

**UNGULATE-PRAIRIE DOG-PLANT INTERACTIONS
IN BADLANDS NATIONAL PARK**

First Annual Report on

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ABSTRACT

This report summarizes data collected during the first field season (May through August, 1995) of a multi-year project designed to evaluate the independent and interactive effects of bison and prairie dogs on plant species composition, plant biomass and nutrient dynamics, and soil nitrogen mineralization at selected sites in the Badlands National Park (BADL), South Dakota. This is being done by sampling vegetation and measuring soil nitrogen dynamics in five different herbivore treatments on and off three different prairie dog town sites. Data from this project will aid park personnel in their herbivore management efforts and a better understanding of the influence of ungulate herbivory on colony patches will assist management decisions regarding the current re-introduction of black-footed ferrets in the BADL.

Five herbivore treatments were established during the fall and winter of 1994: off-colony with bison excluded, off-colony with continued bison utilization, on-colony with bison excluded but continued utilization by prairie dogs, on-colony with utilization by prairie dogs and bison, and on-colony with both herbivores excluded. Three spatially distinct prairie dog town sites were chosen that afforded sufficient space for enclosure construction, that had similar soil characteristics, and that had sufficient grassland space adjacent to prairie dog towns for the off-town treatments. Thus, there were three replicate sites for each of the five herbivore treatments. Aboveground biomass on off-town sites was more than two times greater than on-town sites. This was primarily due to the near elimination of grasses on prairie dog towns. Although plant cover was similar at all the sites, off-town sites were dominated by grasses while on-town sites were dominated by forbs. Plant species diversity was lower for off-town sites and exotic plants constituted a greater proportion of the biomass. Net nitrogen mineralization early in the growing season was four times greater on prairie dog colony sites, but all sites exhibited net immobilization by July. Enhanced nutrient supplies for on-colony sites resulted in lower C:N ratios in plant biomass.

colony gradient, with the highest nitrogen concentrations and highest digestibility found in grasses in the older parts of the prairie dog colonies (Coppock et al. 1983a). Thus, it appears that prairie dogs positively influence forage quality and this may partially account for the preferential use of colony patches by ungulates (Coppock et al. 1983b).

Herbivore selection of colony patches as feeding sites may also be influenced by the modifications in plant community structure resulting from prairie dog colonization. At WCNP, the flat lowland uncolonized sites are typically dominated by cool-season (C_3) grasses. In young colony areas, warm-season (C_4) shortgrasses are often more prevalent while in old colonies plant communities are composed principally of forbs and dwarf shrubs (Whicker & Detling 1988b). Plant species diversity is maximized on colony patches of intermediate age. Ungulates, in particular bison and pronghorn, utilize these compositionally distinct colony sub-areas in patterns that vary spatially and temporally throughout the growing season (Coppock et al. 1983, Krueger 1986).

Modifications of nutrient cycling processes by prairie dogs may have important effects on ungulate habitat usage and nutrition. In preliminary studies at WCNP, colony patches exhibited higher net nitrogen mineralization rates and lower immobilization relative to uncolonized grassland (Holland & Detling 1990). Such changes in the nitrogen cycle within colony patches would produce an increase in plant available nitrogen. This nutrient increase may result from a decrease in carbon allocation to root biomass which reduces the availability of carbon to decomposers (Holland & Detling 1990). Since the foraging behavior of bison during rut is targeted at maximizing intake of grasses high in nutrient quality (Plumb & Dodd 1993), further investigation of ungulate herbivory on colony sites may reveal a linkage between foraging behavior and colony-mediated changes in nutrient cycling and biomass allocation.

Nutrient cycling is significantly altered by herbivory which stimulates nutrient uptake by roots (Jaramillo & Detling 1988), increases denitrification rates (Groffman et al. 1993), redistributes nutrients in the form of feces and urine (Ruess 1987), and increases volatilization of

INTRODUCTION

Natural grassland ecosystems are adapted to disturbance regimes which include fire and grazing episodes of variable intensity. Herbivory by large ungulates, bison (*Bison bison*), pronghorn (*Antilocapra americana*), deer (*Odocoileus* spp.), and elk (*Cervus elaphus*), is an important component of the grassland disturbance regime. The colonization of North American grasslands by prairie dogs (*Cynomys* spp.) represents a significant disturbance both in terms of herbivory and landscape modification. Recent research reveals that the presence of prairie dogs creates a disturbance regime represented spatially by a mosaic of colony patches in the grassland landscape. This increased landscape patchiness modifies ecosystem structure and function (Whicker & Detling 1988a). Colony-induced alterations include changes in patch structure, perturbation of the belowground ecosystem (Ingham & Detling 1984) and soil structure and profile (Munn 1993), variations in species composition and biomass allocation (Archer et al. 1987), modification of seasonal feeding site selection by other herbivores, such as bison and pronghorn (Coppock et al. 1983b, Krueger 1986), and alterations in nutrient cycling (Holland & Detling 1990). These ecological consequences of prairie dog colonization are of interest in terms of ungulate management and black-footed ferret (*Mustela nigripes*) re-introduction (Oldemeyer et al. 1993).

Ungulates exploit the unique forage attributes of colony patches during seasonal grazing (Krueger 1986). Studies conducted at Wind Cave National Park (WCNP) indicate that prairie dog colonization alters the morphology and nutrient content of forage species with the colony patch. Grass species exposed to grazing often demonstrate a unique and apparently ecotypic morphology characterized by reduced aboveground:belowground biomass, higher blade:sheath biomass, and generally prostrate growth form (Detling et al. 1986, Painter et al. 1993). These morphological changes produce grasses with shorter stature which may, in turn, increase grazing resistance (Jaramillo & Detling 1988). Nitrogen content and digestibility of forage species increased along a

OBJECTIVES

The overall objective of this research is to evaluate the individual and interactive effects of bison and prairie dogs on various aspects of plant productivity and species composition and on soil/plant nitrogen dynamics. The studies are being conducted in the Sage Creek Wilderness Area (SCWA) in the North Unit of the Badlands National Park (BADL), South Dakota. To develop an understanding of how these effects vary in different years, and to gain insight into trends in vegetational and mineralization changes, the study is expected to continue for multiple growing seasons. The following specific research objectives are currently being addressed:

1. Assess the effects of each of the five herbivore treatments (described below) on the:
 - a. intraseasonal aboveground biomass dynamics of cool season (C_3) graminoids, warm season (C_4) grasses, forbs, and other plant species;
 - b. ratio of live:dead plant material;
 - c. crude protein concentration of the forage;
 - d. root biomass; and,
 - e. ratio of root:shoot biomass.
2. Compare plant species composition and diversity in each of the five treatments.
3. Quantify soil nitrogen dynamics that occur in response to the five treatments.

ammonia (Schimel et al. 1986). However, investigative efforts linking these impacts to the unique nutrient cycles of prairie dog colonies are rare.

Grazing facilitation occurs among prairie dogs, bison and pronghorn, but this interaction remains largely uncharacterized in terms of its consequences for nutrient cycling, plant biomass allocation and species composition. Attempts to link the disturbance regime of prairie dog colonies to nutrient cycling and the consequences of ungulate herbivory are few. A previous study at WCNP did reveal a decrease in mean nitrogen concentration following the exclusion of either prairie dogs or bison (Cid et al. 1991). However, a broader understanding of the relationship of ungulate herbivory and the nutrient dynamics of colony patches and neighboring uncolonized grassland is useful for sound management of native grassland ecosystems.

IMPLICATIONS FOR MANAGEMENT

The North Unit of the Badlands National Park (BADL) currently supports several populations of black-tailed prairie dogs (*Cynomys ludovicianus*) located in several distinct colonies. It is expected that these colonies have modified the grassland landscape in ways similar to those described above. These colonies offer sites for further investigating ungulate herbivory in terms of biomass allocation, herbivore offtake, species composition, and nutrient cycling. Knowledge gained from these studies will aid park personnel in their herbivore management efforts. Moreover, a better understanding of the influence of ungulate herbivory on colony patches will assist management decisions regarding the current re-introduction of black-footed ferrets. The Badlands National Park system represents a unique opportunity to quantify ecosystem processes in the context of grazing patterns and disturbance regime.

concentration of nitrogen in the forage multiplied by the biomass of that forage, summed across vegetational categories.

C. Species composition and diversity.

Plant species composition and diversity was estimated for all five treatments in each of the three sites in June and July. In each site sampled, twenty 0.10 m² quadrats (sample adequacy was tested using collection curves [Pielou 1977]) were placed every two meters along the longest axis of the site and canopy coverage was estimated for each species (Daubenmire 1959). Percent cover of exposed soil and litter was also estimated in each quadrat. Plant community parameters, such as plant species richness, relative cover and the Shannon diversity index (H'), were then calculated for each treatment. To compare the extent to which species composition diverges between sites and treatments, floristic similarity between sites and treatments were calculated for the cover data with Morisita's similarity index (Morisita 1959).

D. Soil nitrogen dynamics.

To assess the impact of these herbivore treatments on net nitrogen mineralization, soils were incubated *in situ* for 30 days at each site from mid-May to mid-August. This incubation period was expected to capture maximum microbial activity. In mid-May, ten PVC cores (5 cm diameter, 10 cm length) were randomly placed within each treatment and another ten were paired within 20 cm of the first set of cores. All cores were driven into the ground and withdrawn. One member of each pair was immediately sealed in plastic and placed in a cooled chamber for further laboratory analyses. The bottom 1 cm of soil was removed from the other core to accommodate an ion-exchange resin bag and was then replaced in the ground to incubate under field conditions for approximately one month. This second set of cores was then withdrawn from the soil approximately 30 days later, sealed in plastic, cooled, and taken back to the laboratory for analyses.

METHODS

A. Study Area and Treatments.

Three distinct prairie dog towns (Hay Butte, Kalchbrenner, and Kocher Flats) were selected in 1994 in the Sage Creek Wilderness Area (SCWA) in the North Unit of the Badlands National Park (BADL). These three study sites were specifically chosen in an attempt to locate sites in the same or most similar soil series. Two permanent long-term exclosures (ca. 50m X 50m) were built on each prairie dog town, one to keep out bison and the other to keep out both prairie dogs and bison. A third bison exclosure was built at a nearby location off each town. Thus, a total of nine permanent exclosures were built in the winter of 1994 (prairie dog fencing was put up in the Spring of 1995). Two additional plots (ca. 50m X 50m) were chosen at each site, one on the town and the other off the town. Thus, five herbivore treatments were utilized: off-colony with bison excluded (NB), off-colony with continued bison utilization (B), on-colony with bison excluded but continued utilization by prairie dogs (P), on-colony with continued utilization by prairie dogs and bison (PB), and on-colony with exclusion of both prairie dogs and bison (NN).

B. Plant biomass, forage N-content, crude protein determinations.

On each of the five treatments at each site, 10 circular 0.25 m² quadrats were randomly placed and the vegetation clipped to ground level once a month in May, June, and July. Plant material was separated by plant functional group (e.g., graminoids, forbs, and other plant groups), dried to a constant weight at 50°C in the laboratory, and further separated into live (at time of harvest) and dead components.

Aboveground nitrogen concentrations were determined using a CHN analyzer on randomly selected subsamples of each plant category collected, and converted to crude protein by multiplying by 6.25. At any given time, standing crop of nitrogen (g N/m²) can be calculated as the

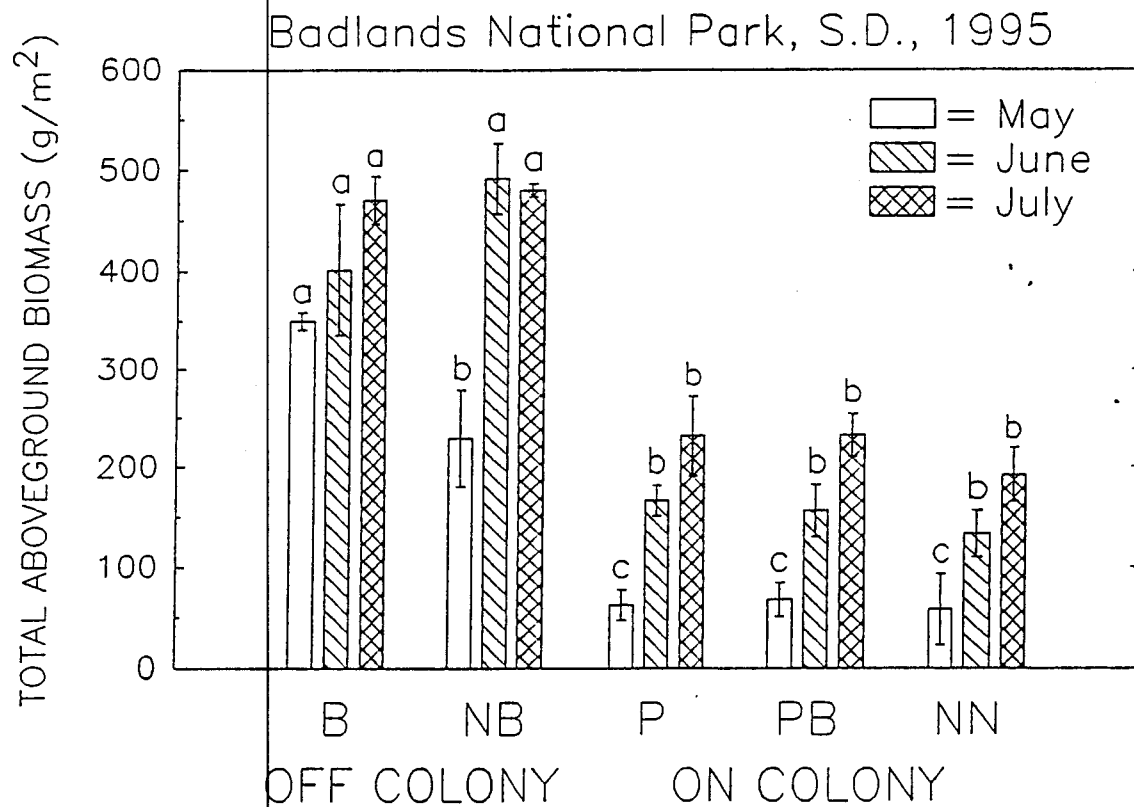


Figure 1. Total aboveground biomass in May, June, and July, 1995, for the five different herbivore treatments. Data are means $\pm$ 1 SE. Significant (<0.05) differences between means are indicated by different letters above each bar.

This procedure was repeated each month from May to August.

Inorganic nitrogen ($\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$) was extracted from each soil sample and resin bag in the lab using 2 M KCl. Inorganic nitrogen (N_i) was analyzed colorimetrically from the extracts of initial soils, 30 day soils, and resin bags: initial N_i was determined from the mid-May extracts, and final N_i was determined by combining values from the soil extracts and resin bag extracts at the end of each month. Bulk density was determined for each sample from a 10 g subsample of initial soil samples that was oven dried at 65°C for 24 hours.

RESULTS AND DISCUSSION

Because this data represents only the first field season of data, and since the exclosures have only been up for a short time, all results and interpretation of them should be regarded as preliminary and subject to change as analyses and additional field seasons are completed.

Plant biomass, forage N-content, crude protein determinations

Total aboveground plant biomass increased seasonally in all treatments with peak standing crop occurring near the end (i.e., late-July) of the growing season (Figure 1). Although there were no significant differences in plant biomass between on-colony treatments or between off-colony treatments, plant biomass was always greater off the colony relative to on-colony treatments (Figure 1). This difference was largely the result of the near absence of grasses on the prairie dog towns (Figure 2). Aboveground biomass off prairie dog towns was dominated by grasses while forbs dominated the on-town treatment sites (Figure 2). This pattern of functional group composition and biomass distribution as a result of herbivore activity associated with prairie dog towns is similar to that which has been observed in other studies (Coppock et al. 1983; Archer et

al. 1987). We expect that in subsequent growing seasons, significant differences in plant biomass between on-colony treatments and between off-colony treatments may develop as vegetation that is protected from prairie dogs, bison, or both, recovers from past herbivore disturbances. (For a more complete listing of the aboveground biomass data, see Appendix Tables A1 - A3.)

Forage N-content, represented in crude protein, generally increased in on-town treatments relative to off-town treatments (Figure 3), but due to the higher total biomass in off-town treatments, standing crop of N (g N/m^2) was much higher in off-town sites (Figure 4). These N patterns did not, however, translate into significant differences in carbon:nitrogen ratios in any of the treatments. Carbon:nitrogen ratios tended to be lowest in May and increase as the season progressed (Figure 5). There was also a general trend for live forbs to have lower C:N ratios than grasses throughout the growing season and for live biomass to have lower C:N ratios than dead biomass (Figure 5). However, there was not any consistent differences between any of the herbivore treatments. There did appear to be a slight trend for on-town treatments to have lower C:N ratios than off-town treatment, especially evident in dead plant material and later in the season, but whether this trend becomes more pronounced in subsequent seasons remains to be seen.

Species composition and diversity

Changes in species composition largely reflected the trends observed in biomass with off-town sites being dominated by grasses and on-town sites dominated by forbs (Table 1). While total live plant cover did not vary much among the treatments, bare ground was nearly three times greater in on-town sites relative to off-town sites (Table 1). Likewise, litter cover was only about 5% in on-town sites but averaged close to 30% off the prairie dog towns (Table 1). One interesting pattern was the greater contribution of exotic plants to total plant cover in off-town sites relative to on-town sites (Table 1). This was primarily due to the large contributions to plant cover of

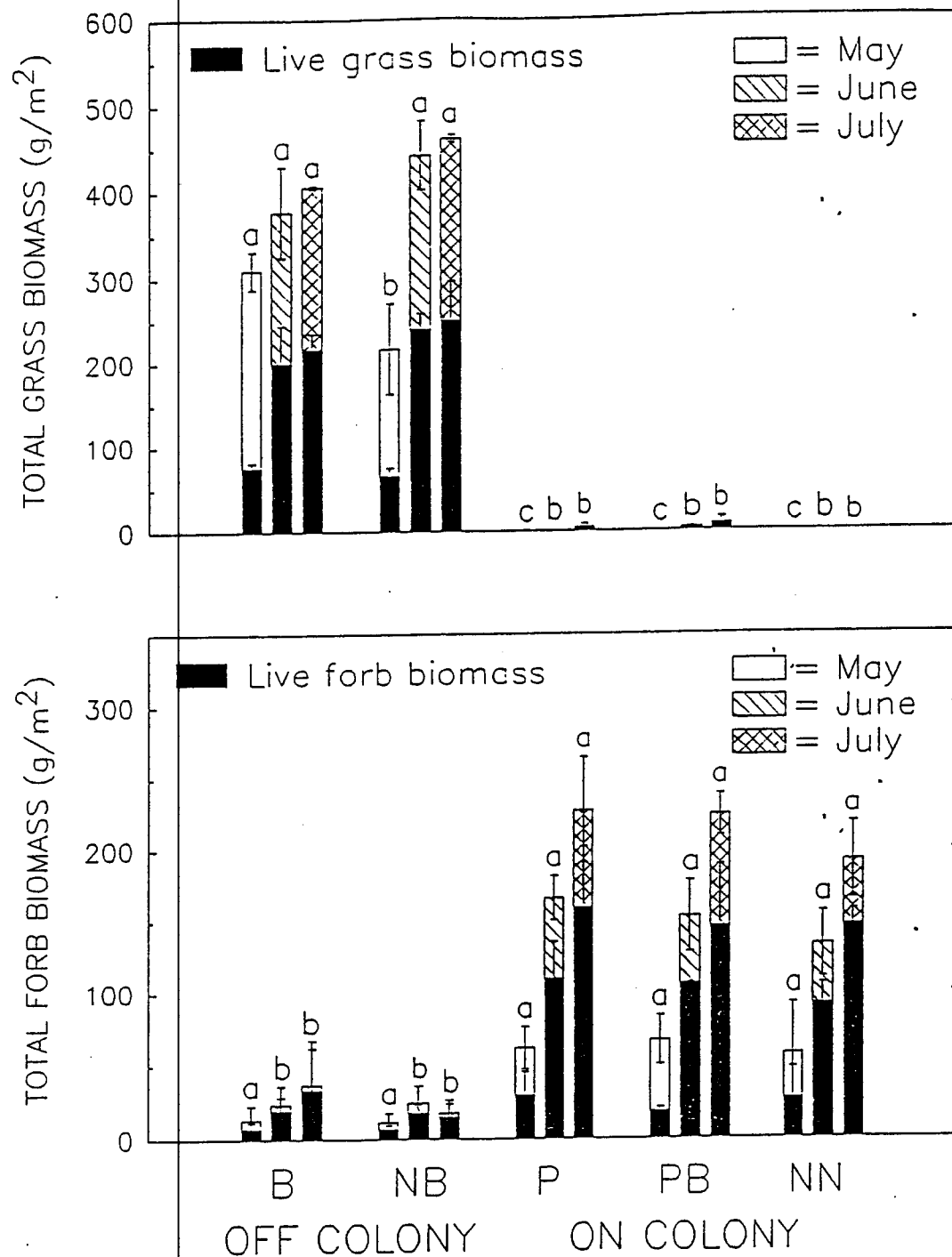


Figure 2. Total and live grass (top) and forb (bottom) biomass in May, June, and July, 1995, for the five different herbivore treatments. Data are means $\pm$ 1 SE. Significant (<0.05) differences between means are indicated by different letters above each bar.

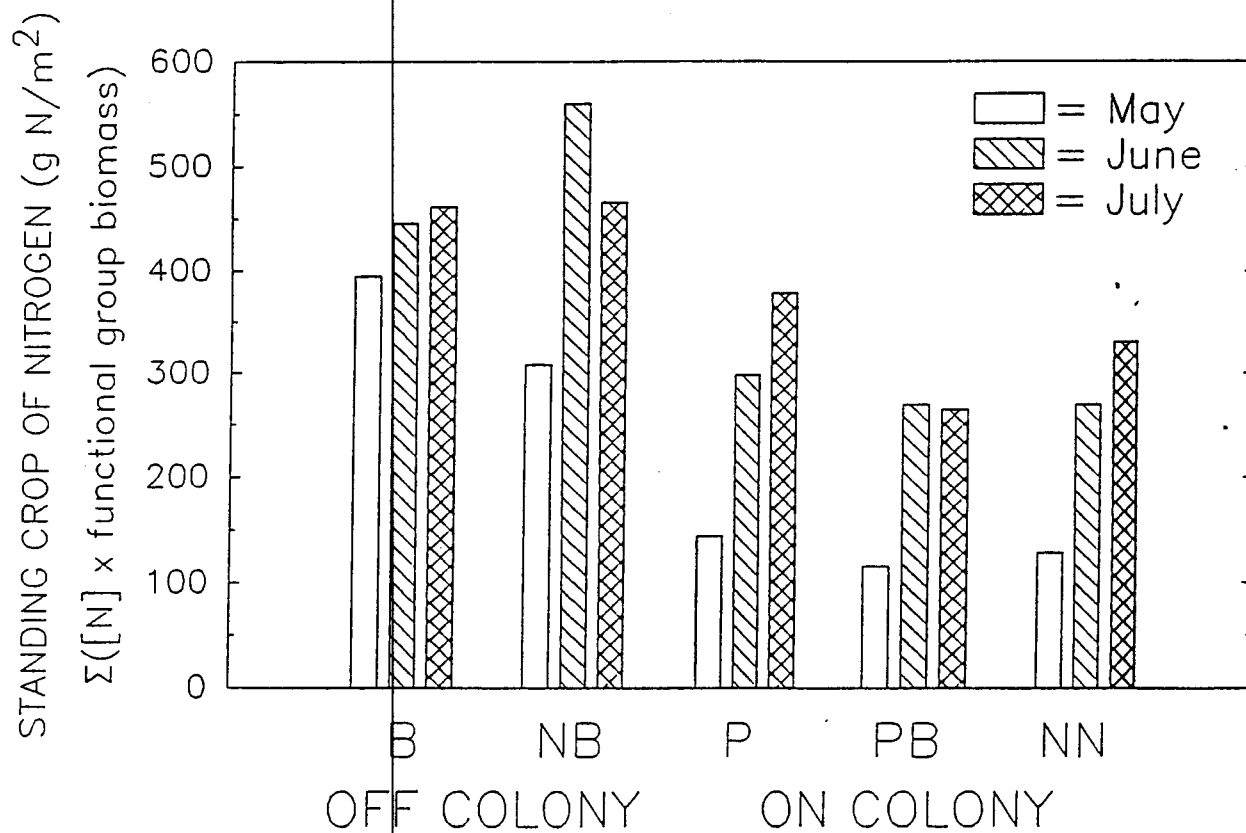


Figure 4. Standing crop of nitrogen in May, June, and July, 1995, for the five different herbivore treatments. Data were determined by multiplying the nitrogen concentration by aboveground biomass of each functional group and then summing functional groups.

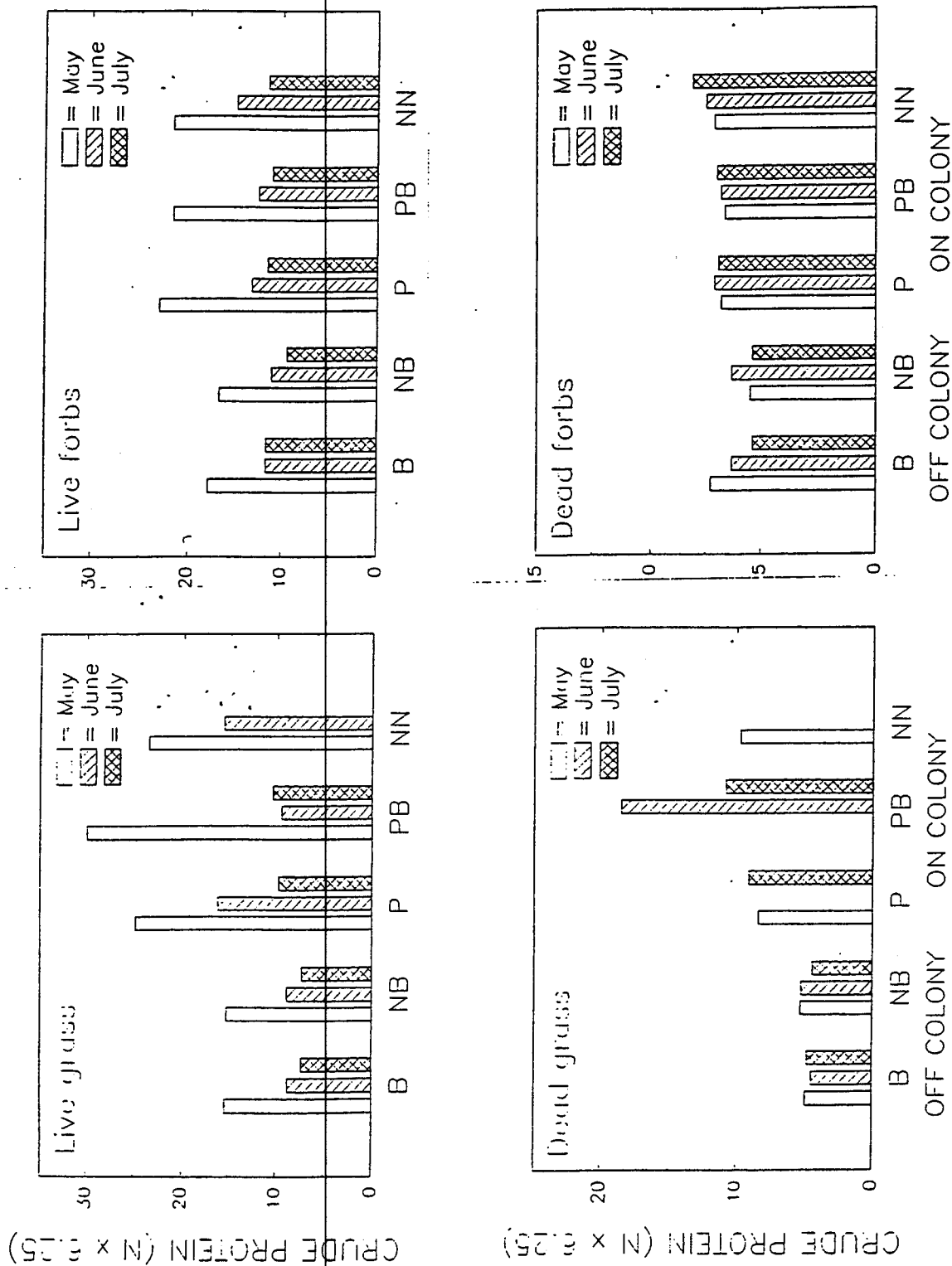


Figure 3. Crude protein concentration in live and dead grass and forb biomass for the five different herbivore treatments.

Bromus japonicus, an introduced grass, and *Melilotus officianalis*, an introduced clover, in off-town sites. In general, these two exotics are not considered a nuisance and may actually contribute substantially to large herbivore diets.

Species diversity was higher in on-town sites relative to off-town sites (Table 1) reflecting the more uniform distribution of biomass among species in on-town sites. Similarity between sites also mirrored biomass and species composition patterns with the off-town treatments, B and NB, having high similarity to each other but low similarity to on-town sites, and on-town treatments, P, PB, and NN, being similar to each other but dissimilar to off-town sites (Table 2). The higher similarity of PB to the off-town sites is largely due to the Kalchbrenner PB site being in a relatively early stage of prairie dog colonization compared to the other two PB sites. (For a complete listing of species composition tables for each site, contact J. Fahnestock).

Soil nitrogen dynamics

Net nitrogen mineralization was highest in May and declined steadily during the growing season (Figure 6). Average net mineralization was positive for on-town sites in May and June and negative by July. For off-town sites, net mineralization was barely positive in May and June and July showed net immobilization (Figure 6). This modification of nutrient cycling on prairie dog towns is similar to that observed in studies at WCNP where colony patches exhibited higher net nitrogen mineralization rates and lower immobilization relative to uncolonized grassland (Holland & Detling 1990).

Most of the inorganic nitrogen in this system appears to very mobile with a high chance of leaching from the system if it is not taken up by plants or microorganisms. This is apparent when separating the net nitrogen mineralization data into soil and resin bag components (Figure 7). In all treatments, soils showed net immobilization of nitrogen throughout the growing season, although less was immobilized in on-town sites. Conversely, nitrogen collected in resin bags always

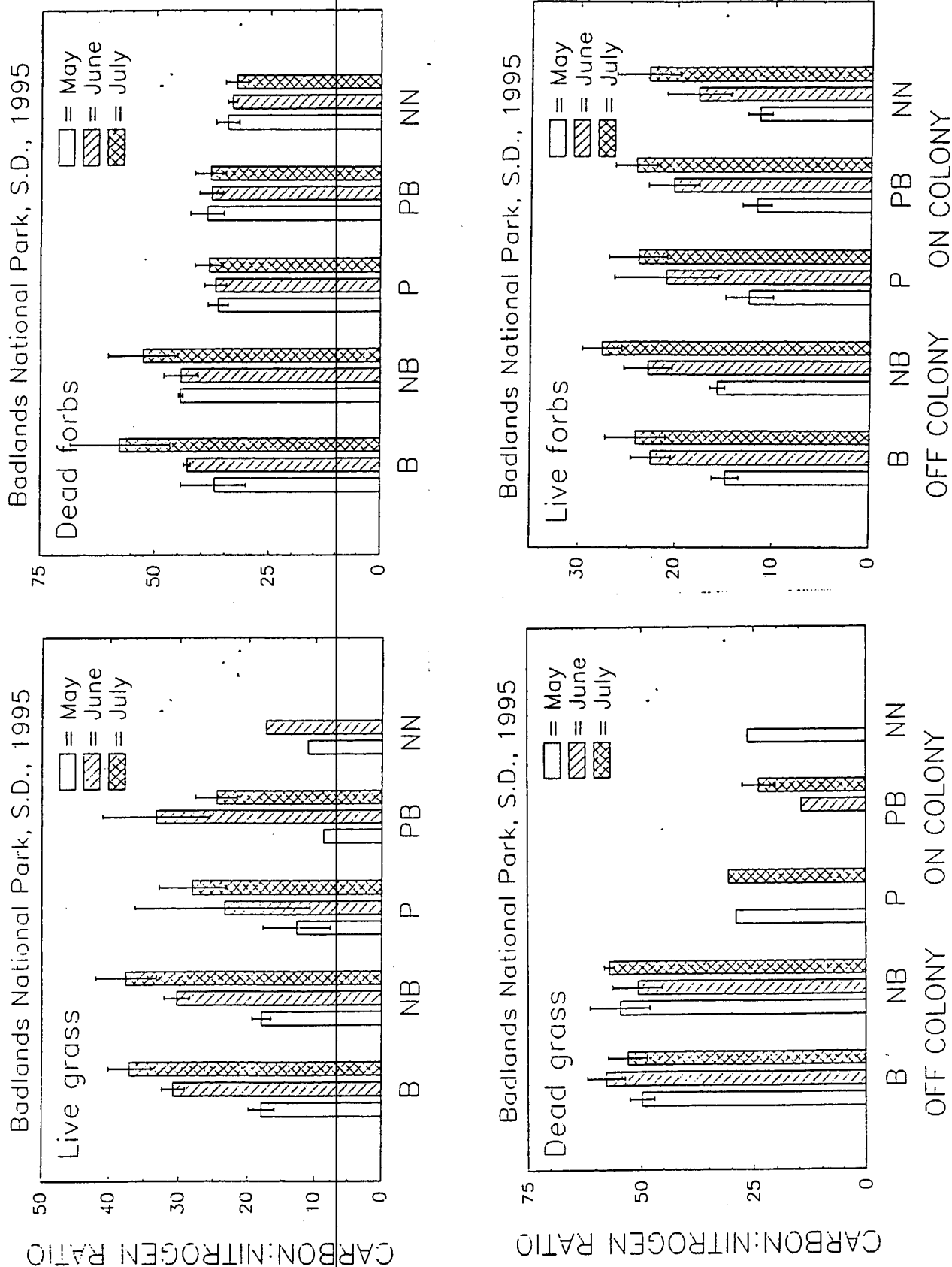


Figure 5. Carbon:nitrogen ratio in live and dead grass and forb biomass for the five different herbivore treatments. Data are means $\pm$ 1 SE.

Table 1. Percentage cover of the ten most abundant species, and other plant community characteristics in June and July 1995. Treatments are as in Table X.

JUNE		JULY	
Treatment B			
<i>Agropyron smithii</i>	27	<i>Agropyron smithii</i>	18
<i>Bromus japonicus</i> *	13	<i>Buchloë dactyloides</i>	8
<i>Buchloë dactyloides</i>	5	<i>Bromus japonicus</i> *	6
<i>Melilotus officianalis</i> *	3	<i>Stipa viridula</i>	4
<i>Poa sandbergii</i>	2	<i>Melilotus officianalis</i> *	3
<i>Hedeoma hispidum</i>	2	<i>Ceratoides lanata</i>	1
<i>Vicia americana</i>	1	<i>Bouteloua curtipendula</i>	< 1
<i>Conyza canadensis</i>	< 1	<i>Hedeoma hispidum</i>	< 1
Unknown forb (#6)	< 1	<i>Camelina microcarpa</i> *	< 1
<i>Draba reptans</i>	< 1	<i>Helianthus annuus</i>	< 1
Total live plant cover	64		47
Bare ground	10		9
Litter	31		19
Species richness	21		15
Shannon diversity index	0.89		0.89
Graminoid/forb cover ratio	3.48		4.01
Native/exotic cover ratio	2.60		3.54
Treatment NB			
<i>Bromus japonicus</i> *	27	<i>Agropyron smithii</i>	22
<i>Agropyron smithii</i>	16	<i>Bromus japonicus</i> *	13
<i>Poa sandbergii</i>	2	<i>Stipa viridula</i>	8
<i>Melilotus officianalis</i> *	2	<i>Buchloë dactyloides</i>	5
<i>Hedeoma hispida</i>	2	<i>Melilotus officianalis</i> *	1
<i>Carex eleocharis</i>	2	<i>Carex eleocharis</i>	1
<i>Buchloë dactyloides</i>	2	<i>Hedeoma hispidum</i>	1
<i>Stipa viridula</i>	1	<i>Conyza canadensis</i>	< 1
<i>Draba reptans</i>	1	<i>Helianthus annuus</i>	< 1
<i>Tradescantia</i> spp.	< 1	<i>Camelina microcarpa</i> *	< 1
Total live plant cover	63		55
Bare ground	4		5
Litter	34		30
Species richness	22		16
Shannon diversity index	0.89		0.79
Graminoid/forb cover ratio	3.99		7.80
Native/exotic cover ratio	1.01		2.61

yielded positive values. Thus, adding soil and resin bag nitrogen together (Figure 7) produced the results seen in Figure 6.

CONCLUSIONS

Since this report represents only the first year of a multi-year study, it is premature to draw definitive conclusions on the effects of these herbivore treatments on various grassland processes. However, some interesting processes are already observable. For instance, on-town sites have much lower plant biomass and nearly all of the species are forbs. Conversely, off-town sites are dominated by grasses and have higher plant biomass. Nitrogen cycling is also being affected by on-town activities with prairie dog town treatments having higher N mineralization rates than off-town sites. This is resulting in higher crude protein for plants on prairie dog towns although total standing crop of N remains higher in off-town treatments simply due to the higher levels of biomass off prairie dog towns.

What is of most interest to us is whether a deviation will occur in subsequent growing seasons from these vegetational and nutrient patterns that we have observed in this first year of the study. Some questions of interest that we will examine in subsequent years include: Will off-town sites that are protected from herbivory accumulate more detritus eventually resulting in less productive sites? Will on-town sites that are protected from both herbivores revert to a condition more reminiscent of off-town sites, or has a new steady state been established? How quickly will changes in vegetation or nutrient cycling occur in sites that are protected from herbivores?

(Table 1 continued)

Treatment NN

<i>Asclepias pumila</i>	7	<i>Dyssodia papposa</i>	9
<i>Sphaeralcea coccinea</i>	5	<i>Conyza canadensis</i>	8
<i>Dyssodia papposa</i>	5	<i>Asclepias pumila</i>	7
<i>Plantago patagonica</i>	5	<i>Sphaeralcea coccinea</i>	4
<i>Conyza canadensis</i>	5	<i>Euphorbia stictospora</i>	4
<i>Verbena bracteata</i>	4	<i>Verbena bracteata</i>	3
<i>Melilotus officianalis</i> *	4	<i>Plantago patagonica</i>	3
<i>Sisymbrium altissimum</i> *	1	<i>Chenopodium desiccatum</i>	1
<i>Hedeoma hispidum</i>	1	<i>Melilotus officianalis</i> *	1
Unknown forb (#20)	< 1	<i>Sisymbrium altissimum</i> *	1
Total live plant cover	42		48
Bare ground	31		34
Litter	2		4
Species richness	17		18
Shannon diversity index	1.09		1.07
Forb/graminoid cover ratio	200.3		62.6
Native/exotic cover ratio	7.16		13.45

(Table 1 continued)

Treatment P

<i>Conyza canadensis</i>	13	<i>Conyza canadensis</i>	16
<i>Hedeoma hispidum</i>	7	<i>Plantago patagonica</i>	5
<i>Plantago patagonica</i>	7	<i>Dyssodia papposa</i>	5
<i>Sphaeralcea coccinea</i>	6	<i>Convolvulus arvensis</i> *	5
<i>Verbena bracteata</i>	3	<i>Sphaeralcea coccinea</i>	4
<i>Dyssodia papposa</i>	3	<i>Verbena bracteata</i>	3
<i>Convolvulus arvensis</i> *	2	<i>Euphorbia stictospora</i>	2
<i>Melilotus officianalis</i> *	2	<i>Melilotus officianalis</i> *	2
<i>Euphorbia marginata</i>	2	<i>Polygonum aviculare</i>	2
<i>Lappula redowskii</i>	2	<i>Hedeoma hispidum</i>	1
Total live plant cover	56		51
Bare ground	33		25
Litter	4		4
Species richness	18		21
Shannon diversity index	1.16		1.08
Forb/graminoid cover ratio	120.3		111.0
Native/exotic cover ratio	7.35		5.05

Treatment PB

<i>Conyza canadensis</i>	12	<i>Conyza canadensis</i>	14
<i>Hedeoma hispidum</i>	8	<i>Convolvulus arvensis</i>	5
<i>Agropyron smithii</i>	6	<i>Plantago patagonica</i>	5
<i>Convolvulus arvensis</i> *	5	<i>Agropyron smithii</i>	4
<i>Verbena bracteata</i>	3	<i>Euphorbia stictospora</i>	3
<i>Lappula redowskii</i>	3	<i>Dyssodia papposa</i>	3
<i>Plantago patagonica</i>	3	<i>Hedeoma hispidum</i>	2
<i>Dyssodia papposa</i>	2	<i>Sisymbrium altissimum</i> *	2
<i>Melilotus officianalis</i> *	2	<i>Melilotus officianalis</i> *	2
<i>Asclepias pumila</i>	2	<i>Asclepias pumila</i>	1
Total live plant cover	54		47
Bare ground	22		23
Litter	6		6
Species richness	20		22
Shannon diversity index	1.17		1.12
Forb/graminoid cover ratio	7.43		9.07
Native/exotic cover ratio	5.27		3.77

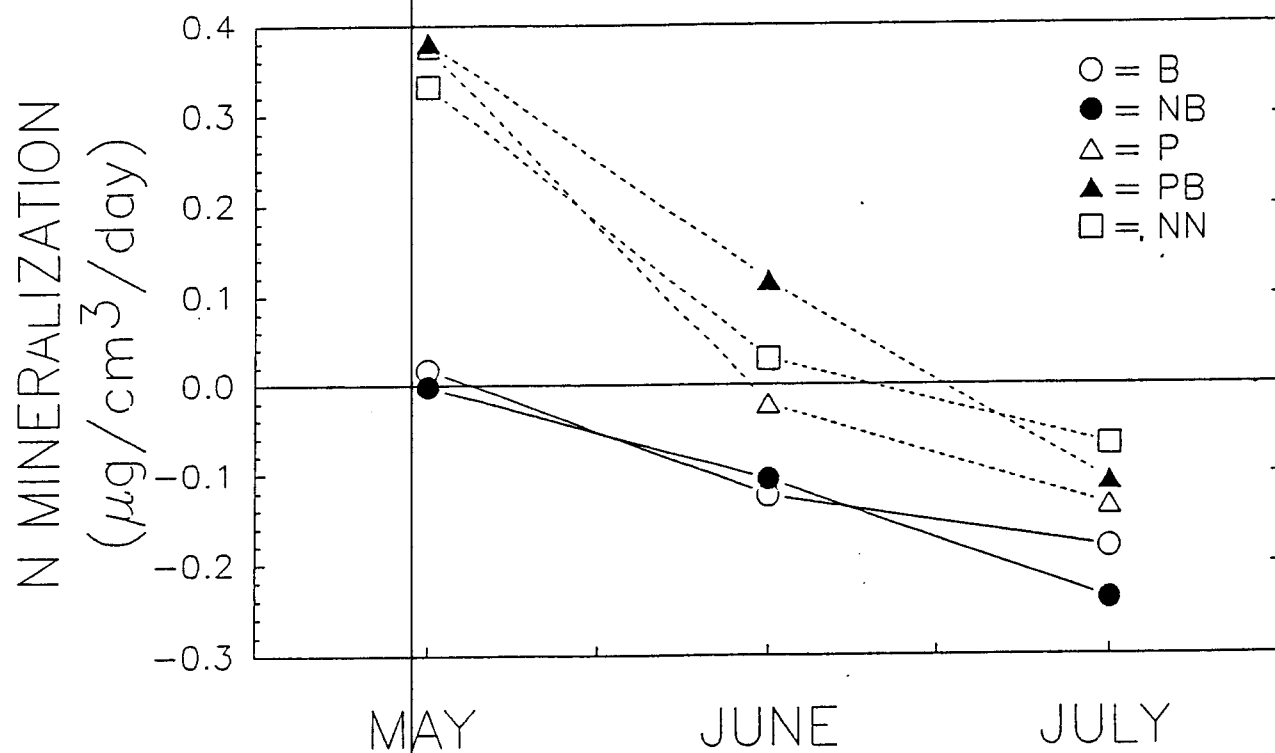


Figure 6. Net nitrogen mineralization for the five different herbivore treatments in May, June, and July, 1995. These values include both the resin bag and soil net mineralization data. See text for additional details.

Table 2. Estimated similarity (Morisita 1959) of plant species composition among five herbivore treatments in June and July 1995. Species composition was measured in three separate study areas within the Sage Creek Wilderness Area, Badlands National Park, S.D. Treatments include two sites that are adjacent to prairie dog towns and three sites that are on prairie dog towns. Treatments are uncolonized prairie with bison (B), uncolonized prairie excluding bison (NB), colonized prairie with prairie dogs but with bison excluded (P), colonized prairie with prairie dogs and bison (PB), and colonized prairie with both bison and prairie dogs excluded (NN).

JUNE						JULY					
	B	NB	P	PB	NN		B	NB	P	PB	NN
B	1.00	-	-	-	-	B	1.00	-	-	-	-
NB	0.86	1.00	-	-	-	NB	1.02	1.00	-	-	-
P	0.07	0.06	1.00	-	-	P	0.06	0.04	1.00	-	-
PB	0.36	0.22	1.02	1.00	-	PB	0.26	0.22	1.08	1.00	-
NN	0.06	0.05	0.89	0.66	1.00	NN	0.05	0.03	0.88	0.77	1.00

LITERATURE CITED

- Archer, S., M.G. Garrett, and J.K. Detling. 1987. Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. *Vegetatio* 72:159-166.
- Cid, M.S., J.K. Detling, A.D. Whicker, and M.A. Brizuela. 1991. Vegetational responses of a mixed-grass prairie site following exclusion of prairie dogs and bison. *J. Range Management* 44:100-105.
- Coppock, D.L., J.E. Ellis, J.K. Detling, and M.I. Dyer. 1983a. Plant-herbivore interactions in a North American mixed-grass prairie I. Effects of black-tailed prairie dogs on intraseasonal above-ground plant biomass and nutrient dynamics and plant species diversity. *Oecologia* 56:1-9.
- Coppock, D.L., J.E. Ellis, J.K. Detling, and M.I. Dyer. 1983b. Plant-herbivore interactions in a North American mixed-grass prairie II. Responses of bison to modification of vegetation by prairie dogs. *Oecologia* 56:10-15.
- Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. *Northwest Science* 33: 43-64.
- Detling, J.K., E.L. Painter, and D.L. Coppock. 1986. Ecotypic differentiation resulting from grazing pressure: evidence for a likely phenomenon. Pages 431-433 in P.J. Jopss, P.W. Lynch, and O.B. Williams, eds. *Rangelands: a resource under siege*. Australian Academy of Science, Canberra.
- Groffman, P.M., C.W. Rice, and J.M. Tiedje. 1993. Denitrification in a tallgrass prairie. *Ecology* 74:855-862.
- Holland, E.A., and J.K. Detling. 1990. Plant response to herbivory and belowground nitrogen cycling. *Ecology* 71:1040-1049.
- Ingham, R.E., and J.K. Detling. 1984. Plant-herbivore interactions in a North American mixed-grass prairie III. Soil nematode populations and root biomass on *Cynomys ludovicianus* colonies and adjacent ungrazed area. *Oecologia* 63:307-313.
- Jaramillo, V.J., and J.K. Detling. 1988. Grazing history, defoliation, and competition: effects on shortgrass production and nitrogen accumulation. *Ecology* 69:1599-1608.
- Krueger, K. 1986. Feeding relationships among bison, pronghorn, and prairie dogs: an experimental analysis. *Ecology* 67:760-770.
- Morisita, M. 1959. Measuring of interspecific association and similarity between communities. *Memoirs Fac. Sci., Kyushu University, Series E (Biology)* 3:65-80.

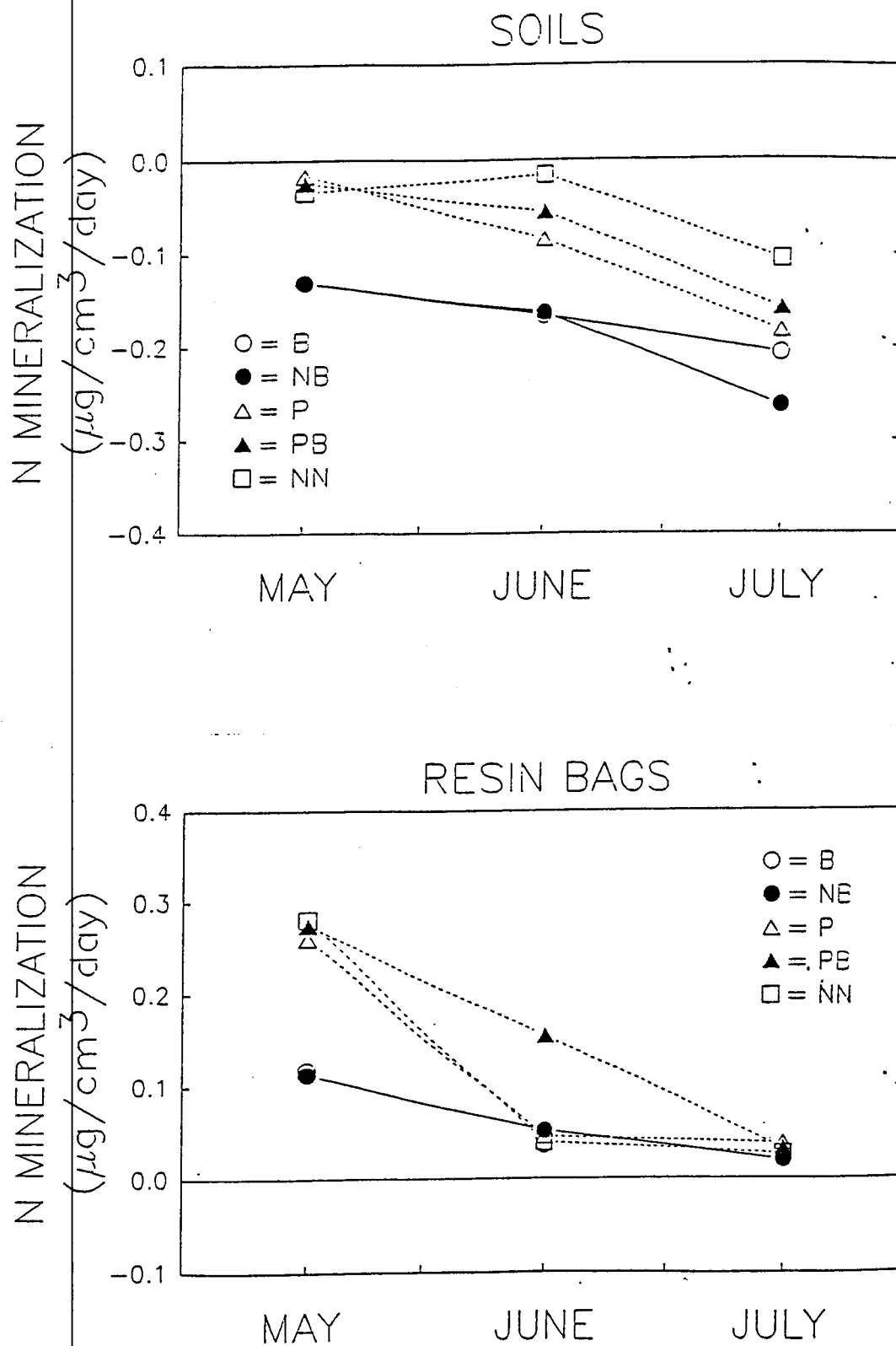


Figure 7. Net nitrogen mineralization/immobilization for soils (top) and resin bags (bottom).

APPENDIX TABLES

Table A1. Mean aboveground biomass (g/m^2) $\pm$ 1 SE of plant functional groups for each site in treatments of off-colony, no bison (NB), off-colony, bison (B), on-colony, no bison, prairie dogs (P), on-colony, no bison, no prairie dogs (NN), and on-colony, bison and prairie dogs (PB). Sites Hay Butte (HB), Kalchbrenner (KA), and Kocher Flats (KF) are in the Sage Creek Wilderness Area of the Badlands National Park, S.D. Values shown are for May 1995 and $n = 10$ for each site ($n = 3$ for final column).

	Hay Butte	Kalchbrenner	Kocher Flats	All Sites
Live graminoids				
NB	46.4 $\pm$ 8.9 ^b	67.3 $\pm$ 9.9 ^{ab}	80.4 $\pm$ 8.0 ^a	64.7 $\pm$ 9.9 ^a
B	76.2 $\pm$ 5.1 ^{ab}	85.5 $\pm$ 11.6 ^a	62.6 $\pm$ 6.9 ^b	74.7 $\pm$ 6.7 ^a
P	0 ^a	< 0.1 ^a	0.7 $\pm$ 0.6 ^a	0.3 $\pm$ 0.2 ^b
NN	0 ^a	0 ^a	0.8 $\pm$ 0.6 ^a	0.3 $\pm$ 0.3 ^b
PB	0 ^a	0.7 $\pm$ 0.5 ^a	0 ^a	0.2 $\pm$ 0.2 ^b
Dead graminoids				
NB	215.4 $\pm$ 66.3 ^a	42.1 $\pm$ 14.9 ^b	198.7 $\pm$ 28.9 ^a	152.1 $\pm$ 55.2 ^a
B	275.8 $\pm$ 41.8 ^a	215.8 $\pm$ 38.4 ^a	213.6 $\pm$ 14.4 ^a	235.0 $\pm$ 20.4 ^b
P	0 ^a	0 ^a	0.7 $\pm$ 0.6 ^a	0.2 $\pm$ 0.2 ^c
NN	0 ^a	0 ^a	0.2 $\pm$ 0.2 ^a	< 0.1 ^c
PB	0 ^a	0 ^a	0 ^a	0 ^c
Total graminoids				
NB	261.8 $\pm$ 73.0 ^a	109.4 $\pm$ 19.3 ^b	279.1 $\pm$ 28.1 ^a	216.8 $\pm$ 53.9 ^a
B	351.9 $\pm$ 42.4 ^a	301.2 $\pm$ 37.4 ^{ab}	276.1 $\pm$ 18.6 ^b	309.7 $\pm$ 22.3 ^b
P	0 ^a	< 0.1 ^a	1.4 $\pm$ 1.3 ^a	0.5 $\pm$ 0.4 ^c
NN	0 ^a	0 ^a	1.0 $\pm$ 0.7 ^a	0.3 $\pm$ 0.3 ^c
PB	0 ^a	0.7 $\pm$ 0.5 ^a	0 ^a	0.2 $\pm$ 0.2 ^c
Live forbs				
NB	8.1 $\pm$ 3.7 ^a	10.5 $\pm$ 1.6 ^a	2.3 $\pm$ 0.6 ^a	7.0 $\pm$ 2.4 ^a
B	2.2 $\pm$ 1.2 ^a	15.0 $\pm$ 6.1 ^a	4.3 $\pm$ 1.5 ^a	7.2 $\pm$ 4.0 ^a
P	16.0 $\pm$ 3.7 ^b	10.0 $\pm$ 3.2 ^b	62.0 $\pm$ 6.4 ^a	29.3 $\pm$ 16.4 ^a
NN	6.7 $\pm$ 2.2 ^b	3.8 $\pm$ 1.6 ^b	69.6 $\pm$ 18.0 ^a	26.7 $\pm$ 21.5 ^a
PB	17.3 $\pm$ 4.2 ^a	14.1 $\pm$ 3.8 ^a	23.4 $\pm$ 5.7 ^a	18.3 $\pm$ 2.7 ^a
Dead forbs				
NB	0.8 $\pm$ 0.6 ^a	12.5 $\pm$ 6.5 ^a	< 0.1 ^a	4.4 $\pm$ 4.0 ^b
B	0.2 $\pm$ 0.2 ^a	17.2 $\pm$ 11.6 ^a	0 ^a	5.8 $\pm$ 5.7 ^b
P	19.2 $\pm$ 3.0 ^b	54.6 $\pm$ 11.2 ^a	24.0 $\pm$ 10.2 ^{ab}	32.6 $\pm$ 11.1 ^{ab}
NN	30.3 $\pm$ 8.9 ^{ab}	6.9 $\pm$ 2.3 ^b	55.7 $\pm$ 30.5 ^a	31.0 $\pm$ 14.1 ^{ab}
PB	19.4 $\pm$ 4.5 ^b	80.1 $\pm$ 20.8 ^a	47.2 $\pm$ 14.7 ^b	48.9 $\pm$ 17.5 ^a

- Munn, L.C. 1993. Effects of prairie dogs on physical and chemical properties of soils. Pages 11-17 in J.L. Oldemeyer, D.E. Biggins, and B.J. Miller, eds. Proceedings on the symposium on the management of prairie dog complexes for the reintroduction of the black-footed ferret. U.S. Fish and Wildlife Service. U.S. Department of the Interior. Washington, D.C.
- Painter, E.L., J.K. Detling, and D.A. Steingraeber. 1993. Plant morphology and grazing history: relationships between native grasses and herbivores. *Vegetatio* 106:37-62.
- Pielou, E.C. 1977. *Mathematical ecology*. John Wiley & Sons, New York. 385 pp.
- Plumb, G.E., and J.L. Dodd. 1993. Foraging ecology of bison and cattle on a mixed prairie: implications for natural area management. *Ecological Applications* 3:631-643.
- Ruess, R.W. 1987. The role of large herbivores in nutrient cycling of tropical savannas. Pages xx-xx in B.H. Walker, ed. *Determinants of tropical savannas*. IRL Press, Oxford, England.
- Schimel, D.S., W.J. Parton, F.J. Anderson, R.G. Woodmansee, R.L. Senft, and M.A. Stillwell. 1986. The role of cattle in the volatile loss of nitrogen from the shortgrass steppe. *Biogeochemistry* 2:39-52.
- Whicker, A.D., and J.K. Detling. 1988a. Ecological consequences of prairie dog disturbances. *BioScience* 38:773-785.
- Whicker, A.D., and J.K. Detling. 1988b. Modification of vegetation structure and ecosystem processes by North American grassland mammals. Pages 301-316 in M.J.A. Werger, P.J.M. van der Art, H.J. During, and J.T.A. Verhoeven, eds. *Plant form and vegetation structure*. SPB Academic Publishing. The Hague.

Table A2. Mean aboveground biomass (g/m²) $\pm$ 1 SE of plant functional groups for June 1995. See legend for Table A1 for additional information regarding notation.

	Hay Butte	Kalchbrenner	Kocher Flats	All Sites
Live graminoids				
NB	237.6 $\pm$ 33.2 ^{ab}	273.0 $\pm$ 34.8 ^a	209.4 $\pm$ 10.7 ^b	240.0 $\pm$ 18.4 ^a
B	159.8 $\pm$ 17.8 ^b	289.0 $\pm$ 31.1 ^a	150.4 $\pm$ 13.5 ^b	199.7 $\pm$ 44.7 ^a
P	0.2 $\pm$ 0.1 ^a	0.2 $\pm$ 0.2 ^a	0.5 $\pm$ 0.1 ^a	0.3 $\pm$ 0.1 ^b
NN	< 0.1 ^a	0 ^a	0.3 $\pm$ 0.2 ^a	< 0.1 ^b
PB	0.5 $\pm$ 0.3 ^a	5.1 $\pm$ 4.2 ^a	3.3 $\pm$ 2.2 ^a	3.0 $\pm$ 1.3 ^b
Dead graminoids				
NB	299.9 $\pm$ 54.4 ^a	133.1 $\pm$ 17.9 ^c	223.1 $\pm$ 18.0 ^b	218.7 $\pm$ 48.2 ^a
B	167.0 $\pm$ 39.6 ^a	192.8 $\pm$ 34.8 ^a	173.5 $\pm$ 26.8 ^a	177.8 $\pm$ 7.7 ^a
P	0 ^a	0 ^a	0.1 $\pm$ 0.1 ^a	< 0.1 ^b
NN	0 ^a	0 ^a	0 ^a	0 ^b
PB	0.2 $\pm$ 0.2 ^a	0.3 $\pm$ 0.2 ^a	0.2 $\pm$ 0.1 ^a	0.2 $\pm$ 0.0 ^b
Total graminoids				
NB	537.4 $\pm$ 62.4 ^a	406.2 $\pm$ 42.6 ^b	432.5 $\pm$ 21.2 ^b	442.6 $\pm$ 40.1 ^a
B	326.4 $\pm$ 50.0 ^b	481.9 $\pm$ 52.1 ^a	323.9 $\pm$ 34.4 ^b	377.4 $\pm$ 52.2 ^a
P	0.2 $\pm$ 0.1 ^a	0.2 $\pm$ 0.2 ^a	0.6 $\pm$ 0.2 ^a	0.3 $\pm$ 0.1 ^b
NN	< 0.1 ^a	0 ^a	0.3 $\pm$ 0.2 ^a	< 0.1 ^b
PB	0.6 $\pm$ 0.5 ^a	5.4 $\pm$ 4.4 ^a	3.5 $\pm$ 2.2 ^a	3.2 $\pm$ 1.4 ^b
Live forbs				
NB	12.8 $\pm$ 12.6 ^a	29.6 $\pm$ 7.9 ^a	9.8 $\pm$ 2.4 ^a	17.4 $\pm$ 6.2 ^b
B	8.2 $\pm$ 4.4 ^a	37.4 $\pm$ 6.0 ^a	12.0 $\pm$ 2.0 ^a	19.2 $\pm$ 9.2 ^b
P	124.1 $\pm$ 16.6 ^a	59.3 $\pm$ 11.0 ^b	145.8 $\pm$ 9.2 ^a	109.7 $\pm$ 26.0 ^a
NN	83.8 $\pm$ 12.0 ^b	72.0 $\pm$ 17.2 ^b	119.5 $\pm$ 13.1 ^a	91.8 $\pm$ 14.3 ^a
PB	105.7 $\pm$ 16.0 ^a	108.2 $\pm$ 16.8 ^a	103.8 $\pm$ 17.4 ^a	105.9 $\pm$ 1.3 ^a
Dead forbs				
NB	1.6 $\pm$ 0.6 ^a	18.4 $\pm$ 10.4 ^a	0.6 $\pm$ 0.4 ^a	6.9 $\pm$ 5.8 ^{bc}
B	0.1 $\pm$ 0.1 ^a	11.7 $\pm$ 4.3 ^a	0.6 $\pm$ 0.3 ^a	4.1 $\pm$ 3.8 ^c
P	48.2 $\pm$ 7.3 ^{ab}	78.4 $\pm$ 11.4 ^a	43.9 $\pm$ 11.6 ^b	56.8 $\pm$ 10.9 ^a
NN	52.3 $\pm$ 28.6 ^a	19.9 $\pm$ 6.0 ^a	52.1 $\pm$ 14.0 ^a	41.4 $\pm$ 10.8 ^{abc}
PB	24.1 $\pm$ 6.2 ^b	95.4 $\pm$ 21.9 ^a	22.8 $\pm$ 7.2 ^b	47.4 $\pm$ 6.0 ^{ab}
Total forbs				
NB	14.4 $\pm$ 4.4 ^a	48.0 $\pm$ 14.8 ^a	10.4 $\pm$ 2.3 ^a	24.3 $\pm$ 11.9 ^b
B	8.4 $\pm$ 4.4 ^a	49.0 $\pm$ 7.7 ^a	12.6 $\pm$ 2.1 ^a	23.3 $\pm$ 12.9 ^b
P	172.3 $\pm$ 21.6 ^a	136.5 $\pm$ 12.6 ^a	189.7 $\pm$ 15.9 ^a	166.2 $\pm$ 15.7 ^a
NN	136.1 $\pm$ 34.8 ^{ab}	91.9 $\pm$ 21.6 ^b	171.6 $\pm$ 25.7 ^a	133.2 $\pm$ 23.1 ^a
PB	129.8 $\pm$ 21.7 ^b	203.6 $\pm$ 31.8 ^a	126.6 $\pm$ 20.9 ^b	153.3 $\pm$ 25.1 ^a

Total forbs					
NB	8.9 ± 3.8 ^a	23.0 ± 6.5 ^a	2.4 ± 0.6 ^a	11.4 ± 6.1 ^a	
B	2.4 ± 1.2 ^a	32.2 ± 12.0 ^a	4.3 ± 1.5 ^a	13.0 ± 9.6 ^a	
P	35.2 ± 4.6 ^b	64.6 ± 10.4 ^{ab}	86.0 ± 14.8 ^a	61.9 ± 14.7 ^a	
NN	37.0 ± 10.3 ^b	10.6 ± 3.1 ^b	125.4 ± 32.8 ^a	57.7 ± 34.7 ^a	
PB	36.7 ± 7.6 ^b	94.2 ± 20.4 ^a	70.6 ± 16.6 ^b	67.2 ± 16.7 ^a	
Total succulents					
NB	1.3 ± 1.2 ^a	0 ^a	4.4 ± 4.4 ^a	1.9 ± 1.3 ^a	
B	9.2 ± 9.2 ^b	0 ^b	71.5 ± 48.6 ^a	26.9 ± 22.5 ^a	
P	0 ^a	0 ^a	0 ^a	0 ^a	
NN	0 ^a	0 ^a	0 ^a	0 ^a	
PB	0 ^a	0 ^a	0 ^a	0 ^a	
Total aboveground plant biomass					
NB	271.9 ± 71.1 ^a	132.4 ± 23.2 ^b	285.9 ± 26.9 ^a	230.1 ± 49.0 ^b	
B	363.5 ± 36.4 ^a	333.4 ± 40.6 ^a	352.2 ± 45.9 ^a	349.7 ± 8.8 ^a	
P	35.2 ± 4.6 ^a	64.6 ± 10.4 ^a	87.4 ± 15.4 ^a	62.4 ± 15.1 ^a	
NN	37.0 ± 10.3 ^b	10.6 ± 3.1 ^b	126.4 ± 32.8 ^a	58.0 ± 35.0 ^a	
PB	36.7 ± 7.6 ^a	95.0 ± 20.1 ^a	70.6 ± 16.6 ^a	67.4 ± 16.9 ^a	

NOTE: Different letters within each functional group denote significant differences among sites for each treatment ($P < 0.05$). Different letters within each functional group in the last column denote significant differences among treatments ($P < 0.05$).

Table A3. Mean aboveground biomass (g/m^2) $\pm$ 1 SE of plant functional groups for July 1995.
See legend for Table A1 for additional information regarding notation.

	Hay Butte	Kalchbrenner	Kocher Flats	All Sites
Live graminoids				
NB	261.2 $\pm$ 24.8 ^b	325.6 $\pm$ 38.1 ^a	164.3 $\pm$ 15.1 ^c	250.4 $\pm$ 46.9 ^a
B	209.8 $\pm$ 20.8 ^{ab}	252.6 $\pm$ 31.9 ^a	186.0 $\pm$ 17.5 ^b	216.1 $\pm$ 19.5 ^a
P	0 ^a	11.5 $\pm$ 7.7 ^a	0.4 $\pm$ 0.1 ^a	4.0 $\pm$ 3.8 ^b
NN	0 ^a	0 ^a	0 ^a	0 ^b
PB	0.2 $\pm$ 0.1 ^a	22.1 $\pm$ 12.2 ^a	1.2 $\pm$ 0.6 ^a	7.8 $\pm$ 7.1 ^b
Dead graminoids				
NB	209.2 $\pm$ 43.3 ^b	128.1 $\pm$ 32.6 ^c	296.9 $\pm$ 40.8 ^a	211.4 $\pm$ 48.7 ^a
B	193.0 $\pm$ 38.2 ^a	154.7 $\pm$ 41.2 ^a	221.2 $\pm$ 33.8 ^a	189.6 $\pm$ 19.3 ^a
P	0 ^a	0.7 $\pm$ 0.7 ^a	0.5 $\pm$ 0.2 ^a	0.4 $\pm$ 0.2 ^b
NN	0 ^a	0 ^a	0 ^a	0 ^b
PB	0.1 $\pm$ 0.1 ^a	0.9 $\pm$ 0.9 ^a	< 0.1 ^a	0.4 $\pm$ 0.3 ^b
Total graminoids				
NB	470.4 $\pm$ 62.2 ^a	453.7 $\pm$ 49.0 ^a	461.2 $\pm$ 47.3 ^a	461.8 $\pm$ 4.8 ^a
B	402.8 $\pm$ 49.8 ^a	407.3 $\pm$ 55.9 ^a	407.2 $\pm$ 47.0 ^a	405.8 $\pm$ 1.5 ^b
P	0 ^a	12.2 $\pm$ 8.2 ^a	0.9 $\pm$ 0.3 ^a	4.4 $\pm$ 3.9 ^c
NN	0 ^a	0 ^a	0 ^a	0 ^c
PB	0.3 $\pm$ 0.2 ^a	23.0 $\pm$ 12.8 ^a	1.3 $\pm$ 0.6 ^a	8.2 $\pm$ 7.4 ^c
Live forbs				
NB	4.5 $\pm$ 1.2 ^a	32.2 $\pm$ 8.1 ^a	8.0 $\pm$ 3.6 ^a	14.9 $\pm$ 8.7 ^b
B	2.1 $\pm$ 0.7 ^b	90.8 $\pm$ 14.8 ^a	6.4 $\pm$ 2.0 ^b	33.1 $\pm$ 28.9 ^b
P	147.6 $\pm$ 9.0 ^b	239.2 $\pm$ 42.3 ^a	91.5 $\pm$ 22.2 ^c	159.4 $\pm$ 43.0 ^a
NN	133.6 $\pm$ 13.4 ^a	168.0 $\pm$ 18.5 ^a	138.9 $\pm$ 23.3 ^a	146.8 $\pm$ 10.7 ^a
PB	189.9 $\pm$ 12.2 ^a	189.5 $\pm$ 36.9 ^a	59.0 $\pm$ 16.0 ^b	146.1 $\pm$ 43.6 ^a
Dead forbs				
NB	4.3 $\pm$ 1.5 ^a	3.1 $\pm$ 0.9 ^a	< 0.1 ^a	2.5 $\pm$ 1.3 ^b
B	2.6 $\pm$ 1.1 ^a	7.4 $\pm$ 2.6 ^a	0.8 $\pm$ 0.4 ^a	3.6 $\pm$ 2.0 ^b
P	52.2 $\pm$ 10.6 ^a	60.8 $\pm$ 10.9 ^a	91.6 $\pm$ 25.3 ^a	68.2 $\pm$ 12.0 ^{ab}
NN	19.8 $\pm$ 4.4 ^b	11.6 $\pm$ 4.2 ^b	104.9 $\pm$ 30.6 ^a	45.4 $\pm$ 29.8 ^{ab}
PB	18.2 $\pm$ 6.1 ^c	63.7 $\pm$ 16.3 ^b	152.9 $\pm$ 35.6 ^a	78.3 $\pm$ 39.6 ^a
Total forbs				
NB	8.8 $\pm$ 1.9 ^b	35.3 $\pm$ 7.7 ^a	8.1 $\pm$ 3.6 ^b	17.4 $\pm$ 9.0 ^b
B	4.7 $\pm$ 1.2 ^a	98.2 $\pm$ 15.6 ^a	7.2 $\pm$ 2.1 ^a	36.7 $\pm$ 30.8 ^b
P	199.9 $\pm$ 15.4 ^b	300.0 $\pm$ 35.4 ^a	183.2 $\pm$ 24.3 ^b	227.7 $\pm$ 36.5 ^a
NN	153.4 $\pm$ 11.6 ^b	179.6 $\pm$ 18.2 ^b	243.8 $\pm$ 31.2 ^a	192.3 $\pm$ 26.9 ^a
PB	208.1 $\pm$ 14.1 ^a	253.2 $\pm$ 49.8 ^a	212.0 $\pm$ 29.0 ^a	224.4 $\pm$ 14.4 ^a

Total succulents					
NB	0 ^a	0 ^a	26.1 ± 26.1 ^a	8.7 ± 8.7 ^a	
B	0 ^a	0 ^a	0 ^a	0 ^a	
P	0 ^a	0 ^a	0 ^a	0 ^a	
NN	0 ^a	0 ^a	0 ^a	0 ^a	
PB	0 ^{a1}	0 ^{a1}	0 ^{a1}	0 ^{a1}	
Total aboveground plant biomass					
NB	551.9 ± 64.2 ^{a1}	454.2 ± 50.8 ^{a1}	469.0 ± 27.5 ^{a1}	491.7 ± 34.6 ^{a1}	
B	335.2 ± 48.2 ^{b1}	530.9 ± 56.8 ^{a1}	336.8 ± 34.0 ^{b1}	401.0 ± 65.0 ^{a1}	
P	172.5 ± 21.6 ^{a1}	137.9 ± 18.3 ^{a1}	190.3 ± 15.8 ^{a1}	166.9 ± 15.4 ^{b1}	
NN	136.1 ± 34.8 ^{a1}	91.9 ± 21.6 ^{a1}	171.9 ± 25.6 ^{a1}	133.3 ± 23.1 ^{b1}	
PB	130.4 ± 22.0 ^{a1}	209.0 ± 29.8 ^{a1}	130.0 ± 21.2 ^{a1}	156.5 ± 26.2 ^{b1}	

NOTE: Different letters within each functional group denote significant differences among sites for each treatment ($P < 0.05$). Different letters within each functional group in the last column denote significant differences among treatments ($P < 0.05$).

**UNGULATE-PRAIRIE DOG-PLANT INTERACTIONS
IN BADLANDS NATIONAL PARK**

**First Annual Report on
Cooperative Agreement: 1445-0009-94-1074 Subagreement #1
(USDI-National Biological Survey)**

and

**Cooperative Agreement: CA1268-2-9004 BADL-R94-0443
(DOI-NPS-National Park Service)**

Time period covered: September 1994 - September 1995

Submitted by

Jace T. Fahnestock

for James K. Detling

Department of Biology

Colorado State University

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Total succulents

NB	0 ^a	0 ^a	0 ^a	0 ^a
B	18.2 ± 18.1 ^a	0 ^a	65.4 ± 65.2 ^a	27.9 ± 19.4 ^a
P	0 ^a	0 ^a	0 ^a	0 ^a
NN	0 ^a	0 ^a	0 ^a	0 ^a
PB	0 ^a	0 ^a	0 ^a	0 ^a

Total aboveground
plant biomass

NB	479.2 ± 61.8 ^a	491.9 ± 43.8 ^a	469.3 ± 48.6 ^a	480.1 ± 6.5 ^a
B	425.7 ± 56.5 ^a	505.5 ± 53.8 ^a	479.8 ± 91.5 ^a	470.3 ± 23.5 ^a
P	199.9 ± 15.4 ^{ab}	312.2 ± 36.0 ^a	184.0 ± 24.2 ^b	232.0 ± 40.3 ^b
NN	153.4 ± 11.6 ^a	179.6 ± 18.2 ^a	243.8 ± 31.2 ^a	192.3 ± 26.9 ^b
PB	208.4 ± 14.0 ^a	276.1 ± 42.6 ^a	213.3 ± 28.6 ^a	232.6 ± 21.8 ^b

NOTE: Different letters within each functional group denote significant differences among sites for each treatment ($P < 0.05$). Different letters within each functional group in the last column denote significant differences among treatments ($P < 0.05$).