

## Effects of Grazing by Ungulates on Upland Bunchgrass Communities of the Northern Winter Range of Yellowstone National Park

### Abstract

Herbivory by native ungulates, primarily elk (*Cervus elaphus*), was studied on xeric, bunchgrass-dominated slopes on the Northern Yellowstone ungulate winter range of Yellowstone National Park. Plant cover, standing green biomass, and nutrient concentrations were compared between grassland sites protected from grazing for 24-27 years and adjacent plots grazed mostly during winter by elk, and to some extent by bison (*Bison bison*). Accumulated litter and standing dead vegetation were four times more abundant on the ungrazed plots. However, few consistent differences were observed in grass or forb biomass from elk herbivory. There was no overall effect of grazing treatment on forbs or other nongrasses ( $P < 0.05$ ). Total grass biomass was less on grazed than ungrazed sites in 1986, after a dry, warm spring, but there was no difference in 1987 ( $P < 0.05$ ). Biomass of junegrass (*Koeleria cristata*) and thick-spiked wheatgrass (*Agropyron dasystachyum*) was greater on grazed than ungrazed sites. Three nongrasses (*Artemisia frigida*, *Phlox hoodii*, *Antennaria microphylla*) were more abundant on some ungrazed sites although the effect on grazing treatment was not significant ( $P > 0.05$ ). The numbers of grasses ( $n = 4.5$ ), forb ( $n = 17.5$ ) and shrub ( $n = 3.5$ ) species did not differ between grazed and ungrazed plots ( $P < 0.05$ ). Vegetative culms of bluebunch wheatgrass (*Pseudoroegneria spicata*), Idaho fescue (*Festuca idahoensis*), bluegrasses (*Poa spp.*), needle-and-thread grass (*Stipa comata*), junegrass, and thick-spiked wheatgrass were shorter on winter grazed plots ( $P < 0.05$ ), but grazing did not affect the numbers of vegetative culms or the height or numbers of reproductive culms of grasses ( $P > 0.05$ ), with the single exception that more vegetative culms of junegrass occurred on grazed sites. Protein content averaged 16% higher in bluebunch wheatgrass, 36% higher in Idaho fescue, and 10% higher in junegrass ( $P < 0.05$ ) on grazed sites. Bare ground averaged 38% more on grazed sites than on ungrazed sites ( $P < 0.05$ ), but pebble cover was 50% less on grazed sites (probably because of hoof compaction); as a result all bare surfaces (bare ground plus pebble cover) averaged only 18% greater on grazed sites. Dead clumps of the grazing sensitive bluebunch wheatgrass and Idaho fescue can be expected on an overgrazed range, but dead bunchgrass clumps did not vary between grazed and ungrazed sites ( $P < 0.05$ ). The effects of herbivory by native ungulates was observed in swale sites that had been disturbed by agricultural activities until the 1930s. Three grasses (*Stipa viridula*, *Poa pratensis*, *P. compressa*) possessed greater cover on grazed swales, but one forb, field pennycress (*Thlaspi arvensis*), was less abundant on grazed sites. Herbivory by native ungulates greatly stimulated grass but not forb cover on these productive swale sites (grass cover was double that of ungrazed sites) ( $P < 0.05$ ), and grazing mostly by elk contributed to the continued dominance of these sites by the exotic, grazing resistant *Poa pratensis* even 54 years following cessation of agricultural activities.

### Introduction

Caughley (1970, 1976, 1979) and Sinclair (1977) suggested that free-ranging ungulates reach an equilibrium with their vegetative food base. Beginning in 1967, Yellowstone National Park embarked upon an experimental program of "hands-off" or natural regulation management of the large ungulates within the park's boundaries (Cole 1971, Houston 1976), although harvest of migratory elk north of the park was encouraged to the greatest extent possible. Cole (1971) stated that over a period of years, naturally regulated ungulate populations were self regulating units. Yellowstone ungulates regulated their own mortality and compensatory natality in relation to available winter food and their population size, and predation seemed a nonessential adjunct. Prior to 1967, elk (*Cervus elaphus*), bison (*Bison bison*), and prong-

horn (*Antilocapra americana*) were reduced by park staff (Craighead et al. 1972, Meagher 1973, Houston 1982, Coughenour and Singer 1991). Elk numbers were reduced to below 5,000 by 1967, and after cessation of artificial controls in 1969, elk increased dramatically (Houston 1982, Merrill and Boyce 1991). Harvests of the northern Yellowstone elk that migrated north of the park averaged only 9% of the herd during the years 1967-88 (Houston 1982, Singer 1991), a level insufficient to control the herd's growth.

Yellowstone's ungulate management since 1967 can not be regarded as a scientific experiment in that there is no ecosystem replication, no control situation(s) with similar climate where wolves exist, where ungulate migrations are uninfluenced by human activities, and where natural fire is unregulated (Cayot et al. 1979, Peek 1980, Kay 1987). Yellowstone National Park's climate is different this century than last—summer temperatures are increasing and January-June

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precipitation levels are decreasing (Balling et al. 1992). The climatic changes might alter vegetation-ungulate relations. Evaluations of the park's management program have been limited mostly to monitoring of range plots (mostly 1958 to present), comparisons inside and outside of ungulate exclosures, and comparisons of current photos to those taken 100-120 years ago (Houston 1982, Houston and Meagher in prep.); inferences from these kinds of monitoring studies are limited (Platt 1964). Few precise criteria for testing hypotheses were provided during the original statement's of the ungulate management experiment (Houston 1976, 1982; Cole 1971), overgrazing was not defined, and equilibrium theories prevalent for the time, which have since been questioned (DeAngelis and Waterhouse 1987), were central to the original experiment (Coughenour and Singer 1991).

Houston (1982:125) who used Parker transect and chart quadrats for his analysis 1957-74, concluded there were "... little or no consistent differences between the treatments of nongrazing and grazing by native ungulates on plant species abundance, basal area, or composition. Differences over time appeared to be related more to fluctuations in growing conditions." Comparative photos from the 1970s compared to historic photos from the 1860-80s suggested no increase in gross evidence of erosion such as in visible erosive rills, exposed tree roots, or bare ground (Houston 1982). Houston (1982) concluded the effects of elk on vegetation did not exceed those expected from a population near ecological carrying capacity; fluctuations in abundance of perennial grasses were influenced more by fluctuating growing conditions, especially rainfall, than ungulate densities.

Several serious questions were raised, however, concerning ungulate densities on the northern Yellowstone winter range following Houston's (1982) study which ended in 1979. Elk counts increased to 16,000 in 1982 and then to 19,000 in 1988 (Singer 1991), raising concerns for overgrazing of the winter range (Chase 1986, Kay 1987). Bison counts also increased 154%, mule deer (*Odocoileus hemionus*) 126%, and pronghorn 215% on the northern Yellowstone winter range during the 1980s (Meagher 1989, Singer 1991), contributing to the concerns. Alternatively, the winter range might not be overgrazed. Useable elk winter range may have increased during mild

winters of the 1980s (seven of the 8 winters between 1980 and 1988 received less than the average amount of snowfall), ungulates ranged over a wider area, forage was more accessible because of the shallower snows, and elk more regularly migrated north of the park boundary beginning at about 1980, thus effectively adding 18% to their area of winter use and dispersing grazing pressures (Singer 1991).

To resolve the controversy, in 1987 the U.S. Congress directed the National Park Service to "start a study on Yellowstone to see whether there is evidence of overgrazing (Congressional Record - Senate S.12613, 1986)."

Studies published from this large research initiative, 1986-88 did not document overgrazing of grasslands by native ungulates. Parker transect data sampled in and out of exclosures 1962-89 suggested vegetation responses to climate were much more significant than changes due to exclosure from grazing. Grasses increased in frequency of abundance until 1986 (in spite of increasing elk numbers) and forbs decreased, reverse trends were observed after 1986, apparently in response to drier conditions (Coughenour et al. 1995). Changes in plant frequency were parallel inside and outside of the ungulate exclosures. Coughenour et al. (1995) concluded elk grazing has not degraded the herbaceous vegetation of the northern winter range, but the authors pointed out problems with the sampling including: no correlation of Parker hits to plant biomass, high variances, and small sample sizes. Coughenour (1991) reported grass and forb biomass production inside and outside of exclosures was largely uninfluenced by elk grazing in 1987, but both were reduced on grazed sites in 1988, a dry year. Root biomass and soil moisture were not affected by grazing. Coughenour's (1991) sampling, however, was restricted to plant groupings; he did not separate herbaceous biomass to the species level.

The purpose of this investigation was to evaluate differences in aboveground biomass production by plant species between grazed and ungrazed sites on Yellowstone's northern elk winter range.

### Methods and Study Area

The Yellowstone northern winter range consists of about 100,000 ha, of which about 82% lies within Yellowstone National Park and 18% lies north of the park on Gallatin National Forest and private lands. The Yellowstone northern winter

range is lower (1,500 m-2,400 m), warmer, and receives less precipitation than the higher plateaus of the park. Total precipitation averages less than 75 cm for most of the northern winter range. Mean annual precipitation at the lower elevations (1,620 m) at the park boundary near Gardiner, Montana, is 30 cm, but precipitation is 55 cm at 2,000 m near the Lamar Ranger Station.

The majority of the winter range is undisturbed by human activities with two major exceptions:

- (1) The 4,900 ha Boundary Line Area described by Houston (1982) was subjected to a livestock grazing, irrigation and haying of meadows and swales, and the introduction of a variety of exotic hay meadow plants (timothy, *Phleum pratense*; Kentucky bluegrass, *Poa pratensis*; smooth brome, *Bromus inermis*; quackgrass, *Agropyron repens*; cheatgrass, *Bromus tectorum*). Houston (1982) felt that prior to the agricultural activities the Boundary Line Area was dominated by needle-and-thread grass (*Stipa comata*) and bluebunch wheatgrass (*Pseudoroegneria spicata*). I studied swales and the intervening rolling grasslands in this area, near the two Gardner ungulate exclosures.
- (2) Bison were largely restricted in the park to the Lamar Valley from about 1904-52, when bison were fed hay cut from both the native meadows, and from irrigated, cultivated fields of exotic grasses (Meagher 1973, Houston 1982). Exotic grasses that still persist in the Lamar Valley area include smooth brome, timothy, Kentucky bluegrass, and quackgrass.

About 41% of the northern winter range is forested, largely with Douglas-fir (*Pseudotsuga menziesii*) stands and a grass understory (Houston 1982, Despain 1991). About 55% of the area is grassland, especially Idaho fescue (*Festuca idahoensis*) and big sagebrush (*Artemisia tridentata*) habitat types (Mueggler and Stewart 1980), about 2% is aspen (*Populus tremuloides*) stands, and about 0.4% is willow (*Salix spp.*) and riparian shrub stands. My investigation focused on two plant community types used mostly by elk: (1) upland bunchgrass communities (ridge and slope) never subjected to agricultural activities, and (2) lower elevation, swale winter range sites grazed mostly by elk, but subjected to cattle

grazing and haying activities until 1932 on the Boundary Line Area (since my study, these swales are also being grazed by the park's expanding bison population (Meagher 1989).

#### Upland Bunchgrass Communities Never Disturbed by Haying Activities

Sampling was conducted within upland bunchgrass communities both inside (ungrazed) and immediately adjacent (grazed) to 8 2-ha exclosures for ungulates. The exclosures were erected in 1957 and 1962 between Gardiner and the Lamar Ranger Station. All 8 exclosures are on dry, upland ridges or slopes within a complex of gently rolling swales and ridges. These ridges and slopes are windblown and receive high use by elk, especially in late winter (Houston 1982). The ridges and slopes at the Gardiner exclosures were grazed by livestock until 1932, but were not subjected to the seeding or haying of grasses—no soil disturbances occurred on these sites.

Measurements in bunchgrass communities in 1986 and 1987 included biomass and cover in 10 pairs of 10x10 m macroplots (grazed and ungrazed) located with similar slope, aspect, and soil characteristics at each exclosure site. Sampling of paired plots was conducted simultaneously. Lane (1991) described the soils at the macroplot sites as Typic Calciborolls, Aridic Haploborolls, and Aridic Calciborolls. Lane (1991) found no consistent trends in soil organic matter, nitrogen, sulfur, electrical conductivity, iron, and zinc between grazed and ungrazed plots. Slopes between paired sites varied less than 6%, and aspects varied less than 18%. Ten 1x1 m quadrats or 15 0.25x0.25 m quadrats were located randomly within each larger (10x10 m) macroplot. Percent cover of each plant species, along with cover of dead litter, dung, bare ground, rocks (>6 m diameter), pebble (<6 m diameter), and pavement was estimated with a grid frame placed on the quadrats. Percent cover by dead bunchgrass clumps was estimated from the grid frame. All herbaceous and subshrub above-ground biomass was then clipped and frozen, later sorted into green and dead material by species, oven-dried for 48 hours at 60°C and weighed.

#### Swale Communities Subjected to Haying Activities

Swale communities in the Boundary Line Area were studied inside and outside of the two Gardiner

exclosures, but sampling was restricted to measurements of percent plant cover only. I selected 5 paired macroplots (10 m x 10 m) located inside and outside of each exclosure in swales. Each swale site was separated from the other by rolling ridges and slopes (n=10 paired macroplots total). Since these swales were small in size (about 0.1 ha) and since they were separated spatially by intervening rolling steppe vegetation, I treated each swale as an independent replicate sample, but I pooled the data within each swale. A single mean value from all the plots in each swale was used in a 1-way ANOVA with grazing as the treatment and individual swales as replicates. Physical evidence (farm machinery parts, ditches) indicated these swales were seeded and grazed by livestock, and some were irrigated prior to 1934. These swales were likely mechanically seeded, but were probably not plowed under.

Nutritional and fibrous constituents were sampled after senescence in August at 2 of the eight total exclosures. The two exclosures sampled were located on the Blacktail Deer Creek. Crude protein, fat fiber, Van Soest fibers, total ash, gross energy, in vitro digestibility (IVDDM, Tilley and Terry), and Calcium, Phosphorus, Manganese, Potassium, and Magnesium levels were determined (Wildlife Management Habitat Lab, Pullman) for the three most common forage grasses, bluebunch wheatgrass, junegrass (*Koeleria pyramidata*), and Idaho fescue. Heights and numbers of reproductive culms and vegetative leaves were counted and measured for the same three grasses on a 20 cm x 30 cm subplot within each quadrat.

Each exclosure represented one replicate (Hurlbert 1984) of the grazing treatment (grazed vs. ungrazed). One mean value for each exclosure was compared for only the most common species and plant categories (forb, subshrub, total grasses) that were present at all locations with 1-way ANOVA. Percent ground cover categories were compared between grazed and ungrazed sites, with the non-parametric Kruskal-Wallis test. The data was not transformed because of the large number of small and zero values of cover categories and biomass.

Grass morphology and reproductive characteristics were compared with Mann-Whitney U tests because the data were not normal (Kolmogorov-Smirnov test), and the variances were heteroscedastic (F-max test, Sokal and Rohlf 1969). Nutritional and fibrous constituents were

compared between grazed and ungrazed sites with the t-test.

## Results

Most of the ungulate herbivory near the eight exclosures was attributed to elk, with some herbivory by bison. Herbivory by pronghorn and mule deer occurs at the Boundary Line Area near the Gardiner exclosures, but these ungulates are primarily browsers in the study area (Singer and Norland 1995). Elk outnumber other ungulates on the northern Yellowstone winter range by ratios of 100 elk:14 mule deer:3 bison:2 pronghorn:2 bighorn sheep (*Ovis canadensis*):1 moose (*Alces alces*) (Singer 1991). Bighorns and moose were not observed near the exclosures. Rodents (*Lepus townsendi*, *L. americanus*, *Spermophilus armatus*) occur near the exclosures and pass freely in and out of the fences.

Ungulate herbivory at the exclosure sites was restricted almost entirely to winter, but some grazing of early spring grass occurs just prior to elk leaving the winter ranges (Houston 1982). Spring off-take was zero near the Blacktail exclosure in 1990 (Singer and Harter unpubl. data), but spring off-take was more significant in the Lamar Valley (Frank and McNaughton 1992). Elk vacated the winter range sites during the remainder of the growing season (Houston 1982). Bison, however, recently shifted their area of winter range use westward (Meagher 1989) and began wintering near the Junction Butte in 1983, and to a limited extent near the Gardiner exclosures since 1988.

### Comparisons of Herbaceous Biomass in Grazed and Ungrazed Bunchgrass Communities Not Subjected to Agricultural Activities

Less standing crop of annual green herbage biomass was collected on grazed sites than on ungrazed sites in 1986 ( $F = 45.7$ ,  $P < 0.01$ , Table 1), but not in 1987 ( $P > 0.05$ ). Forb biomass was not influenced by grazing in 1986 ( $F = 2.0$ ,  $P = 0.12$ ), but the difference due to grazing approached significance in 1987 ( $F = 2.4$ ,  $P = 0.10$ ). Less grass biomass was produced on grazed sites in 1986 ( $F = 28.0$ ,  $P < 0.01$ ), but not in 1987 ( $P > 0.05$ ). Numerically, 85% less biomass of rosy pussytoes (*Antennaria microphylla*) and 33% less fringed sage (*Artemisia frigida*) was collected from grazed sites, but the differences were statistically not significant ( $P > 0.05$ ).

TABLE 1. Comparisons of biomass between grazed and ungrazed bunchgrass communities on Yellowstone's northern elk winter range.

	1986 (n = 4 macroplots)						1987 (n = 6)					
	Ungrazed			Grazed			Ungrazed			Grazed		
	$\bar{x}$	$\pm$	SE	$\bar{x}$	$\pm$	SE	$\bar{x}$	$\pm$	SE	$\bar{x}$	$\pm$	SE
Bluebunch Wheatgrass	13.4	6.6		8.3	2.9		7.6	2.8		7.6	2.8	
Idaho Fescue	8.3	2.9		5.9	2.7		7.2	1.6		10.0	2.0	
Junegrass	7.3	2.5		4.7	1.4		4.8	1.6		10.0	2.0 <sup>1</sup>	
Total Grasses	49.8	4.7		18.9	1.9**		24.4	5.6		31.6	5.2	
Total Sedges	0.2	0.1		0.4	0.1		0.4	0.3		0.4	0.2	
Rosy Pussy-toes	1.0	0.2		0.9	0.4		10.8	6.8		0.8	0.4	
Total Forbs	22.5	6.6		10.9	2.5		26.0	8.8		10.8	3.6 <sup>-</sup>	
Fringed Sage	3.3	1.8		1.4	0.7		4.8	2.0		4.0	2.0	
Total Shrubs and Subshrubs	3.8	2.0		2.0	1.0		10.8	1.6		6.4	2.8	
Total Green Herbage Production	76.1	4.3		31.8	3.8**		62.0	11.2		49.2	6.0	

\*\* P < 0.01, \* P < 0.05, - P < 0.01. Biomass differences were tested using 1-way ANOVA with location as replicates and grazing as the treatment.

<sup>1</sup>Does not include biomass of the perennial succulents, *Opuntia spp.*, which occurred at the lowest elevation, Gardiner exclosures, because I could not differentiate annual from perennial growth. *Opuntia spp.* biomass (annual plus perennial) was  $19.2 \pm 9.64$  g/m<sup>2</sup> on protected sites and  $9.6 \pm 7.4$  g/m<sup>2</sup> on grazed sites.

Several other plant species were less ubiquitous in the study plots, and inferences concerning grazing treatment effects are tenuous. For example, thick-spiked wheatgrass (*A. dasystachum*) was found at only the two highest enclosure locations in the Lamar Valley where it was more abundant on grazed ( $6.2 \pm 0.9$  g/m<sup>2</sup>) than on ungrazed sites ( $3.5 \pm 0.7$  g/m<sup>2</sup>) (P < 0.05).

Elk herbivory did not influence the frequency of grass, forb or shrub species (Table 2, P > 0.05). An average of 4.5 grass species, 17.5 forb species and 3.5 shrub species were identified on each 10 m x 10 m macroplot in bunchgrass communities. One species, *Arabis holboellii*, was recorded from only grazed plots.

Lichen cover was not influenced by elk herbivory (P > 0.05, Table 3), but moss cover was significantly greater on ungrazed sites in 1986 (P < 0.05), but not in 1987 (P > 0.05). Litter and standing dead vegetation averaged 3.5 times more biomass on ungrazed plots (P < 0.05, Table 3), and as a result bare ground averaged 3.8 times more on grazed sites both years (Table 3). Pebble cover, however, averaged 50% less on grazed sites (P < 0.05), probably because pebbles were less obvious on grazed areas due to hoof action and soil compaction by ungulates. When bare ground and pebble cover were combined, all bare surfaces averaged only 18% more on grazed versus

ungrazed sites in 1987 (P < 0.05), but the difference was not significant in 1986 (P > 0.05, Table 3). Small pebble cover was greater on ungrazed plots both years. Animal dung from ungulates and rabbits provided a minor amount of ground cover (1.2-4.1%) and its abundance was greater on grazed than ungrazed sites (P < 0.05) (Table 3).

I observed no evidence of any significant increase in bunchgrass mortality due to elk herbivory (P > 0.05, t-test, t = 0.54). Dead bunchgrass clumps averaged 4.3% cover for both treatments.

#### Grass Morphology

Numbers and heights of reproductive culms and numbers of vegetative culms did not vary between grazed and ungrazed paired plots for bluebunch wheatgrass, Idaho fescue, junegrass, thick-spiked wheatgrass, needle-and-thread grass (*Stipa comata*), or bluegrasses (Table 4). The single exception was more vegetative culms of junegrass were sampled per individual plant on grazed sites. Heights of vegetative leaves were shorter in grazed sites of bluebunch wheatgrass (t = 5.7, P < 0.001), Idaho fescue, junegrass, thick-spiked wheatgrass, and bluegrasses (P < 0.05). Reproductive ratio (the number of reproductive vs. the number of vegetative culms per plant) did not vary between grazed and ungrazed paired plots for any grass species (P > 0.05).

TABLE 2. Number of grass, forb, and shrub species compared between 10 pairs of grazed and ungrazed macroplots, in 1986 and 1987 from upland bunchgrass communities on Yellowstone's northern range.

No. Plant Species	1986							
	Mammoth-W		Mammoth-E		Blacktail-W		Blacktail-E	
	Control	Grazed	Control	Grazed	Control	Grazed	Control	Grazed
No. Grasses	6	4	4	5	4	4	6	3
No. Forbs	8	7	15	10	26	25	16	21
No. Shrubs	5	3	3	5	2	3	2	2
TOTAL	19	14	22	20	32	32	24	26

  

No. Plant Species	1987					
	Gardiner-E		Gardiner-W		Blacktail	
	Control	Grazed	Control	Grazed	Control	Grazed
No. Grasses	2	2	4	3	4	4
No. Forbs	11	16	21	17	10	12
No. Shrubs	0	1	3	2	2	3
TOTAL	13	19	28	22	16	19

  

No. Plant Species	1987					
	Junction Butte		Lamar-E		Lamar-W	
	Control	Grazed	Control	Grazed	Control	Grazed
No. Grasses	3	8	5	5	3	4
No. Forbs	19	17	22	21	27	32
No. Shrubs	2	2	1	1	3	3
TOTAL	24	25	28	27	33	39

TABLE 3. Ground cover categories and standing dead and downed litter on grazed and protected bunchgrass communities in Yellowstone National Park, 1986-87. Differences were tested using the Kruskal-Wallis 1-way ANOVA with grazing as treatment and locations (n = 4 or 6) as replicates.

	1986 (n = 4)						1987 (n = 6)					
	Ungrazed			Grazed			Ungrazed			Grazed		
	$\bar{x}$	$\pm$	SE	$\bar{x}$	$\pm$	SE	$\bar{x}$	$\pm$	SE	$\bar{x}$	$\pm$	SE
Lichen Cover(%)	6.3		3.3	9.8		8.0	4.2		1.1	5.1		3.9
Moss Cover (%)	10.4		3.9	1.7		0.2*	1.9		0.4	0.6		0.3
Bare Ground (%)	11.7		5.1	20.2		2.5*	4.4		0.3	35.1		6.5*
Pebble Cover <sup>1</sup> (%)	29.4		4.5	18.3		8.9	37.0		8.2	13.8		0.7**
All Bare Surfaces <sup>2</sup> (%)	41.1		5.1	38.5		2.5	41.4		4.1	48.8		2.7*
Animal Dung <sup>3</sup> (%)	0.2		0.1	34.3		11.6**	1.2		0.3	4.1		1.2*
Litter and Standing Dead												
Vegetation (g/m <sup>2</sup> )	84.4		16.4	21.1		7.2**	67.0		9.3	23.3		3.9**
Dead Wood <sup>4</sup> (g/m <sup>2</sup> )	2.1		0.6	1.7		0.5	3.2		0.7	2.0		0.7

<sup>1</sup>Pebbles were defined as < 6cm diameter.

<sup>2</sup>Bare ground and pebble cover combined.

<sup>3</sup>Elk, pronghorn, deer and rabbits pellets as percent of ground cover in 1987, and total number of pellets per m<sup>2</sup> in 1986.

<sup>4</sup>Dead stems of shrubs (big sagebrush, horsebrush, rabbitbrush) and subshrubs (fringed sage, Phlox) lying on the ground surface.

TABLE 4. Mean morphological measurements for 3 common grasses at 8 grazing exclosures on Yellowstone's Northern Winter Range (n= 130 grazed and 130 ungrazed plots, 1-m<sup>2</sup>).

	Bluebunch Wheatgrass		Idaho Fescue		Junegrass	
	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
No. Vegetative Culms	15.4±13.3	18.6±15.8	94.0±50.1	127.6±107.2	23.1±17.9	44.7±21.4*
No. Reproductive Culms	2.0±1.7	2.3±2.1	4.2±3.3	3.2±2.9	2.5±2.6	3.2±2.7
Tallest Vegetative Culm (cm)	22.3±2.5	18.0±1.6*	15.4±3.1	7.8±0.4*	10.1±2.3	7.6±1.0*
Tallest Reproductive Culm (cm)	27.1±13.7	29.5±11.6	33.2±9.6	24.4±9.7	18.5±10.1	13.9±7.8

\* Significant difference,  $p < 0.05$ , Mann-Whitney U tests.

### Nutritional Responses of Grasses to Grazing

Elk herbivory enhanced the protein content of live grasses. Protein content averaged 16% higher on grazed versus ungrazed paired plots for bluebunch wheatgrass ( $t = 9.8$ ,  $P < 0.0001$ ), 36% higher for grazed Idaho fescue ( $t = 11.8$ ,  $P < 0.001$ ), and 10% higher for grazed junegrass ( $t = 6.8$ ,  $P < 0.05$ , Table 5). Grazing did not significantly influence digestibility (IVDDM) or fibers (NDF, ADF, ADL,  $P > 0.05$ ). Ash content was significantly higher in grazed Idaho fescue and junegrass ( $P < 0.05$ , Table 5).

Grazing resulted in a minor enhancement of macronutrients. Calcium levels were higher in grazed than ungrazed Idaho fescue ( $0.56 \pm 0.07$  ppm vs.  $0.41 \pm 0.06$  ppm,  $t = 15.8$ ,  $P < 0.001$ , d.f. = 18) as were Phosphorous levels ( $0.16 \pm 0.01$  ppm vs.  $0.14 \pm 0.04$  ppm,  $t = 6.20$ ,  $P < 0.01$ ) and Magnesium levels ( $0.14 \pm 0.01$  ppm vs.  $0.09 \pm 0.01$  ppm,  $t = 15.8$ ,  $P < 0.001$ ). Potassium levels were higher in grazed bluebunch wheatgrass ( $1.14 \pm 0.10$  ppm vs.  $0.99 \pm 0.03$  ppm,  $t = 7.9$ ,  $P < 0.001$ ). No other differences attributable to elk herbivory were observed for 5 elements (Phosphorus, Calcium, Magnesium, Potassium, Manganese) in Idaho fescue or bluebunch wheatgrass, and no differences in any elements were observed in junegrass.

### Effects of Native Ungulate Grazing in the Former Agricultural Zone

*Bunchgrass Communities Formerly Grazed by Livestock.* Vegetation on elk grazed and ungrazed rolling bunchgrass-dominated ridges and slopes in the Boundary Line Area was similar; apparently both treatments recovered in a parallel fashion from livestock grazing terminated 54 years be-

fore. No exotic plants were sampled on either treatment and no biomass differences by plant species occurred with the single exception that more biomass of *Phlox hoodii* was sampled on sites ungrazed by elk ( $P < 0.05$ ).

*Swales Formerly Hayed and Grazed by Livestock.* Swale communities in the Boundary Line Area, however, where seeding and limited soil disturbance from agriculture occurred, differed on sites grazed by native ungulates during the 54 recovery period versus those sites ungrazed by native ungulates. The differences did not suggest decreased productivity on the elk grazed sites, in fact, grass cover was nearly double and bare ground less on the elk grazed sites (Table 6,  $P < 0.05$ ). Three grasses (green needlegrass; Kentucky bluegrass; Canadian bluegrass, *Poa compressa*) were more abundant on elk grazed sites ( $P < 0.05$ ,  $F = 5.7, 5.1, 3.6$ , respectively), but one of these grasses is an exotic (Kentucky bluegrass) suggesting elk grazing promoted continued dominance of the sites by an exotic grass. Field pennycress (*Thlaspi arvensis*), an exotic forb, however, was more abundant on sites ungrazed by elk ( $F = 3.9$ ,  $P < 0.05$ ).

### Discussion

Grass biomass on upland bunchgrass types was reduced in 1986 by grazing, but there was no effect from grazing in 1987. The winter of 1985-86 which preceded the 1986 growing season was characterized by an early spring snowmelt and less than normal spring precipitation (83% of average). Grazing effects on grasslands may be exacerbated during dry conditions (Coughenour 1991, Frank and McNaughton 1993) and recovery from a drought is slower on heavily-grazed sites (Young 1943). Growing season consumption by ungulates was negligible at the study sites

TABLE 5. Nutritional values of grazed and ungrazed (exclosed) grasses on Yellowstone's northern winter range, 1986 ( $\bar{x} \pm S.D.$ ).

	Bluebunch Wheatgrass		Idaho Fescue		Junegrass	
	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
Protein (%)	7.74 $\pm$ 0.49	9.01 $\pm$ 0.80**	7.02 $\pm$ 0.56	9.58 $\pm$ 1.02**	7.95 $\pm$ 0.31	8.78 $\pm$ 0.75**
Digestibility (IVDMD, %)	60.98 $\pm$ 1.83	61.18 $\pm$ 2.46	60.06 $\pm$ 4.50	64.93 $\pm$ 3.08	61.74 $\pm$ 2.70	62.89 $\pm$ 3.26
Fiber (NDF, %)	68.69 $\pm$ 2.76	68.21 $\pm$ 1.09	73.15 $\pm$ 1.74	68.13 $\pm$ 3.69	69.63 $\pm$ 2.33	69.23 $\pm$ 2.93
Ash (AIA, %)	1.54 $\pm$ 0.32	1.49 $\pm$ 0.18	1.20 $\pm$ 0.36	2.15 $\pm$ 0.42**	0.78 $\pm$ 0.33	2.09 $\pm$ 0.57**

\*Significant difference between grazed and ungrazed grasses,  $P < 0.05$ . \*\*  $P < 0.01$ , t-tests.

TABLE 6. Percent cover of common plant species in swale communities of the boundary line area (BLA) of Yellowstone's northern winter range.  $n = 10$  plots of 1 m<sup>2</sup> randomly located in each of 10 swales within each treatment. Ungrazed sites were protected from grazing for 27 and 29 years. Each swale was considered 1 replicate sample and only 1 mean value from subplots in each swale ( $n = 10$ ) was used a 1-way ANOVA with grazing as the treatment ( $P < 0.05$ ). The BLA was grazed by domestic livestock until the 1930s and some areas were seeded with exotics for hay crops, thus exotic plants are more prevalent in this part of the winter range.

Plant Species	Ungrazed		Grazed	
	$\bar{x}$	SE	$\bar{x}$	SE
Grasses:				
<i>Stipa viridula</i>	0.4	0.4	5.5	2.0**
<i>Bromus tectorum</i> (exotic)	4.7	2.8	3.1	1.4
<i>Poa pratensis</i> (exotic)	17.1	6.2	43.8	9.1**
<i>Poa compressa</i>	0		4.5	3.1*
<i>Hordeum jubatum</i>	1.0	0.6	1.4	0.9
<i>Koeleria cristata</i>	2.1	0.8	2.2	1.0
<i>Agropyron spicatum</i>	0.9	0.5	0.3	0.1
Other Grasses <sup>1</sup>	5.2	2.8	3.8	1.8
Total Grasses	31.4	1.8	64.6	19.4
Forbs:				
<i>Thlaspi arvensi</i> (exotic)	2.9	1.2	0.9	0.6*
<i>Taraxacum</i> spp. (exotic)	1.0	0.5	0.3	0.2
Other Forbs <sup>2</sup>	3.5	1.5	1.2	0.4
Total Forbs	7.4	3.2	2.4	1.2
Moss	5.1	2.2	0	

<sup>1</sup>Other grasses included *P. sandbergii*, *H. punctuata*, *A. smithii*, *S. comota*, *A. cristatum*, *A. caninum*, *Elymus cinerius*, *B. inermis*, *Sitanton hystrix* in frequencies too low for analysis.

<sup>2</sup>Other forbs included low frequencies of *Polygonum*, *Eurotia*, *Alyssum gabrum*, *Tragapogon dubius*, *Chenopodium*, *Descurainia richardsonii*, *Lappula redowskii*.

in 1990 (F. Singer and M. Harter in press) and growing season consumption was suspected to be negligible most other years, since so few elk were observed near the study plots. But spring consumption by elk was not sampled in 1986 or

1987, and it may have been more significant than I suspected.

The response of individual plant species to grazing were minimal. Only 4% (5 of 133) of the plant species found on the macroplots reflected

biomass differences that might be attributed to grazing. Three species (rosy pussytoes, fringed sage, *Arabis holboellii*) might have decreased due to grazing (not statistically different, but a consistent trend), but two other species (junegrass and thickspiked wheatgrass) might have increased due to elk herbivory (statistical differences).

Smith (1960) rated junegrass as an increaser species in response to elk herbivory in the nearby Jackson Hole region of Wyoming and thickspiked wheatgrass was resistant to grazing; these observations are consistent with these Yellowstone northern range data. The lack of any consistent grazing responses in other grasses on the study plots is noteworthy since both Idaho fescue and bluebunch wheatgrass are sensitive to grazing and clipping experiments (Daubenmire 1940, Young 1943, Evanko and Peterson 1955, Pond 1960, Caldwell et al. 1981). However, most native ungulate herbivory of Yellowstone northern winter range occurred during winter when grasses are dormant and during the first 2 weeks of initial grass growth (Houston 1982). Other research suggests that winter combined with minimal spring grazing, as occurred on the study plots, might have few effects on grass production. For example, clipping of Idaho fescue and bluebunch wheatgrass after they had cured had minimal effects on future production (Mueggler 1969). Early spring grazing has minimal effects on production of many grasses and forbs (McCarthy and Price 1942, Stoddart 1946, Blaisdell and Pechanec 1949).

Total forb and subshrub biomass was not consistently influenced by elk herbivory. A few forbs and subshrubs were less abundant at some paired grazed sites (fringed sage, rosy pussytoes, phlox). Perhaps some of these sites received elk herbivory into the spring on newly growing forbs. Jameson (1963) concluded that forbs were more sensitive to grazing than were grasses, as my data indicates. Elk eat very few forbs during the winter months in Yellowstone National Park (only 3% of winter diets), apparently because of deep snows and forb desiccation (Singer and Norland 1995), but less litter and more bare ground on grazed sites may provide conditions that are more (or less) suitable to some plants' needs for seedling establishment, for example some forb species.

Grass cover was substantially greater on elk grazed swales in the BLA. These swales are more productive than bunchgrass communities (Hous-

ton 1982). High nutrient return in urine and feces, and stimulation of grass growth were likely in the more productive swale communities (Frank and McNaughton 1992, 1993). These swales were seeded to exotic hay grasses prior to inclusion in the park during the 1930's. Apparently, grazing by native ungulates, especially by elk, contributed to the persistence of exotic grasses, while complete protection from ungulates since 1958 contributed to the decline of exotic grasses. The dominance of exotic grasses on Lamar Valley study sites (Frank and McNaughton 1993) also suggests heavy grazing by native ungulates, both elk and bison, contributes to the persistence of the Eurasian grasses.

The maintenance of aboveground and belowground biomass of grasses on heavily grazed sites on Yellowstone's northern range may be due to the benefits of ungulate defecation and urination (Williams 1966, McNaughton 1979) and to the accelerated decomposition of plant material (Gusev and Guseva 1983). Furthermore, grass meristems may be activated by grazing (McNaughton 1984), and the growing season may be extended by enhanced water availability (McNaughton 1983) and by higher early season soil temperatures on grazed sites (Whitman 1971, Archer and Detling 1985). Total protection of bunchgrass winter range sites from native ungulate grazing for 24-27 years resulted in a 4-fold increase in accumulated dead litter and standing dead vegetation. Excessive accumulations of mulch may reduce grass production (Weaver and Rowland 1952, Jameson 1963) due to a cooler soil surface (Johnston et al. 1971, Whitman 1971), but the addition of litter increased production in other studies (Ellison 1960). Whatever the mechanism, we observed no difference in total standing crop biomass between grazed and ungrazed sites during the first year, but only about one-half the total standing crop biomass was produced on grazed sites versus ungrazed sites during a second, drier year. In contrast, Frank and McNaughton (1993) reported more consistent and numerically more biomass increases due to grazing (47% more aboveground primary production from grazed sites) in Yellowstone National Park. However, their study involved different years than mine (1988 and 1989) and they sampled primary production (I sampled standing crop only). Frank and McNaughton's (1992, 1993) study sites were more mesic, and more productive than mine. Five of

their 12 study sites were dominated by grazing resistant, exotic grasses (timothy, Kentucky bluegrass, and/or smooth brome). Their study sites were located on summer range, transition range, and upper elevation - winter range, nearly all of their sites were located at higher elevations with more precipitation than my study sites. The swale sites I studied were more similar to study sites of Frank and McNaughton's (1992, 1993), i.e., depositional, productive sites and the swale comparisons were more supportive of their conclusions. Apparently grasses were stimulated by grazing in swales, and the exotic grass, Kentucky bluegrass, continued to dominate sites grazed by elk following cessation of agricultural activities.

Grass heights and shapes did not differ following 28 years of protection from native ungulate herbivory, with the single exception that vegetative culms of most grasses were shorter in grazed areas. Grazing results in shorter, more prostrate forms of grasses (Jameson 1963, McNaughton 1984) and more horizontal leaf angles (Detling and Painter 1983). My study indicated no effect on the height or numbers of seed heads of grasses from winter and early spring grazing. In contrast, most clipping or grazing during the growing season reduced seed production of grasses (Jameson 1963, Mueggler 1975, Owen and Wiegart 1981, McNaughton 1983, Ruess et al. 1983). The effects of winter grazing on seed production, as occurred on the Yellowstone northern range study sites, are less significant than are the effects of grazing during the growing season.

Grazing enhanced protein content in grasses by an average of 21% on the study sites. Several macronutrient concentrations (Ca, Ph, Mg, K) averaged 13-36% higher in grazed versus ungrazed grasses. The average crude protein content on the northern winter range for 3 common cured grasses in early August was 7.6% on ungrazed sites and 9.1% on grazed sites. Mould and Robbins (1981) indicated dry-matter intake of forage by elk sharply increased when dietary protein concentration fell below 8%. Therefore, enhancement of protein content on the northern winter range from grazing thus may be critical to elk over-winter survival. Increases in foliage N concentrations of grasses in response to grazing have been reported elsewhere (Jameson 1963, Everson 1966, Chapin 1980, Detling and Painter 1983, Day and Detling 1990). Enhanced N content has been attributed

to greater proportion of younger stems after grazing which are higher in N and other nutrients (Jameson 1963, Owensby et al. 1970). Uptake rates of N are higher after clipping (Ruess et al. 1983), soil nutrient pools may be enhanced by dung and urine deposition (Williams 1966, Ruess and McNaughton 1987), and increased net mineralization rates (Holland and Detling 1990).

Compensatory growth of grazed grasses (sensu Belsky 1986 = any positive increase in plant growth due to herbivory) may have occurred in years of adequate precipitation on my study sites and also on Coughenour's (1991) and Frank and McNaughton's (1993) study sites. Total protein yield (biomass x % protein) produced in 1986 on grazed sites was only 50% that of ungrazed sites, but in 1987 grazed sites produced 156% of the total protein yield of ungrazed sites. Gordon (1988) observed greater biomass and a higher proportion of green grass available for red deer (*C. elaphus*) on sites grazed by cattle (*Bos taurus*) during the previous winter.

### Conclusions

The upland bunchgrass sites under study on Yellowstone's northern winter range apparently were not overgrazed at the time of this investigation in 1986 and 1987, at least in terms of declines in aboveground biomass production, while only the most minor changes in species composition were observed. There were very few differences in plant species composition or numbers of plant species between grazed and ungrazed plots, and there was no evidence of accelerated mortality of bunchgrasses from elk herbivory. Protein concentrations and the concentrations of several nutrients were enhanced in grasses by elk herbivory. Very few differences were observed on the heights or growth form of grazed grasses. An increase in bare ground and a large decrease in accumulated litter and standing dead vegetation were observed on grazed sites which, combined with higher bulk densities, contributed to slightly lower soil infiltration rates on grazed sites (Lane 1991). Numerically less total forbs and shrubs were found on grazed sites, but the differences were not statistically significant. Less total grass biomass was found during 1 of 2 years on grazed sites. Limitations of the study include the small number of replicate comparisons (n = 10 paired macroplot comparisons) over only 2 years. Te-

dious hand sorting of all live and dead materials by species for this study was enormously labor intensive (> 1.3 person years) and limited the number of replicates. In addition, pre-exclosure differences in species abundance or microsite characteristics might have occurred, and possibly obscured real effects due to grazing. Parker transect data gathered at the time of exclosure in 1958 and 1962, however, does not suggest any consistent site differences at the time of exclosure (Houston 1982, Coughenour et al. 1995). Data from swale grassland types was limited to species cover data. Elk grazing on these more productive sites apparently resulted in stimulation of grasses (double the total herbaceous plant cover in grazed sites), but the elk herbivory also resulted in continued persistence of a grazing resistant exotic grass, Kentucky bluegrass, following cessation of agricultural activities. The work of Frank and McNaughton (1993) also suggests exotic grasses persist with intense elk and bison herbivory (45% consumption) in the Lamar Valley where haying activities persisted until 1952. Exotic grasses apparently declined more rapidly in ungrazed swales in the Boundary Line Area, but one exotic weed, field pennycress, was more abundant on ungrazed sites. National Park Service policy states that native animal populations be managed under conditions representing as near as possible natural conditions. Natural conditions include herbivory by native ungulates. At the time of this study,

Yellowstone's northern elk winter range supported 21 elk/km<sup>2</sup> during the winter months (Singer 1991), yet only minor differences were detected between grazed bunchgrass sites and paired sites protected from native ungulates for nearly three decades. I propose the minimal number of grazing effects observed on the study plots are due to the restriction of direct and indirect effects from ungulate activity (grazing, trampling, bedding, trailing) to the winter season only. During the winter, plants are in senescence, the ground is frozen and, in most situations, the ground is also snowcovered, minimizing the effects from herbivory by elk. I stress these findings apply only to the upland bunchgrass sites under study and to sites where native ungulate herbivory was restricted to the winter period only.

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### Literature Cited

- Archer, S., and J.K. Detling. 1985. Evaluation of potential herbivore mediation of plant water status in a North American mixed-grass prairie. *Oikos* 47:287-291.
- Balling, Jr., R.C., G.A. Meyer, and S.G. Wells. 1992. Climate change in Yellowstone National Park: Is the drought-related risk of wildfires increasing? *Climate Change* 22:35-45.
- Belsky, A.J. 1986. Does herbivory benefit plants? A review of the evidence. *Am. Nat.* 127:870-892.
- Blaisdell, J.P., and J.F. Pechanec. 1949. Effect of herbage removal at various dates on vigor of bluebunch wheatgrass and arrowleaf balsamroot. *Ecology* 30:298-305.
- Caldwell, M.M., J.H. Richards, D.A. Johnson, R.S. Nowak, and R.S. Dzurea. 1981. Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. *Oecologia* 50:14-24.
- Caughley, G. 1970. Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. *Ecology* 51:53-72.
- \_\_\_\_\_. 1976. Wildlife management and the dynamics of ungulate populations, pp. 183-246. *In*: T. H. Croaker (ed), *Applied Biology Vol. 1*. Academic Press, New York.
- \_\_\_\_\_. 1979. What is this thing called carrying capacity?, pp. 2-8. *In*: M.S. Boyce and L. D. Hayden-Wing (eds), *North American elk: ecology, behavior and management*. University of Wyoming, Laramie.
- Cayot, L.J., J. Prukop, and D.R. Smith. 1979. Zootic climax vegetation and natural regulation. *Wildl. Soc. Bull.* 7:162-169.
- Chapin, F.S., III. 1980. The mineral nutrition of wild plants. *Ann. Rev. Ecol. Syst.* 11:223-260.
- Chase, A. 1986. *Playing God in Yellowstone*. Atlantic Monthly Press, New York, NY. 446 pp.
- Cole, G.F. 1971. An ecological rationale for the natural or artificial regulation of native ungulates in parks. *Trans. N. Am. Wildl. Conf.* 36:417-425.
- Congressional Record. 1986. Senate hearings. S12612. U.S. House of Representatives.
- Coughenour, M.B. 1991. Biomass and nitrogen responses to grazing of upland steppe in Yellowstone's northern winter range. *J. Appl. Ecol.* 28:71-82.

- Coughenour, M.B., and F.J. Singer. 1991. The concept of overgrazing and its application to Yellowstone's northern range. Pages 209-230 in: M.S. Boyce and R. Keiter (eds), Examining the Greater Yellowstone. Yale Univ. Press.
- Coughenour, F.J. Singer and J. Reardon. 1995. Parker transects revisited. In: D. Despain and R. Hamre (eds.), Plants and Their Environments: First Biennial Scientific Conference on the Greater Yellowstone Ecosystem. U.S. National Park Service, Trans. and Proc. Ser. (in press).
- Craighead, J.J., G. Atwell, and B.W. O'Gara. 1972. Elk migrations in and near Yellowstone National Park. Wildl. Monogr. 29:1-48.
- Daubenmire, R. 1940. Plant succession due to overgrazing in the *Agropyron* bunchgrass prairie of southeastern Washington. Ecology 21:55-64.
- DeAngelis, D.L., and J.C. Waterhouse. 1987. Equilibrium and non-equilibrium concepts in ecological models. Ecol. Monogr. 57:1-21.
- Despain, D. 1991. Yellowstone vegetation: consequences of environmental and history in a natural setting. Roberts Rinehart Publ., Boulder, CO. 239 pp.
- Detling, J.K., and E.L. Painter. 1983. Defoliation responses of western wheatgrass populations with diverse histories of prairie dog grazing. Oecologia 57:65-71.
- Day, T.A., and J.K. Detling. 1990. Grassland patch dynamics and herbivore grazing preference following urine deposition. Ecology 71:180-188.
- Ellison, L. 1960. Influence of grazing on plant succession of rangelands. Bot. Rev. 26:1-78.
- Evanko, A.B., and R.A. Peterson. 1955. Comparisons of protected and grazed mountain rangelands in southwestern Montana. Ecology 36:71-82.
- Everson, A.C. 1966. Effects of frequent clipping at different stubble heights on western wheatgrass (*A. smithii*). Agron. J. 58:33-35.
- Frank, D.A., and S.J. McNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. Ecology 73:2043-2058.
- Frank, D.A. and S.J. McNaughton. 1993. Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. Oecologia 96:157-161.
- Gordon, I.J. 1988. Facilitation of red deer grazing by cattle and its impact on red deer performance. J. Appl. Ecol. 25:1-10.
- Gusev, A.A., and N.A. Guseva. 1983. Participation of wild ungulates in the decomposition of vegetation in forest-steppe ecosystems. Ekologiya 6:51-55. (Translated into English)
- Holland, F.A. and J.K. Detling. 1990. Plant responses to herbivory and belowground nitrogen cycling. Ecology 71:1040-1049.
- Houston, D.B. 1976. Research on ungulates in northern Yellowstone National Park, pp. 11-27. In: Research in the parks. Trans. Natl. Park Centennial Symp., Natl. Park Serv. Symp. Ser. No. 1.
- \_\_\_\_\_. 1982. The northern Yellowstone elk: ecology and management. MacMillan Publ. Co., Inc., New York.
- Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54:184-211.
- Jameson, D. 1963. Responses of individual plants to harvesting. Bot. Rev. 29:532-594.
- Johnston, A., J.E. Dormaar, and S. Smoliak. 1971. Long-term grazing effects on fescue grassland soils. J. Range Manage. 24:185-188.
- Kay, C.E. 1987. Too many elk in Yellowstone - book review. Western Wildlands 13:39-44.
- Lane, J. 1991. Characterization and comparisons of soils inside and outside of grazing exclosures on Yellowstone National Park's Northern Winter Range. M.S. Thesis, Mont. State Univ., Bozeman, MT.
- McCarthy, E.C., and R. Price. 1942. Growth and carbohydrate content of important mountain forage plants in central Utah as affected by clipping and grazing. USDA, Tech. Bull. 818. 51 pp.
- McNaughton, S.J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. Am. Nat. 113:691-703.
- \_\_\_\_\_. 1983. Compensatory plant growth as a response to herbivory. Oikos 40:329-336.
- \_\_\_\_\_. 1984. Grazing lawns: animals in herds, plant form and coevolution. Am. Nat. 124:863-886.
- Meagher, M. 1973. The bison of Yellowstone National Park. Natl. Park Serv. Sci. Monogr. 1:1-161.
- \_\_\_\_\_. 1989. Range expansion by bison of Yellowstone National Park. J. Mammal. 70:670-675.
- Merrill, E.H., and M.S. Boyce. 1991. Summer range and elk population dynamics. Pages 263-273 in: R.A. Keiter and M.S. Boyce, eds. The Greater Yellowstone Ecosystem: Redefining America's Wild Heritage. Yale Univ. Press, New Haven.
- Mould, E.D., and C.T. Robbins. 1981. Digestive capabilities of elk compared to white-tailed deer. J. Wildl. Manage. 46:22-29.
- Mueggler, W.F. 1969. Responses of mountain grassland vegetation to clipping in southwestern Montana. Ecology 48:942-949.
- \_\_\_\_\_. 1975. Rate and pattern of vigor recovery in Idaho Fescue and bluebunch wheatgrass. J. Range Manage. 28:198-204.
- Mueggler, W.F., and W.L. Stewart. 1980. Grassland and shrubland habitat types of western Montana. USDA Gen. Tech. Report INT-66. 154 pp.
- Owens, D.F., and R.G. Wiegert. 1981. Mutualism between grasses and grazers: an evolutionary hypothesis. Oikos 36:376-378.
- Owensby, C.E., R.M. Hyde, and K. Anderson. 1970. Effects of clipping and supplemental N and water on loamy upland bluestem range. J. Range Manage. 23:341-346.
- Peek, J.M. 1980. Natural regulation of ungulates. Wildl. Soc. Bull. 8:217-227.
- Platt, J.R. 1964. Strong inference. Science 16:347-353.
- Pond, F.W. 1960. Vigor of Idaho fescue in relation to different grazing intensities. J. Range Manage. 13:28-30.
- Rohlf, F.J., and R.R. Sokal. 1969. Statistical tables. W. H. Freeman and Co., Publ., San Francisco. 253 pp.
- Ruess, R.W., S.J. McNaughton, and M.B. Coughenour. 1983. The effects of clipping, nitrogen source, and nitrogen concentration on the growth responses and nitrogen uptake of an East African sedge. Oecologia 59:253-261.
- Ruess, R.W., and S.J. McNaughton. 1987. Grazing and the dynamics of nutrients and energy regulated microbial processes in the Serengeti grasslands. Oikos 49:101-110.

- Sinclair, A.R.E. 1977. The African buffalo—a study of resource limitation of populations. Univ. of Chicago Press, Chicago.
- Singer, F.J. 1991. The ungulate prey base for large predators in Yellowstone National Park. Pages 323-348. In M.S. Boyce and R. Keiter, eds. Examining the Greater Yellowstone, Proc., Laramie, Wyo. Yale Univ. Press, New Haven.
- Singer, F.J. and J.E. Norland. 1994. Niche relationships within a guild of ungulates following release from artificial controls, Yellowstone National Park, Wyoming. Can. J. Zool. 72:1383-1394.
- Singer, F.J. and M.K. Hauter. 1995. Comparative effects of elk herbivory and 1988 fires on northern Yellowstone National Park grasslands. Ecol. Applic. (in press).
- Stoddart, L.A. 1946. Some physical and chemical responses of *Agropyron spicatum* to herbage removal at various seasons. Utah Agr. Exp. Sta., Bull. 324. 24 pp.
- Weaver, J.E., and N.W. Rowland. 1952. Effects of excessive natural mulch on development, yield and structure of native grassland. Bot. Gaz. 114:1-19.
- Whitman, W.C. 1971. Influence of grazing on microclimate of mixed grass prairie. pp. 207-218 in K.M. Kreitlow and L. Hart, eds. Plant Morphogenesis as a Basis for Scientific Management of Range Resources. USDA Agric. Res. Serv. Misc. Publ. No. 1271.
- Williams, C.H. 1966. Nitrogen, sulfur and phosphorus, their interactions and availability. Trans. Internatl. Soil Sci. Soc. (Aberdeen, Scotland) 1966:93-111.
- Young, V.A. 1943. Changes in vegetation and soil of Palouse prairie caused by overgrazing. J. For. 41:834-838.

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