

HERBIVORE EFFECTS ON PLANT AND NITROGEN DYNAMICS IN OAK SAVANNA

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Abstract. Herbivores can often control plant dynamics by mediating positive feedbacks in plant species' influence on nutrient cycling. In a 7-yr field experiment in a nitrogen-limited Minnesota oak savanna, we tested whether herbivores accelerated or decelerated nitrogen (N) cycling through their effects on plants. We measured effects of excluding insect (primarily Orthoptera and Homoptera) and mammalian herbivores (primarily white-tailed deer, *Odocoileus virginianus*) on above- and belowground plant biomass, plant species composition, plant tissue nitrogen concentration, available soil N and light, and total N and carbon (C) in different pools (soil, roots, litter, etc.). Herbivore exclusion strongly increased cover and biomass of the legume *Lathyrus venosus* and a few species of woody plants. These effects were associated with greater aboveground standing crop, reduced belowground standing crop, and reduced light penetration to the ground surface. Herbivore exclusion also modified N cycling through greater N content of live, aboveground plant tissue early in the growing season and of litter and belowground tissue late in the growing season. Herbivore exclusion also increased soil nitrate and total available N concentrations but did not alter total soil or plant N. Our results support the hypothesis that herbivores indirectly decelerate N cycling by decreasing the abundance of plant species with nitrogen-rich tissues. However, other factors, such as disturbance from fire, may mediate herbivore effects on long-term changes in N and C pools. Herbivores may therefore indirectly control productivity, N cycling, and succession by consuming nitrogen-fixing and woody plants that have strong effects on plant resources (e.g., nitrogen and light).

Key words: herbivores; legumes; nitrogen; plants; positive feedback; savanna.

INTRODUCTION

Herbivores can have a variety of direct and indirect effects on plant communities (Huntly 1991, Davidson 1993, Jefferies et al. 1994, Hixon and Brostoff 1996). Direct negative effects of herbivores on a subset of plant species can produce strong indirect effects on plant species composition, above- and belowground plant productivity, and nutrient cycling (e.g., Naiman et al. 1986, Brown and Heske 1990, Power 1990, DeAngelis 1992, McInnes et al. 1992, Pastor et al. 1993). Such effects may be particularly strong when herbivores limit the abundance of one or a few important plant species that control resource abundance, e.g., nitrogen fixers (Vitousek et al. 1987, Ritchie and Tilman 1995) or other efficient nutrient competitors (Sterner 1994, Wedin 1994). As a result, herbivores may indirectly control the form and function of ecosystems (Naiman et al. 1986, Pastor and Naiman 1992, Jones and Lawton 1994, Lawton 1994).

A major way that herbivores control ecosystem function is by modifying feedbacks between dominant plant species and nutrient cycles (e.g., Crawley 1983, Coley

et al. 1985, McNaughton 1985, Chapin et al. 1986, Holland et al. 1992, Pastor and Naiman 1992). These studies suggest two hypotheses (Fig. 1). One hypothesis predicts that herbivores have an *accelerating effect* on nutrient cycling (Fig. 1A) (McNaughton 1976, 1985, Tilman 1982, 1988, DeAngelis et al. 1989, Ruess et al. 1989, Holland et al. 1992, Sterner 1994). This hypothesis argues that herbivores increase tissue loss rates of plant species that tolerate herbivory but have nutrient-rich tissue. These plant species may compensate for herbivory with faster nutrient uptake, faster relative growth rates, and higher tissue nutrient concentrations. Such changes yield faster litter decomposition and nutrient turnover, which, together with herbivore waste products, increase nutrient supply rate. A greater nutrient supply rate then favors these same plant species in competition with others. Thus, herbivores enhance a positive feedback mechanism that increases aboveground plant productivity and the rate of nutrient cycling.

An alternative hypothesis predicts that herbivores have a *decelerating effect* on nutrient cycling (Fig. 1B) (Naiman et al. 1986, Tilman 1988, Leibold 1989, Bryant et al. 1991, Pastor and Naiman 1992, Wilson and Agnew 1992, Wedin 1994). This hypothesis argues that herbivores feed selectively on plant species with nu-

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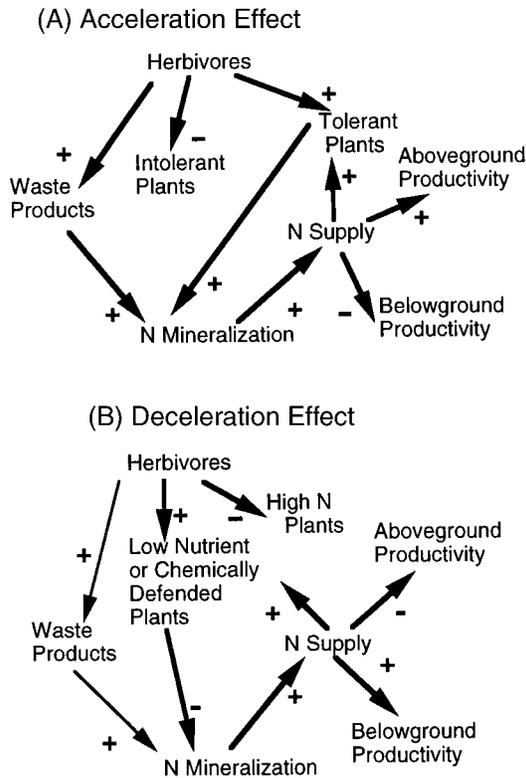


FIG. 1. Feedback loops that represent (A) the acceleration effect and (B) the deceleration effect of herbivores on positive feedbacks between plant species and nutrient cycling. Arrows indicate the net indirect effect of herbivores on the abundance of plants or the rate of the process. Note how the two alternative effects depend on whether herbivores favor tolerant plants with high tissue N or defended, low-tissue-N plants. The type of herbivore effect may be determined by whether the resource-limiting plant growth is the same as that controlling herbivore preference.

trient-rich tissue and increase the dominance of plant species with tissue that is nutrient-poor or defended by secondary compounds. Litter from these latter species decomposes slowly and reduces nutrient turnover and availability. Reducing nutrient availability favors nutrient-poor species because they are often better nutrient competitors. In this case, herbivores enhance a positive feedback that reduces aboveground productivity and the rate of nutrient cycling.

These hypotheses differ critically in their assumptions about how plants respond to herbivory (Hobbie 1992). The acceleration effect assumes that dominant plants can tolerate herbivory through compensatory growth and are limited by a resource other than that which determines palatability to herbivores. In some terrestrial systems, herbivores appear to "stimulate" compensatory responses in plants with nitrogen-rich tissues (Coppock et al. 1983, McNaughton 1985, Day and Detling 1990, Holland and Detling 1990, Frank and McNaughton 1992, Jefferies et al. 1994). Rapid decomposition of litter, coupled with herbivore return

of mineralized N through waste products, accelerates N mineralization rates. Plants in these systems are potentially limited by resources other than nitrogen (e.g., water). In other, apparently nitrogen-limited systems (Belsky 1986, Bryant et al. 1991, McInnes et al. 1992, Pastor et al. 1993), herbivores select plants with nitrogen-rich tissue and increase the dominance of plant species with low tissue N or with chemical defenses. Litter from these species decomposes slowly and reduces N mineralization and availability.

These conflicting results suggest that the type of resource limiting plant growth may determine the effects of herbivores on N cycling. If plant productivity is nitrogen-limited and dominant species are likely to have lower tissue N (Tilman 1988, Hobbie 1992), then herbivores may slow nitrogen cycling. If the dominant plants have high tissue N to maintain efficiency in using another resource (e.g., water, light) and/or tolerate herbivory in ways unrelated to tissue chemistry, then herbivores may accelerate N cycling.

In a Minnesota oak savanna maintained by frequent prescribed burns (Tester 1989), herbivores can potentially influence succession to either grassland or woodland (Inouye et al. 1994). Soils are sandy and low in nitrogen, and plant productivity is primarily nitrogen-limited (Tilman 1987, 1988). Based on the above hypotheses and previous results (Ritchie and Tilman 1995), we expected herbivores, especially white-tailed deer (*Odocoileus virginianus*), to selectively reduce plant species with greater tissue N, e.g., legumes. We expected that these effects might increase plant species with low N concentrations in plant tissue and litter (e.g., grasses). We further expected that shifts in plant community composition toward species with low tissue N would lead to lower soil N availability (Wedin and Pastor 1993, Wedin 1994). Finally, we expected that herbivore effects would lead to lower aboveground productivity and total soil N.

To address these predictions, we examined the effects of 7 yr of herbivore exclusion on plant dynamics and cycling of N and C in this savanna. We measured plant productivity, species composition, and tissue N and C in response to a replicated set of herbivore exclosures and control plots. Exclosures kept out mammalian herbivores with fences and reduced insect abundances with window screen and with limited pesticide applications. We compared cover and biomass of different plant species among treatments to assess herbivore effects on the plant community, and we compared biomass of litter and live plant tissue (above- and belowground) to assess herbivore effects on productivity. The effects of herbivores on N cycling were measured from the N content of plant tissue (litter, belowground, and aboveground live) and concentrations of ammonium, nitrate, and total N in soil. Finally, we combined N and C concentrations of soil and plant tissue with biomass estimates to compare herbivore effects on overall N and C pools.

METHODS

Study site

The experiment was conducted in a single 0.2-ha opening in an oak savanna at Cedar Creek Natural History Area (CCNHA), 50 m away from long-term plant dynamics experiments conducted by Tilman (1987, 1988). The savanna is burned two out of every three years (White 1983, Tester 1989, Faber-Langendoen and Tester 1993), and, during this experiment (1989–1995), it was burned in the spring (1–10 May) of 1990, 1991, 1993, and 1994. Dominant herbaceous plants include grasses (e.g., *Andropogon gerardi*, *Sorghastrum nutans*, *Schizachyrium scoparium*, *Poa pratensis*, *Stipa spartea*, and *Panicum praecocius*), forbs (e.g., *Asclepias tuberosa*, *Asclepias syriaca*, *Ambrosia coronopifolia*, *Lithospermum carolinense*, *Comandra richardsoniana*, and *Artemisia ludoviciana*), and legumes (*Lathyrus venosus*, *Amorpha canescens*, and *Lespedeza capitata*). Our experimental plots also initially contained seedlings and saplings of several woody species (e.g., *Quercus ellipsoidalis*, *Quercus macrocarpa*, *Rhus glabra*, *Rosa arkansana*, and *Corylus cornuta*).

The dominant mammalian herbivores at the site are white-tailed deer, which occurred at densities of 15–30 individuals/km² during the experiment, primarily during October–April. CCNHA is a wildlife refuge and historical wintering area, and these densities are typical for such preserves in the midwestern United States (McCullough 1979). Low densities of cottontail rabbits (*Sylvilagus floridanus*) and meadow voles (*Microtus pennsylvanicus*) were also present. A variety of herbivorous insects occurred in the experimental plots at the beginning of the experiment. Although we did not survey insects, the most visually abundant herbivore species were grasshoppers (Orthoptera: Acrididae), aphids (Homoptera: Aphidae), scales (Homoptera: Coccidae), and beetles (Coleoptera).

Experimental design and sampling

In June of 1989, 10 plots, each 2 × 2 m, were placed randomly on existing vegetation within a 40 × 40 m area. Five of these plots excluded mammalian herbivores with 0.8 m high fences made of an inside layer of 0.8 cm mesh wire cloth. Insects were excluded by applying carbaryl methylcarbate (Sevin) insecticide (800 µL/L solution at 0.2 L/m²) in mid-June each year to kill insects that emerged or immigrated during early spring. Following pesticide application, we discouraged further insect invasion by covering each enclosure plot with a 1.5-mm mesh window-screen “lid” and by installing side panels that extended to the ground and were held taut with steel bars. Covers were in place during the principal insect growing season, mid-June–late August, but were removed to avoid snow damage in winter. The cages effectively reduced insect damage and excluded small mammals and deer (see *Results*). We never observed pocket gopher mounds inside plots.

We used primarily physical barriers to exclude insects because repeated insecticide applications might have modified soil invertebrate faunas (which were presumably similar among treatments at the start of the experiment) and could have biased our measurements of belowground standing crop and N cycling (Brown and Gange 1989). Some insects, e.g., ground-dwelling species, undoubtedly re-entered plots after insecticide application, but damage from the major folivorous insect herbivores (see *Study site*) was greatly reduced in enclosure plots (see *Results*). Although repeated fires prevented most woody plants from growing taller than 0.8 m, some plants (oaks and tall grasses) were occasionally bent by lids. However, bending did not appear to limit growth, as some tree saplings, despite being bent by lids, grew taller (maximum height 1.1 m) in enclosure plots than the maximum height (0.91 m) among 20 randomly selected saplings in surrounding savanna.

The remaining five plots were “controls” that received a window-screen lid during mid-June–late August to standardize the shading effects of lids, but had no wire cloth fence or window-screen side panels, so as to allow herbivores to feed. Deer browsed, walked, and eliminated wastes in these plots during September–May, and they continued to browse the outer 0.8 m of each plot even when lids were in place. We did not explicitly quantify fecal pellet deposition, but we routinely found deer pellets in some control plots each year, and we never found pellets in enclosure plots. Given that deer densities are highest at CCNHA during October–April, “control” plots probably experienced 80–90% of the use of unmanipulated savanna by deer. Plots burned along with surrounding savanna during prescribed fires (see *Study site*); we detected no visual difference in fire intensity (e.g., the proportion of litter burned) among treatments.

We visually assessed herbivore damage to individual plant species. In 1994 and 1995, we measured the height of the tallest plant or ramet for woody plants and legumes. In 1994, we estimated the percentage of plants or ramets that exhibited damage for all woody plants and legumes, because these were the groups that appeared to be most affected by herbivores. In the course of estimating percent cover, we also noted any other species that had been damaged.

We sampled plant species composition as visual percent cover (Inouye et al. 1987, Tilman 1988, Ritchie and Tilman 1995) in June and August in 1989, 1992, 1994, and 1995. We estimated percent cover by covering portions of plots with a 1 × 1 m grid divided into 10 × 10 cm sections. We counted the total number of sections (or parts of sections) that covered each species' areal canopy, so that total cover could be >100%. Cover was highly correlated with the number of plants or ramets of each species (Ritchie and Tilman 1995). A species was represented by its largest cover value (June or August) for a given year. Total cover was the

sum of each species' maximum cover. By using maximum cover for each species to assess plant community composition, we represented the contribution of plant species with different phenologies.

We sampled aboveground plant biomass in June and August of 1989 and 1995 by clipping a 10 cm × 2 m strip perpendicular to the edge of each plot. Herbaceous vegetation was clipped to ground level, but only current annual growth was clipped from woody plants. Each strip was sorted to species, dried at 55°C for one week, and later weighed. As a crude measure of production, we used the greatest biomass for each species (either June or August) as an estimate of peak biomass. Total peak biomass was the sum of peak biomass for all species.

We also sampled belowground biomass in 1995 by taking a 5 cm diameter, 20 cm deep soil core from three random locations along each strip immediately after clipping. These cores were immediately washed over a 1-mm mesh screen to remove soil and dead or decayed plant material. All live material (roots and rhizomes combined) was then dried at 55°C for one week and later weighed. This method reliably samples 70–90% of total belowground biomass (Wedin and Tilman 1990, 1993). However, frequent fires left abundant charcoal particles in the soil; these were difficult to rinse from roots and probably inflated estimates of belowground biomass. However, each root sample was rinsed by the same person according to a standard technique, so that values could be compared fairly among treatments.

We analyzed plant tissue and soil from each plot for total N and C in 1995 with a Carlo Erba autoanalyzer (Carlo Erba Strumentazione, Milan, Italy). Dried samples of litter, belowground tissue, and aboveground tissue for each species were ground through a 0.8-mm mesh screen in a Wiley mill. After grinding, samples for each species from each plot were combined to form one sample per functional group: legumes, other forbs, woody plants, and grasses. We then determined N and C from each plot for each of these groups as well as for belowground tissue and litter. We estimated N and C for total aboveground live tissue by weighting N and C contents for each functional group by their respective biomass proportions in each plot. We measured total soil N and C in July of 1995. We took 2.5 cm diameter, 20 cm deep soil cores from four random points in each plot, and then combined cores to form a single sample for each plot. Soil samples were dried at 55°C for one week and then kept at 28°C until they were analyzed.

We also measured resources available to plants in each plot. We measured light penetration to the ground surface in August 1989, after the construction of herbivore exclosures, and again in August 1995. We took light readings from 1100–1200 on a clear day with a LI-COR Integrating Quantum/Radiometer/Photometer, model LI-188B (LI-COR, Lincoln, Nebraska). We took readings from above the window-screen lid and from

four locations within each plot. Light penetration was measured as percentage of light above the window-screen lid reaching the ground surface. We also measured ammonium (NH_4^+) and nitrate (NO_3^-) in the soil of each plot in August of 1994 and in June and August 1995 using the methods of Wedin and Tilman (1990) and Inouye et al. (1987). We took three 2.5 cm diameter, 20 cm deep cores from random points within each plot and then combined cores to form a single sample for each plot. Ammonium and nitrate were immediately extracted in 0.01 mol/L KCl and their concentration per kilogram of dry soil was determined with an AlpKem autoanalyzer (AlpKem, a division of O. I. Analytical, Wilsonville, Oregon). Total available soil N was the sum of ammonium and nitrate concentrations.

We estimated the total amount of N and C (g/m^2) and C:N ratio in soil, belowground plant tissue, litter, and aboveground live plant tissue in August 1995. Concentrations in soil (percentage dry mass) were multiplied by bulk density of dry soil (130 kg/m^3 for the top 10 cm layer of soil; Zak and Grigal 1991) to obtain total pool sizes in soil. Aboveground live tissue concentrations (in milligrams per gram) of N and C for each plant functional group and for litter and belowground tissue were multiplied by their respective biomasses to obtain N and C pools in plant tissue.

Statistics

For plant and N responses measured in different years (percent cover, biomass, light), we tested for significant effects of herbivore exclosures and year by using two-way ANOVA. To control for unmeasured pretreatment differences among plots, we judged treatments to have significant ($P < 0.05$) effects only if both the main effect of herbivore exclusion and the herbivore × year interaction were significant, thus indicating a stronger difference among treatments in later years. For ammonium and nitrate concentrations, which were measured in August 1994 and June and August 1995, we used repeated-measures ANOVA. For other responses, we tested for herbivore exclosure effects with one-way ANOVA. A posteriori contrasts in responses between controls and herbivore exclosures were tested with Tukey's multiple-comparisons test, because the design is balanced (five replicates of each treatment).

RESULTS

Herbivores visibly damaged relatively few plant species in our plots. In 1995, deer reduced the average height of the tallest stem of the dominant legume *Lathyrus venosus* from 110 ± 9.1 cm (mean ± 1 SE) in herbivore exclosures to 51.4 ± 5.6 cm ($F = 29.6$, $df = 1, 8$, $P = 0.0006$) in control plots. Herbivores also reduced the average number of *Lathyrus* inflorescences per plot from 75.8 ± 11.3 to 2.2 ± 7.3 ($F = 21.3$, $df = 1, 8$, $P = 0.002$). Deer and insect herbivores reduced the height of the tallest woody plant from 106.8 ± 7.0

TABLE 1. ANOVA results for the effects of herbivore exclusions on different cover and biomass variables, as well as proportion of light penetrating to the ground surface, once year effects are considered.

Response	Treatment effect					Treatment × year interaction			
	ss†	ss expl.‡	df	F	P	ss expl.‡	df	F	P
Total cover (%)	14 816.6	19.6	1, 32	13.5	0.0009	16.6	3, 32	3.8	0.017
Legume cover (%)	2 798.6	23.9	1, 32	37.8	<0.0001	15.1	3, 32	8.0	0.0004
Woody cover (%)	3 962.6	15.3	1, 32	11.7	0.0017	17.2	3, 32	4.4	0.01
Grass cover (%)	7 091.5	8.6	1, 32	4.2	0.04	4.6	3, 32	0.7	0.53
Forb cover (%)	4 844.4	16.3	1, 32	8.3	0.007	2.6	3, 32	0.4	0.72
Total live biomass (g/m ²)	202 754.5	29.5	1, 16	21.5	<0.0001	7.1	1, 16	5.1	0.03
Legume biomass (g/m ²)	12 043.9	16.6	1, 16	8.3	0.011	14.7	1, 16	7.3	0.015
Woody biomass (g/m ²)	9 286.5	21.2	1, 16	6.2	0.02	9.5	1, 16	2.8	0.11
Grass biomass (g/m ²)	63 908.4	15.0	1, 16	3.6	0.07	0.5	1, 16	0.1	0.74
Forb biomass (g/m ²)	37 098.2	4.8	1, 16	1.2	0.28	5.5	1, 16	1.4	0.26
Litter biomass (g/m ²)	529 684.6	3.2	1, 16	2.2	0.16	2.9	1, 16	2.0	0.17
Light (proportion)	0.085	39.5	1, 16	31.6	<0.0001	2.4	1, 16	2.3	0.15

† Total sum of squares in ANOVA.

‡ Percentage of total sum of squares explained by either the main effect of herbivore exclusions or by the herbivore × year interaction.

cm in herbivore exclusions to only 44.8 ± 13.4 cm in control plots. In 1994, $74.3 \pm 8.3\%$ of oak stems (*Quercus ellipsoidalis* and *Q. macrocarpa*) were damaged in control plots, whereas only $4.5 \pm 6.2\%$ of stems were damaged in herbivore exclusions ($F = 32.1$, $df = 1$, 8 , $P = 0.0002$). All (100%) *Lathyrus* plants were damaged by both deer and insects in control plots, whereas only $23.4 \pm 9.3\%$ of plants were damaged in herbivore exclusions, and then only by insects. The only other plant species showing evidence of deer browsing were the forbs *Asclepias tuberosa* and *Lithospermum canescens* and the woody plant *Rosa arkansana*. In 1989, these six plant species represented only 10–15% of the species present and <10% of total cover in each plot. By 1995, they represented the same proportion of species but >50% of total cover inside herbivore exclusions.

Percent cover and peak biomass for all plants combined and for each functional group except grasses (Table 1, Figs. 2, 3) increased from 1989 to 1995, as plants recovered from a major drought during 1987–1988 (Tilman and El-Haddi 1992). After accounting for these year effects, herbivore exclusions had numerous effects on the abundances of different plant functional groups. By 1995, legumes and woody plants were significantly more abundant within herbivore exclusions, as they increased in cover by almost 300% and 400%, respectively, and in peak biomass by 500% and 800%, respectively (Table 1, Fig. 2A, B, Fig. 3A, B). Year × herbivore interaction terms for legume cover and biomass and woody cover were significant (Table 1), indicating that herbivore exclusion effects were significantly stronger in 1995 than in 1989. The interaction term for woody biomass was not significant, but pairwise contrasts indicated that herbivore exclusion effects were significant in 1995 but not 1989. Although cover of both grasses and forbs was significantly higher outside herbivore exclusions, the interaction between

year and exclusion was not significant (Table 1, Fig. 2C). Grass and forb biomass were not significantly affected by herbivore exclusions. Nevertheless, total percent cover and total biomass were significantly greater inside herbivore exclusions (Fig. 2E, 3E). These differences were significantly greater in 1995 than in 1989, as indicated by significant year × exclusion interaction terms (Table 1). Peak biomass of litter was not significantly affected by herbivore exclusions, but belowground biomass was almost 50% lower inside herbivore exclusions. Total biomass (live above- and belowground) and litter biomass were not significantly affected by herbivores (Table 2, Fig. 3F).

Herbivore exclusion also affected plant resources, particularly light and available soil N (Fig. 4). Although light penetration to the soil surface was significantly lower in 1989 in herbivore exclusions (probably due to shading by window screen on the sides of plots), by 1995 light penetration decreased significantly within herbivore exclusions to less than half that in control plots (Table 1, Fig. 4A). The decline in light penetration within control plots over the same period was not significant. Nitrate concentrations were more than twice as high inside herbivore exclusions (Table 2, Fig. 4A), although soil ammonium was not significantly affected by herbivore exclusions (Table 2, Fig. 4C). Consequently, total available N concentrations in soil (ammonium + nitrate) were significantly greater in herbivore exclusions, especially in 1995 (Fig. 4D, Table 2).

Aboveground plant tissue N was significantly higher inside herbivore exclusions only in June (Table 2, Fig. 5A), but litter and belowground tissue N were significantly higher inside herbivore exclusions only in August (Table 2, Fig. 5B). Plant functional groups differed significantly in the N content of aboveground live tissue, with legumes having a significantly higher N content than other groups (Table 3). However, plant groups did

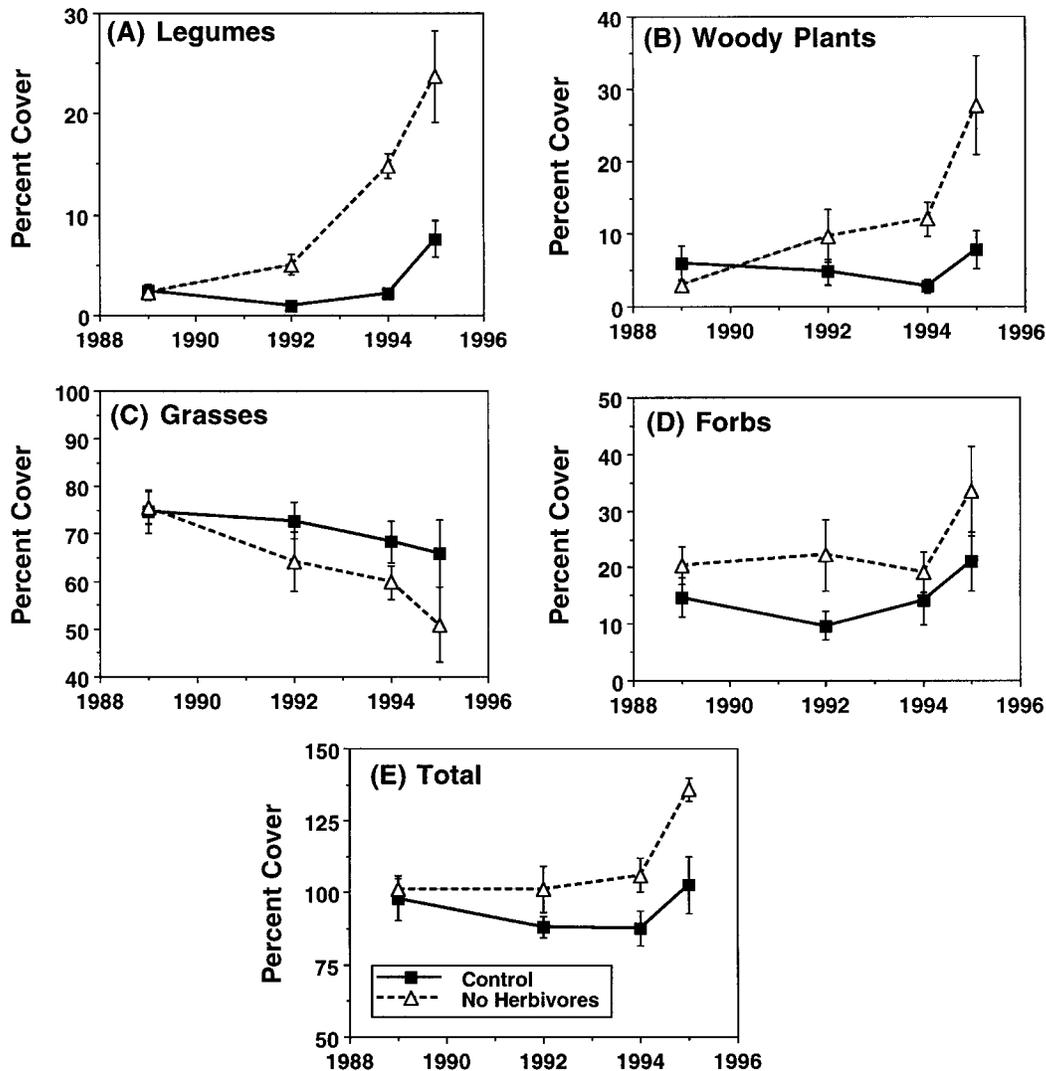


FIG. 2. Trajectories of mean (± 1 SE, $N = 5$) percent cover of four major plant groups: (A) legumes, (B) woody plants, (C) grasses, (D) forbs, and (E) all plants combined, from 1989 to 1995. Non-overlapping standard errors imply significant differences ($P < 0.05$).

not differ in their N content between control plots and herbivore exclosures ($F = 0.16$ – 3.1 , $df = 1, 16$, $P = 0.09$ – 0.7). Tissue C differed among plant groups, with forbs and grasses having a significantly lower C content than legumes and woody plants (Table 3). However, herbivores did not significantly affect C content of aboveground live tissue, litter, belowground tissue, or soil ($F = 0.01$ – 2.51 , $df = 1, 8$, $P = 0.17$ – 0.92). Because C varied little among plots or plant tissues, responses in C:N ratios perfectly reflected responses in N.

We calculated N and C pools for control plots vs. herbivore exclosures. Herbivores significantly affected total N for aboveground live tissue (Fig. 6) but not soil or belowground tissue. Soil C was not significantly different between control plots and herbivore exclosures ($F = 0.33$, $df = 1, 8$, $P = 0.56$). C pools in herbivore exclosures were greater for aboveground tis-

sue but lower for belowground tissue, as reflected in responses of plant and litter biomass (Fig. 3). However, soil C:N ratio was not different inside (11.9 ± 1.1) vs. outside herbivore exclosures (12.2 ± 1.3) ($F = 0.33$, $df = 1, 8$, $P = 0.48$; ANOVA on log-transformed data).

DISCUSSION

Our results suggest that insect and mammalian herbivores have dramatic direct effects on a few species of legumes and woody plants in this savanna. Moreover, herbivore indirect effects appeared to influence productivity and nitrogen cycling. Specifically, herbivore exclusion increased soil N availability, plant tissue N, and aboveground biomass but decreased light penetration and belowground biomass. Consequently, our results are most consistent with the hypothesis that herbivores have decelerating effects on the feedback be-

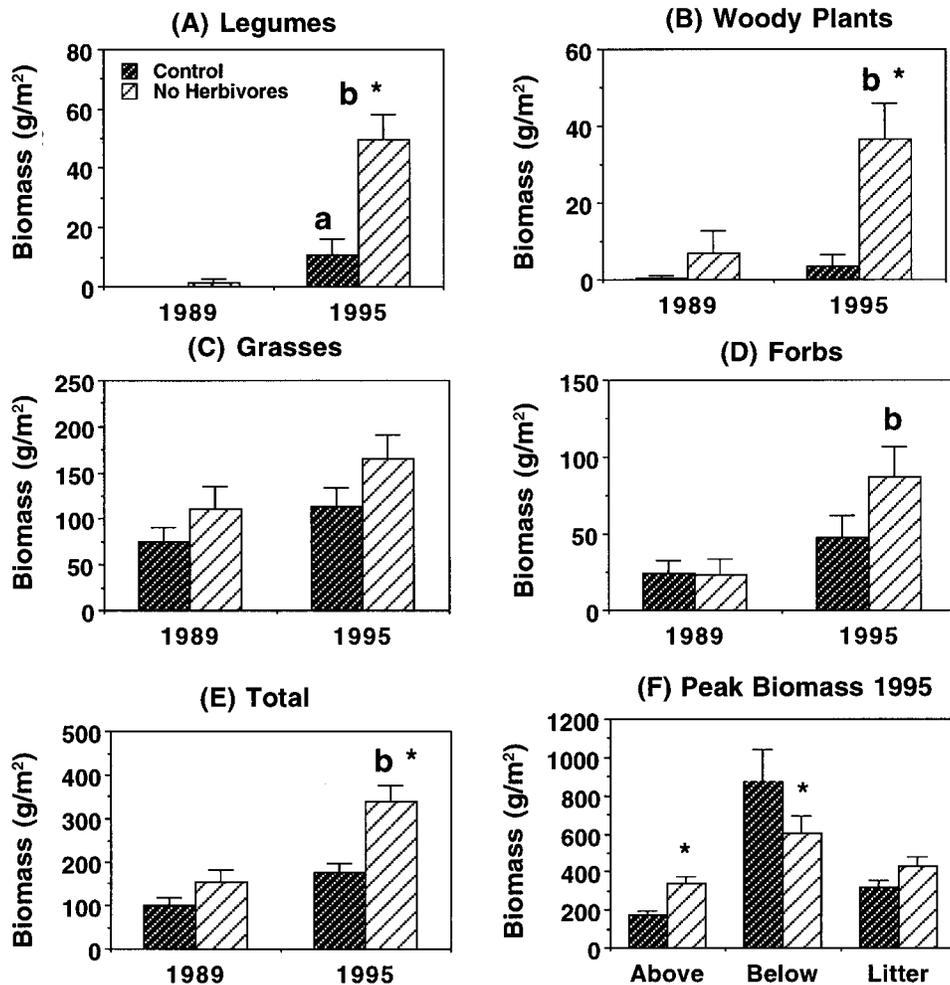


FIG. 3. Mean (± 1 SE) peak biomass for the four main plant groups: (A) legumes, (B) woody plants, (C) grasses, (D) forbs, and (E) all plants combined. Means are compared between herbivore exclusions and control plots, and between 1989 and 1995. An asterisk indicates a significant difference between herbivore treatments, and a lowercase letter indicates a significant difference ($P < 0.05$) between 1989 and 1995 within a treatment. (F) 1995 effects of herbivore exclusions on peak live aboveground, belowground, and litter biomass.

tween plants and nitrogen cycling (Naiman et al. 1986, Tilman 1988, Leibold 1989, Pastor and Naiman 1992, Wilson and Agnew 1992). Counter to arguments that terrestrial ecosystems should show weak trophic effects (Strong 1992, Polis and Strong 1996), herbivores in our savanna had strong "top-down" effects on plants, plant resources, and succession despite consuming a relatively small proportion of species (Leibold 1989, 1996). Our results come from relatively small plots (4 m²) and we do not know how they apply at larger scales (Brown and Allen 1989). However, they appear to give important insights about interactions among herbivores, plants, and ecosystem processes at local scales.

Herbivore effects on plant abundance

Seven years of exclusion of mammalian and insect herbivores produced a five-fold increase in the cover and biomass of some legume and woody plant species,

particularly *Lathyrus venosus* and *Quercus* spp. Cover of two other plant groups, grasses and forbs, changed significantly with herbivore exclusion, but the year \times exclusion interaction for each group was not significant. Thus, initial differences among plots might explain herbivore treatment effects on grass and forb cover but not legumes and woody plants

These results are consistent with previous studies, which show that herbivores may strongly limit abundances of nitrogen-fixers such as legumes (Ehrlén 1992, 1995, Ritchie and Tilman 1995) and even prevent their dominance in nitrogen-limited systems (Tilman 1982, Vitousek and Howarth 1991, Ritchie and Tilman 1995). Such effects may greatly reduce the positive effects of nitrogen-fixers on N availability and primary productivity (Vitousek et al. 1987, Vitousek and Howarth 1991) and on other plant species (Van Sanbeek et al. 1986, Posler et al. 1993). In our savanna, her-

TABLE 2. ANOVA results for the effects of herbivore exclosures on phytomass, tissue N, and soil N.

Response	ss [†]	ss expl. [‡]	df	F	P
Peak aboveground live biomass (g/m ²)	44 944.3	52.3	1, 8	8.74	0.02
Peak belowground biomass (g/m ²)	642 311.2	65.9	1, 8	15.40	0.004
Litter (g/m ²)	12 769.1	24.9	1, 8	2.66	0.14
Aboveground tissue N (%)					
June	0.079	59.0	1, 8	12.02	0.008
August	0.016	22.5	1, 8	2.27	0.17
Litter tissue N (%)					
June	0.079	1.6	1, 8	0.13	0.78
August	0.273	38.9	1, 8	5.10	0.04
Belowground tissue N (%)					
June	0.064	0.6	1, 8	0.05	0.83
August	0.562	40.7	1, 8	5.5	0.04
Nitrate (mg/kg) [§]	0.097	72.0	1, 16	98.4	<0.0001
Ammonium (mg/kg) [§]	0.816	1.2	1, 16	1.0	0.34
Available N (mg/kg) [§]	1.25	31.4	1, 16	6.4	0.03
Total soil N (g/m ²)	10 032.3	3.2	1, 8	0.26	0.65

[†] Total sum of squares in ANOVA.

[‡] Proportion of total sum of squares explained by the main effect of herbivore exclosures.

[§] Results from repeated-measures ANOVA (August 1994, June 1995, and August 1995).

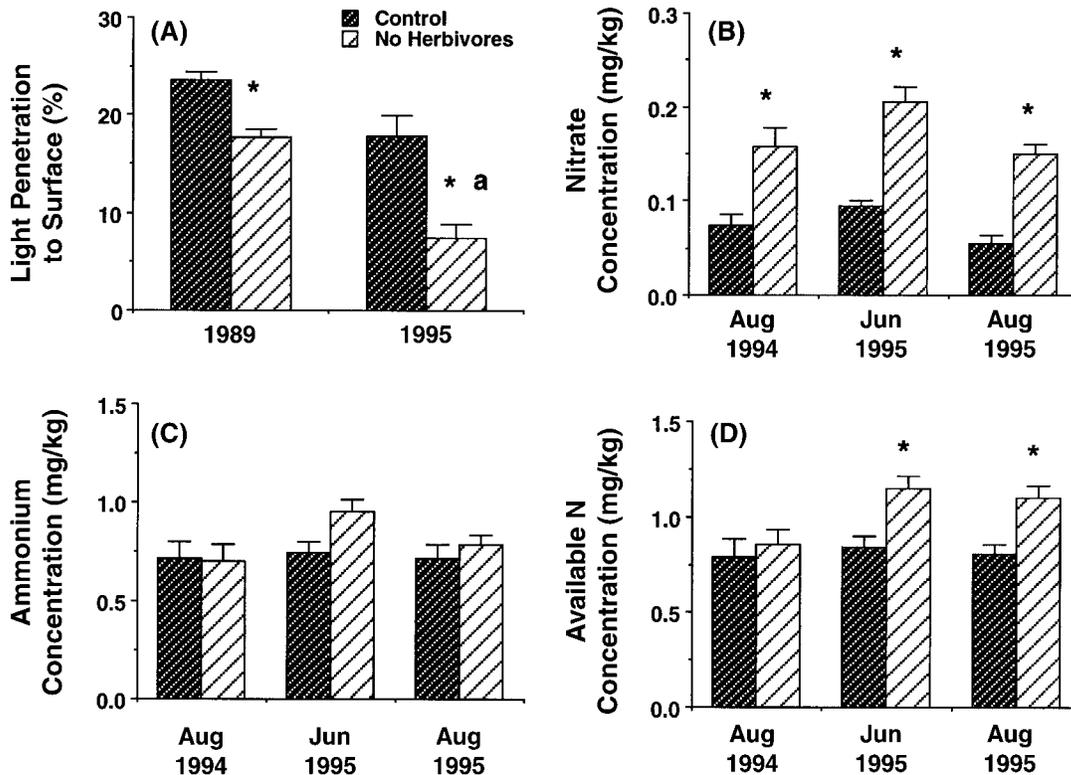


FIG. 4. Differences between exclosures and controls in mean (+1 SE) resource availability: (A) light penetration to the ground surface, (B) nitrate NO_3^- , (C) ammonium NH_4^+ , and (D) available soil nitrogen (ammonium + nitrate). Means are compared between herbivore exclosures and control plots, and between different sampling times. An asterisk indicates a significant difference between herbivore treatments, and a lowercase letter indicates a significant difference ($P < 0.05$) between 1989 and 1995 within a treatment (for light only).

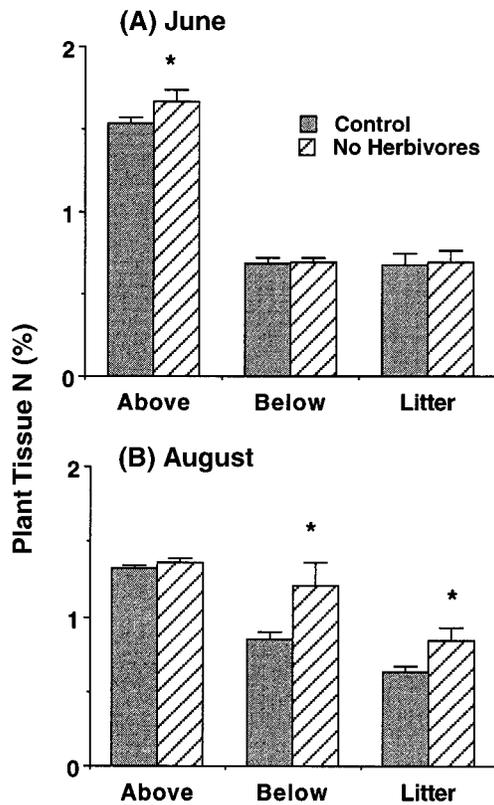


FIG. 5. Mean (+1 SE) N content (percentage dry mass) of aboveground live (Above), belowground live (Below), and litter tissue in control plots and herbivore exclosures in (A) June and (B) August 1995. An asterisk indicates a significant difference ($P < 0.05$) between herbivore treatments.

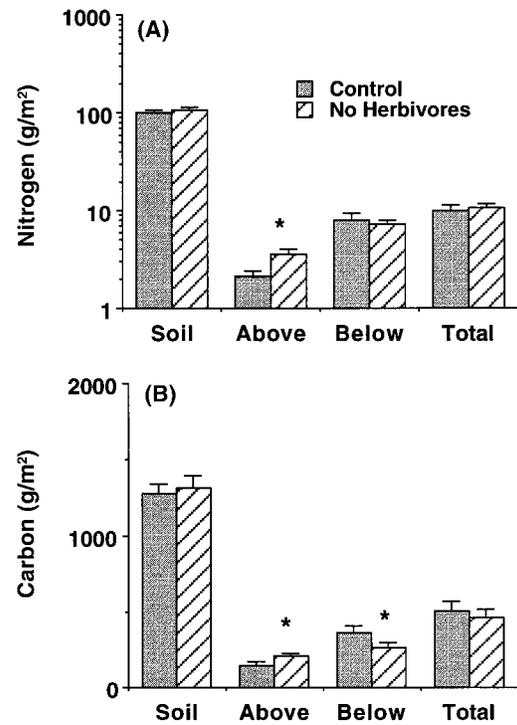


FIG. 6. Mean (+1 SE) size of (A) nitrogen and (B) carbon pools in soil, aboveground (live tissue + litter, Above), belowground live tissue (Below), and total plant tissue (Total). Data are compared among control plots and herbivore exclosures. An asterisk indicates a significant difference ($P < 0.05$) between herbivore treatments.

bivore exclusion led to 30% greater total peak cover and 50% greater peak aboveground biomass (Figs. 2, 3). However, these increases appear to result directly from increases in species consumed by herbivores (legumes and woody plants) rather than indirect benefits to other species (grasses and forbs). Nevertheless, removal of herbivory from legumes did alter nitrogen availability (see *Herbivore effects on nitrogen cycling*, below). Such indirect consequences of herbivore effects on nitrogen-fixers may have been previously overlooked, because nitrogen-fixers are kept rare by herbivores and other factors, such as nutrients other than

N and drought (Vitousek and Howarth 1991, Ritchie and Tilman 1995).

The dramatic increase in woody plants with herbivore exclusion suggests that, in this savanna, herbivores may inhibit succession to woodland within grass-dominated savanna openings. Herbivory of woody species might explain why tree invasion of old fields and prairies at CCNHA is so slow (Inouye et al. 1987, 1994). Our results provide another example of how selective herbivory can alter succession (Huntly 1991, Davidson 1993), particularly in savannas that feature a transition from grassland to woodland (Belsky 1986, Wilson and Agnew 1992).

TABLE 3. Mean N and C (± 1 SE) in aboveground live tissue of the dominant plant functional groups in the savanna.

	Function group			
	Forbs	Woody	Legumes	Grasses
Nitrogen content (%)				
June	1.68 ^a \pm 0.06	1.38 ^a \pm 0.12	2.38 ^b \pm 0.11	1.43 ^a \pm 0.08
August	1.50 ^a \pm 0.09	1.19 ^a \pm 0.11	2.23 ^b \pm 0.10	1.25 ^a \pm 0.08
Carbon content (%)				
June	43.0 ^a \pm 0.4	45.3 ^b \pm 0.4	45.1 ^b \pm 0.4	43.9 ^a \pm 0.1
August	42.9 ^a \pm 0.2	45.2 ^b \pm 0.3	45.4 ^b \pm 0.2	43.7 ^a \pm 0.1

Note: Different superscript lowercase letters within a row indicate significantly different means ($P < 0.05$).

Herbivore effects on plant resources and allocation

In addition to changing plant abundances, exclusion of herbivores appeared to change plant resource availability. Extractable soil nitrate doubled, total available N (ammonium + nitrate) increased by 30%, and light penetration to the ground surface declined by half in the absence of herbivores (Fig. 4). These changes are consistent with the result that herbivore exclusion increased legumes and woody plants. Legumes, with their nitrogen-fixing capability, may increase soil nitrate through turnover of nitrogen-rich leaves or roots (Table 3, Fig. 5) (Vitousek et al. 1987, Vitousek and Howarth 1991, Ledgard and Steele 1992). Reduced light levels may be associated with shading by the greater abundance of broad-leaved legumes and woody plants such as *Lathyrus venosus* and *Quercus* spp. By reducing these species, herbivores may prevent a potential shift in the light:nitrogen ratio during succession, as hypothesized by Tilman (1985). Consequently, indirect herbivore effects on plant resources might explain why succession in CCNHA grassland occurs through mechanisms other than shifts in resource ratios, e.g., a trade-off between colonization and N competition (Tilman 1987, 1988).

Herbivore effects on above- vs. belowground biomass and tissue N are consistent with current hypotheses about the relationship between nutrient availability and plant allocation. Tilman (1988, 1991) proposed that increased soil nutrient availability and lower light availability would favor plants that allocate less to roots and more to stems or leaves. As expected from this hypothesis, aboveground live biomass increased significantly and belowground biomass decreased significantly in association with the higher soil nitrate and lower light penetration in the absence of herbivores (Figs. 3F, 4). However, total standing crop (above- plus belowground) was not affected by herbivore exclusion (Fig. 3F). Thus, changes in biomass from below- to aboveground likely resulted from shifts in allocation rather than an increase in total productivity. Because we could not identify roots to species, we could not determine whether shifts from roots to shoots in herbivore exclosures occurred within plant species or because of changes in species composition.

Resource availability may also control overall nutrient content of plant tissue (Bryant et al. 1983, Coley et al. 1985, Chapin et al. 1986, Tilman 1988, 1991). Increasing available soil N may favor plant species that rapidly take up N and grow relatively faster, because higher N content of plant tissue may be required to support greater metabolic activity and growth (Chapin et al. 1986, Tilman 1988). If plants with lower allocation to roots are favored by increased available soil N, these plants may have lower nitrogen-use efficiency and require greater N in plant tissue (Wedin and Tilman 1990). These changes in tissue N might result from either changes in species composition or changes with-

in species. Our results support the hypothesis that resource availability controls total plant tissue N, but only through changes in species composition. While herbivores did not induce significant changes in aboveground live tissue N within plant species (see *Results*), they did reduce species with high tissue N (legumes, Table 3, Figs. 2, 3). Overall, herbivores led to decreased N content in live aboveground tissue in June and belowground tissue and litter in August (Fig. 5). These effects coincide with decreased available soil N and increased light penetration (Fig. 4).

Plant allocation of C may also change with resource availability (Bryant et al. 1983, Coley et al. 1985, Chapin et al. 1986, Tilman 1988). However, we found no difference in plant C content between control plots and exclosures (see *Results*), even though legumes and woody plants had significantly greater C content in their live aboveground tissue. Overall C content may not have differed among treatments for several reasons, e.g., either C-rich plants do not alter their C content in response to light, light was not a limiting resource even in herbivore exclosures, or light limitation affects the form of C in tissue (soluble vs. structural carbohydrates) rather than total C. However, we lack the data to test these hypotheses.

Plant and N responses to herbivore exclosures might be due to shading by the window screen on the sides of exclosures rather than herbivore effects. However, this seems unlikely. Although lower than in control plots, mean light penetration to the soil surface in herbivore exclosures in 1989 was still 18% (Fig. 4A). This level is probably not low enough to affect plant nitrogen budgets and competitive interactions in these soils (Tilman and Wedin 1991, Wedin and Tilman 1993). Furthermore, light declined significantly from 1989 to 1995 only inside herbivore exclosures (Fig. 4A). These patterns suggest that low light levels in herbivore exclosures were not due to a "cage effect," because differences in light levels between 1989 and 1995 for the same treatment should be due only to plant responses. However, the initial difference in light levels among treatments may have augmented herbivore-induced shifts in the relative abundance of plant species and aboveground biomass. Therefore, the strength of herbivore effects on plants, N, and light might not have been as strong if we had excluded herbivores without reducing light. Repeated applications of insecticide might have accomplished this, but we were concerned that such applications would modify soil herbivore faunas (which were presumably similar among treatments at the start of the experiment) and bias our results in other ways (Brown and Gange 1989).

Herbivore effects on nitrogen cycling

Herbivore exclusion appeared to enhance N cycling through a series of linked effects on plant community composition, the allocation of biomass and N among plant structures, and resource availability. These linked

effects appear similar to those predicted by the decelerating effect hypothesis (Fig. 1), but with seasonal shifts in N among different plant tissues. By reducing the abundance of nitrogen-fixing legumes and light-reducing woody plants, herbivores leave prairie grasses (*Andropogon gerardi* and *Sorghastrum nutans*) that have high nitrogen-use efficiency, are good N competitors, and can significantly reduce available soil nitrate (Wedin and Tilman 1990, Tilman and Wedin 1991). Litter from these grasses often decomposes slowly, and may increase microbial uptake of N released from the litter of other plant species (Wedin and Pastor 1993). In our study, herbivores reduced nitrogen-rich plant species, e.g., legumes, that peaked in abundance in June and contributed to an increase in belowground tissue and litter N in August (Fig. 5). Because available soil nitrate is strongly correlated with N mineralization in this savanna (Zak and Grigal 1991), higher N mineralization rates may have resulted from herbivore exclusion (Fig. 4B). This occurred even though control plots received nitrogenous waste products from both insect and mammalian herbivores. Lower N availability favors prairie grasses due to their strong competitive ability for N (Tilman and Wedin 1991, Wedin and Tilman 1993), so herbivores may enhance a positive feedback between prairie grasses and N cycling.

Shading by plants and window screen associated with herbivore exclosures might have altered N availability due to changes in microhabitat rather than plant tissue N. In particular, reduced light levels in exclosures might have cooled soil temperatures, thereby altering decomposition and N mineralization rates. However, such effects are unlikely to explain our results, because cooler temperatures should lead to slower N mineralization rates in our system. Decomposition and N mineralization rates appear to increase with temperature in our savanna (Zak and Grigal 1991, Wedin and Pastor 1993), so the greater N availability in herbivore exclosures would appear to occur in spite of cooler temperatures associated with greater shade. Consequently, changes in plant species composition that alter overall plant tissue N appear to be the most likely explanation for the observed effects of herbivore exclusion on N availability.

Faster N cycling should coincide with greater accumulation of N and C in soils (Vitousek and Howarth 1991, Pastor et al. 1993). However, total soil N was not greater in herbivore exclosures (Table 2, Fig. 6). Although herbivores shifted C in above- vs. belowground plant tissue, they did not change total C in plants or soil. These results suggest that the faster N cycling in herbivore exclosures did not result in greater total soil N. This lack of difference may be due to the short duration (7 yr) of the experiment and the comparatively small difference in plant N pools between control plots and exclosures (Fig. 6). Belowground tissue N in August was greater in herbivore exclosures

(Fig. 5), but the total plant N pool was virtually identical between control plots and exclosures (Fig. 6), as belowground biomass was much lower inside exclosures. Frequent fires (two every three years) prescribed for this savanna may also contribute to this pattern. Volatilization of aboveground N during fire (Ojima et al. 1994) may reduce the contribution of aboveground N to soil pools. Thus, herbivores may have little effect on short-term soil N accumulation despite their effects on plant tissue and available soil N.

Because CCNHA features nitrogen-poor soils and nitrogen-limited aboveground production, our results support the hypothesis that herbivores should have decelerating effects on N cycling in nitrogen-limited systems. Our results are similar to those at Isle Royale (McInnes et al. 1992, Pastor et al. 1993), where moose browsing favored succession to coniferous trees (with nitrogen-poor tissue and litter) and led to slower N mineralization rates. This pattern may occur in other nitrogen-limited ecosystems, given that herbivores generally selectively feed on plant species with nitrogen-rich tissue (Mattson 1980, Belovsky 1986), and plants with nitrogen-poor tissue may be superior N competitors (Wedin and Tilman 1990, 1993, Tilman and Wedin 1991, Wedin and Pastor 1993). Alternatively, accelerating effects on N cycling by herbivores may occur in systems that are limited by other resources, e.g., light-limited forests affected by insect outbreaks (Holling 1973) or water-limited grasslands grazed by mammals (McNaughton 1985, Holland and Detling 1990). In some cases, however, herbivores might have accelerating effects in nitrogen-limited systems if plant decomposition rates are constrained by some factor other than plant tissue N, e.g., temperature (Bazely and Jefferies 1985, 1986, Jefferies et al. 1994). In addition, effects of herbivores on N cycling are likely to interact with effects of other disturbances, such as drought and fire. A major avenue of future research will be to determine the combination of resource limitation, soil fertility, and disturbance that leads to accelerating vs. decelerating herbivore effects on nutrient cycling.

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