

Carbon and nitrogen dynamics in elk winter ranges

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Abstract

Recent increases in elk (*Cervus elaphus* L.) herbivory and changes in hydrology towards drier conditions have contributed to declines in willow (*Salix* spp. L.) communities in the winter ranges for elk in Rocky Mountain National Park. In 1994, we constructed 12 large elk exclosures in 2 watersheds of the winter range for elk in the park, and conducted field experiments from 1995 to 1999 to investigate the effects of herbivory and proximity to surface water on the dynamics of C and N. Litterfall biomass averaged 65.6 and 33.0 g m⁻² inside and outside the exclosures, respectively. Elk herbivory increased (P < 0.05) N concentration of willow litter from 1.25 to 1.49%, but there were no differences in losses of C and N from litterbags placed in grazed and ungrazed plots in any of the growing seasons. Carbon losses from litterbags were higher in lower landscape positions (P = 0.001), in comparison to upper landscape positions. Shoot biomass of willow plants fertilized with N averaged 27.3 g and was higher (P < 0.05) than that of unfertilized plants, which averaged 20.2 g, indicating that N availability limits plant growth in our study sites. Elk herbivory had no effect on soil inorganic N availability, even though we estimated that the return of N to the soil in grazed plots could be as much as 265% of the N return in exclosed plots. In the long-term, greater return of N to the soil combined with increased litter quality in the grazed plots could contribute to increases in N cycling rates and availability, and these changes could affect ecosystem structure and function in the winter range for elk in Rocky Mountain National Park.

Key Words: Willow, *Salix*, *Carex*, litterfall, litter decomposition, nitrogen availability.

Since 1968, elk (*Cervus elaphus* L.) numbers in Rocky Mountain National Park, Color. have been managed under a policy of natural regulation, which rests on the assumption that density-dependent mechanisms would result in an equilibrium between large ungulate herbivores and plant resources. During this period, elk numbers have increased from approximately 1,000 to about

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Resumen

El reciente incremento en la herbivoría del alce (*Cervus elaphus* L.) y los cambios en la hidrología hacia condiciones más secas han contribuido a la disminución de las comunidades de "Willow" (*Salix* spp. L.) en los pastizales de invierno para alces del Parque Nacional de las Montañas Rocallosas. En 1994 construimos 12 grandes exclusiones contra alce en 2 cuencas hidrológicas de pastizales de invierno para alce del parque y de 1995 a 1999 condujimos experimentos de campo para investigar los efectos de la herbivoría y proximidad de la superficie de agua en las dinámicas de C y N. La biomasa de mantillo promedió 65.6 y 33.0 g m⁻² dentro y fuera de las exclusiones respectivamente. La herbivoría del alce aumentó (P < 0.05) la concentración de N del mantillo de "Willow" de 1.25 a 1.49%, pero no hubo diferencias en las pérdidas de C y N de bolsas con mantillo colocadas en parcelas con y sin pastoreo en ninguna de las estaciones de crecimiento. Las pérdidas de carbón de las bolsas con mantillo fueron mayores en las posiciones de terrenos bajos (P = 0.001), en comparación con las posiciones de terrenos altos. La biomasa de tallos de plantas de "Willow" fertilizadas con N promedió 27.3 g y fue mayor (P < 0.05) que la de las plantas sin fertilizar, la cual promedió 20.2 g, indicando que la disponibilidad de N limita el crecimiento de las plantas en nuestros sitios de estudio. La herbivoría del alce no tuvo efecto en la disponibilidad del N inorgánico del suelo, a pesar de que estimamos que el retorno de N al suelo en las parcelas con pastoreo pudiera ser tanto como el 265% del N retornado en las parcelas excluidas. A largo plazo, el mayor retorno de N al suelo, combinado con un aumento en la calidad del mantillo de las parcelas con pastoreo contribuir a incrementar las tasas de reciclaje de N y su disponibilidad, y estos cambios podrían afectar la estructura y función del ecosistema en los pastizales de invierno para alce del parque Nacional de la Montañas Rocallosas.

3,300 animals, and park managers are concerned about the effects of these increases on the soils and vegetation of the elk winter range within the park (Singer et al. 1998b).

Willow (*Salix* spp. L.) communities have reportedly been declining in elk winter ranges of the park during the last few decades (Hess 1993, Singer et al. 1998b), and several studies are currently being conducted to investigate the extent of these changes (R. Peinetti, pers. comm., 1999). Similarly, declines in willow populations have also been reported for Yellowstone National Park (Chadde and Kay 1991, Kay and Wagner 1994, Singer et al. 1998a). In addition to increased elk herbivory, 2 other factors have been proposed to explain these apparent

declines in willow communities of Rocky Mountain National Park: (1) climates are warmer and drier this century, possibly resulting in lowered stream flows and less water availability to plants (Singer et al. 1998b); and (2) beaver populations have declined on the eastern slope of the park (Stevens and Christianson 1980), which may further contribute towards the drying of these ecosystems.

Large herbivores can significantly influence plant community structure and biogeochemical cycles within the soil-plant system (Frank et al. 1994, Frank and Groffman 1998, Hamilton et al. 1998, Schuman et al. 1999, Wijnen et al. 1999). Herbivores can influence nutrient cycling by removing plant biomass and returning more readily available nutrients to the soil (McNaughton et al. 1988, Frank et al. 1994, Hamilton et al. 1998), increasing soil N mineralization rates and plant N uptake (Frank and Groffman 1998, Wijnen et al. 1999), spatially redistributing nutrients within the landscape (McNaughton 1985, Afzal and Adams 1992, Russelle 1992), or decreasing the amount of litter-fall and nutrient return to the soil in litter (Pastor et al. 1993).

Beaver (*Castor canadensis* Kuhl) can also influence plant communities and biogeochemical cycles of ecosystems. By building dams, beavers contribute to the entrapment of sediment and organic matter and modify water availability, nutrient cycling, and the dynamics of organic matter decomposition (Naiman et al. 1986, Naiman and Melillo 1984). It has been suggested that the observed declines in beaver populations in the eastern slope of Rocky Mountain National Park have contributed to a decrease in the surface area of water (ponds and streams) within the winter range of elk since the beginning of this century, therefore decreasing water availability for willows. These reductions in water availability could further reduce the ability of willow to respond to elk herbivory (Singer et al. 1998b) and could also alter the biogeochemical cycles of those ecosystems. However, the extent of the influences of these changes over the elk winter ranges of the park is unknown.

Plant-available N is usually a limiting element for plant growth in terrestrial ecosystems (Power 1977, Kiehl et al. 1997, Wijnen et al. 1999) and the cycling of N in these systems is linked to the C cycle by interactions between decomposers, plants, and herbivores (Aber and Melillo 1991, Pastor and Naiman 1992). There is no available information about the effects of elk herbivory or the reduction in

surface water on the dynamics of C and N in the winter ranges of elk in Rocky Mountain National Park. This information is necessary for helping park managers formulate policies that will maintain herbivore populations at levels that are adequate for preserving the natural functioning of these ecosystems. Therefore, the objective of this study was to perform experimental field manipulations to investigate the effects of elk herbivory and proximity to surface water on the C and N cycles in the winter ranges of elk in the park.

Methods

Study Sites

The winter range for elk in Rocky Mountain National Park encompasses about 10,000 ha, which includes land within the eastern side of the park and private and national forest lands outside the park in the town of Estes Park and Estes Valley, Colo. (Singer et al. 1998b). Our study sites were located in 2 riparian ecosystems on the northeastern side of Rocky Mountain National Park: 1) Moraine Park, along the Big Thompson River watershed, at an elevation of 2,481 m and 2) Horseshoe Park, along the Fall River watershed, at an elevation of 2,598 m. The latitude and longitude of the area of the watersheds are 105° 36' N and 40° 22' W. The 2 watersheds are within 5 km of each other and have perennial alpine snowfields at their headwaters. Mean annual precipitation for the sites is 41 cm (Singer et al. 1998b) and peak stream flow usually occurs in early to mid-June (USDA 1995, 1996, 1997). The 30-year average temperature for the adjacent Estes Valley ranges from 9 to 17°C during the 5-month growing season of May through September (Alstad et al. 1999). The study area consists of wet meadows dominated by willow (mainly *Salix monticola* L., *S. geyeriana* Anderss., and *S. planifolia* Pursh), other shrubs such as birch (*Betula* spp. L.), sedges (*Carex* spp. L.), rushes (*Juncus balticus* Willd.), and grasses (*Phleum* spp. L., *Calamagrostis* spp. Adans., *Bromus* spp. L., *Poa* spp. L.). The elk population of Estes Valley numbers about 3,300 animals, of which about one third generally spends the winter within the park (Larkins 1997, Singer et al. 1998b).

Experimental Treatments

In the wet meadows of both parks, 12 exclosures (30 m x 46 m each) were erected within willow communities along the rivers between August and November of 1994. Next to each exclosure, 30 m x 46 m

plots were chosen and marked off as paired plots open to grazing (grazed plots). The area within each exclosure was subdivided into 15 m x 23 m sub-plots and 2 treatments were imposed throughout the period of the study: (1) 75% current annual growth removal (clipped plots), and (2) no clipping at all (ungrazed plots). The 75% current annual growth removal treatment was applied between January and April of 1995, 1996, 1997, and 1998, and consisted of clipping all forage shrubs and herbaceous plants in each sub-plot. All clipped plant biomass was removed from the exclosures. Therefore, each site consisted of: (1) grazed plot (outside the exclosure); (2) ungrazed plot; and (3) clipped plot (both inside the exclosure).

Eight sites (4 in Moraine Park and 4 in Horseshoe Park) were placed in areas with little or no beaver activity, and contained heavily browsed willow plants, which had their height suppressed by elk browsing (short willow). The other 4 sites (2 in each park) were located in nearby (about 1 to 2 km) wetter areas, generally containing taller willow plants subjected to less browsing by elk (tall willow). The difference between the willow plants in the 2 areas (tall willow and short willow) was strictly morphological since the willow species composition of the communities in the 2 areas was the same. In half of the short willow sites (2 in each park), hydro-manipulation treatments were imposed by placing sheet metal check dams on ephemeral stream channels both inside the exclosures and in the grazed plots. We expected these check dams to catch snowmelt and rain runoff through the spring and raise the water table at the sites. Twenty-five dams were installed in April and May 1995 and were relatively successful in holding additional water at these sites. The dams were intended to add water, but in no way was the treatment able to simulate water additions in the amounts accomplished by beaver dams on larger, permanent streams (Singer et al. 1997). In each exclosure and associated grazed plot, an average of 5 shallow (0.5 to 2 m) wells were installed in the spring of 1995 for the purpose of monitoring groundwater levels. During early 1996 and 1997, 3 beaver dams were constructed near 2 sites within the wetter area of Moraine Park, but these dams were washed out during the spring flood of 1996 and 1997.

Litterfall

Litter was collected in each experimental plot during the fall of 1995, 1996, and

1997, through the use of 15 greenhouse trays (totaling ~ 2.3 m²) arranged in a 5 x 3 regularly spaced grid (9.1 m x 15.9 m). The grids were established randomly within each sub-plot before willow senescence began, and each tray was anchored to the ground using 2 or more large spikes. Litter was collected weekly from early September to late October until litterfall was complete. The litter was then composited within each experimental replication, sorted by genus and litter type, air dried, and weighed. Oven-dry corrections were applied within each category by drying a subsample at 60°C. Litterfall biomass was calculated as oven dry mass per unit area. Total N and C content of litter was determined using a LECO CHN-1000 analyzer.

Litter Decomposition

During September and October of 1994, before the establishment of the exclosures, we collected litter material throughout the study area to generate a standard litter that was used in the decomposition experiments. Willow leaf litter was obtained by locating greenhouse trays directly under willow canopies throughout the study area (dominated by *S. monticola*, *S. geyeriana*, and *S. planifolia*) and collecting the leaves periodically. *Carex* litter was collected by clipping and collecting standing dead biomass. We dried all litter in a 35°C forced air oven, and subsamples (2 g) from the 2 standard litter types (willow leaves and *Carex* tissue) were enclosed in 1 mm nylon mesh bags. These bags containing the standard litter were used in litter decomposition experiments to investigate the effects of herbivory, landscape position, and plant cover on the decomposition rates of willow and *Carex* litter during the growing seasons of 1995, 1996, and 1997. During the growing season of 1995, we investigated the effect of herbivory on litter decomposition by randomly placing 4 bags of each litter type (willow leaves and *Carex* tissue) in the ungrazed plots within the exclosures and in the grazed plots outside the exclosures (no bags were placed in the clipped plots) for all of the 12 sites. The results from the 4 bags of each litter type within each treatment replicate were combined to reduce microsite variability within each of the 12 treatment replicates. In 1996 and 1997, we investigated the effect of herbivory, landscape position, and plant cover on litter decomposition. For this, we selected, in each of the ungrazed and grazed plots within the 12 sites, 2 willow shrubs located at 2 different landscape positions: (1) lower landscape positions, next to a stream or a pond, and (2) upper landscape positions, at

least 10 m away from a stream or a pond and 0.5 m higher in the landscape than lower landscape positions. Bags of both willow and *Carex* litter were placed under the canopies of the selected shrubs ('willow canopies') and in open grass areas ('*Carex* plots') located within 2 m of the shrubs. Two bags of each litter type were placed within each treatment replicate and their results pooled in order to reduce microsite variability.

In all experiments, the litterbags were placed on the soil surface and left in the field during the entire length of the growing season (from late May until mid-September). At the end of the season, they were collected, air-dried, weighed, ground to a fine powder to pass a 40 mesh sieve, and stored until analysis. Carbon and N in the decomposed litter were analyzed using a LECO CHN-1000 analyzer, and C and N losses were calculated in an ash-free dry weight basis by subtracting the amounts in the post-decomposition from the pre-decomposition litter.

Elk Dung Quantification

We estimated the amount of C and N returned to the soil in elk dung by counting the number of scat piles along 30 m transects within our experimental grazed plots, and measuring the concentrations of C and N in the dung. The survey was conducted after the elk herds left the winter range for the summer range during late spring 1997. We selected 8 grazed plots (4 in each park) and established 4 randomly placed transects per plot. In each transect, we measured the distance from the scat piles to the transect, and calculated the density of piles per area. Only scat piles that were visually identified as from the previous fall and winter were counted. To estimate dry matter and C and N content in each dung pile we obtained 51 samples (26 from Horseshoe Park and 25 from Moraine Park) by collecting all dung from fresh piles during late Fall of 1997. After collection, the samples were oven-dried at 50°C, weighed, ground to a fine powder, and sub-sampled for determination of moisture (oven-dried at 105°C) and ash content (500 °C). The concentrations of C and N in the dung were determined using a LECO CHN-1000 analyzer and expressed on an ash-free dry weight basis.

Soil Characteristics and N Availability

Soil samples (0–15 cm) were collected in July 1997 from the grazed, ungrazed, and clipped plots. Within each treatment replication, a total of 25 to 30 cores were randomly collected with a soil core sampler 2 cm in

diameter and combined in a paper bag. After collection, the samples were taken to the laboratory, air-dried, and passed through a 2 mm sieve. Soil particle distribution was measured in each sample using the hydrometer method (Gee and Bauder 1986). Sub-samples (10 g) of each sample were ground to a fine powder with a ball mill. The sand fraction (> 53 µm) of each sample was ground to a fine powder with a ball mill, for determination of particulate organic matter (POM) C and N (Cambardella and Elliott 1992). Total C and N in the total soil and sand fraction were determined with a LECO CHN-1000 analyzer.

In addition, during the summer of 1996 we collected soil samples (0 to 20 cm) under willow trees and in associated open grass areas next (within 2 m) to the trees. A total of 33 pairs of samples (shrub canopy plus open grass) were taken from the 12 ungrazed plots within the exclosures of Moraine Park and Horseshoe Park. The samples were air-dried and sieved through a 2 mm screen. Sub-samples (10 g) of each sample were ground to a fine powder with a ball mill, and total soil C and N were determined using a LECO CHN-1000 analyzer.

Soil moisture (0 to 14 cm) measurements were performed weekly in 8 sites in Moraine Park and Horseshoe Park (4 in each watershed) by Time Domain Reflectometry (TDR) (Ledieu et al. 1986) with a Trase System model 6050x1 during the growing season of 1997. The TDR rods were vertically placed in each measurement position and left there for the whole season. Within each site and grazing treatment, soil moisture was measured under willow canopies and in associated *Carex* plots next to the willow shrubs in both upper and lower landscape positions. Within 3 ungrazed plots in each park, soil temperature was measured using HOBO® temperature data loggers during the growing season of 1997. The loggers were wrapped with a thin plastic film to avoid damage by soil moisture, and were buried in a vertical position from 1 to 6 cm of depth. In each of the sites, we performed comparisons of soil temperature between (1) willow canopies and *Carex* plots and (2) streamside and upper landscape positions. The temperature measurements were performed every 15 minutes for periods of 7 to 14 days.

In 1995, 1996, and 1998 in situ soil N availability in the experimental plots was assessed using ion-exchange resin bags. Paired cation and anion resin bags made from nylon stockings and containing about 15 cm³ of exchange resins were placed 5

cm beneath the soil surface (Binkley 1984). In 1995 and 1996, fifteen pairs of resin bags were placed in a regularly spaced grid (9.1 x 15.9 m) within each treatment (grazed, ungrazed, clipped) in the 12 sites. To analyze the temporal variability of N availability, 2 sets of bags were placed in each of the 3 treatments during each of the growing seasons of 1995 and 1996. The first set was left in place from mid-June to mid-July, and the second set from mid-July to mid-August. A different experimental procedure was utilized in 1998, in which 6 pairs of resin bags were randomly placed within each of the 12 ungrazed and grazed plots (no bags were placed in the clipped plots), and left in the field from May to October. For all 3 years, after removal of the bags, the N adsorbed in the resins was extracted with 50 ml of 2 M KCl, and the extracts were frozen until analysis for NO₃⁻-N and NH₄⁺-N on an Alpkem automated spectrometer.

In 1997 and 1998, in situ measurements of net N mineralization were performed by conducting field soil incubations as described in Kolberg et al. (1997) using aluminum cores 15 cm long and 5 cm in diameter. During the 1997 growing season, cores were placed in upper and lower landscape positions within the 12 ungrazed and grazed plots of the 2 watersheds. Within each landscape position and grazing treatment, cores were placed under willow shrubs and in associated *Carex* patches within 2 m of the willow plants. Four cores were placed inside each treatment replicate to reduce micro-site variability. Cation and anion resin bags were placed in the bottom of each core to capture the inorganic N leached from the core. During the 1998 growing season, 6 open-top field soil incubation cores were placed within the ungrazed and grazed plots in 3 different 6-week incubation periods (June to July, July to August, and August to October). Net soil N mineralized during the incubation periods was calculated by subtracting the initial amount of inorganic N in the soil from the final amount of inorganic N after the incubations, and the results were expressed in g N m⁻².

Nitrogen Fertilization

In each ungrazed and grazed plot in the 12 sites, we placed 2 paired circular subplots (each with 2 m radius) around willow plants at the end of the growing season of 1998. Within each pair of circular subplots, we applied 2 fertilization treatments: (1) no fertilization, and (2) 10 g N m⁻² as ammonium nitrate. During late July 1999, before the elk returned from the summer range at

Table 1. Litterfall biomass in ungrazed, clipped, and grazed plots of Moraine Park and Horseshoe Park during 1995, 1996, and 1997. Values represent means (n = 12) with standard errors in parentheses. Means within the same group followed by different letters are significantly different at P < 0.05.

Treatment	Willow (<i>Salix</i> spp.) leaves	Other shrub leaves ¹	Herbs ²	Wood	Unidentified material	All litter
----- (g m ⁻²) -----						
1995						
Ungrazed	32.9 (9.8) a	5.9 (2.7) ab	10.1 (2.4)	3.0 (1.0)	0.6 (0.2)	52.5 (10.2) a
Clipped	34.1 (8.5) a	13.2 (6.3) a	8.0 (1.0)	4.4 (1.4)	0.3 (0.1)	60.0 (8.9) a
Grazed	19.1 (7.1) b	1.7 (0.6) b	6.4 (0.9)	3.1 (1.4)	0.5 (0.2)	30.9 (8.5) b
1996						
Ungrazed	55.0 (13.6) a	9.1 (3.9) ab	3.1 (0.6)	3.1 (1.1)	1.4 (0.4)	71.6 (12.6) a
Clipped	47.1 (10.6) ab	18.3 (8.6) a	2.6 (0.5)	1.6 (0.4)	0.8 (0.2)	70.2 (9.7) a
Grazed	26.6 (8.1) b	3.7 (0.8) b	3.4 (0.5)	5.1 (2.2)	0.7 (0.3)	39.4 (9.1) b
1997						
Ungrazed	45.3 (12.3) a	8.7 (4.0) ab	14.3 (3.3)	3.1 (1.0)	-	71.5 (11.1) a
Clipped	41.6 (10.4) a	15.5 (6.3) a	7.2 (0.7)	2.2 (0.7)	-	66.4 (10.1) a
Grazed	15.9 (6.0) b	3.0 (0.9) b	7.5 (1.0)	2.4 (1.1)	-	28.8 (7.1) b

¹Mostly birch (*Betula* spp.) leaves.

²Litter material from forbs and *Carex* spp. combined.

higher elevations, willow shoots (current year growth) were collected from the plants inside the subplots, dried at 60°C, weighed, and ground to a fine powder to pass a 40 mesh sieve. Concentrations of C and N in shoots were determined using a LECO CHN-1000 analyzer.

Statistical Analyses

Statistical analyses were performed using the SAS Statistical Package (SAS, Version 6.12, SAS Institute Inc., Cary, N.C., 1995). The data on litterfall, litter nutrient content, litter decomposition, soil characteristics, N availability, and N fertilization were analyzed using a split-plot factorial design where watershed was considered a random effect. Watersheds and height of willow plants were not significantly different (P < 0.05) for any of the variables analyzed, therefore the data values from tall and short willow sites in both Moraine Park and Horseshoe Park were pooled (12 replications) in the analyses to determine the effect of browsing on litterfall and N availability, and the effects of browsing, proximity to surface water, and canopy position on litter decomposition. The data on soil nutrient content between willow canopies and open grass areas was analyzed using paired t-tests.

Results and Discussion

Litterfall

Litterfall biomass in the ungrazed and clipped plots was greater than in the grazed plots for the 3 growing seasons (Table 1). Across all growing seasons, litterfall biomass averaged 65.6 and 33.0 g

m⁻² inside and outside the enclosures, respectively. On average, willow leaves accounted for 58% of the litterfall biomass followed by herbs (20%), other shrub leaves (16%), wood (5%), and unidentified material (1%). However, the use of trays for collecting litterfall may underestimate the amount of grass litterfall, since a significant portion of the senescent tillers still remain attached to the plant and were not collected and counted as litter. Willow leaf litterfall in the ungrazed and clipped plots was greater than in the grazed plots during the 1995 and 1997 seasons, but in 1996 there were no significant differences between clipped and grazed plots (Table 1). Leaf litter from other shrubs, mostly birch (*Betula* spp.), was significantly lower in the grazed plots when compared to the clipping treatment inside the enclosures, but there were no differences between grazed and ungrazed plots. No treatment differences were observed for the amounts of herb or wood litter during the three growing seasons.

Inside the enclosures, even the removal of 75% of current annual growth in the clipped plots did not result in significant differences between the ungrazed and clipped plots during the growing seasons. We suggest this lack of difference between clipped and ungrazed plots occurred in part because the artificial clipping of willow did not satisfactorily simulate elk browsing. Other studies have demonstrated the limitations of clipping experiments to reflect accurately the natural patterns of herbivory (Paige 1999). Visual observations in our field plots suggested that clipped plants inside the enclosures were morphologically similar to the

Table 2. Nitrogen content and carbon to nitrogen ratio of different litter types in ungrazed, clipped, and grazed plots of Moraine Park and Horseshoe Park in 1997. Values represent means (n = 12) with standard errors in parentheses. Means within the same group followed by different letters are significantly different at P < 0.05.

Treatment	Willow (<i>Salix</i> spp.) leaves	Other shrub leaves ¹	Carex	Forbs
Nitrogen (%)				
Ungrazed	1.25 (0.10) b	1.23 (0.15)	1.40 (0.11)	1.79 (0.13)
Clipped	1.27 (0.09) b	1.11 (0.13)	1.22 (0.08)	1.71 (0.15)
Grazed	1.49 (0.08) a	1.09 (0.11)	1.23 (0.09)	1.82 (0.12)
Carbon to nitrogen ratio				
Ungrazed	45.8 (3.2) a	48.5 (12.0)	37.2 (2.9)	31.0 (3.0)
Clipped	43.0 (4.2) a	53.4 (11.6)	42.1 (2.8)	32.6 (2.9)
Grazed	37.7 (3.1) b	49.9 (14.3)	43.5 (3.1)	31.4 (2.6)

plants in the ungrazed treatment, regarding height and canopy structure, while the grazed plants were apparently more suppressed and shorter than the plants in the 2 treatments inside the exclosures. These patterns probably result from the additional damage to willow leaders caused by elk when stripping off leaves from the plants, as compared to artificial clipping. On average, elk may browse on more than 70% of the leaders in each plant in our study sites, and may remove nearly 40% of the length of each leader (Singer et al. 1998b). Additional field observations from our experiments demonstrate that an average of 20% of the length of browsed willow leaders may die after elk browsing due to bark damage, while only 2% of the length of the leader may die in the case of artificially clipped plants (R. Peinetti, pers. comm., 1999). We suggest that the differences in litterfall observed between grazed and clipped treatments in our study may result from: (1) greater leader damage during elk browsing, in comparison to artificial clipping, and/or (2) greater increases in plant height in clipped plants, in comparison to grazed plants, due to differences in the patterns of tissue removal during elk browsing or artificial clipping, which may influence canopy architecture.

Willow leaf litter in the ungrazed and clipped plots had lower N content and higher C to N ratio than willow leaf litter in the grazed plots, but no significant treatment differences were found in litter from other shrubs, *Carex*, or forbs (Table 2). Similar to our findings, Alstad et al. (1999) reported that early season willow tissue N concentration in plants under elk herbivory in our sites was significantly higher than in plants protected from herbivory. Often, grazing leads to increases in plant tissue N (McNaughton 1985, Holland and Dettling 1990, Coughenour 1991, Hamilton et al. 1998) due to faster nutrient cycling and uptake by plants or a reduction in tissue biomass for allocation of N. Higher N concentration and lower C

to N ratios in litter may lead to faster litter decomposition and greater nutrient availability (Ritchie et al. 1998, Irons et al. 1991). In our study site, the effects of elk herbivory on willow litter N concentration could lead to increases in the rate of litter decomposition and nutrient cycling, which could lead to changes in species composition and ecosystem functioning (Aber and Melillo 1991, Holland et al. 1992, Ritchie et al. 1998, Stohlgren et al. 1999).

Litter Decomposition

Losses of C and N from willow and *Carex* litter bags was not affected by grazing treatments in any of our experiments. However, in the 3 growing seasons, C losses from willow litter bags were higher than from *Carex* litter bags and, interestingly, N losses from willow litter were lower than from *Carex* litter (Table 3).

In 1996, C losses from litter bags were higher in streamside positions than in upper landscape positions, but no significant differences were observed for N losses during 1996 or C and N losses during 1997 (Table 4). Soil moisture is usually an

Table 3. Carbon and nitrogen losses from willow (*Salix* spp.) and *Carex* leaf litter bags in Moraine Park and Horseshoe Park during the growing seasons of 1995, 1996, and 1997. Values represent means (n = 12) with standard errors in parentheses.

Litter type	C loss (%)	N loss (%)
1995		
Willow	30.2 (2.7)	6.3 (2.0)
Carex	22.9 (2.6)	10.3 (2.1)
P-value	N.S. 1	0.026
1996		
Willow	29.0 (1.9)	3.4 (5.1)
Carex	22.9 (2.4)	15.2 (4.7)
P-value	0.046	0.005
1997		
Willow	22.1 (1.4)	2.7 (2.4)
Carex	16.4 (1.8)	16.7 (4.3)
P-value	0.013	0.005

¹Not significantly different at P < 0.05.

important factor contributing to decomposition and, in general, litter decomposition increases with increasing soil moisture in semi-arid ecosystems (Schlesinger 1997). Higher C losses observed in streamside positions in our study are likely due to high-

Table 4. Carbon and nitrogen losses from litter bags placed in upper and lower landscape positions of Moraine Park and Horseshoe Park during the growing seasons of 1996 and 1997. Values represent means (n = 12) with standard errors in parentheses.

Landscape position	C loss (%)	N loss (%)
1996		
Streamside	31.7 (2.3)	5.7 (6.1)
Upper landscape	20.3 (1.9)	12.8 (6.0)
P-value	0.001	N.S. ¹
1997		
Streamside	18.1 (1.9)	6.5 (4.2)
Upper landscape	20.4 (1.3)	12.9 (2.7)
P-value	N.S.	N.S.

¹Not significantly different at P < 0.05.

er soil water availability (Fig. 1), suggesting that eventual reductions in surface water may lead to reductions in litter decomposition rates in our sites. However, no significant differences in willow or *Carex* litter decomposition were observed between streamside and upper landscape positions around the 2 beaver ponds in 1996. Average C and N losses from litter bags of the 2 litter types placed in streamside and upper landscape positions around the ponds were 36.4 and 2.9%, respectively.

Litter bags placed under willow canopies lost significantly more C and N than bags placed in *Carex* plots (Table 5), even though soil moisture levels were slightly lower under willow canopies, compared to *Carex* plots, especially in Horseshoe park (Fig. 1). Average maxi-

Table 5. Carbon and nitrogen losses from litter bags placed under willow (*Salix* spp.) canopies and in *Carex* spp. plots in Moraine Park and Horseshoe Park during the growing seasons of 1996 and 1997. Values represent means (n = 8) with standard errors in parentheses.

Position	C loss (%)	N loss (%)
1996		
Willow canopies	35.7 (1.7)	24.2 (1.8)
Carex plots	7.7 (2.9)	-1.6 (2.4)
P-value	0.001	0.022
1997		
Willow canopies	23.1 (1.5)	15.5 (1.7)
Carex plots	16.0 (3.5)	3.4 (3.5)
P-value	0.001	0.012

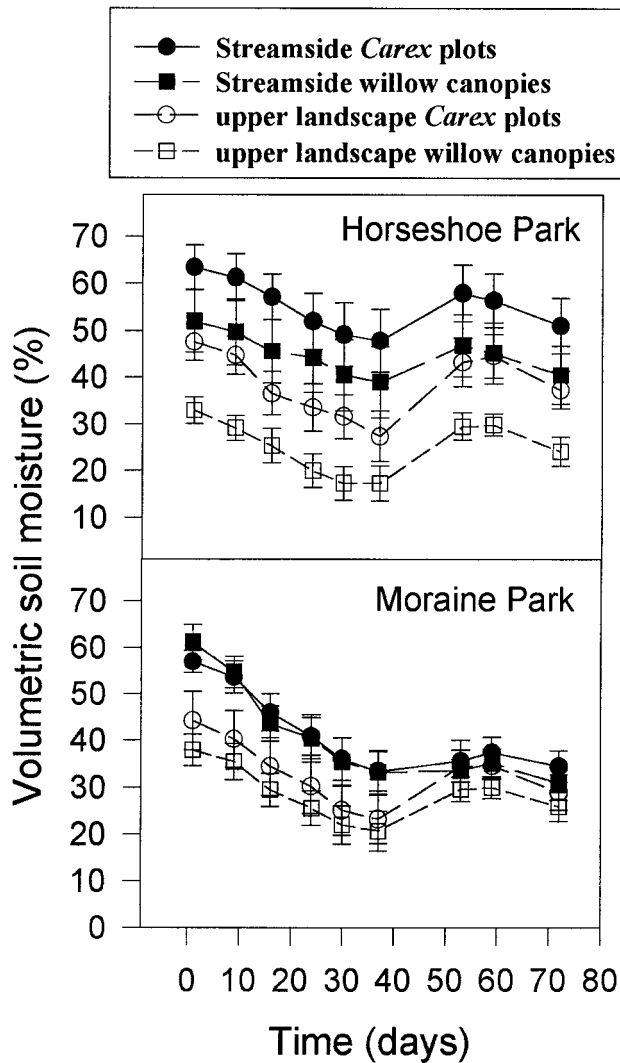


Fig. 1. Soil moisture (0 to 14 cm) under willow canopies and in *Carex* plots in upper and lower landscape positions of Horseshoe Park and Moraine Park from early June to late August of 1997. Error bars represent standard errors of the means (n = 8).

mum soil temperatures from 1 to 6 cm in depth during the 1997 growing season were significantly lower under willow canopies than in *Carex* plots in both Moraine and Horseshoe parks (Fig. 2). These results indicate that the presence of willow shrubs has a significant influence on microclimatic conditions in our sites,

contributing to reductions in soil temperature and soil moisture. We suggest that the rate of nutrient loss from litter bags was higher under willow canopies because: (1) shading by willow canopies may decrease soil temperature and help preserve moisture at the top few centimeters of the litter layer and soil, and this may enhance litter

decomposition and/or (2) *Carex* plants may have held litter bags off the soil, which may have let them dry out more and decompose less than bags placed under willow canopies.

Return of N to the Soil

Based on the biomass and N content of aboveground litter in our sites (Tables 2 and 3), we calculated that the N return to the soil in aboveground litter during the 1997 growing season was greater in the ungrazed and clipped plots (0.83 and 0.82 g N m⁻², respectively) than in the grazed plots (0.42 g N m⁻²), excluding the contribution of N in wood litter in all treatments. Litter from willow, other shrubs, and herbs contributed to 62, 17, and 21% of the N returned to the soil in litter inside the exclosures, and 51, 16, and 33 % of the N returned to the soil in litter within the grazed plots, respectively. Elk dung biomass deposited on the soil during the 1997-98 season averaged 42.2 ± 6.2 g m⁻² across all sites. This value is similar to those reported by Frank and McNaughton (1992), who found that average herbivore dung deposition during the 5 month season in the winter range of Yellowstone National Park was 76.9 ± 30.1 g m⁻². In our sites, average elk dung N concentration in the samples collected in late fall of 1997 was 2.0 %. Based on our results, we estimated that approximately 0.87 ± 0.12 g N m⁻² returned to the soil in elk dung during the 1997-98 winter season in our study site. Therefore, the amount of N returned to the soil as elk dung plus aboveground plant litter averaged 1.3 g m⁻² in the grazed plots. The estimated amount of N returned to the soil in elk urine in our sites, based on the diet and specific characteristics of the herd, could be approximately 98% of the N returned to the soil in dung (K. Schoenecker, pers. comm., 1999). Based on these estimates, after including the potential N inputs from urine, the total amount of N returned to the soil in the grazed plots could be as high as 2.2 g N m⁻², which corresponds to 265%

Table 6. Soil characteristics (0-15 cm) of ungrazed, clipped, and grazed plots of Moraine Park and Horseshoe Park in July 1997. Values represent means (n = 12) with standard errors within parentheses.

Treatment	Total C	Total N	POM ¹ C	POM N	Sand	Silt	Clay	pH ²
----- (g kg soil ⁻¹) -----								
Ungrazed	50.3 (9.0)	3.38 (0.63)	15.9 (3.5)	0.81 (0.19)	523 (59)	209 (40)	152 (19)	4.64 (0.10)
Clipped	47.7 (7.1)	3.27 (0.54)	13.3 (2.0)	0.63 (0.09)	494 (55)	235 (47)	161 (25)	4.67 (0.12)
Grazed	42.7 (6.2)	2.82 (0.44)	11.3 (2.0)	0.53 (0.12)	549 (37)	234 (29)	118 (19)	4.60 (0.11)

¹Particulate Organic Matter

²Measured in water (2:1, water:soil)

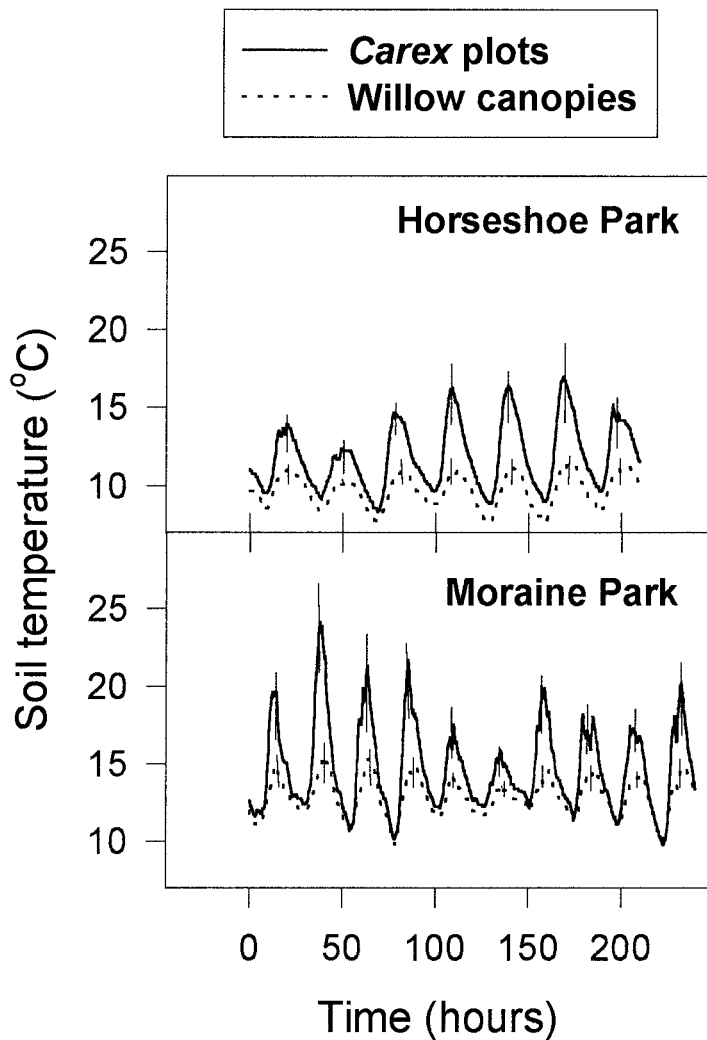


Fig. 2. Soil temperature (1 to 6 cm) under willow canopies and in *Carex* plots in Horseshoe Park and Moraine Park during July 1997. Vertical lines represent the range of the 95% confidence interval for the means of maximum temperatures ($n = 3$).

of the N returned as aboveground litter in the excluded plots. Our results are consistent with the findings of Frank and McNaughton (1992), who found that elk and bison populations in Yellowstone National Park excreted 0.81 to 4.60 g N m⁻² year⁻¹, an amount that corresponded to roughly 4 times the amount of N returned in litterfall in their study site.

Soil Characteristics and N Availability

There were no significant differences in total soil C and N, POM C and N, soil texture, and soil pH between grazing treatments in our sites 4 years after the establishment of the exclosures (Table 6). Similar to our findings, Frank and Groffman (1998) found no differences in soil total C and N between grazed plots and excluded plots that had been protected from herbivory for 33 to 37 years in

Yellowstone National Park. In addition, we found no differences in total soil C and

Table 7. Inorganic nitrogen adsorbed to ion exchange resin bags during different incubation periods during 1995 and 1996, and from 1 incubation period during 1998. Values represent means ($n = 12$) with standard errors within parentheses.

Incubation period	NO ₃ ⁻ -N	NH ₄ ⁺ -N	NO ₃ ⁻ -N + NH ₄ ⁺ -N
	----- (mg bag ⁻¹) -----		
1995			
June to July	1.08 (0.23)	4.45 (0.63)	5.53 (1.45)
July to August	0.64 (0.32)	2.12 (0.44)	2.78 (1.29)
P-value	0.0151	0.001	0.001
1996			
June to July	0.95 (0.52)	3.39 (0.81)	4.34 (1.14)
July to August	1.05 (0.55)	1.44 (0.53)	2.49 (0.87)
P-value	N.S. ²	0.001	0.001
1998			
July to October	3.01 (0.55)		
	7.29 (1.98)	10.30 (2.43)	

¹P-value of comparisons between means of incubation periods.

²Not significantly different at $P < 0.05$.

N (0 to 30 cm) between soil samples taken in *Carex* plots or under willow canopies. Total soil C and N averaged 62 and 4.4 g kg⁻¹ in *Carex* plots and 58 and 4.0 g kg⁻¹ under willow canopies, respectively.

In all experiments with both ion-exchange resin bags and field soil core incubations, there were no significant differences in soil N availability between grazing treatments during the years of the study. Several studies have reported increases in the rates of soil N mineralization with herbivory (McNaughton et al. 1988, Holland and Detling 1990, Frank and Evans 1997). Frank and Groffman (1998), reported that N availability in plots grazed by elk was 100% higher than excluded plots. It is possible that the short time (4 years) since the establishment of the exclosures in our study did not allow for the development of detectable differences in soil N mineralization and availability between grazing treatments. Alternatively, since the explanations for the influences of herbivores on N availability are not quite well understood, other mechanisms may have contributed to the lack of differences in N availability between grazing treatments.

The assessment of N availability with ion-exchange resin bags during 1995 and 1996 indicated that, in general, both NH₄⁺-N and NO₃⁻-N availability were higher during early to mid-season and declined afterwards (Table 7). In 1998, there was only 1 resin bag incubation period, and the total amount of N adsorbed to the bags was slightly higher than the sum of both periods of either 1995 or 1996, probably because the incubation period in 1998 was a few weeks longer. On average, the amount of NH₄⁺-N adsorbed to the resin bags was 137 to 412% higher than NO₃⁻-N during the 3 growing seasons.

Table 8. Inorganic nitrogen mineralized during field soil incubations (0 to 15 cm) using aluminum cores during 1997 and 1998. Values represent means for all treatments (n = 12) with standard errors within parentheses.

Incubation period ¹	NO ₃ ⁻ -N	NH ₄ ⁺ -N	NO ₃ ⁻ -N + NH ₄ ⁺ -N
	----- (g N m ⁻²) -----		
1997			
June to July	0.11 (0.04)	0.55 (0.15)	0.66 (0.16)
1998			
June to July	0.71 (0.44)	0.81 (0.80)	1.51 (0.77)
July to August	1.13 (0.38)	1.33 (0.95)	2.46 (1.17)
August to October	0.51 (0.23)	0.34 (0.52)	0.85 (0.59)

¹Length of incubation period: 1997 = 4 weeks; 1998 = 6 weeks each period.

The higher proportions of soil NH₄⁺-N could benefit plant productivity in our sites, since plants with an evolutionary history of grazing show elevated growth responses to ammonium relative to other

Table 9. Inorganic nitrogen adsorbed to ion exchange resin bags under willow (*Salix* spp.) canopies and in *Carex* spp. plots during different incubation periods of the 1995 and 1996 growing seasons. Values represent means (n = 12) with standard errors within parentheses.

Position	June to July	July to August
	----- (g N m ⁻²) -----	
1995		
Willow canopies	5.69 (2.13)	2.87 (1.20)
Carex plots	5.80 (1.92)	2.87 (1.11)
P-value	N.S. ¹	N.S.
1996		
Willow canopies	4.98 (0.77)	3.07 (0.55)
Carex plots	4.01 (0.68)	2.42 (0.37)
P-value	0.018	N.S.

¹Not significantly different at P < 0.05.

inorganic forms of N, particularly when subject to defoliation (Ruess 1984, Ruess and McNaughton 1987, Hobbs 1996). Similarly to the results from the experiments with ion-exchange resin bags, the amounts of net NH₄⁺-N mineralized in the soil cores were usually higher than NO₃⁻-N (Table 8). In addition, total inorganic N in the soil was higher during early to mid-season during the 1998 growing season (Table 8). If plant uptake is higher

Table 10. Effects of nitrogen fertilization on willow (*Salix* spp.) growth and N assimilation during the growing season of 1999. Values represent means (n = 12) followed by standard errors between parentheses.

Treatment	Shoot length	Shoot biomass	Shoot concentration	Amount of N per shoot
	(cm)	(g)	(%)	(g)
N fertilizer (10 g N m ⁻²)	28.6 (1.4) a ¹	27.3 (2.5) a	2.25 (0.05)	0.62 (0.06) a
No fertilization	22.5 (1.1) b	20.2 (2.4) b	2.14 (0.06)	0.43 (0.05) b

¹Means followed by different letters are significantly different at P < 0.05.

during early to mid-season when plant growth and nutrient requirements are probably greater, the higher availability of nutrients during that period may contribute to the synchronization of nutrient supply and demand and enhance primary production and nutrient retention within the system (Myers et al. 1994).

Interestingly, the presence of willow had a significant effect on N availability in our experiments with ion-exchange resin bags. During both incubation periods of 1996, the amounts of inorganic N adsorbed to resin bags located under willow canopies was higher (P < 0.05) than in bags placed in *Carex* plots (Table 9), but no significant differences were observed during 1995. The higher N availability may be a consequence of higher amounts of litter N inputs and higher rates of N loss from litter under willow canopies, as indicated by our findings in 1996.

The data from the N fertilization experiment demonstrated that willow growth in the winter ranges for elk is limited by N availability, independently of grazing treatment. Both inside and outside the exclosures, N fertilizer additions increased willow shoot length, shoot biomass, and the amount of N in the shoots (Table 10).

Based on our findings, we conclude that proximity to surface water had little effect on the dynamics of C and N in the winter ranges for elk during the period of our studies. In addition, we suggest that elk herbivory could lead to long-term increases in N availability in our sites, because of induced increases in both litter quality and

return of N to the soil. Stohlgren et al. (1999) reported that exotic species were more likely to invade landscape patches higher soil N and moisture, which could lead to a decline in native plant species and ecosystem diversity (Billings 1990, D'Antonio and Vitousek 1992). Therefore, eventual increases in N availability in our sites due to elk herbivory could lead to changes in plant species composition and alter ecosystem functioning, because of shifts in the competitive interactions between plant species (Tilman 1982, 1988, Holland et al. 1992, Sterner 1994, Ritchie et al. 1998).

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