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Photo courtesy of Yellowstone National Park.

Ungulate regulation of ecosystem processes in Yellowstone National Park: direct and feedback effects

Douglas A. Frank

Abstract Ungulates are highly integrated components of grassland food webs that exert strong direct and indirect influences on ecosystem dynamics. Although wildlife ecologists and managers are aware of the impacts of ungulate herbivory on vegetation and the carrying capacity of habitats, the indirect effects of ungulates on ecosystems are rarely considered. I review research in Yellowstone National Park documenting a positive, ecologically significant feedback of ungulates on their forage. Ungulates increase aboveground production of grasslands in Yellowstone by stimulating grazed plants to allocate resources aboveground and by facilitating the rate of net nitrogen (N) mineralization and the availability of N to plants. Moreover, the migration of ungulates from winter to summer range in Yellowstone is associated with animals following the spatio-temporal pattern of nutrient-rich forage across the ecosystem. This is likely critical in the positive feedback of herbivores on their forage by providing grazed plants extended periods to recover while soil conditions are suitable for plant growth. These findings from Yellowstone, in addition to similar findings of research in other ecosystems, documenting the importance of feedback effects of ungulates on habitats, indicate the need for managers to look beyond direct influences of herbivory to understand factors controlling ecosystem processes and the dynamics of managed ungulate populations.

Key words bison, diet, elk, forage, grassland, herbivory, migration, nitrogen, ungulates, Yellowstone National Park

The principle goals of wildlife management are the manipulation and protection of wildlife populations. The former includes effecting population increases, reductions, or sustained yields through the judicious use of predators, competitors, habitat modification, hunting, water holes, mineral licks, and feed, while the latter could simply mean leaving the system alone and observing what happens (Caughley and Sinclair 1994). The successful management of ungulates is predicated upon understanding how the target population interacts with other components of its ecosystem, because these interactions often dictate the dynamics of even the most intensively manipulated populations. The *direct* effects of wildlife herbivory on ecosystems are appreciated. For example, the degree to which ungulate consumption can influence vegetation and the carrying capacity of ecosystems is one of the most well-studied and thoroughly discussed subjects in wildlife ecology (Caughley 1976, McCullough 1979). In contrast, however, wildlife managers and ecologists have paid less attention to *indirect* effects of herbivory on ecosystems (Hobbs 1996).

I draw attention to ungulates as a highly integrated and interactive component of the grassland food web that imparts strong indirect and feedback influences on the functioning, i.e., energy and material flows, of the entire ecosystem. I examine grassland-ungulate interactions in Yellowstone National Park. Although the park is a relatively pristine system, the findings from Yellowstone can be applied to manipulated- and protected-grassland ecosystems supporting large herds of ungulates. In addition to their direct effects on the ecosystem through consumption of vegetation, ungulates in Yellowstone have surprisingly strong indirect effects that feed back on the ungulates themselves and have profound regulatory influences on flows of energy and nutrients within the ecosystem.

Study area

Yellowstone National Park is 9,000 km² in size and is located in the northwest corner of Wyoming (44°08'–45°07' N, 111°10'–110° W). The research reviewed was conducted in the northern range, operationally defined as habitat that is grazed by migratory elk (*Cervus elaphus*) and bison (*Bison bison*) populations that overwinter on the northern winter range. The northern winter range is approximately 140,000 ha of relatively low-elevation grassland and shrubland lying in the Yellowstone and Lamar river drainages (Coughenour and Singer 1996). Pronghorn (*Antilocarpa americana*), mule deer (*Odocoileus hemionus*), bighorn sheep (*Ovis canadensis*),

and moose (*Alces alces*) also occupy the northern range.

Elevations of the northern range are 1,700 to >3,000 m. The climate is cool and dry, with temperature declining and precipitation increasing with elevation. For example, mean temperature and precipitation at Mammoth Hot Springs (1,899 m), on winter range, and Lake (2,360 m), in the middle of the summer range, are 4.3°C and 42 cm, and 0.2°C and 47 cm, respectively (Houston 1982). Most of the precipitation in this ecosystem falls as snow. I will concentrate on grassland and shrub-grassland of the northern range, which is the primary habitat for elk, bison, and pronghorn.

The seasonal migration

Long-distance mass migration is a conspicuous feature of most of the earth's tundra and grassland ecosystems that support herds of wild ungulates (Fryxell and Sinclair 1988). On the northern winter range of Yellowstone National Park, ungulates migrate between low-elevation winter range and high-elevation summer range (Meagher 1973, Houston 1982). After spending ≤7 months on the northern winter range, ungulates begin moving to higher elevations as the surrounding slopes and hillsides become free of snow in spring. During this migration, animals graze grassland and shrub-grassland intensively for the first 1–2 months after snowmelt, then move progressively upslope (Frank and McNaughton 1992). Thus, the movement to summer range is associated with ungulates grazing phenologically young plant tissue that sweeps upslope through spring and summer. In fall, animals return to the winter range when the first "winter" storms deposit snow on high-elevation habitat.

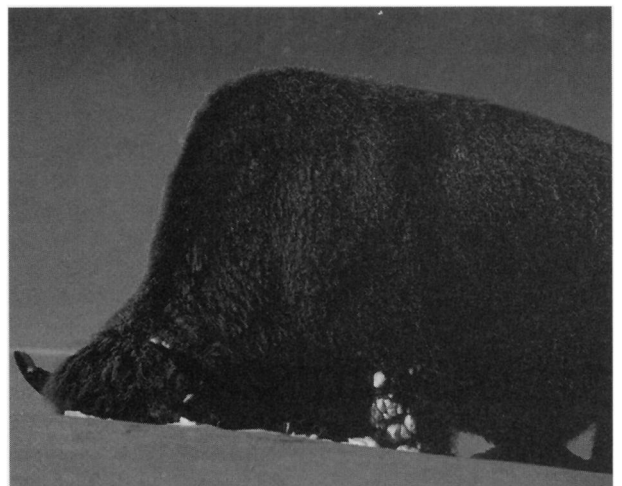


Photo courtesy of Yellowstone National Park.

Table 1. Mean mineral concentrations ($\mu\text{g/g}$) of graminoids collected 1–5 months after snowmelt at sites on the winter, transitional, and summer ranges in Yellowstone National Park. Table revised from Frank et al. (1998).

Element	No. months after snowmelt				
	1	2	3	4	5
Ca	3,187A ^a	3,272A	3,691AB	4,267B	4,562B
Co	0.43	0.37	0.12	0.52	0.35
Cu	7.17C	5.47AB	6.16BC	4.37A	5.68ABC
Fe	83.4	81.3	112.9	100.1	61.9
K	22,380C	20,033C	14,174B	10,446AB	7,908A
Mg	1,415	1,265	1,436	1,509	1,670
Mn	58.4	64.6	75.9	83.3	92.0
N	33,997D	22,512C	17,866B	13,033A	9,855A
Na	168C	123B	94A	100AB	82A
P	2,709D	1,643C	1,242B	885A	665A
Se	1.67B	0.46A	1.51B	1.89B	2.29B
Zn	35.62	6.2	29.2	27.7	35.1

^a Means within the same rows with different letters are significantly different from one another ($P \leq 0.05$).

There are 2 common reasons given for the migrations of ungulates: predation reduction and diet enhancement (Fryxell and Sinclair 1988). In Yellowstone National Park, the migration from winter to summer range is closely related to the nutrient content of forage (Frank and McNaughton 1992, Frank et al. 1998). Dominant graminoid species at winter, transitional (intermediate elevation), and summer range sites were collected each month throughout the growing season in 1989. Plants were analyzed for the contents of 12 essential minerals. The results indicated that N, P, and Na contents were significantly higher in the first month after snowmelt, and K was elevated during the first 2 months of the growing season (Table 1). Thus, forage mineral content was highest at sites when ungulates were present.

Native ungulates have dietary requirements similar to those of domesticated livestock (Taylor and Murray 1987). Average levels of nutrients during the first month after snowmelt in Yellowstone met mineral requirements for beef cattle, with the exception of Cu, which was marginal, and Na (McDowell 1985). Phosphorus and Zn were below required levels by the second month of the growing season, and N was deficient after the third month. Season-long deficiencies of Cu, Mg, Na, and Zn existed for lactating, domesticated cows that required higher concentrations of several nutrients.

Grasslands support, in addition to graminoids, significant dicot biomass. For example, among the sites where graminoid samples were collected in Yellowstone, dicots represented 9–55% ($\bar{x} = 24 \pm 5\%$) of the plant biomass during the first month after

snowmelt. An analysis of common dicot species that ungulates grazed at the sites indicated that most minerals were more concentrated in dicots than in graminoid species during the first 2 months of the growing season, when animals were present (Tables 1, 2). Nutrient content of dicots met the dietary requirements for all livestock, with the exception of Na, a mineral supplemented in Yellowstone by geophagy (Tracy and McNaughton 1995).

Results of analysis of forage nutrients suggest that Yellowstone ungulates must make a correct series of hierarchically organized feeding decisions to meet their mineral require-

ments. At the landscape or regional levels, grazers must follow young, nutritious vegetation as it sweeps upslope through the growing season. At the level of the individual plant, ungulates, particularly lactating females, may need to discriminate among forage species that vary considerably in mineral content.

These findings also have several implications for the management of ungulate populations. First, they indicate a potentially tenuous nutritional status of grazing mammals in the wild. Second, they identify minerals that may be particularly important supplements for wild populations. And third, the results emphasize the importance of seasonal migration of ungulates for maintaining the animals' nutritional condition and suggest potential deficiencies for animals whose migratory movements are restricted.

Forage production and consumption

Yellowstone National Park grassland, similar to most grassland ecosystems around the world, is topographically variable. A number of edaphic properties covary along topographic gradients from hilltop to slope-bottom, including soil texture, moisture, organic material, and nutrients (Frank and McNaughton 1992, Frank and Groffman 1998). An important consequence of this edaphic variation is that forage production also varies considerably across the landscape.

Aboveground production was determined on the northern range of Yellowstone using moveable exclo-

Table 2. Mean mineral concentration ($\mu\text{g/g}$) of dicots collected at sites 1 and 2 months after snowmelt.

Element	No. months after snowmelt	
	1	2
Ca	7,288A ^a	8,444B
Co	0.49	0.56
Cu	10.2	9.5
Fe	166	229
K	25,909	24,509
Mg	3,349	3,644
Mn	55.2	69.1
N	35,202B	25,104A
Na	227B	187A
P	3,114B	2,167A
Se	1.30	0.90
Zn	41.4	40.0

^a Means within the same rows with different letters are significantly different from one another ($P \leq 0.05$).

tures (Frank and McNaughton 1992). This technique measures forage production while taking into account the amount of plant biomass removed by grazers (McNaughton et al. 1996). Mean annual (1988, 1989) productivity at the 11 winter, transitional, and summer range sites varied from 21 to 447 g/m^2 ($\bar{x} = 216 \text{ g/m}^2$), indicating that production ranged by >1 order of magnitude among sites. Highly productive sites were located in mesic valley bottoms and swales, and low productive sites were on dry hilltops and slopes.

There was also marked variation in the amount of forage consumed across the ecosystem in Yellowstone. Consumption during the growing season, arbitrarily defined as that portion during 1988–1989, when $\geq 20\%$ of the plant biomass was green, ranged from 0 to 168 g/m^2 ($\bar{x} = 68 \text{ g/m}^2$).

Regression of consumption on plant production at these sites revealed a positive and linear relationship between the 2 variables (Fig. 1). This relationship indicates that herbivores graze patches in the landscape according to forage availability. Ungulates consume more forage as plant production increases among sites, an indication of the importance of productive habitat in supporting Yellowstone ungulate herds. In addition, the relationship suggests that grazing intensity increases with patch production. Using the calculated regression line as an estimate of consumption along the productivity gradient, I found that grazing intensity (i.e., percent of aboveground production consumed) increased from 14% at a site producing 50 $\text{g/m}^2/\text{year}$ of forage to 41% at a site producing 400 $\text{g/m}^2/\text{year}$ of forage. Thus, both the flux of energy and nutrients to herbivores, and the intensity of grazing experienced by plants, increased as plant production increased in Yellowstone.

Effects of ungulates on plant production

Ungulates can have net negative, neutral, or positive effects on aboveground plant production depending on the intensity and frequency of grazing (Hilbert et al. 1981, Georgiadis et al. 1989, Michaud 1991, Turner et al. 1993), environmental conditions (Ruess et al. 1983, Chapin and McNaughton 1989, Dyer et al. 1991b, Oesterheld and McNaughton 1991, Thorton 1991), and the evolutionary history of the plant-herbivore complex (Mack and Thompson 1982, Coughenour 1985, Lennartsson et al. 1997). Frank and McNaughton (1993) compared productivity of grazed grassland, measured with moveable enclosures, to production of permanently fenced, ungrazed grassland to determine how ungulates influenced aboveground plant production in Yellowstone National Park. This experiment was conducted at 2 sites (1 winter, 1 transitional range) in 1988 and at 4 sites (2 winter, 1 transitional, 1 summer) in 1989. At each site, in each year, productivity of grazed grassland was greater than that of fenced grassland (Fig. 2). Grazers increased production by an average of 45%, indicating that the positive feedback of grazers on their forage is an ecologically significant process, exerting a major impact on the rates of energy and material flows through the Yellowstone ecosystem.

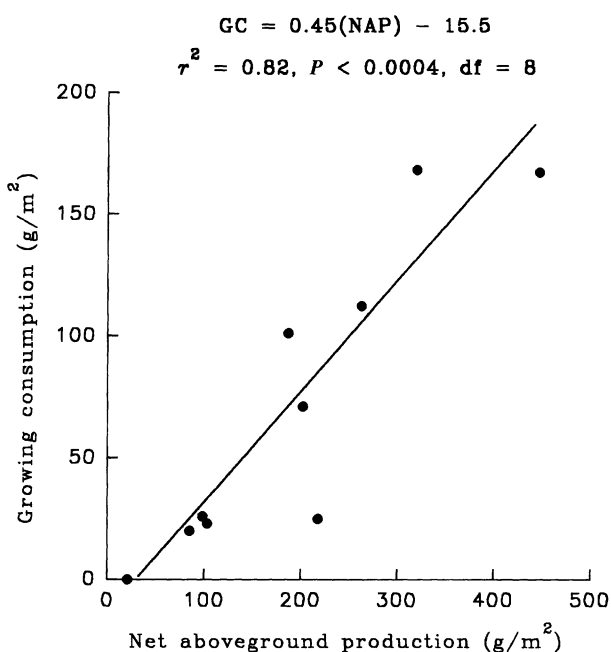


Fig. 1. The relationship between mean (1988, 1989) consumption during the growing season and mean (1988, 1989) aboveground plant production at winter, transitional, and summer range sites on the northern range, Yellowstone National Park.

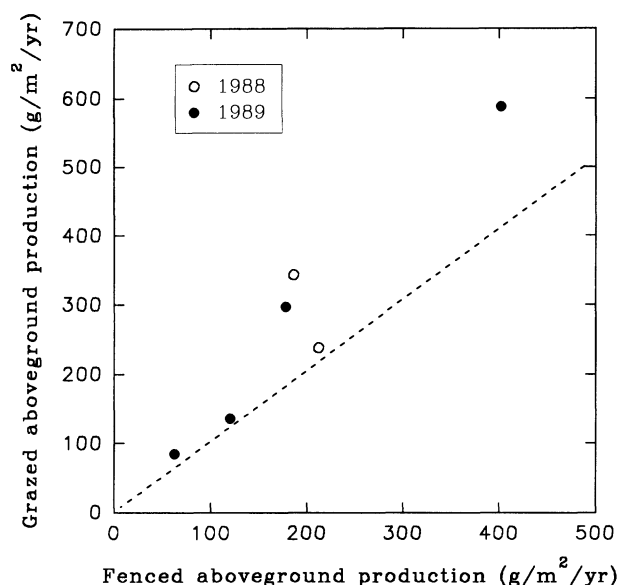


Fig. 2. Comparison of grazed and fenced, ungrazed aboveground plant production on the northern range, Yellowstone National Park. Dashed line represents unity. Figure adapted from Frank and McNaughton (1993).

Several mechanisms may account for this stimulatory effect of ungulates on shoot production. In controlled growth-chamber and greenhouse experiments, defoliation increased aboveground production in grasses (Oesterheld and McNaughton 1988, Wegener and Odasz 1997), including a common Yellowstone northern range species, western needlegrass (*Stipa occidentalis*; Wilsey 1996). These results are a consequence of (1) defoliated plants increasing resource allocation to shoot growth (Welker et al. 1985, Oesterheld and McNaughton 1988, Dyer et al. 1991a) and (2) production of young plant tissue, in response to defoliation, with higher photosynthetic rates than older material that was removed (Caldwell et al. 1981, Wallace 1990, Senock et al. 1991).

In addition to affecting the physiological responses of plants by removing shoot material, large herbivores also influence the growing environment of defoliated plants. Grazing increases light penetration through the canopy and light absorption by young, photosynthetically active plant tissue near the soil surface (Laude 1972, Monsi et al. 1973). The reduction of transpirational surface area may reduce loss of soil moisture and water stress of plants (McNaughton 1985, Wraith et al. 1987). In addition, trampling and ungulate waste products can enhance decomposition and rates of nutrient cycling in grazed grassland (Ruess 1987, Holland and Detling 1990, Holland et al. 1992, Shariff et al. 1994, McNaughton et al. 1997).

Finally, and of critical importance, the responses of plants and soils to herbivores are modulated by the spatio-temporal pattern of ungulate movement in Yellowstone. The length of time between grazing bouts has been reported to be positively associated with aboveground production of plants in field (Georgiadis et al. 1989) and laboratory (Oesterheld and McNaughton 1991) studies. In Yellowstone, ungulates typically graze grassland for 1-2 months after snowmelt, then migrate off sites, possibly to satisfy dietary requirements (Frank and McNaughton 1992). This ensures that grazed plants have an extended period of time to recover (i.e., the remainder of the growing season). In addition, because animals leave sites when soils are still moist (soils progressively dry during most growing seasons), conditions are suitable to support plant growth when grazing ceases. Thus, the seasonal migration of animals guarantees a sufficient period of time and suitable growing conditions for plants to compensate for material lost to herbivores.

There are 2 management implications related to ungulates having indirect effects on aboveground production. First, changing the natural migratory patterns of ungulates by herding or fencing may lessen, break, or reverse the positive feedback between herbivores and their forage. Second, because grazers can indirectly influence their food supply, a grassland's carrying capacity can be modified by the ungulates themselves. The influence of grazing intensity on positive, neutral, or negative effects of grassland production has been examined (Hilbert et al. 1981, McNaughton 1985). However, to my knowledge, this information has never been incorporated into standard models that predict the fluctuations of an ungulate population around a habitat's carrying capacity (Crawley 1983, McCullough 1997).

Effects of ungulates on nutrient cycling

The growth-chamber study by Wilsey (1996), indicating that clipping increases shoot production of a common grass in Yellowstone, suggests that the herbivore-induced increase in forage production measured in the field is, at least in part, a physiological response of plants to grazing. However, other mechanisms may be involved. For example, herbivores may indirectly change the rate of nutrient cycling. Because nitrogen (N) is a well-known limiting resource in grasslands (Vitousek and Howarth 1991), the effects of herbivores on N cycling should be considered in investigating nutrient-based mechanisms causing grazers to stimulate grassland production in Yellowstone.

Efforts to examine herbivore effects on N dynamics in Yellowstone have focused on changes made by grazers on 1 key step in the soil N cycle, net N mineralization (Frank et al. 1994, Frank and Evans 1997, Frank and Groffman 1998). Net N mineralization is the rate at which organic N is converted to $\text{NH}_4^+\text{-N}$. Thus, this process reflects the rate at which N becomes available for plant uptake.

Frank and Groffman (1998) measured annual rates of mineralization inside and outside of 35-year-old, permanent exclosures at 7 sites on the northern winter range to investigate the influence of large herbivores on net N mineralization in Yellowstone. Because of the complex topo-edaphic gradients in grasslands, nutrient cycling can vary markedly among sites at different topographic locations with different soil properties (Aandahl 1948, Charley and West 1977, Schimel et al. 1985, Frank et al. 1994). Selected exclosure sites were topographically diverse, ranging from dry hilltops to mesic slope-bottoms, so that the relative importance of ungulates versus topography on N mineralization could be evaluated (Frank and Groffman 1998). Results indicated that grazers increased net N mineralization by 2-fold; average mineralization was 1.9 ± 0.32 g of N/m²/year in fenced, ungrazed grassland and 3.8 ± 0.84 g of N/m²/year in grazed grassland (Fig. 3). Ungulates stimulated N mineralization in an amount (1.9 g of N/m²/yr) roughly equivalent to the difference among the ungrazed sites (2.2 g/m²/yr), which reflected the maxi-

mum topographic effect measured. The similarity in the levels at which grazers and topography affected N mineralization was surprising, because soil characteristics varied substantially among the topographically diverse sites. For instance, average soil moisture (measured monthly during a growing season) varied by 4-fold, and total C and N content of soil ranged by >10-fold among the sites. In contrast, herbivores had no effect on any soil property, except that animals reduced moisture of soil 0–10 cm deep by 7%; this likely would have suppressed mineralization, not stimulated it, as grazers were observed to have done in Yellowstone. Therefore, ungulates increased N mineralization without enhancing soil-resource pools. Moreover, the magnitude at which herbivores stimulated net mineralization was similar to variation along topo-edaphic gradients that encompassed a wide range in soil properties.

So, how did ungulates facilitate N mineralization in Yellowstone? A 62-week laboratory incubation was performed on Yellowstone soils to determine if herbivores influenced soil organic matter quality (Frank and Groffman 1998). This method, which was first formulated by Stanford and Smith (1972) and later revised by Nadelhoffer (1990), calls for incubating soils at ideal temperature and moisture conditions and periodically extracting inorganic N with a weak salt solution to derive the temporal pattern of net N mineralization. At the time that the inorganic N is extracted, CO₂ evolution often is measured to determine the rate of microbial respiration, or carbon mineralization. Typically, when soils are sampled in this manner, N and C mineralization rates are high early in the incubation and decline to relatively low, quasi-steady-state levels late in the incubation. The explanation for this pattern is that soil organic matter represents a continuum from quickly processed, labile to slowly metabolized, recalcitrant material. Rates are elevated early during the incubation while labile organic matter is present. Rates decline throughout the incubation as organic material becomes more recalcitrant.

Incubating grazed and fenced soil, collected at sites where field mineralization rates were measured, demonstrated that large herbivores increased both N and C mineralization early in the incubation and inhibited those rates late during the process (Fig. 4). This temporal pattern of mineralization during the incubation indicated that large herbivores enhanced the labile fraction and reduced the recalcitrant fraction of soil, i.e., grazers improved the quality of soil organic matter. Consequently, ungulates elevated the rate at which N became available to plants in the field, at least in part, by enhancing the turnover rate

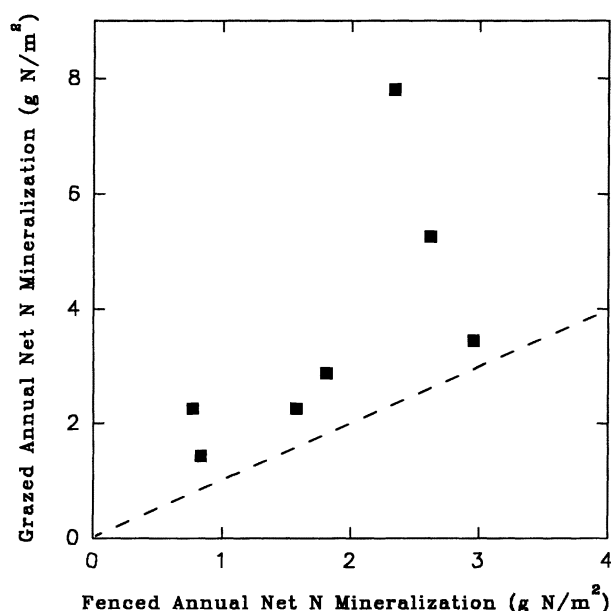


Fig. 3. Comparison of net N mineralization in grazed and fenced, ungrazed grassland on the northern winter range, Yellowstone National Park, measured May 1995–April 1996. Dashed line represents unity (after Frank and Groffman 1998).

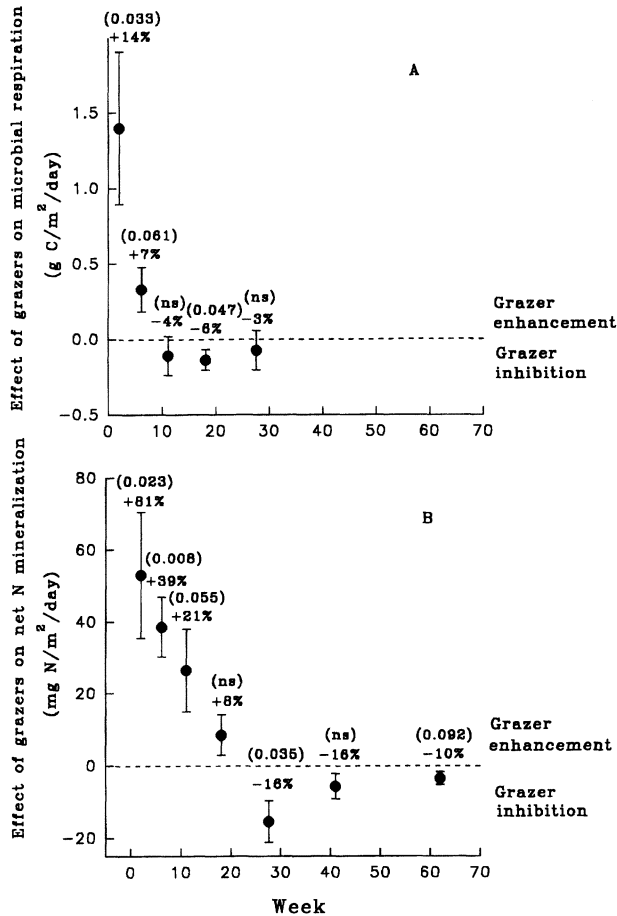


Fig. 4. The effect of grazers on (A) potential microbial respiration and (B) net N mineralization during a long-term lab incubation. Points indicate average ($N = 7$) differences between daily rates measured in soils collected in grazed and fenced grassland. Bars are standard errors. Percentage that herbivores altered process and results of paired tests (in parentheses) are provided above the bars. No significance ($P > 0.10$) is indicated by "ns." (After Frank and Groffman 1998).

of soil N (i.e., the proportion of soil N mineralized during the year). The process by which this occurs is the subject of current research.

Browsers in forest ecosystems: a caveat

Wildlife ecologists and managers working in forest ecosystems that support populations of browsers should note that the positive feedbacks by grazing ungulates on plant production and nutrient cycling described for Yellowstone, and which have been reported for other grassland habitats (Holland and Detling 1990, McNaughton et al. 1997, Frank et al. 1998), may not apply to forest habitats. Studies of long-term exclosures in the boreal forest of Isle Royale National Park (McInnes et al. 1992, Pastor et

al. 1993), which supports the highest recorded densities of moose in the world, indicate that browsing can reduce rates of net N mineralization and forest production. This negative feedback was a consequence of moose reducing abundance of several highly preferred tree species that produced labile litter and increasing the abundance of less preferred species that produced recalcitrant litter. Thus, the consequence of browsers increasing the abundance of species that produced recalcitrant leaf litter was an indirect reduction of energy and material flow through the system. The research conducted at Isle Royale demonstrated that the direction in which grazers shift ecosystem processes may differ between forest and grassland habitats. Furthermore, results from this browsed, boreal forest reinforce the conclusion that indirect and feedback effects of ungulates can have ecologically significant impacts on ecosystem dynamics.

Conclusions

The ungulate mass migration to summer range in Yellowstone National Park is closely associated with the nutritional quality of forage. Animals graze young, nutritionally rich forages as they migrate up the elevation gradient through the spring and summer. Elemental requirements determined for domesticated cattle (McDowell 1985) suggest that the seasonal migration, combined with selective feeding, is necessary for wild ungulates, particularly lactating cows, to meet dietary requirements.

Ungulates graze patches in spatially heterogeneous landscapes according to the rate of aboveground plant production. Herbivores obtain more energy and nutrients and graze more intensively as patch production increases.

Grazers play an ecologically significant role in stimulating aboveground plant production. Both a physiological response by plants to defoliation and a grazer-induced increase in N availability are involved in this positive effect on forage. The seasonal migration is a critical component of this feedback, allowing grazed vegetation an extended period to recover when resources are sufficient to support plant growth.

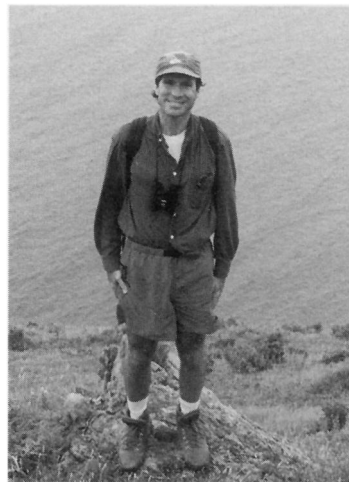
This research in Yellowstone National Park indicates that large herbivores, in addition to their direct impacts on ecosystems through consumption of plant material, have major indirect effects on ecosystem processes. Ecologically important feedbacks of ungulates have been demonstrated in other ecosystems and suggest that these interactions are a widespread phenomenon that needs to be considered by managers of ungulate populations.

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