gains. Cette étude révèle que les herbivores, par une dominance trophique descendante, peuvent influencer profondément les pools d'azote d'écosystèmes terrestres et que les légumineuses peuvent jouer un rôle déterminant en remplaçant les pertes d'azote causées par le feu dans les savanes arborées du Midwest.

Mots-clés : herbivorie, légumineuses, fixation, azote, recyclage, savane, chêne, exclos.

Introduction

Selective herbivory frequently causes changes in the structure of plant communities (Batzli & Pitelka, 1970; Huntly, 1991; 1987; McNaughton, 1978; Ross, Bray & Marshall, 1970). However, these changes may not affect ecosystem nutrient pools significantly (Buechner & Dawkins, 1961; Hatton & Smart, 1984; Tiedemann & Berndt, 1972; Pletscher, Bormann & Miller, 1989; but see Schlesinger *et al.*, 1990). This lack of ecosystem response is likely to be caused by the competitive release of non-grazed species that can acquire resources left available by the species experiencing herbivory (Louda, Keeler & Holt, 1990). However, ecosystem nutrient cycling can be changed if a feedback between herbivores, plants and decomposers occurs (Pastor & Naiman, 1992) or if the plant species held in check by herbivory can disproportionately influence nutrient inputs, such as nitrogen fixing legumes. Legumes can strongly influence ecosystem nitrogen inputs, nitrogen pools, and primary productivity (Binkley *et al.*, 1992; Bormann *et al.*, 1993; Fahey *et al.*, 1985; Kohls *et al.*, 1994;

Vitousek *et al.*, 1987; Vitousek & Walker, 1989). Because legumes have a larger supply of nitrogen than non-legumes, they also often have higher quality tissue which can result in higher herbivory. Herbivory can substantially reduce growth, survival, and fruit production of legumes (Ehler, 1995a,b). However, this increased herbivory of legumes due to the increase in tissue quality can be modified by the presence of plant secondary compounds (Bryant & Kuropat, 1980; Hjalten & Palo, 1992).

Ritchie & Tilman (1995) showed that herbivore exclusion dramatically increased legume abundances at Cedar Creek, especially for *Lathyrus venosus* (viney peavine or bushy vetchling). *Lathyrus* is a native perennial legume with herbaceous, deciduous viney shoots up to 1 m long, and overwintering rhizomes that can be locally common in open woodlands and prairies (McGregor, Barkley & Association, 1986; Stubbendieck & Conard, 1989). *Lathyrus* has a distinct phenology, in that it grows early, relative to the dominant C₄ grasses, reaches peak biomass in June and senesces in July or August depending on the weather. Roots are nodulated and show nitrogenous activity (Knops, pers. observ.). In this study, we compared nitrogen pools within and outside a long-term herbivore exclosure over 13 years to examine if lack of herbivory, which

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increased legume abundance (Ritchie & Tilman, 1995), also influenced nitrogen pools, and if changes in these nitrogen pools are reflected in overall productivity.

Material and methods

STUDY SITE

This study was conducted in an oak savanna at Cedar Creek Natural History Area that has never been cultivated (Field D; Tilman, 1987). Cedar Creek Natural History Area is located 45 km north of Minneapolis, Minnesota, U.S.A. (45° 24' N, 93° 12' W) and has a typical mid-continent climate with hot, humid summers and cold winters. Soils consist of fine sands from the Sartell series (Grigal *et al.*, 1974) and nitrogen is the only detectable mineral nutrient limiting plant productivity within this field (Tilman, 1984; 1987). This savanna has an open overstory canopy of two oak species *Quercus ellipsoidalis* and *Q. macrocarpa* with an understory dominated by native tallgrass prairie species such as *Sorghastrum nutans*, *Carex sp.*, *Rubus sp.*, and *Artemisia ludoviciana*. This landscape has been maintained by burning since 1964, and is part of a larger experiment on the effect of fire frequency in oak savanna (White, 1983; Tester, 1989; Faber-Langendoen & Tester, 1993). Both the fenced and unfenced areas are burned as part of one burn unit, every two out of three years. Recent burns occurred in 1981, 1982, 1984, 1985, 1987, 1988, 1990, 1991, 1993, 1994.

We studied nitrogen pools and plant productivity in two areas with the same site and burn history. One 0.125 ha area was fenced in 1982 to exclude white-tailed deer (*Odocoileus virginianus*), cottontail rabbits (*Sylvilagus floridanus*), and pocket gophers (*Geomys bursarius*). Note that there are no other large herbivores present at Cedar Creek. Plots within this fenced area are part of a long-term nitrogen fertilization experiment sampled annually (Tilman & El Haddie, 1992; Tilman & Downing, 1994; Tilman, 1996; 1987). Herbivores were excluded with 15 cm mesh wire up to 1.8 m high and hardware cloth buried to a depth of 84 cm. Gophers were regularly trapped and removed, and other small mammals on an occasional basis. A separate unfenced area comprises a series of ten 20 m × 50 m "macro plots" that are part of an experiment investigating the effects of nitrogen addition on oak savanna. These two experiments are located next to each other and all plots are within 200 meters of one another.

Cedar Creek is a protected area in which no deer were hunted from 1985 to 1994. No good estimates on total deer density are available, but a regulated hunt in 1994 removed 150 adult deer and a similar hunt in 1995 removed 191. Cedar Creek comprises 2200 ha, and this puts a minimum on deer density of 0.16 deer per ha. This density is similar to that in other protected areas (Ross, Bray & Marshall, 1970; McCullough, 1979), where deer herbivory has caused shifts in the dominant tree species. Pocket gopher densities are low in savanna fields (Inouye *et al.*, 1987).

SOIL SAMPLES

Samples were collected before the fertilizer treatments were established in both the unfenced and fenced areas in 1982. One composite sample from four soil cores was

collected in each of 45 plots in the fenced area and four composite samples were collected per macroplot ($n = 10$) in the unfenced area in 1982 and 1995. All cores were 15 cm deep, 2.5 cm wide in both areas and at both sampling times.

FERTILIZER TREATMENTS

Fertilization methods are detailed by Tilman (1987). In summary, the fenced experiment was established in 1982 and has nine fertilizer treatments with five replicates per treatment, a control, and eight different rates of NH_4NO_3 addition with the same amount of other nutrients (P, K, Ca, Mg, S and trace elements) for a total of 45 plots of 1.5 m × 4 m. Rates of N addition are 0, 1, 2, 3.3, 5.3, 9.3, 16.7, and 26.7 g nitrogen/m² year. Fertilizer was applied twice each year, once in early May and once in late June. The unfenced fertilizer experiment also started in 1982 and consisted of ten 20 m × 50 m "macro plots" with one control plot, and three treatments with three replicates each of different rates of NH_4NO_3 addition with the same amount of other nutrients (P, K, Ca, Mg, S and trace elements). Rates of N addition are 0, 5.3, and 26.7 g nitrogen/m² per year.

STANDING BIOMASS

The same vegetation sampling methods were used from 1982 through 1997 (see Tilman, 1987, for an in-depth description). In summary, standing biomass was sampled by clipping a 10 cm × 3 m strip at the soil level in each 1.5 m × 4 m plot in the fenced area and in four subplots within each of the 10 macro plots. Herbivory was only detected on the standing biomass of *Lathyrus* in the unfenced area. Note that deer are the only large herbivore present, and browses only on specific plants like *Lathyrus*. We are confident that the standing biomass of the dominant grasses and forbs are reflecting their annual productivity. The fenced area was sampled each year, whereas the unfenced area was only sampled in 1982 and in 1995. Plant samples were taken into the laboratory, sorted to functional group or standing dead biomass (*e.g.*, litter), weighed, and ground in a Cyclone mill. Root biomass was estimated from three 2.5-cm diameter by 25-cm long soil cores per clipped strip in each plot, and three in each of the four subplots of each macroplot. Samples were lumped per plot or subplot and rinsed to remove all soil; dead and live roots were not distinguished. All plots were sampled in late August of 1982 and in both late June and early September of 1995.

NITROGEN MINERALIZATION

This was determined by using the *in situ* sequential coring technique (Raison, Connell & Khanna, 1987). Six PVC pipes 5 cm wide and 25 cm long were placed into each clipped strip in the fenced plots and the unfenced macroplots after clipping in June 1995. Three cores from each strip were immediately removed and combined, extracted in 1N KCL, and subsequently analyzed for NH_4 and NO_3 . The other three cores from each strip were removed at the time of the second clipping in 1995, and combined and extracted in the same way as the first samples. Samples were analyzed with a Alpchem RFA-300 autoanalyzer for NH_4 -N and NO_3 -N, following standard methods. Net mineralization was calculated as the sum of the final extraction minus the first extraction.

NITROGEN AND CARBON ANALYSIS

All soil and plant samples were dried to constant mass at 60°C, weighed, ground, and analyzed for carbon and nitrogen with a Carlo-Erba NA1500 N/C analyzer. One extreme value (three times higher than the other replicates) from the fenced area was analyzed four times and found to be consistently higher; consequently, we used the average value. Nineteen of the 884 functional group plant samples were too small to analyze (less than 0.5 g) and the average of a category (by harvest data, experiment, and fertilizer treatment) was used to calculate total plot N and C. All soil samples were analyzed in 1995.

STATISTICAL ANALYSIS

All of the plots used in this study are located within the same stand of savanna and are either within or outside of one enclosure. Many of our statistical analyses are comparisons of plots inside versus outside of the enclosure. As such, there is no actual replication for effects of fencing (Hulbert, 1984). We offer our analyses despite this major limitation because we believe that the long-term trends we have observed are unique and may well give an important insight into the effects of herbivory on ecosystem nitrogen dynamics. We used a GLM analysis to test for differences between the herbivore enclosure and the unfenced area using fencing as the main effect and the nitrogen addition rate for each plot as a co-variant. Any differences detected by such analyses cannot be unambiguously ascribed to herbivore exclusion (Hulbert, 1984). Rather, we use them to generate testable hypotheses. There were no significant differences between the control plots and the plots with no nitrogen added; consequently, they were pooled together. Samples from strips within each of the 10 unfenced macro plots were averaged to avoid subsampling (Hulbert, 1984), resulting in a sample size of 10 for the unfenced area and a sample size of 45 for the fenced area. This analysis uses a GLM Type III sums of squares to deal with the unbalanced design. Changes over time are analyzed as the percent change on an individual plot basis. All statistical tests were done in SPSS 7.0 for Windows.

Results

We found significant differences between the fenced and unfenced area in above-ground plant biomass in both 1982 and 1995 (Table I). The control plots of the fenced area showed a long-term increase (Figure 1). Note that the

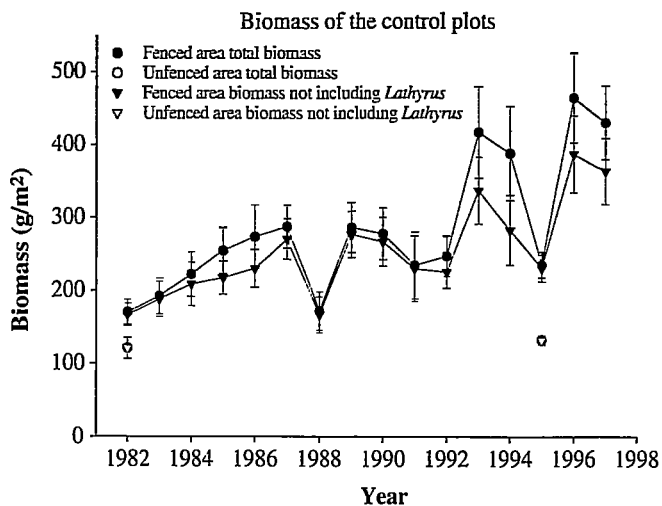


FIGURE 1. Above-ground biomass of the control plots from the fenced experiment with (●, $n = 10$) and without *Lathyrus* (▼, $n = 10$), and the unfenced experiment with (○, $n = 4$) and without *Lathyrus* (▽, $n = 4$) sampled in late August or early September of each year. Given are the means \pm SE.

decrease in biomass in the fenced area in 1988 was caused by an extreme drought (Tilman & El Haddie, 1992). The decrease in 1995 was caused by the early senescence of *Lathyrus*, e.g., above-ground biomass was 165 g (SE 45) in June versus 5 g (SE 2) in September. We do not have enough sample points of the unfenced area to determine if there was any change over time.

The fenced area had a significantly higher above-ground biomass, total biomass (above- and below-ground) and per area total nitrogen and carbon in above-ground and total biomass in both June and September (Table I, Figure 2). This difference in productivity and in nitrogen and carbon in above-ground vegetation corresponds, in June, with a large amount of *Lathyrus* foliage in plots receiving 5.3 or fewer grams of nitrogen and a strong increase in woody plant foliage in the plots receiving 9.3 or more grams of nitrogen (Figure 3). The *Lathyrus* foliage had senesced and decayed by September, but woody plant foliage increased later in the season in plots receiving the highest rate of nitrogen addition.

The amount of nitrogen added had a strong significant effect on plant biomass in September over the entire fertilization gradient, but a much smaller effect in June (Figure 2).

TABLE I. *F*-values from a GLM (type III) for the effect of enclosure on plant above-ground biomass, nitrogen, carbon, and total plant biomass, nitrogen and carbon. Annual fertilized nitrogen amount was added as a covariant. All data are $\ln(x + 1)$ transformed. ($n = 45$ for the fenced area and $n = 10$ for the unfenced area). n.s. = not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Variable (df)	Nitrogen (1) <i>F</i> -value	Enclosure (1) <i>F</i> -value	Model (2) <i>F</i> -value	<i>R</i> ²
Plant above-ground biomass June 1995	2.81 ^{n.s.}	8.07**	5.57**	0.176
Plant above-ground nitrogen June 1995	4.72*	5.74*	5.37**	0.171
Plant above-ground biomass September 1995	100.07***	22.04***	62.29***	0.706
Plant above-ground nitrogen September 1995	105.41***	16.39***	62.00***	0.705
Plant total biomass June 1995	4.24*	9.85**	7.21**	0.217
Plant total nitrogen June 1995	10.09**	9.19**	9.89***	0.276
Plant total biomass September 1995	20.96***	9.37**	15.53***	0.374
Plant total nitrogen September 1995	56.59***	15.70***	36.93***	0.587
Plant above-ground biomass August 1982	56.05***	27.37***	44.26***	0.630

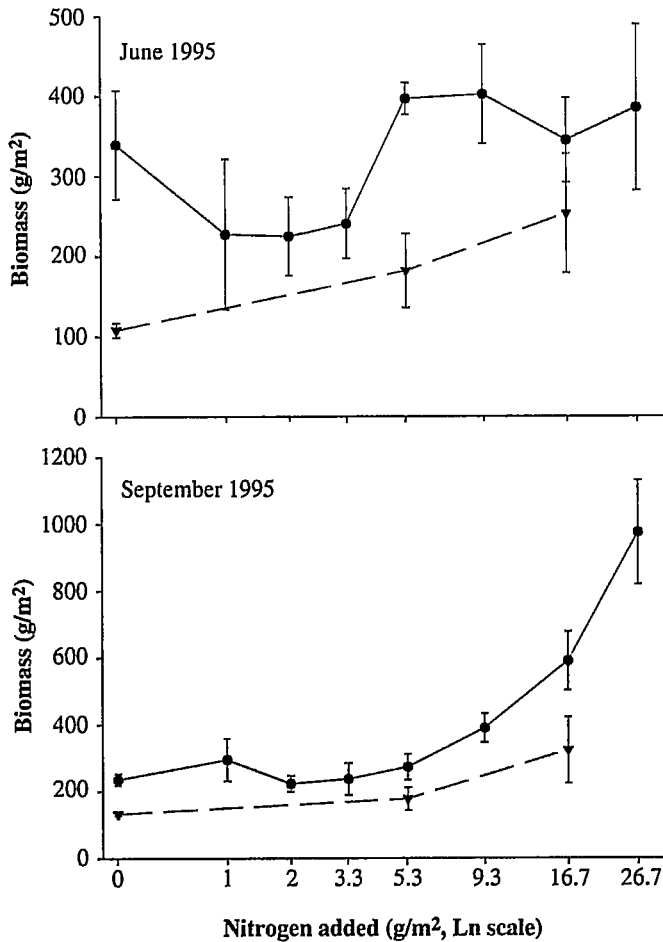


FIGURE 2. Above-ground biomass (live and standing dead) of the fenced (circles) and the unfenced experiment (triangles) in June and September 1995 across a nitrogen fertilization gradient. Given are the means \pm 1 SE.

This was caused in the excluded plots by the strong increase in biomass in the plots receiving 9.3 and more grams of nitrogen (Figure 2), which corresponds with an increase in woody plants and a relative decrease in grasses (Figure 3).

Soil nitrogen levels of the two areas differed initially by 40% (Figure 4a), but were similar by 1995 (Figure 4b), due to a decrease in the unfenced area (Figure 4c, Table II). Nitrogen fertilization did not have a significant effect on soil nitrogen when the two areas were combined (Table II), but it did for the unfenced area alone in 1995 (Table III).

TABLE II. *F*-values from a GLM (type III) for the effect of enclosure on soil nitrogen, carbon, C/N ratio, and nitrogen, carbon, and C/N ratio change. Nitrogen was added as a covariant. ($n = 45$ for the fenced area and $n = 10$ for the unfenced area). n.s. = not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Variable (df)	Nitrogen (1) <i>F</i> -value	Enclosure (1) <i>F</i> -value	Model (2) <i>F</i> -value	<i>R</i> ²
Soil N 1982 ¹	0.24 ^{n.s.}	15.20***	7.67***	0.228
Soil N 1995 ¹	2.71 ^{n.s.}	0.28 ^{n.s.}	1.52 ^{n.s.}	0.055
Soil C/N 1982	0.14 ^{n.s.}	32.52***	16.29***	0.385
Soil C/N 1995 ¹	0.34 ^{n.s.}	2.04 ^{n.s.}	0.31 ^{n.s.}	0.043
Soil C 1982 ¹	0.22 ^{n.s.}	21.67***	10.90***	0.295
Soil C 1995 ¹	2.03 ^{n.s.}	0.02 ^{n.s.}	1.03 ^{n.s.}	0.038
Soil N change ²	2.42 ^{n.s.}	10.75**	6.72**	0.205
Soil C/N change ³	0.01 ^{n.s.}	17.31***	8.67**	0.250
Soil C change ⁴	2.06 ^{n.s.}	11.85**	7.09**	0.214
N mineralization ⁵	14.24**	0.47 ^{n.s.}	7.43**	0.222

¹Ln ($x + 1$) transformed.
²Ln ($x + 41$) transformed.
³Ln ($x + 7$) transformed.
⁴Ln ($x + 40$) transformed.
⁵Ln ($x + 130$) transformed.

Soil nitrogen mineralization did not differ between the fenced and unfenced areas (Table II), even for only the control plots (One-way ANOVA, $df = 1, 12$ $F = 0.02$ $p = 0.89$).

Discussion

THE EFFECT OF ENCLOSURE ON THE VEGETATION

We found that 13 years of herbivore enclosure caused an increase in both above-ground and total plant biomass (Table I, Figures 1, 2). This increase corresponds with an increase in *Lathyrus* biomass at the lower end of the fertilization gradient (Figure 3). The biomass difference between the fenced and unfenced areas was reflected in the nitrogen in the above-ground biomass, because the tissue nitrogen content of *Lathyrus* was substantially higher than for the other functional groups, with the exception of forbs in the unfenced area in June (Table IV). This higher tissue quality makes *Lathyrus* a preferred food for browsing mammals, and herbivory almost completely eliminated *Lathyrus* outside the fenced area (Figure 3; Ritchie & Tilman, 1995; Ritchie, Tilman & Knops, 1998).

We are unable to determine if there was a change in biomass in the unfenced area, because we did not sample that area repeatedly over time. Ritchie, Tilman & Knops (1998) reported from a separate experiment in the same

TABLE III. Regression of the effect of nitrogen fertilizer on soil nitrogen change and soil nitrogen in 1982 and 1995. ($n = 45$ for the fenced area and $n = 10$ for the unfenced area). n.s. = not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Variable	Field	Regression		Parameter estimate	
		<i>F</i> -value	<i>R</i> ²	Constant	Nitrogen
Change in soil total nitrogen ¹	fenced	1.20 ^{n.s.}	0.027	3.72***	0.0001 ^{n.s.}
	unfenced	8.6*	0.517	2.69***	0.0140*
Soil total nitrogen 1982 ²	fenced	0.13 ^{n.s.}	0.003	0.07***	0.0000 ^{n.s.}
	unfenced	0.96 ^{n.s.}	0.107	0.10***	0.0001 ^{n.s.}
Soil total nitrogen 1995 ²	fenced	1.50 ^{n.s.}	0.034	0.08***	0.0001 ^{n.s.}
	unfenced	14.79**	0.649	0.07***	0.0004**

¹Ln ($x + 41$) transformed.
²Ln ($x + 1$) transformed.

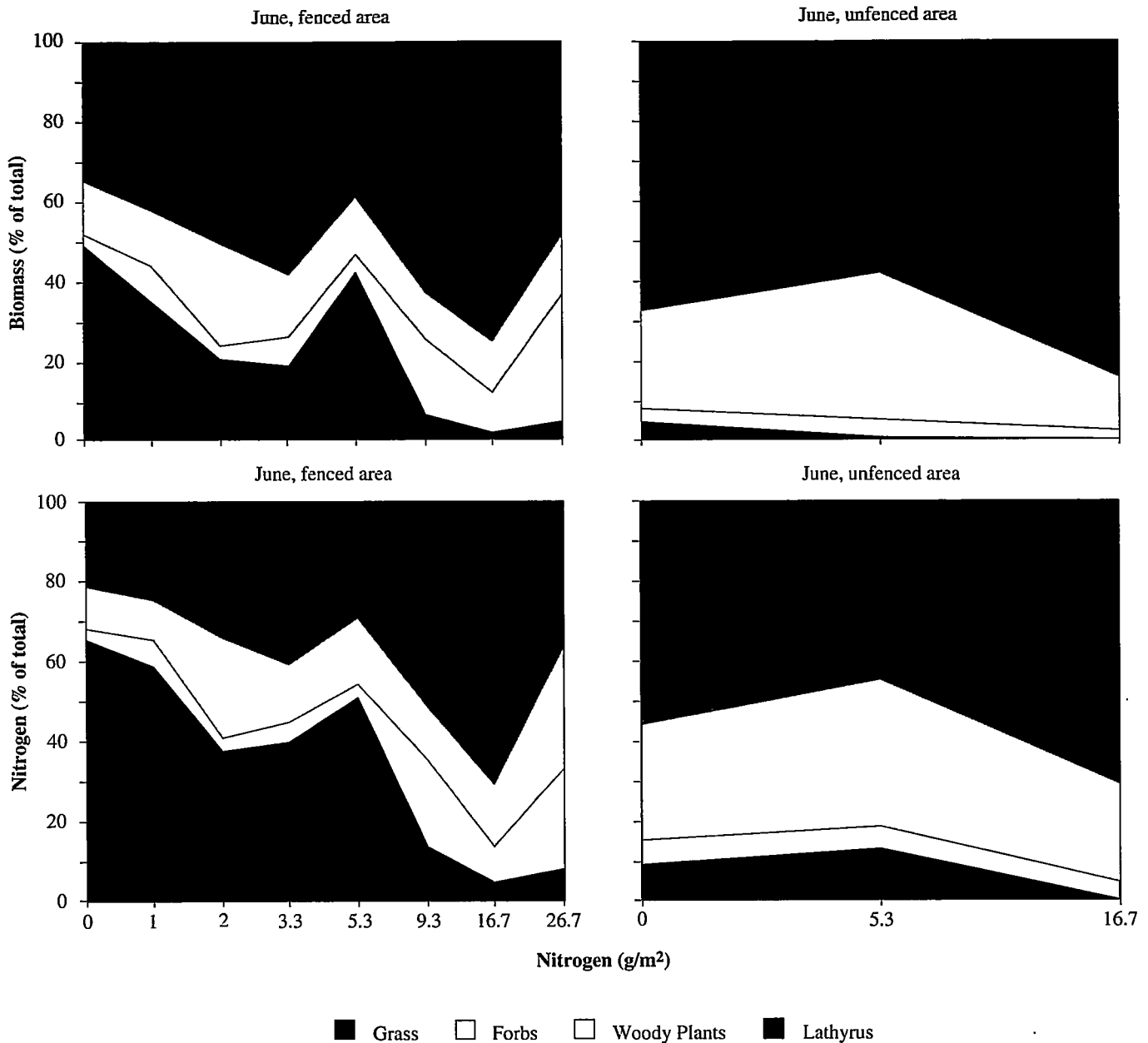


FIGURE 3. Relative functional group above-ground biomass and nitrogen of the fenced (circles) and the unfenced (triangles) experiment in June 1995.

field that fencing from 1989 to 1995 significantly increased the biomass of *Lathyrus* and *Quercus sp.* and also resulted in a significant increase in above-ground biomass in the fenced as compared to the unfenced area. They also found changes in soil nitrate, but no change in soil total nitrogen. The length of the experiment might have caused the lack of a significant change in total nitrogen, as ours was 13 years old, whereas Tilman & Ritchie was only 6 years old. We found no indication of a change in *Lathyrus* biomass in the unfenced area (Figures 1, 3), and Tilman (1996) reported no systematic increase in biomass in fenced areas in other fields, where *Lathyrus* has not increased. These two studies, and our data, are consistent with the hypothesis that *Lathyrus* can increase plant above-ground biomass over time in areas where it is present and herbivory is prevented.

Deer populations have reached abnormally high levels in many regions of the western, mid-west and eastern United States because suitable habitat has greatly expanded and because predators such as wolves, mountain lions, and grizzly bears have been eliminated. Human hunting has replaced predation in some areas, but in many residential areas and nature preserves, where hunting is not intense or not allowed, deer densities are at historically high levels. Such high deer densities can have a substantial impact on plant communities by virtually eliminating the deer's preferred forage plants (De Jong *et al.*, 1995; Hernandez & Silva-Pando, 1996; Inouye, Allison & Johnson, 1994; Phillips & Maun, 1996; Ross, Bray & Marshall, 1970; van Hees, Kuiters & Slim, 1996). Our results, and similar results in other prairies (Phillips & Maun, 1996; D'Ulisse & Maun, 1996) and forests

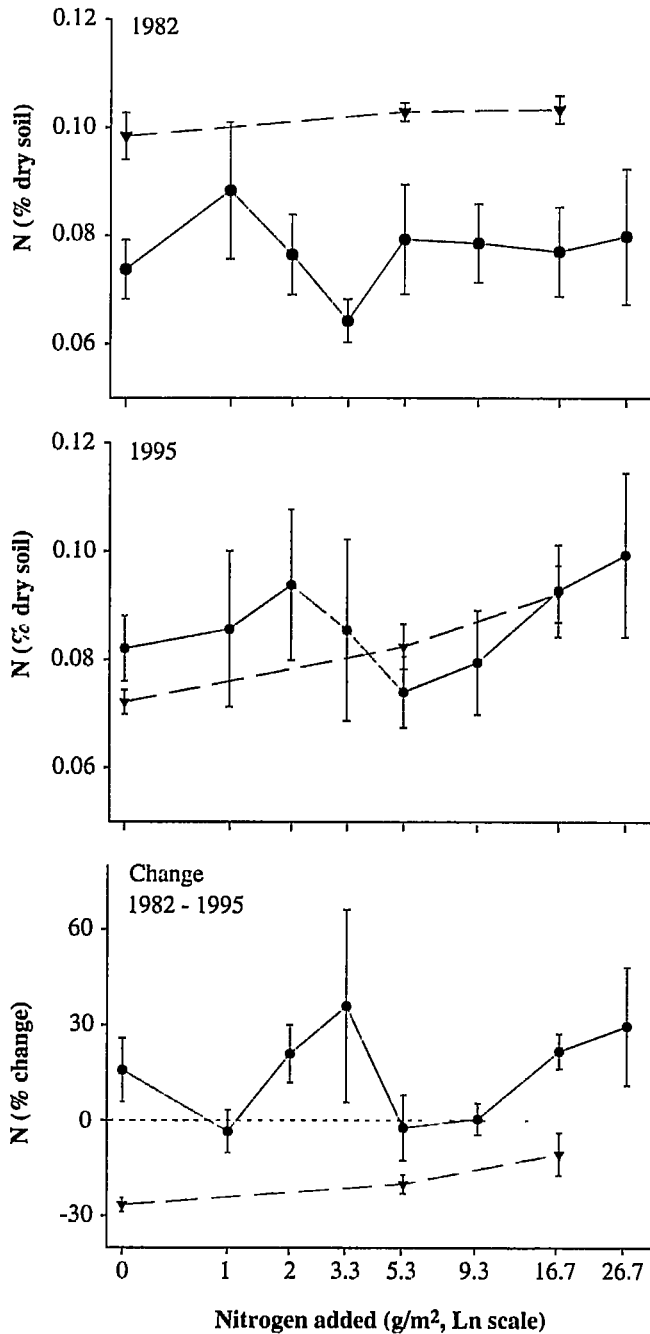


FIGURE 4. Total soil nitrogen of the fenced (circles) and the unfenced (triangles) experiment in 1982, 1995, and the change from 1982 through 1995. Given are the means \pm 1 SE.

(De Jong *et al.*, 1995), are consistent with the hypothesis that deer browsing can substantially influence the vegetation, altering the plant functional group abundance and ecosystem productivity by eliminating legumes.

THE EFFECT OF EXCLOSURE ON NITROGEN POOLS

Initially, soil total nitrogen was quite different between the fenced and unfenced area, which corresponds with the higher tree density in the unfenced area during the entire period. Tree canopies often result in higher soil nitrogen, both in the Midwest (Ko & Reich, 1993) and in other savannas worldwide (Kellman, 1979; Knops *et al.*, 1996; Vetaas, 1992) and tree canopy cover is variable within this savanna. During the 13 years of the experiment, soil nitrogen decreased significantly outside the enclosure, resulting in similar nitrogen pools and mineralization rates in 1995 (Table II). The decrease outside the enclosure likely resulted from nitrogen volatilization of above-ground biomass caused by prescribed burns (Hobbs *et al.*, 1991; Ojima *et al.*, 1994; Raison, 1979), which was not replaced by fixed nitrogen as in the enclosure. Atmospheric deposition amounts to about 0.7 g per m² and is the main input pathway for nitrogen when symbiotic nitrogen-fixing plants are absent (Schlesinger, 1991). September above-ground plant biomass contained 1.56 g N per m² in the unfenced area (Table V). If we assume that 50% of the above-ground nitrogen is retranslocated and that fire-induced nitrogen losses from litter are in the order of 80% (Raison, 1979), there is still a negative balance, which may explain the decrease in total soil nitrogen.

By contrast, within the enclosure that was burned identically, soil nitrogen did not change (Figure 4). *Lathyrus* contributed 49% of the biomass and 82% of the nitrogen in the control plots of the fenced area in June. This decreased to 2% and 4% in September (Table V). Fixed nitrogen is either retranslocated to below-ground storage organs and/or roots, or present in high quality litter that can decompose quickly in the humid, warm Minnesota summers. It is also likely that the above-ground *Lathyrus* litter contributes relatively more to the soil nitrogen pools than the grass and forb biomass produced later in the season because it abscises earlier in the season and is of much higher quality. If we again assume that 80% of the nitrogen present in the above-ground litter is lost to the atmosphere due to fire, and 50% of the nitrogen present in the September biomass is still present in the litter, we find a loss of 1.63 gram per m². Atmospheric inputs are about 0.7 grams, resulting in a net loss of 0.9 gram per m² per year. The above-ground biomass of *Lathyrus* contained 5.62 grams of nitrogen per m², and if we assume that *Lathyrus* has the same amount below-ground

TABLE IV. Tissue percent nitrogen content of the functional groups in the control plots. Given are the means \pm SE (sample size)

Group	Fenced area		Unfenced area	
	June 1995	September 1995	June 1995	September 1995
Forbs	2.06 \pm 0.08 (42)	1.96 \pm 0.08 (43)	2.55 \pm 0.31 (10)	1.81 \pm 0.17 (10)
Grasses	1.62 \pm 0.05 (45)	1.48 \pm 0.05 (45)	1.67 \pm 0.14 (10)	1.39 \pm 0.11 (10)
<i>Lathyrus</i>	2.59 \pm 0.07 (31)	4.08 \pm 0.35 (25)	2.42 \pm 0.14 (6)	2.25 \pm 0.34 (4)
Woody plants	1.87 \pm 0.08 (40)	1.72 \pm 0.08 (38)	1.88 \pm 0.13 (10)	1.82 \pm 0.09 (9)
Roots	1.28 \pm 0.04 (45)	1.34 \pm 0.06 (45)	1.17 \pm 0.08 (10)	1.15 \pm 0.09 (10)
Litter	0.94 \pm 0.04 (45)	1.55 \pm 0.08 (45)	1.27 \pm 0.19 (10)	1.31 \pm 0.11 (10)

TABLE V. Biomass and nitrogen (g/m^2) of the control plots in the fenced and unfenced areas in 1995

	Fenced	Unfenced
Above-ground biomass June	339 \pm 68	108 \pm 9
<i>Lathyrus</i> biomass June	165 \pm 45	5 \pm 2
<i>Lathyrus</i>	49%	5%
Above-ground nitrogen June	6.84 \pm 1.49	1.66 \pm 0.14
<i>Lathyrus</i> nitrogen June	5.63 \pm 0.85	0.16 \pm 0.05
<i>Lathyrus</i>	82%	10%
Above-ground biomass September	235 \pm 17	133 \pm 6
<i>Lathyrus</i> biomass September	5 \pm 3	1 \pm 0
<i>Lathyrus</i>	2%	1%
Above-ground nitrogen September	4.09 \pm 0.64	1.56 \pm 0.12
<i>Lathyrus</i> nitrogen September	0.18 \pm 0.07	0.03 \pm 0.01
<i>Lathyrus</i>	4%	2%

we get a total of 11.2 grams of nitrogen per m^2 present in *Lathyrus*. Thus, a fixation rate of nitrogen that supplies *Lathyrus* with at least 10 percent of its tissue nitrogen can account for the net long-term accumulation of nitrogen in these plots. This 10% fixation would result in a net input of 11 kg per ha per year, which is in line with nitrogen fixed annually by other legumes (Fahey *et al.*, 1985; Halvorson *et al.*, 1992). However, this is likely a low estimate, because estimates range from 10-30% in *Acacia* (Schulze *et al.*, 1991), up to 60% in lupines (Halvorson *et al.*, 1992), and total amounts fixed can be as high as 100 kg per ha per year (Bormann *et al.*, 1993; Youngberg & Wollum, 1976).

Similar enclosure studies have documented large shifts in the dominant tree species due to herbivory of deer (Howard, 1964; Ross, Bray & Marshall, 1970; Tiedemann & Berndt, 1972) and other large herbivores (Buechner & Dawkins, 1961; Hatton & Smart, 1984; Pastor *et al.*, 1993). However, most of these studies did not find significant changes in total soil nitrogen (Pastor *et al.*, 1993; Tiedemann & Berndt, 1972). This study reiterates the critical role that legumes can play in ecosystem nitrogen inputs, as has been documented for other symbiotic nitrogen-fixing plants (Maron & Connors, 1996; Stock & Baker, 1995; Vitousek *et al.*, 1987; Vitousek & Walker, 1989). This study also documents the fact that herbivore impacts on legumes can be reflected in ecosystem-wide soil nitrogen pools. This supports the hypothesis that cascading "top-down" effects of terrestrial herbivores, like deer (Estes, 1995; Paine, 1980) also have an impact on nutrient cycling (Hunter & Price, 1992; Pastor & Naiman, 1992; McNaughton, Banyikwa & McNaughton, 1997).

NITROGEN LIMITATION

Fire is considered a critical tool in maintaining prairies and savannas of the upper mid-western U.S.A. (Collins & Wallace, 1990; Leach & Givnish, 1996) and most other grassland savanna ecosystems. Both the fenced and unfenced areas are burned frequently as part of the same burn compartment. Our results suggest that fire-induced nitrogen losses may be higher than atmospheric deposition, resulting in a net loss of soil nitrogen over time. Thus, fire may control vegetation structure and nitrogen availability at Cedar Creek, as it does in other grasslands (Seastedt, Briggs

& Gibson, 1991; Blair, 1997). This suggests that fire might be a useful tool to minimize nitrogen accumulation from increased atmospheric deposition (Vitousek, 1994; Wedin & Tilman, 1996).

Vitousek & Howarth (1991) explored the mechanisms that keep nitrogen fixation from reversing nitrogen limitation and concluded that, in terrestrial ecosystems, energetic constraints or limitation by another nutrient can be the cause. However, they also point out that ecological constraints have received less attention and may be important. This paper documents such an ecological constraint. *Lathyrus*, which is the dominant legume present in this study area (Ritchie & Tilman, 1995) is strongly limited both by selective herbivory by deer and by cations or phosphorus (Ritchie & Tilman, 1995). In addition, *Lathyrus* has big seeds like most legumes, which leads to slow dispersal (Tilman, 1993). High herbivory and poor dispersal are likely explanations for why legumes are not more abundant in these strongly nitrogen-limited prairie ecosystems (Ritchie & Tilman, 1995).

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