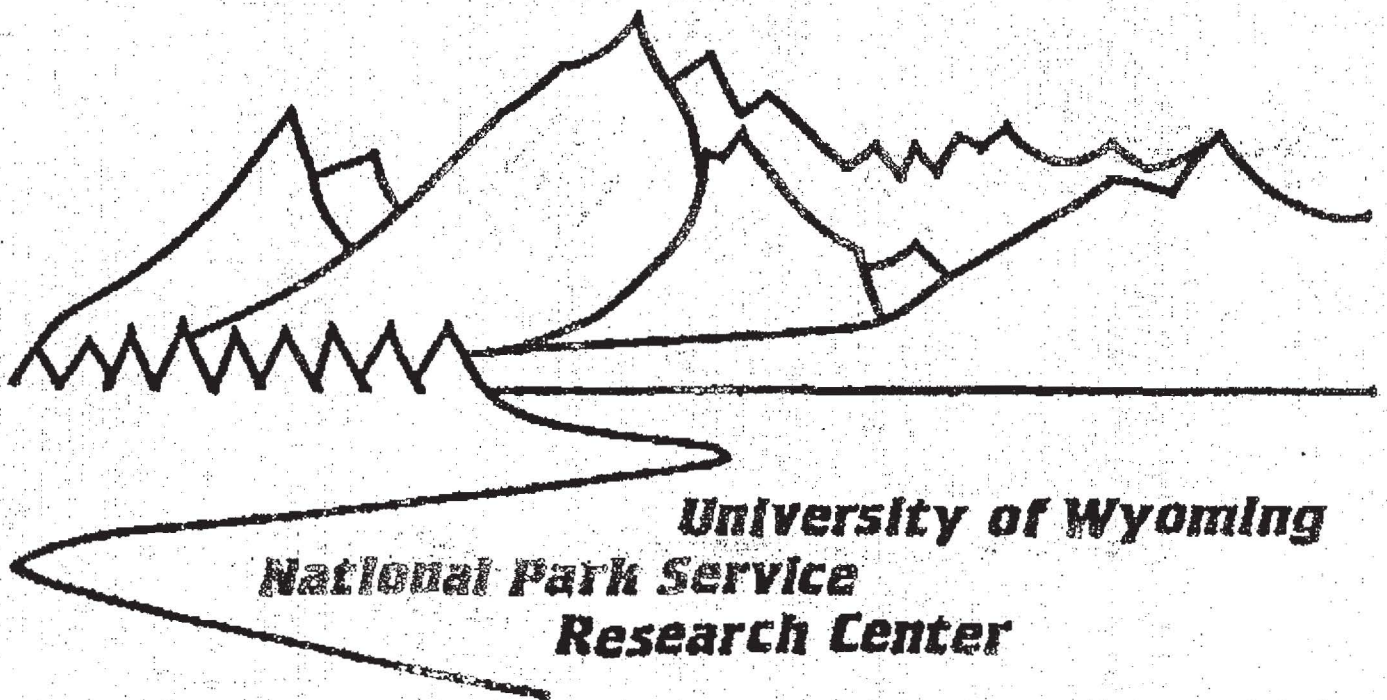


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INTERACTIVE ECOLOGY OF PLANTS, LARGE
MAMMALIAN HERBIVORES AND DROUGHT IN
YELLOWSTONE NATIONAL PARK



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INTERACTIVE ECOLOGY OF PLANTS, LARGE MAMMALIAN HERBIVORES,
AND DROUGHT IN YELLOWSTONE NATIONAL PARK

FINAL REPORT

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ABSTRACT

Yellowstone National Park possesses large, free-roaming herds of native large mammalian herbivores. The objective of this study was to explore the effects of large grazers, primarily elk (Cervus elaphus) and bison (Bison bison), on energy and nutrient flows in Yellowstone Park's northern range. Net aboveground primary production, ungulate consumption, and ungulate fecal deposition were measured in a variety of mostly non-forested sites in winter, transitional, and summer range areas. Measurements were concentrated in 1988, a drought year, and 1989, a year of near-average precipitation. Movable exclosures at 13 sites were used to measure consumption and aboveground production under grazing regimes (aPn), and permanent exclosures at 4 sites were used to measure production without grazers.

Ungulates stimulated aboveground production at 3 of 4 sites from 36 to 85%. Ungulates had no effect on production at a summer range site that experienced the severest drought of any site. These results indicate ungulates regulate primary production in the Yellowstone ecosystem, and suggest their regulatory influence is constrained by climate.

Growing season consumption (gH), that period when green biomass was at least 20% of total standing crop, and aPn were positively related, except at sites that

possessed a single species contributing over 90% of the biomass, where no grazing occurred. Grazing was positively associated with both plant growth, when green biomass concentration and forage N were highest, and dung deposited at sites. These results indicate that ecosystem processes are spatially and temporally linked in the Yellowstone landscape.

Both aPn and gH declined from 1988 to 1989. The decline in gH was likely due to the dramatic reduction in elk and bison from 1988 to 1989. The aPn reduction may have resulted from death or injury to plants during the 1988 drought and/or a decline in herbivore-induced stimulation. Species composition of vegetation shifted dramatically between years, and grazing appeared to have an increasing impact on plant community species composition with increasing drought severity.

ACKNOWLEDGEMENTS

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There were innumerable park service employees who assisted with logistics during the project. The entire Yellowstone Park Research Division staff was indispensable throughout the study. In particular, we thank John Varley for his key and never-wavering support and Frank Singer, who was the park's contact person for the study, and who generously provided horses, packer, and many other necessities. We also extend special gratitude to Mary Meagher, whose recommendations were impeccable, and who is a principal reason for the success of the project. District ranger Steve Frye always attempted to help, even during the 1988 fires, when he could have easily, and understandably, claimed preoccupation with other concerns. Subdistrict ranger Joe Fowler's ecological insights were

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INTRODUCTION

The form and function of large mammalian herbivores reflect the forage they have evolved with and the ecosystems they have evolved in. Grasses and hypsodont - toothed mammalian herbivores appeared simultaneously during the Eocene Epoch (Stebbins 1981) and both experienced radiations from the Miocene into the Pleistocene (Love 1972, Morton 1972) as orogeny created large arid grasslands in regions around the world (Raven and Axelrod 1974, Stebbins 1981). The development of hypsodont (high crowned) dentition, well suited to a diet of abrasive, siliceous grass (Stebbins 1981) was associated with digestive systems specialized for fermentation of graminoid forages high in fiber (Demment and van Soest 1985, Hofmann 1989), as well as cursorial and saltatorial body forms adapted for efficient travel to follow a spatio-temporally shifting forage base in large, open environments (Stebbins 1981).

Prior to the worldwide spread of European influence, as much as one half of the terrestrial surface of the Earth was occupied by grasslands with fauna in most areas dominated by large mammalian herbivores representing Artiodactyla, Perissodactyla, Proboscidea, or Macropodidae (McNaughton 1989). The conversion of grassland to cropland and the replacement of native with domesticated

herbivores has reduced the extent of these areas to the brink of elimination. Today, this once common ecosystem in its most basic intact unit, e.g., full-year habitat for its native large herbivores, is restricted to a few of the world's largest grassland reserves.

Native large herbivores have tremendous effects on ecosystem function (Naiman 1988, McNaughton et al. 1988, Detling 1988). Although much is known about the functional properties of grassland-dominated habitats in general (Coupland 1979, French 1979, Huntley and Walker 1982), and the impact of native grazers on grasslands in particular (e.g., Coppock et al. 1983, Collins and Barber 1985, Krueger 1986, Polley and Wallace 1986, Day and Detling 1990), little is known about the properties of such ecosystems when still possessing large, free-ranging herds of their Pleistocene mammalian herbivore fauna. The tropical savanna habitat of Africa, supporting the largest herds of grazing mammals and highest herbivory rates on Earth (Lock 1972, Sinclair 1975, Edoma 1981, McNaughton 1983, 1985), until now has been the only reference point. Here I present a second example from Yellowstone National Park, a temperate mountainous reserve, which maintains one of the highest concentrations of ungulates in North America.

The objectives of this study were to measure rates of primary production, consumption, and nutrient return from

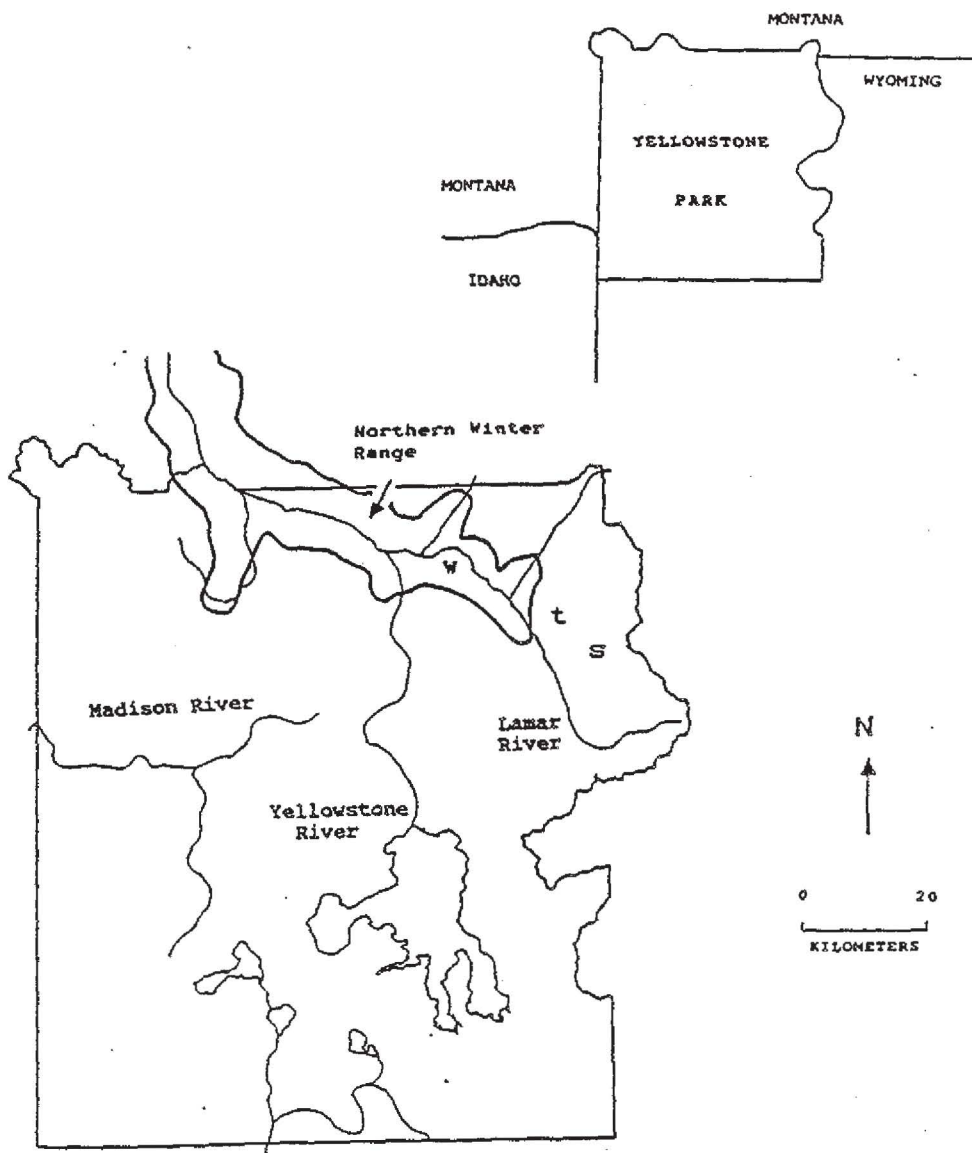
ungulates to the soil at a variety of sites in all seasonal ranges in Yellowstone National Park. The study used both temporary, movable exclosures and large, permanent exclosures to examine primary production with and without large mammalian grazers. Measurements were made during two dramatically disparate years in regards to weather and ungulate numbers and, thus, provide an opportunity to explore the effect of these different prevailing conditions on ecosystem structure and function.

STUDY AREA

Yellowstone National Park was established in 1872 and today occupies 8995 km² located between 44° 08' and 45° 07' N and 111° 10' and 110° W in the northwest corner of Wyoming (Fig 1). Elevations range from 1500 m to over 3000 m. However, much of the area is a gently rolling plateau between 1200 and 2600 m (Meagher 1973, Houston 1982). The Park is mostly covered by tertiary and quarternary volcanic deposits that have been glaciated several times during and after their deposition (Keefer 1971).

Eight ungulate species are found in Yellowstone National Park, elk (Cervus elaphus), bison (Bison bison), mule deer (Odocoileus hemionus), white-tailed deer (O. virginianus), pronghorn (Antilocapra americana), bighorn sheep (Ovis canadensis), moose (Alces alces), and mountain goats (Oreamnos americanus). The focus of the study was non-forested habitat in the northeastern portion of the park primarily used by northern range elk and bison. Herds of elk and bison forage during the winter in the northern winter range that occupies lower portions of the Yellowstone, Lamar, Gardner, Slough, and Soda Butte drainages (Fig. 1). The northern winter range is about 1000 km² in area, roughly 83% of which is in the park and the remainder outside the park down the Yellowstone River

Fig. 1. Map of study region, indicating deliniation of the northern winter range and the winter (w), transitional (t) and summer (s) range study site locations. Adapted from Houston (1982).



valley (Houston 1982). Some elk and bison are shot each fall and winter when they exit the park.

Northern range elk and bison migrate off the winter range in spring to forage at higher elevations, and return to the winter range in late-summer and fall. Northern elk disperse during the summer throughout the park where they mix with animals of the Madison herd, the park's only other resident elk herd, and members of several other herds that winter outside the park (Houston 1982).

Northern bison summer movements are restricted to the upper Lamar drainage, Specimen Ridge, and the Mirror Plateau where they mix with Pelican Valley herd members (Meagher 1973).

Climate of the park is generally cool and moist, with most of the precipitation falling as snow or as rain on snowpack (Despain 1987). The northern winter range is warmer and drier than the rest of the park. Houston (1982) summarized 30 years of climatic data from 4 winter range sites and 2 higher elevation sites characteristic of elk and/or bison summer range. Mean annual temperature and precipitation of winter range sites was 3.8° C and 349 mm compared to 0.6° C and 536 mm for summer range sites, respectively.

Vegetation of the northern winter range is grassland and shrub-grassland with isolated trees or small copses of aspen (Populus tremuloides) or cottonwood (Populus spp.)

in mesic sites and lodgepole pine (Pinus contorta) and Douglas fir (Pseudotsuga menziesii) primarily on rocky outcrops and north facing slopes. Ridges of the upper Lamar drainage, the location of the transitional and summer range study area, are densely forested on their flanks with lodgepole pine (Pinus contorta), Engelmann spruce (Picea engelmannii), subalpine fir (Abies lasiocarpa), and whitebark pine (Pinus albicaulis), and covered with grassland and shrub-grassland on much of their ridgelines. Vegetation of the central plateau of the park is mostly forest comprised primarily of lodgepole pine, but also includes locally abundant areas of subalpine fir, Englemann spruce, and whitebark pine.

The management of northern range elk and bison has varied considerably, reflecting the evolution of national park management (Houston 1982, Meagher 1973). Northern range elk management has included: (1) hunting and poaching before and for several years after the establishment of Yellowstone National Park in 1872, (2) protection, characterized by winter feeding programs and sporadic, aggressive reductions of coyotes (Canis latrans), mountain lions (Felis concolor), and wolves (Canis lupus) from the mid-1890s into the 1930s, and (3) intensive elk reductions from 1935 to 1968. Yellowstone bison were hunted and poached to near extirpation by 1880 when fewer than 50 survived in the park. Today's Yellowstone bison

are a hybrid of the descendants of the remnant native park bison and plains bison, which were introduced in 1902 and closely herded until 1915. Reductions of northern range bison, which likely began as a normal ranching objective in the early 1900s, continued into the late-1960s, when there were roughly 200 bison in the northern herd (Meagher 1973).

Since 1969, all ungulate species have fluctuated without human interference in the park, e.g., "natural regulation" (Cole 1971, Houston 1982). Northern elk increased from about 4000-5000 in 1968, the last year of reductions, to 12,000-16,000 by the late-1970s (Houston 1982). In 1988, the first year of this study, after several wet summers and mild winters in the early and mid-1980s, northern range elk had increased to 22,500 (Singer et al. 1988), and northern range bison comprised over 577 individuals (Meagher pers. comm.).

STUDY SITES

The focus of the study was winter, transitional, and summer range areas used by northern range elk and bison in the northeastern portion of Yellowstone Park (Fig. 1). Winter range sites were located in the upper northern winter range; near Crystal Creek (w1), in the Lamar Valley (w2 and w3) and along Slough Creek (w4). Transitional range sites (t1-3, tb) and summer range study sites (s1-5) were on the same ridge, situated between Cache and Calfee Creeks in the Lamar River drainage, e.g., Cache-Calfee ridge (Table 1). All transitional range communities were within .5 km of each other, and summer range sites were separated by no more than 1 km.

Vegetation was markedly heterogeneous in each of the seasonal range areas due to steep, complex soil and moisture gradients created by uneven topography. Study sites were selected to represent a spectrum of topographic positions, primary productivities, and plant community species compositions in each of the seasonal-use areas (Table 1).

Measurements span two profoundly disparate years: 1) 1988, a year of record drought and large landscape-scale wildfires, when northern range elk and bison populations were at their highest levels in recent decades, and 2) 1989, a near-average year in terms of temperature and

Table 1. Study site descriptions.

SITE	TOPOGRAPHIC POSITION	VEGETATION	HERBACEOUS DOMINANTS
W1	BENCH	GRASSLAND	<u>Festuca idahoensis</u> , <u>Lupinus sericeus</u>
W2	RIVER TERRACE	GRASSLAND	<u>Phleum pratense</u> , <u>Poa pratensis</u>
W3	VALLEY BOTTOM	GRASSLAND	<u>Bromus inermis</u>
W4	RIVER TERRACE	SEDGE MEADOW	<u>Carex rostrata</u>
T1	RIDGETOP	GRASSLAND	<u>Koeleria cristata</u> , <u>Astragalus miser</u>
T2	BENCH	GRASSLAND	<u>Phleum pratense</u> , <u>Juncus hallii</u>
T3	MID-SLOPE	SHRUB-GRASSLAND	<u>Phleum pratense</u> , <u>Agropyron caninum</u>
TB	MID-SLOPE	GRASSLAND*	<u>Bromus carinatus</u> , <u>Agropyron caninum</u>
S1	RIDGETOP	GRASSLAND	<u>Danthonia unispicata</u> , <u>Poa scabrella</u>
S2	MID-SLOPE	SHRUB-GRASSLAND	<u>Stipa occidentalis</u> , <u>Bromus carinatus</u>
S3	BENCH	GRASSLAND	<u>Phleum pratense</u> , <u>Carex sp.**</u>
S4	BENCH	GRASSLAND	<u>Poa sp***</u> , <u>Stipa occidentalis</u>
S5	BENCH	FOREST	<u>Calamagrostis rubescens</u>

* a shrub-grassland community that burned in 1988 and was sampled in 1989 only.

** includes C. xerantica and C. raynoldsii.

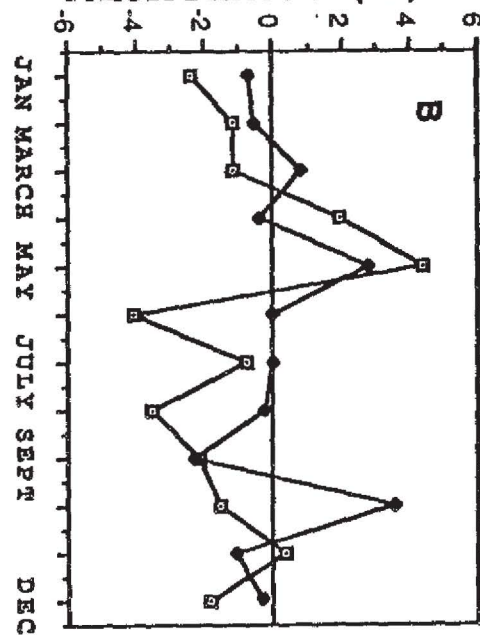
*** includes P. nevadensis and others.

precipitation (Fig. 2), when northern range elk and bison populations declined to 38-43% (Singer et al. 1989) and 50% (Meagher pers. comm.) of their 1988 levels, respectively. The onset of the 1988 drought was early June, following a wetter than average April and May. Precipitation from June through August in 1988 was 32% of average, compared to 97% of average in 1989. Because growing season initiation among sites ranged from late-March to early-June, and was inversely related to elevation, a gradient of drought severity existed from mild in the winter range, where conditions were wet for the first 2 months of the growing season, to severe in the summer range, where no precipitation fell after the growing season commenced. Although no study site burned, wildfires occurred within a kilometer of all sites. A sagebrush community that was thoroughly burned (all aboveground standing biomass was consumed) in 1988 (tb) and located immediately adjacent to a sampled transitional range sagebrush site (t3), was added to the study in 1989.

Soils within the major rooting zone (0-10 cm) at the sites were loams, silt loams, and sandy loams (Table 2.). Soil pH values were all slightly acidic, ranging from 5.14 in a summer range lodgepole pine forest to 6.75 at the summer range ridgetop site. Bulk density, field capacity, organic matter, and soil nitrogen ranged from 0.83-1.32 g cc⁻¹, 16.0-65.2%, 5.2-25.5%, and 0.1-0.9%,

Fig. 2. Departures from (a) mean monthly temperature, calculated from daily midpoint temperatures, and b) monthly precipitation for 1988 (—■—) and 1989 (—●—). Data are from Mammoth, Wyoming (U. S. Department of Commerce 1988, 1989).

DEPARTURE FROM AVERAGE
PRECIPITATION (cm)



DEPARTURE FROM AVERAGE
MONTHLY TEMPERATURE (C)

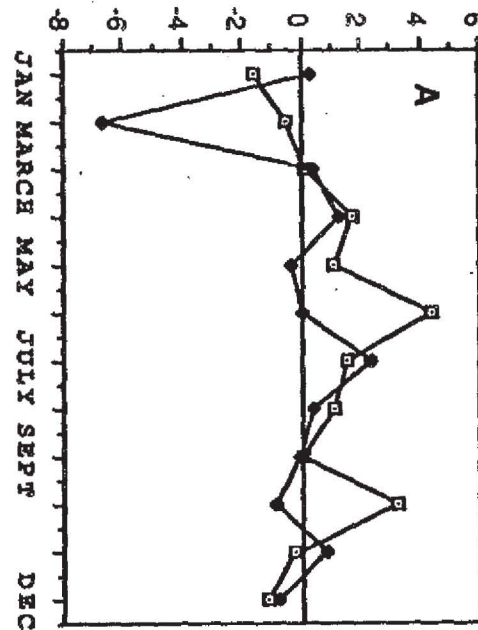


Table 2. Study site soil properties.

SITE	pH	BULK DENSITY (g/cc)	FIELD CAPACITY (% H ₂ O)	%OM ^a	%N	USDA TEXTURE CATAGORIES (%)			SOIL CLASSIFICATION
						SAND	SILT	CLAY	
W1	6.30	1.31	16.0	5.4	0.2	69.7	26.5	3.8	sandy loam
W2	6.66	1.16	23.6	6.1	0.2	32.2	61.7	6.1	silt loam
W3	5.84	0.91	34.3	14.2	0.5	38.1	49.4	12.6	loam
W4	5.67	0.64	65.2	25.5	0.9	23.6	64.1	12.2	silt loam
T1	6.14	0.95	35.2	13.8	0.7	43.4	49.9	6.7	silt loam
T2	5.62	0.90	37.1	18.8	0.7	40.1	52.1	7.9	silt loam
T3	5.61	0.91	39.6	14.7	0.7	40.1	55.2	4.8	silt loam
TB	5.83	0.98	34.1	13.6	0.7	48.5	45.4	6.1	sandy loam
S1	6.75	1.32	19.8	5.2	0.1	59.4	30.1	10.4	sandy loam
S2	5.89	1.02	30.6	11.3	0.5	48.4	43.1	8.5	loam
S3	5.57	0.83	46.6	16.6	0.8	42.6	48.2	9.1	loam
S4	5.45	0.90	35.0	14.5	0.6	37.6	54.1	8.2	silt loam
S5	5.14	1.06	24.8	7.7	0.2	29.5	52.3	18.2	silt loam

a Percent organic matter from loss on ignition.

respectively. Omitting the burned site, tb, from analysis, Spearman rank correlations revealed pH was negatively associated with organic matter ($P=.046$) and positively associated with bulk density ($P=.036$); field capacity was positively associated with organic matter ($P<.002$) and N ($P<.002$), and negatively associated with bulk density ($P<.002$); and N was positively associated with organic matter ($P=.002$) and negatively associated with bulk density ($P<.003$). There was a tendency for pH and bulk density to increase, and field capacity, percent organic matter, and percent N to decline from the base to top of a slope. Soil properties are well known to be closely tied to topographic gradients in semiarid habitats (Schimel et al. 1985, Burke 1989). Site w4, a wet sedge meadow, was notable as having the lowest bulk density and the highest field capacity, percent organic matter, and percent N.

METHODS

Net aboveground primary production and large herbivore consumption were measured at each of the sites. Aboveground biomass of each species was estimated with canopy intercept, except at site w4 where vegetation was too tall for canopy intercept and, therefore, was clipped. Details of canopy intercept in this study have been described elsewhere (Frank and McNaughton 1990). Briefly, canopy intercept relates aboveground standing crop to the number of contacts a pin makes when passed at a fixed angle through vegetation. The technique was strongly affected by plant growth form. Slopes for the relationship of biomass (g m^{-2}) on mean contacts for 5 functionally separate plant growth forms encountered in the study ranged from 0.175 to 0.853, and r^2 for the 5 groups ranged from 0.831 to 0.956, indicating the method affords a high degree of precision for estimation of standing crop.

Temporary exclosures (1.5 x 1.5 m, n=5-7 per site) were randomly moved approximately every 28 days to estimate net aboveground production under grazing and large herbivore consumption. Site production was calculated as the sum of significant (ANOVA, $P < .05$) increments of standing crop inside exclosures. Consumption was defined as a significant difference

(ANOVA, $P < .05$) in standing crop inside versus outside the exclosures. Total consumption for a site was calculated as the sum of the differences. Variances of production and consumption for periods greater than one sampling interval were calculated by summing sampling interval variances, since

$$\text{var}(a+b) = \text{var}(a) + \text{var}(b).$$

The 28 day sampling interval was a compromise between limiting microenvironmental effects by fencing (intensive sampling), and the desire to embrace system diversity (extensive sampling). Notable exceptions to the normal sampling regimen were 34-36 day intervals for summer range sites during July - August, 1988, due to restricted backcountry access during the wildfires. Since most of the vegetation had browned and no detectable plant growth or consumption occurred during this period, fencing effects were negligible. Nevertheless, it should be borne in mind that fencing can influence vegetation in confounding ways (Cowlinshaw 1951, Heady 1957).

To determine the existence of feedback mechanisms between herbivores and vegetation, production of grazed vegetation was compared with production of ungrazed vegetation in large, permanent exclosures at 4 sites. Ungrazed production was estimated as peak standing crop

inside permanent exclosures (n=3 per site) which were erected in August of 1987 (w1, t2, s4) and 1988 (w4).

Canopy height was estimated in 1989 as the resting height of a styrofoam sheet (5.0 g, 26x21cm) when gently laid on the vegetation (n=10). Canopy height and standing biomass estimates were made at the same time, but different random locations at each site throughout the snow-free year. Vegetation biomass concentration (C, mg cc⁻¹) was calculated by dividing standing crop by canopy height (McNaughton 1976, 1984, 1985). This estimate does not include a term for the covariance between the variables (Welsh et al. 1988), since height and standing crop measurements were decoupled spatially. To explore the maximum potential spurious effect of omitting the covariance term when calculating C, extreme values of covariance were approximated from the data. Among samples from three sites where standing crop varied widely, the mean maximum proportional departure from C due to covariance was 5% (SE=0.02, n=12). There was no trend in deviation through the season (P=.37), and no difference between sites (P=.39). This amount of unknown error would have no effect on the conclusions.

In an effort to index the amount of nutrient flow from ungulates to the soil, dung deposition was calculated as

$$D = \sum_{i=1}^m \left(\sum_{j=1}^{10} p_{ij} \times b_{ij} / 20 \right) / 10 \quad (1)$$

where D (g m^{-2}) is dung deposition at a site, and p_{ij} and b_{ij} are the number of fecal piles in a 10×2 m transect and the mean dry weight for a fecal pile, respectively, for the i th of m ungulate species and the j th of 10 transects. Mean oven-dry weights of elk, bison, and pronghorn fecal piles randomly collected near the study sites were 92 g m^{-2} ($\text{SE}=10.6$, $n=38$), 294 g m^{-2} ($\text{SE}=25.6$, $n=36$), and 37 g m^{-2} ($\text{SE}=4.2$, $n=10$), respectively.

Measured vegetation state variables were standing crop inside permanent exclosures (ug), inside temporary exclosures (pg) and in grazed vegetation (g). Derived variables were:

cPn = control, ungrazed aboveground net production

(Pn) = peak ug;

aPn = actual, grazed Pn = sum of pg increments;

dPn = rate of Pn per day for a sampling interval = pg increments/#days of sampling interval;

H = consumption = aPn - gPn;

H% = percent consumption = H/aPn;

dH = rate of H per day for a sampling interval = H/days of sampling interval;

C = standing biomass concentration (g cc^{-1}) = g or ug

divided by vegetation canopy height measured with styrofoam sheet;

D = dung deposited.

Consumption and/or percent consumption are reported for the entire snowfree year (e.g., H, H%) the growing season (e.g., gH, gH%), and the late-snowfree season (e.g., LH) separately. Terminology and definitions largely follow McNaughton (1985).

Standard statistical methods were used for analyses. All proportions were arcsine-transformed to meet parametric test requirements. Nonparametric tests were employed when satisfying requirements was impossible. All relationships were least square fits, except where noted. Plant nomenclature follows Hitchcock and Cronquist (1973) and species diversity was indexed with H' (MacArthur 1955). Nitrogen concentration of forages was determined with a Carlo Erba CNS Analyzer using standard protocol.

RESULTS: PROCESSES

Plants

An early objective of the study was to select sites representing a spectrum of herbaceous primary productivities (aPn). Ranges for aPn were 27-539 g m⁻² in 1988 and 16-589 g m⁻² in 1989 (Fig 3). During both years the least productive community was a summer range, xeric ridgetop (s1, Table 3), and the most productive community was a winter range, wet sedge meadow (w4, Table 3). Herbaceous production declined from 1988 to 1989 at 6 of 11 sites (Table 3). Moreover, mean aPn of paired sites, sites where aPn was measured both years, declined from 278 g m⁻² in 1988 to 226 g m⁻² in 1989 (paired comparison ANOVA, $F_{1,271}=5.9$, $P<.05$), indicating the reduction in aPn was a landscape phenomenon. Production of Artemisia tridentata at two shrub-grassland sites, t3 and s2, did not differ between years (Table 3).

Production was associated with several soil properties. Spearman rank correlations showed 1989 aPn was negatively related to bulk density ($P=.05$) and percent sand ($P=.02$), and weakly positively related to percent silt ($P=.06$) and field capacity ($P=.10$).

In this study, an A. tridentata - graminoid community was sampled one year after it had burned in 1988. The fire caused complete mortality of A. tridentata

Fig. 3. Frequency histograms of α Pn in A) 1988 and B) 1989. Gray bars are sites for which data exist for both years.

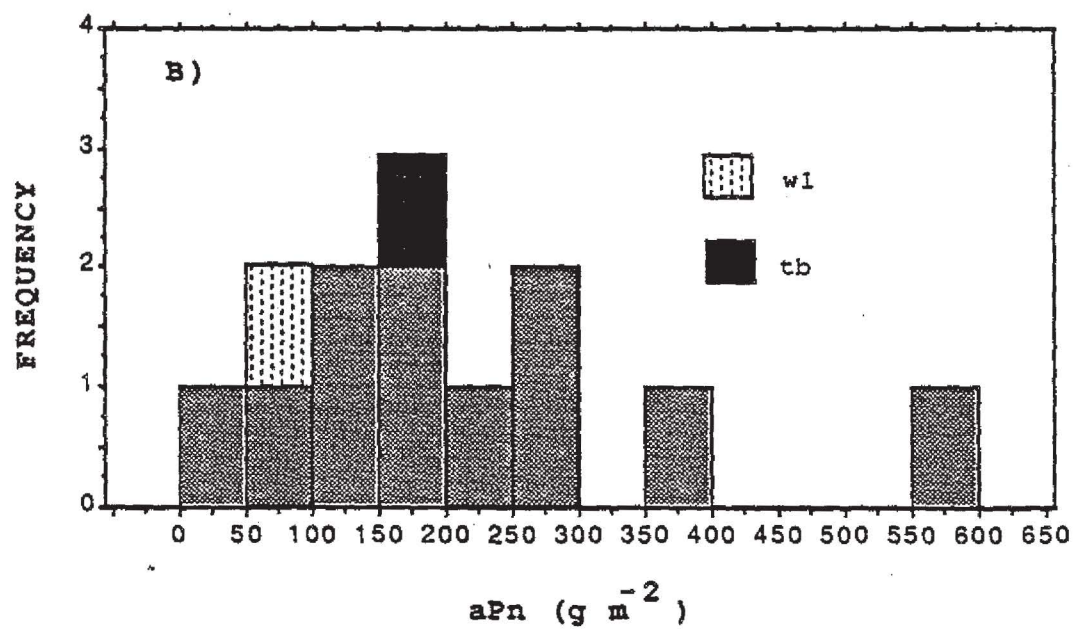
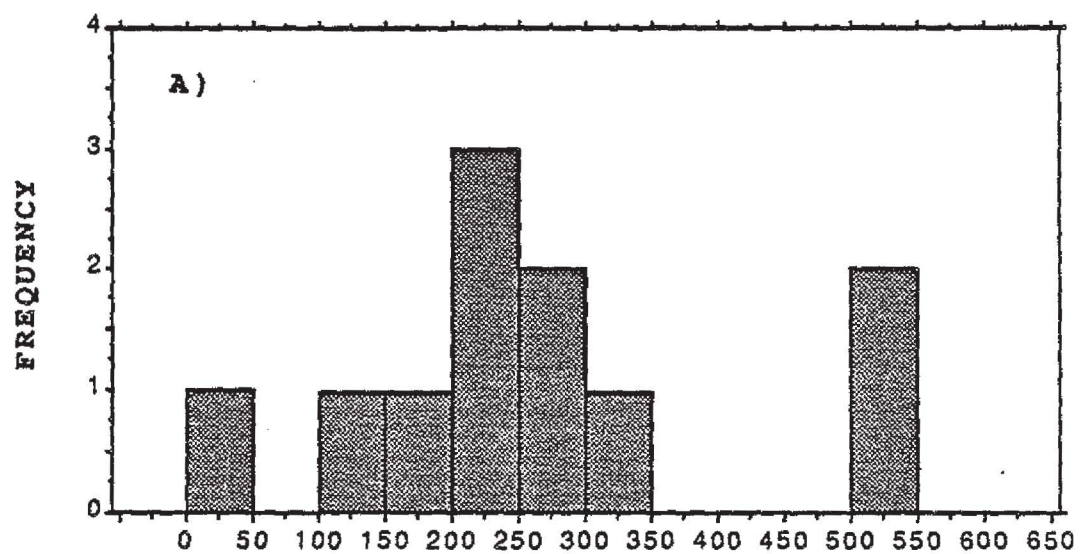


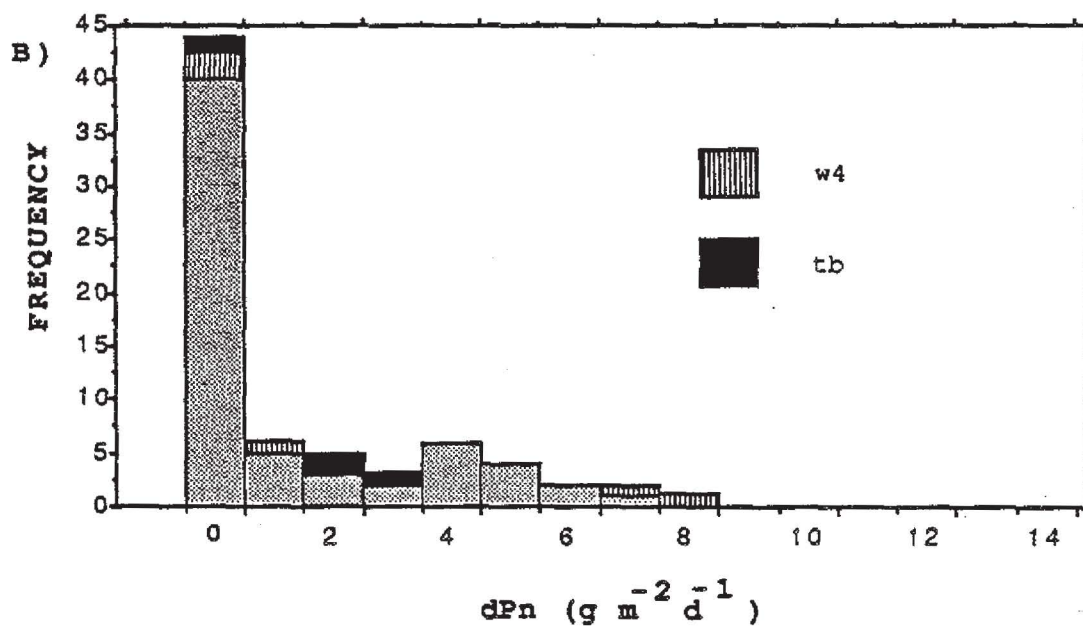
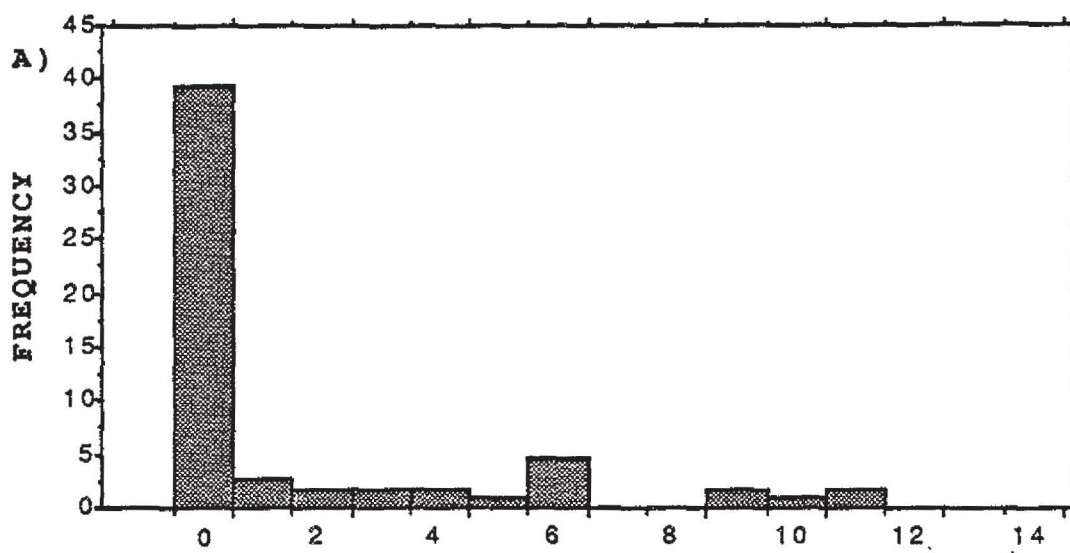
Table 3. Net aboveground primary production (aPn), consumption during the growing season (gH), late-season consumption (lH), consumption during the snow-free season (H), and the F-test probabilities that 1988 and 1989 values are from the same sample populations. NS denotes nonsignificance ($\alpha=0.05$). Whole-community, shrub (S), and herbaceous (H) portions of t3 and s2 are provided. All units are g m⁻².

SITE	aPn			gH			lH			H		
	1988	1989	PROB	1988	1989	PROB	1988	1989	PROB	1988	1989	PROB
Winter Range												
w1	a	85	-	a	20	-	a	0	-	a	20	-
w2	513	380	<0.001	249	86	<0.01	0	0	NS	249	86	<0.01
w3	232	204	NS	50	0	<0.001	56	0	<0.001	106	0	<0.001
w4	539	589	NS	0	0	-	0	0	-	0	0	-
Transitional Range												
t1	145	60	<0.001	47	0	<0.001	63	0	<0.001	111	0	<0.001
t2	343	297	NS	199	137	<0.05	107	0	<0.001	306	137	<0.001
t3	290	223	NS	90	53	NS	0	0	NS	90	53	NS
t3H	241	163	NS	90	53	NS	0	0	NS	90	53	NS
t3S	49	60	NS	0	0	-	0	0	-	0	0	-
tb	b	104	-	b	53	-	b	19	-	b	72	-
Summer Range												
s1	27	16	<0.01	0	0	-	0	0	NS	0	0	-
s2	166	183	NS	32	20	<0.01	0	0	NS	32	20	<0.01
s2H	112	84	<0.01	32	20	<0.01	0	0	NS	32	20	<0.01
s2S	54	99	NS	0	0	-	0	0	-	0	0	-
S3	278	248	NS	97	127	NS	51	0	<0.001	148	127	NS
S4	238	136	<0.001	124	77	<0.01	24	0	<0.05	149	77	<0.001
S5	247	198	<0.05	0	0	-	0	0	-	0	0	-

and in 1989 the community was a mosaic of vegetated and bare patches. Line intercept samples 28 days after snowmelt and just prior to snowfall indicated no discernable recolonization ($F_{1,18}=.783$, $P=.397$) of bare areas had occurred during the first year after the fire, and unvegetated patches covered 32% of the total area of the community. Charred A. tridentata stumps located in the center of bare areas suggested temperatures produced during combustion of bushes killed nearby herbaceous vegetation and created the barren patches.

The frequency distributions of daily production (dPn), calculated as growth during a sampling interval divided by the number of days of the interval, for both 1988 and 1989 were most distinguished by their large number of zero growth intervals (Fig. 4). For sites sampled in both years no significant growth occurred in 66.1% and 63.5% of the intervals during 1988 and 1989, respectively. Positive dPn at these sites ranged from 0.4-10.7 g m⁻² d⁻¹ in 1988 and 0.3-6.8 g m⁻² d⁻¹ in 1989. Mean positive dPn was 5.7 g m⁻² d⁻¹ in 1988 and 3.2 g m⁻² d⁻¹ in 1989 ($F_{1,42}=2.827$, $P=.11$). Maximum dPn at each of the sites was greater in 1988 than 1989 (paired-t=5.09, $P<.001$, df=9). The duration of growth, the number of days during which significant growth occurred, was indistinguishable between years ($P=.371$, Wilcoxon) and averaged 51.3 days; although, it is notable that the power

Fig. 4. Frequency histograms of dPn, daily aboveground primary production, in A) 1988 and B) 1989. Gray bars represent samples from sites dPn was measured in both years.

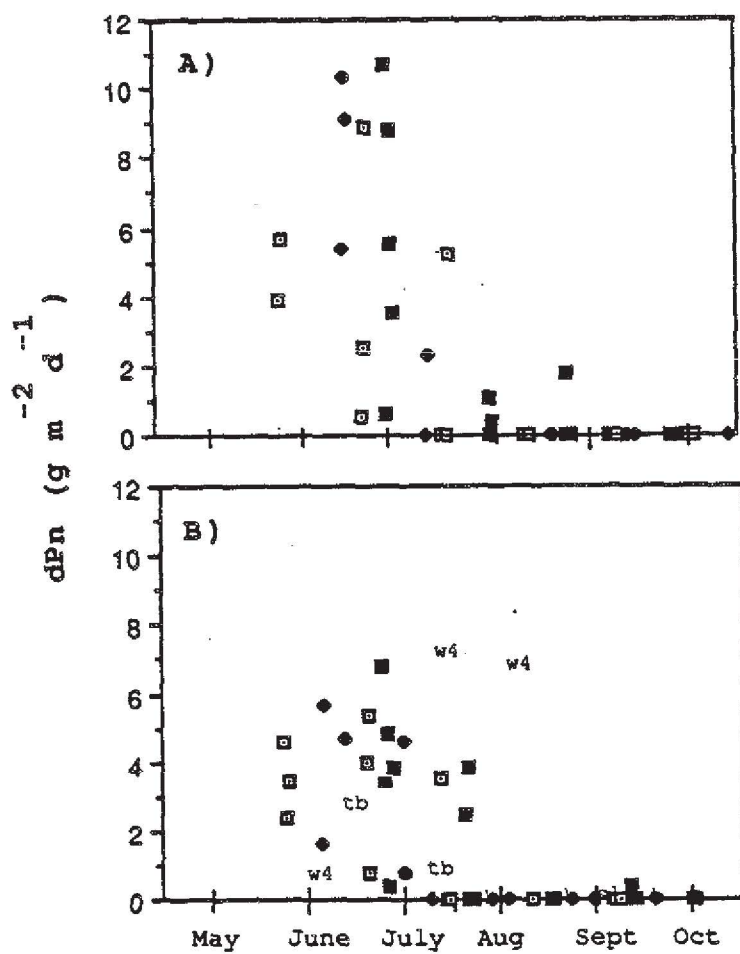


to discriminate a between-year difference in the length of the growing period was diminished to an unknown extent by the duration of the sampling interval.

Plant growth in Yellowstone is a spatiotemporal wave. Growth usually begins in mid-March in the lower winter range and proceeds along an elevational gradient that is locally influenced by topography to the upper summer range, lasting in most years through late-August. The sites sampled in this study represent a midsection of this gradient, from the upper winter range to the lower summer range (Fig. 5). Production begins after snowmelt and lasts for 1-2 months in most sites and 3 months in mesic-wet valley bottom sites (in this study w2 and w4). The growth wave is not reflected in Fig. 5 because of the narrow elevation gradient sampled, 1888-2477 m, and the relatively high representation of lush, valley bottom winter range sites that have extended plant growth periods. A wet sedge meadow, w4, for which daily production was determined for 1989 only, had among the highest rates of growth that continued well into the summer (Fig. 5).

Effects of climatic variation at the base of the food web will pervade through all trophic levels. I further explored the effect of climate during this study by examining the persistence of green biomass through the growing season in two ways. Green biomass is a central

Fig. 5. Scattergram of dPn, daily aboveground production, on calendar day during A) 1988 and B) 1989 for winter (■), transitional (◆), and summer (■) range sites. There are no 1988 dPn data for w4 or tb.



variable in an ecosystem, since it is critical to both plant carbon gain, and herbivore nutrition. First, green biomass was summed over sites in each seasonal range for each sampling interval in 1988 and 1989 (Fig. 6).

Although there was more green biomass early in the 1988 season in each seasonal range, by early-August, values for 1988 were lower than 1989 (for winter range, $t_{23}=16.5$, $P<.001$; for transitional range $t_{23}=21.5$, $P<.005$; for summer range, $t_{39}=12.9$, $P<.001$). This indicates an important drought effect of limiting the availability and, potentially, the flow of nutrients to higher trophic levels in aboveground food webs.

Second, the proportional contribution of green biomass to total biomass through the season in each seasonal range was compared between years. Green biomass considered as a proportion in this way corrects for between year differences in aPn, and perhaps more clearly reveals the effect of the 1988 drought on plants, while providing an index of bulk forage quality for herbivores. By early-August there was relatively less green biomass represented in the standing crop in 1988 compared with 1989 in each seasonal range (Fig. 7). In addition, seasonal ranges differed with respect to how long after snowmelt between-year differences were evident. Paired-t tests on mean site values revealed the proportion of green biomass was indistinguishable between years for the first

Fig. 6. Relationship of summed green biomass in A) summer, B) transitional, and C) winter range sites to calendar day for 1988 (—□—) and 1989 (—●—). Symbols are means.

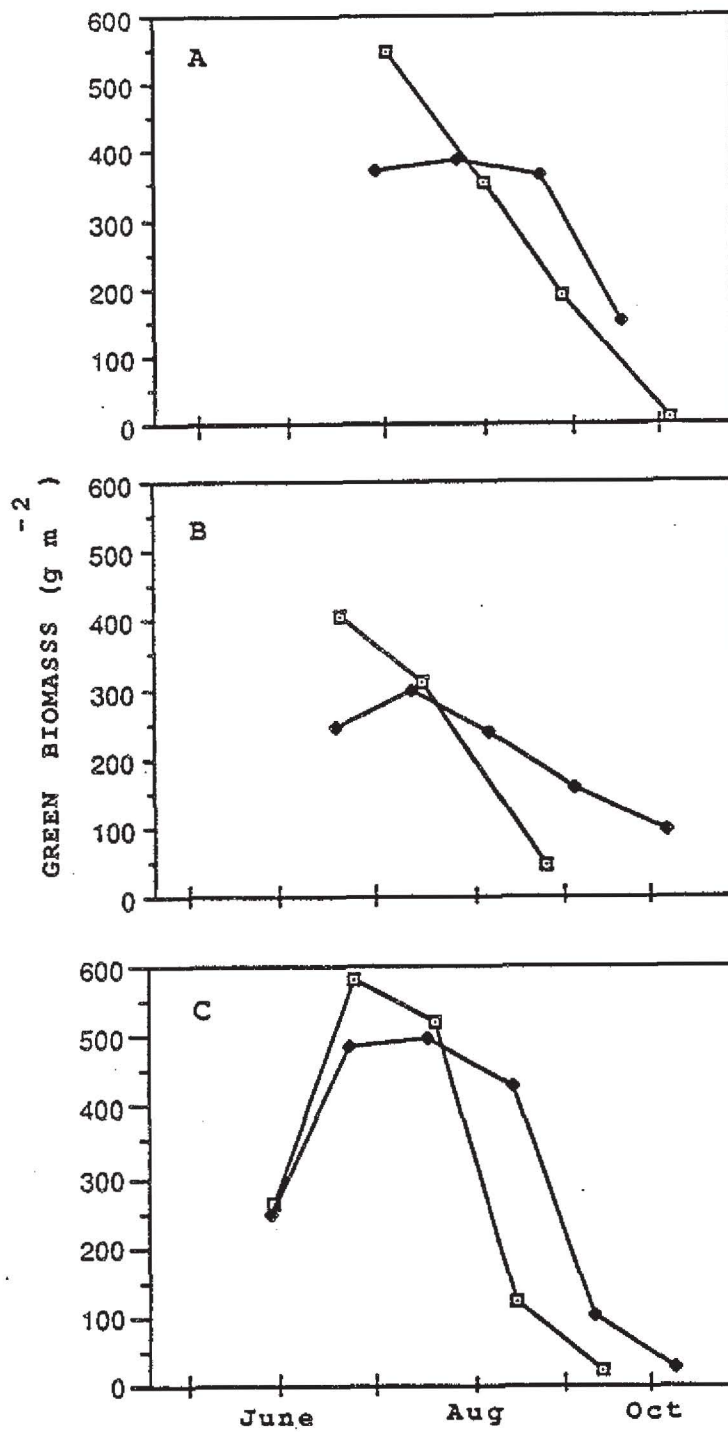
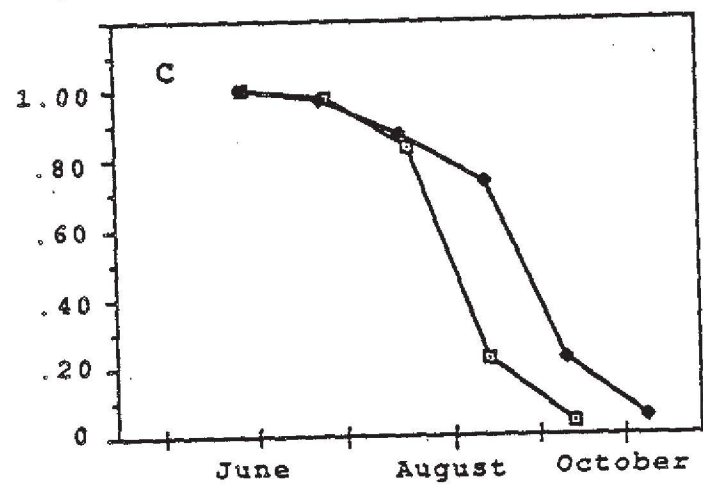
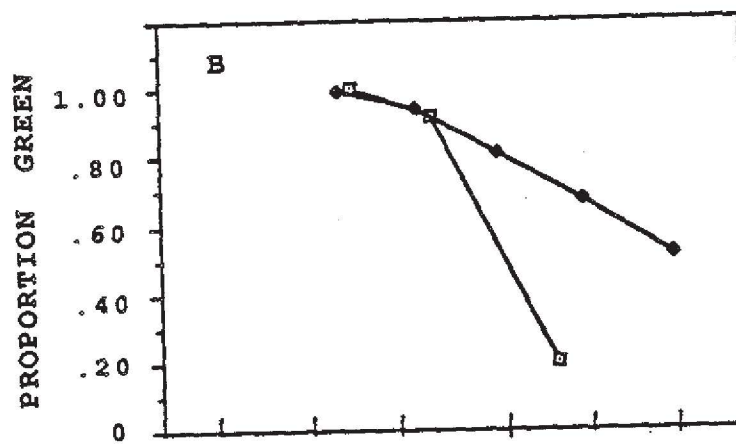
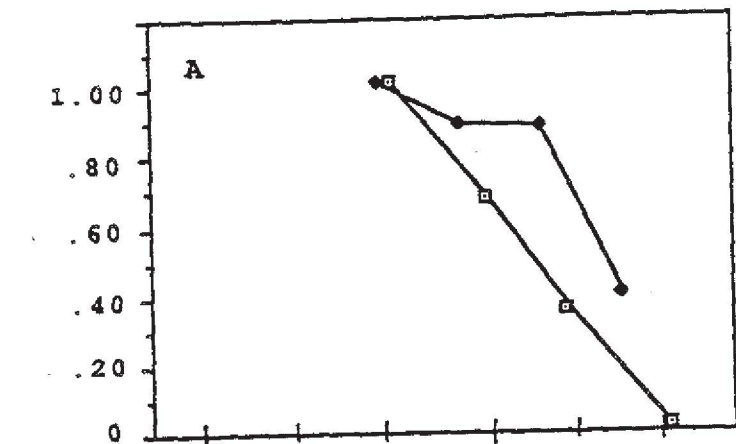


Fig. 7. Relationship of green proportion of total biomass for A) summer, B) transitional, and C) winter range sites to calendar day in 1988 and 1989. Lines are through means. Symbols as Fig. 6.



3 samples in the winter range (May, $t_2 < 0.01$; June, $t_2 = 0.02$; July, $t_2 = 2.17$), 2 samples in the transitional range (June, $t_2 = 0.35$, July, $t_2 = 1.00$), and only one sample in the summer range (early-July, $t_4 = 0.47$). This is an elevation gradient which may reflect an associated drought severity gradient. It was already mentioned that the onset of the 1988 drought was in June, after 2 months of above-average spring precipitation. Drought severity was likely inversely related to the period that sites were free of snow before the beginning of the drought. This period ranged from up to approximately 60 days at the winter range sites to 0 days at the summer range sites.

Nitrogen content was determined for a subset of forages, comprising the dominant grass species at each of seven grazed sites throughout the 1989 snowfree season. All species were grazed (pers. obs.). Plants were harvested at the same time biomass estimations were made at each site. Forage nitrogen of the first harvests, approximately 28 days after snowmelt, ranged from 2.5-3.7% and were significantly greater than harvests later in the year ($F_{1,31} = 53.3$, $P < .0001$), which ranged from 1.1-2.4%. Percent nitrogen (N) was related to days after snowmelt (dy) ($r^2 = .713$, $df = 30$) by

$$\arcsin N^{1/2} = 6.90 (1 + 1.05e^{-.03(dy)})$$

(Fig. 8). Implicit in this relationship is a nitrogen wave, tied to the plant growth wave already discussed, from low to high elevations following snowmelt patterns.

Green biomass concentration (C , g cc^{-1}) and the number of days after snowmelt (dy) were negatively related ($r^2=.470$, $df=56$) by

$$C = 106.3 - .640(dy)$$

(Fig. 9). Highest values for C occurred during the first sample, approximately 28 days after snowmelt, at all sites, except $s1$ and $s5$. Variation among sites was highest at this time (Fig 9). When restricting analysis to the earliest samples at each site, 32.9% of the variation in C was explained by aPn ($F_{1,9}=4.41$, $P=.065$), in contrast to aPn explaining only 4% of the variance ($F_{1,55}=3.3$, $P=.075$) when both dy and aPn are included as variables in a multiple regression over the entire snowfree season. From Fig. 9 it is clear that site quality, e.g., aPn , accounts for little of the variation in C during the snowfree season, because of the homogenization of patches in the landscape with respect to C as the season progresses.

Correlation analyses of the relationship between the 2 components of C , green biomass and canopy height, with dy showed the decline in C with length of season was due

Fig. 8. Relationship of arcsine-transformed forage nitrogen concentration (N) of dominant grasses at 7 sites on days after snowmelt.

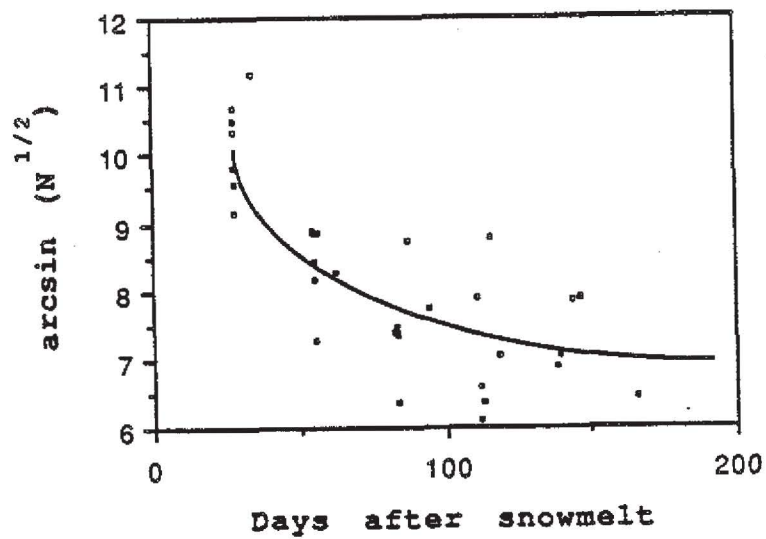
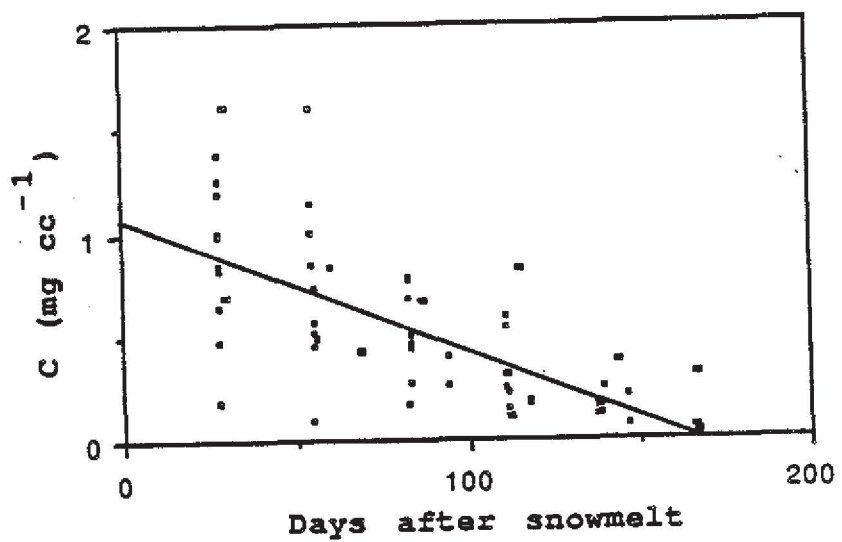


Fig. 9. Relationship between C, green biomass concentration, and days after snowmelt.

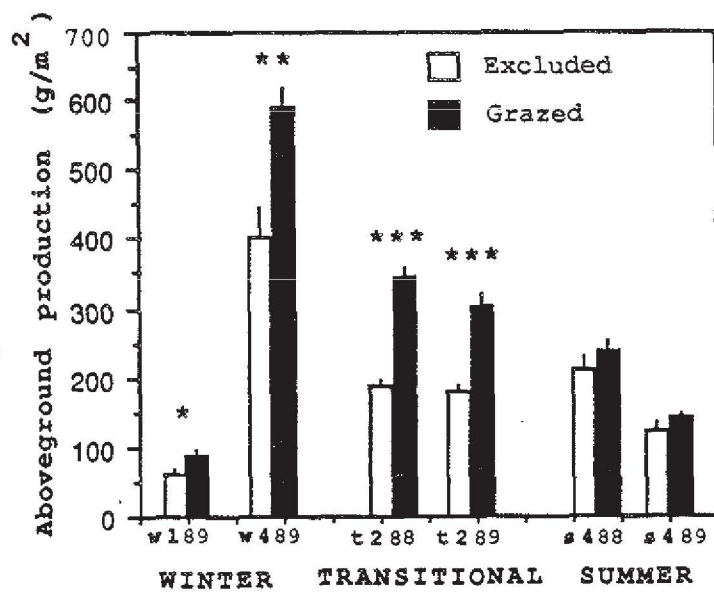


to a contemporaneous decline in standing green biomass and increase in canopy height. Days after snowmelt (dy) was negatively related to green biomass ($P=.02$, $r=-.31$, $df=56$) and positively related to canopy height ($P=.002$, $r=.41$, $df=56$). At all 4 sites with permanent exclosures, grazed vegetation had a higher concentration of green biomass than fenced sites at peak standing crop: C of grazed and fenced vegetation was .78 and .45, .92 and .70, .69 and .55, and .55 and .22 mg cc^{-1} at w1, w4, t2, and s4, respectively.

To determine the composite effects of large herbivores on aboveground primary production, ungrazed production (cPn) was compared to grazed production (aPn) in 4 communities. For 3 of the communities aPn was significantly higher than cPn (Fig. 10). The results were consistent at sites where cPn data were obtained during both years. Herbivores stimulated production by 36.0% in w1, 46.2% in w4, and 84.5% and 67.0% in t2 in 1988 and 1989, respectively.

There was considerable variation in the season(s) the four communities were grazed. Ungulates grazed t2 and s4 principally during the snowfree portion of the year, w1 throughout the entire year, and w4 only in the winter. Site w4 was the only community where no green tissue was consumed. This temporal feature of herbivore utilization

Fig. 10. Net aboveground primary production of grazed, aPn, and ungrazed, cPn, vegetation in four communities Sites t2 and s4 were sampled in 1988 and 1989. * denotes $P < .05$. ** denotes $P < .01$. *** denotes $P < .0001$



bears substantially on the mechanisms that may cause herbivores to stimulate production.

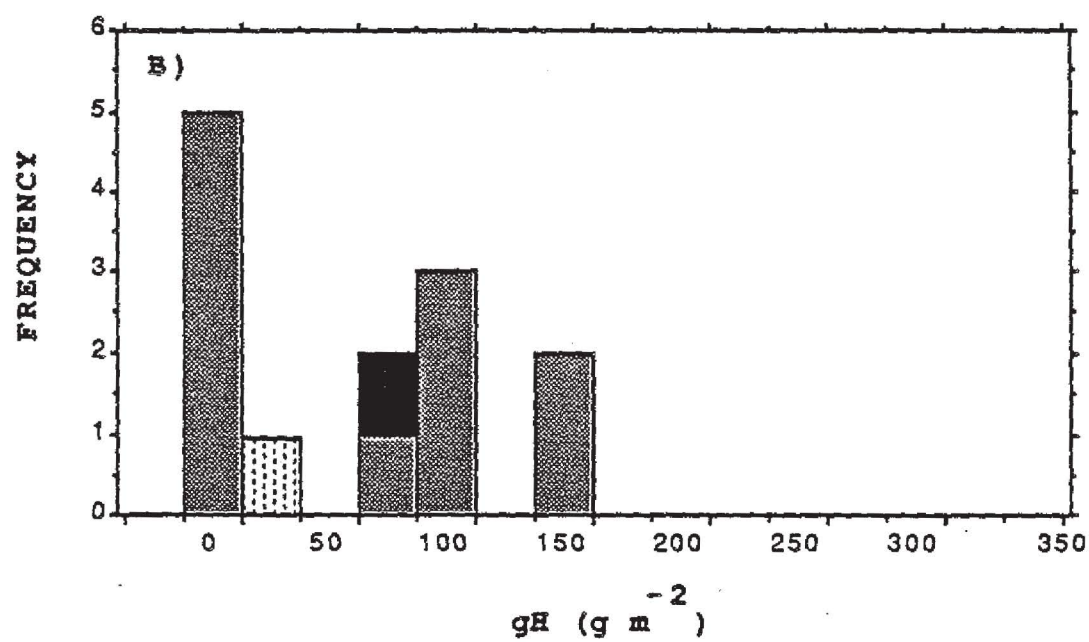
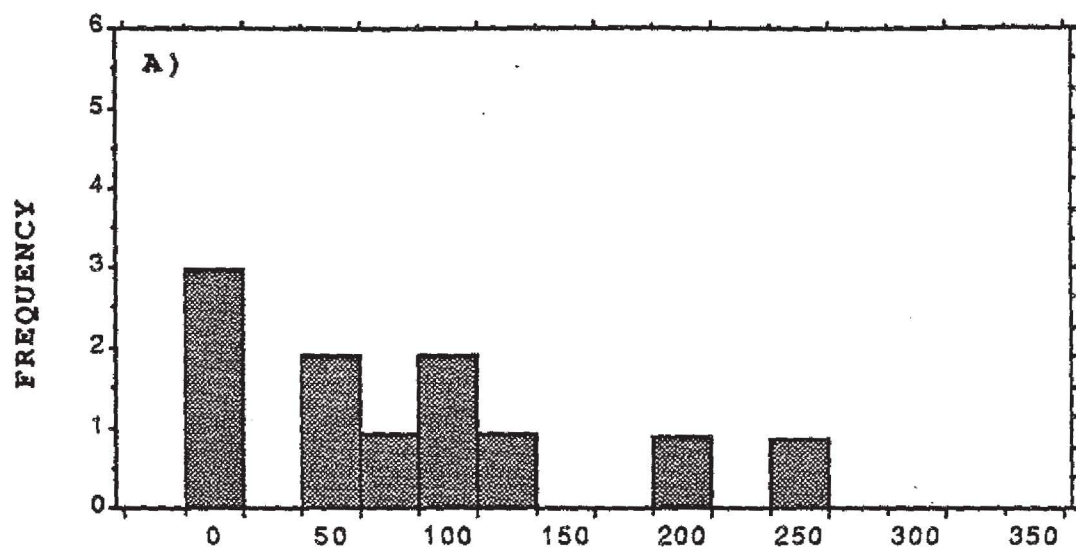
Herbivores

Whether a herbivore grazes green or browned tissue has important consequences for both the herbivore and the plant that is grazed. Therefore, in addition to presenting data on consumption during the entire snowfree period, I report offtake during the growing season, arbitrarily defined as that portion of the year that green biomass represents at least 20% of the total standing crop, and the late-season, that period after the growing season until snowfall.

Consumption varied widely and was strongly affected by ungulate numbers. Growing season consumption (gH) at sites sampled in both years and grazed in at least one year ranged from 32-249 g m⁻² in 1988 and 20-137 g m⁻² in 1989 (Fig. 11). At w1 and tb where only 1989 data exist, offtake was 20 g m⁻², the lowest of any site sampled that year, and 53 g m⁻², respectively. When considering just vegetated areas at tb, gH was 78 g m⁻². There was no significant grazing in 3 and 5 communities sampled in 1988 and 1989, respectively.

Mean gH for grazed sites measured in both years declined from 111 g m⁻² in 1988 to 63 g m⁻² in 1989 (paired

Fig 11. Frequency histograms of gH, growing season consumption, for A) 1988 and B) 1989. Codes of bars are as Fig. 3.



comparison ANOVA, $F_{1,337}=5.93$, $P<.05$). Reductions in gH occurred at 6 of 8 sites (Table 3). Most notable was a 65% decline at w2, which in 1988 had the highest rate of gH.

At t3 and s2, where A. tridentata occurred, herbaceous vegetation between and under shrubs was sampled separately. At no time during the study did significant offtake of herbaceous biomass occur under A. tridentata (Table 3). This suggests a reciprocal relationship between sagebrush cover and herbivory across the landscape.

The percentage of aPn consumed during the growing season (gH%) at grazed sites ranged from 22-58% in 1988 and 23-51% in 1989 (Fig. 12). Mean gH% for sites grazed in either year declined somewhat from 39.2% in 1988 to 29.0% in 1989 ($P=.07$, $t_g=2.17$, $df=7$), and the number of sites not grazed increased from 3 in 1988 to 5 in 1989.

Offtake late in the season (lH) differed markedly between years. In 1988 detectable lH occurred in 5 communities, averaging 60 g m^{-2} (Fig 13, Table 3). In contrast, during 1989 measurable lH occurred at tb only. Whole-community lH equalled 20 g m^{-2} at tb, and 28 g m^{-2} in vegetated areas.

Total consumption (H) was defined as consumption between spring snowmelt and late-autumn snowfall. In 1989 gH and H were identical at all sites, except tb, where H

Fig. 12. Frequency histograms of gH%, percent net aboveground primary production grazed during the growing season, for A) 1988 and A) 1989. Codes of bars are as Fig. 3.

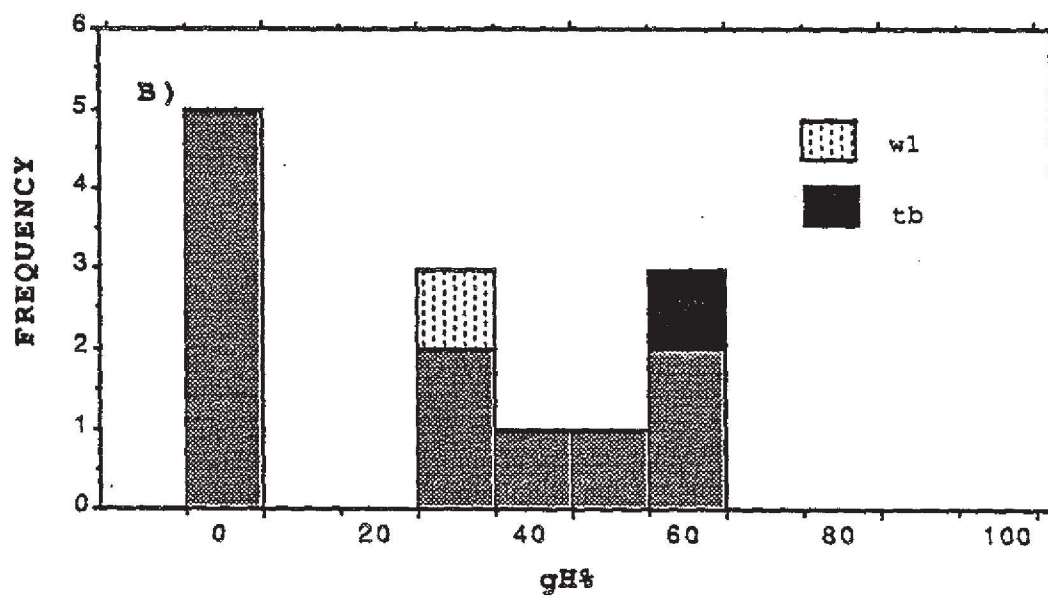
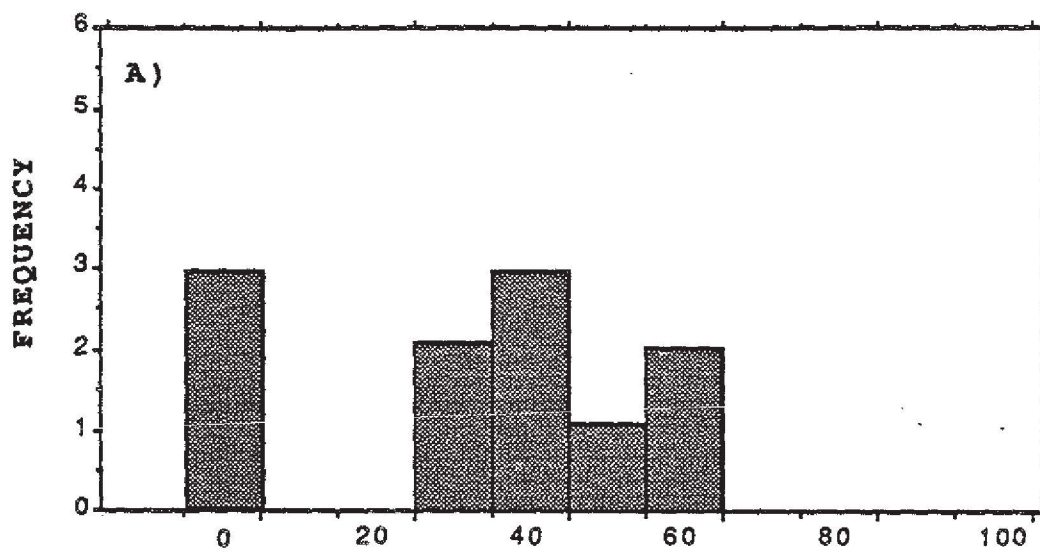
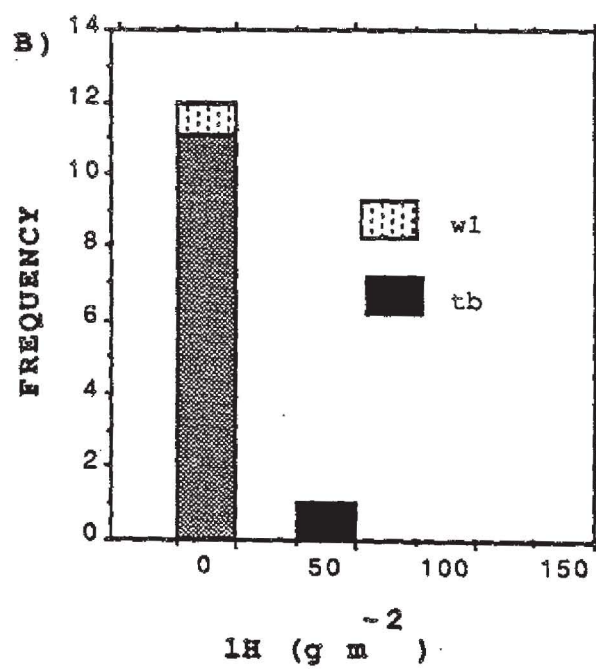
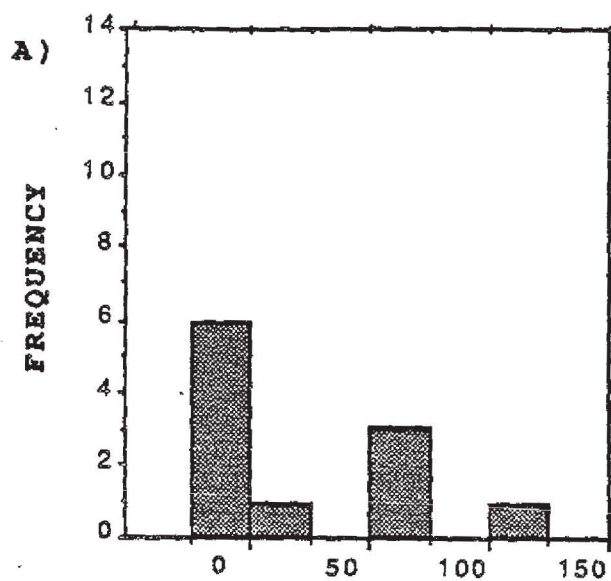


Fig. 13. Frequency histograms of LH, late-season consumption, for A) 1988 and B) 1989. Codes of bars are as Fig 3.



equalled 72 (Table 3). For vegetated areas at tb, H was 106 g m^{-2} . For grazed sites sampled in both years, H ranged from $32\text{--}306 \text{ g m}^{-2}$ in 1988 and $20\text{--}137 \text{ g m}^{-2}$ in 1989 (Fig 14). Mean H declined from 154 in 1988 to 71 g m^{-2} in 1989 (paired comparison ANOVA, $F_{1,418}=9.28$, $P<.01$). Consumption declined in 7 of 8 communities (Table 3). No grazing occurred at 3 sites in 1988 and 5 sites in 1989.

The percentage of aPn grazed during the entire snowfree season (H%) was bimodal in 1988 (Fig. 15). Three communities were not grazed, and H% of others ranged from 28–89%. It was no surprise that H% was greater than gH% in 1988 ($P=.02$, $t=3.09$, $df=7$), since many sites were regrazed in the late-season. As above, in 1989 H% and gH% were identical at unburned sites. Among sites where consumption was measured in both years, H% was higher in 1988 than 1989 ($P=.02$, $t=3.12$, $df=7$). Site tb had the highest H%, 51%, of all sites in 1989.

Daily consumption (dH) was calculated as the amount consumed during an interval divided by the number of days of the interval. Frequency histograms of dH at grazed sites for 1988 and 1989 (Fig. 16) are similar to those for dPn (Fig. 4). In both years, no consumption occurred during the majority of the sampling intervals. Daily consumption was not significantly different from 0 for 60.7% and 76.2% of the growing season samples, and 56.8% and 76.4% of all samples in 1988 and 1989, respectively.

Fig. 14. Frequency histograms of H, consumption during the snow-free season for A) 1988 and B) 1989. Codes of bars as Fig. 3.

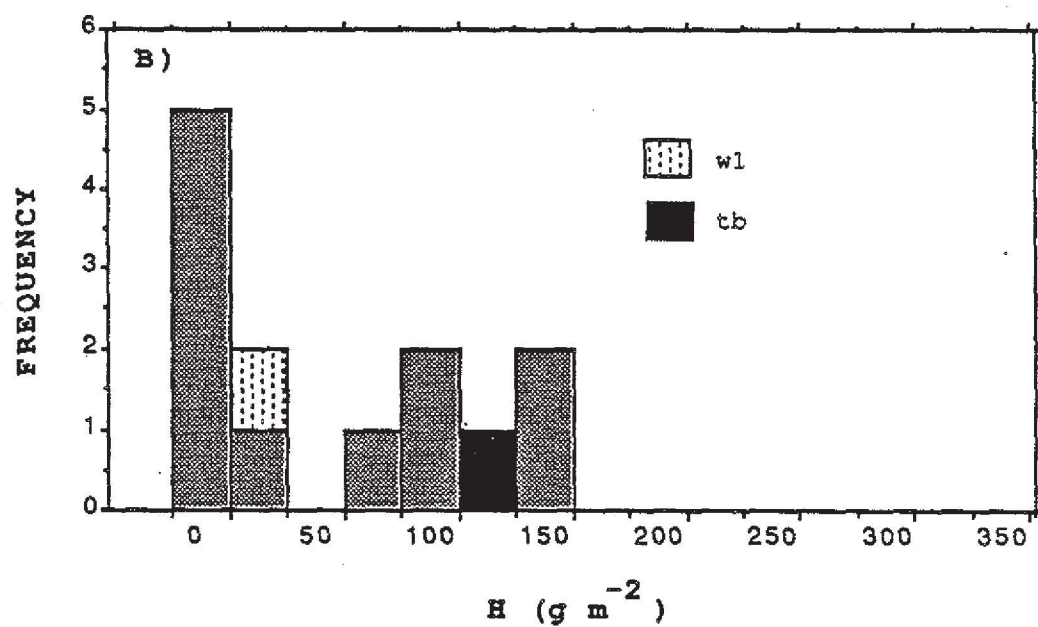
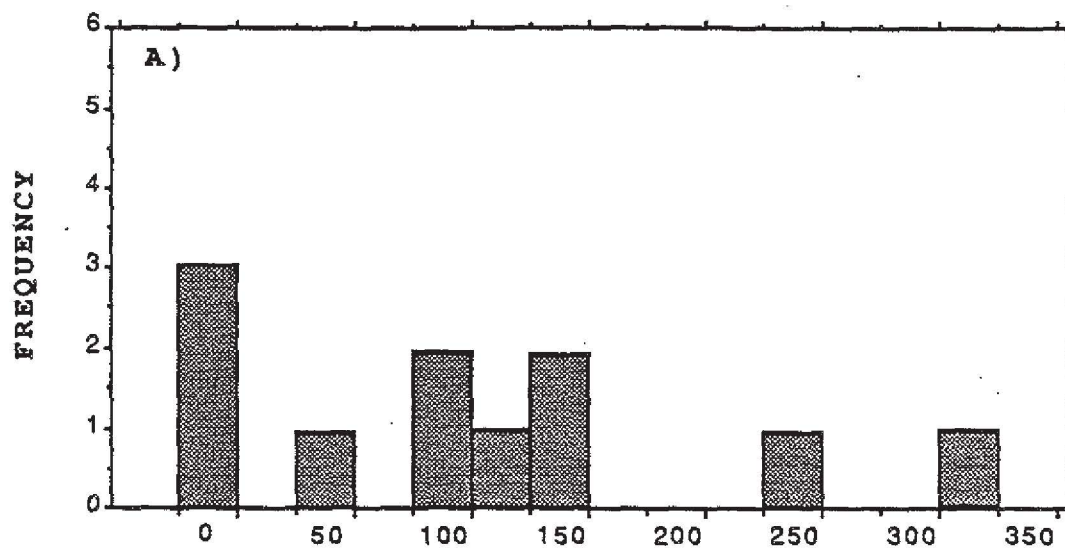


Fig. 15. Frequency histogram of H%, percent consumption during the snow-free season, for 1988.

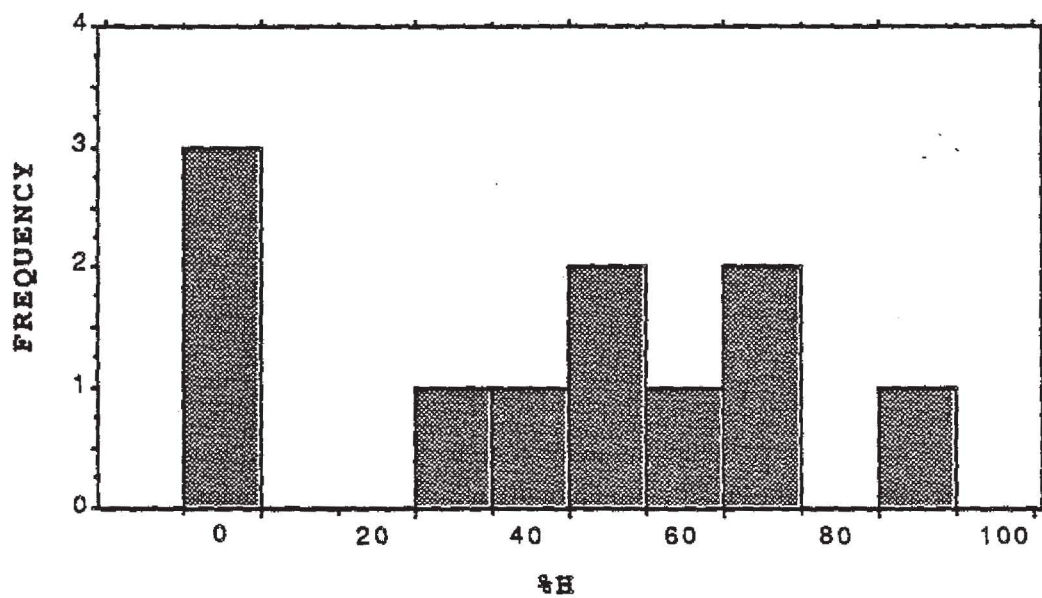
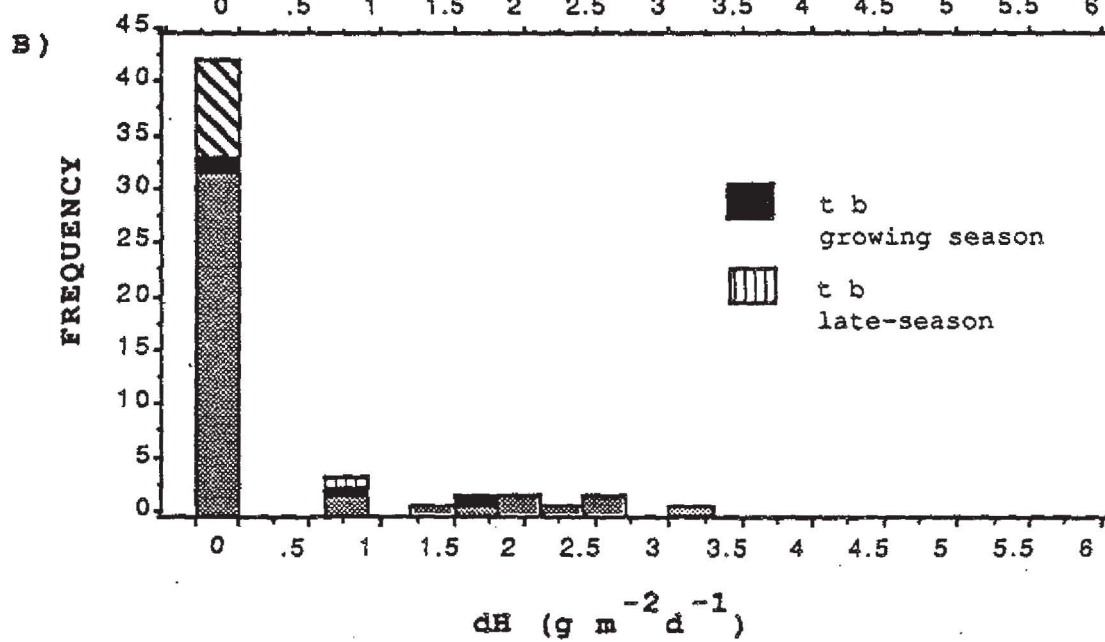
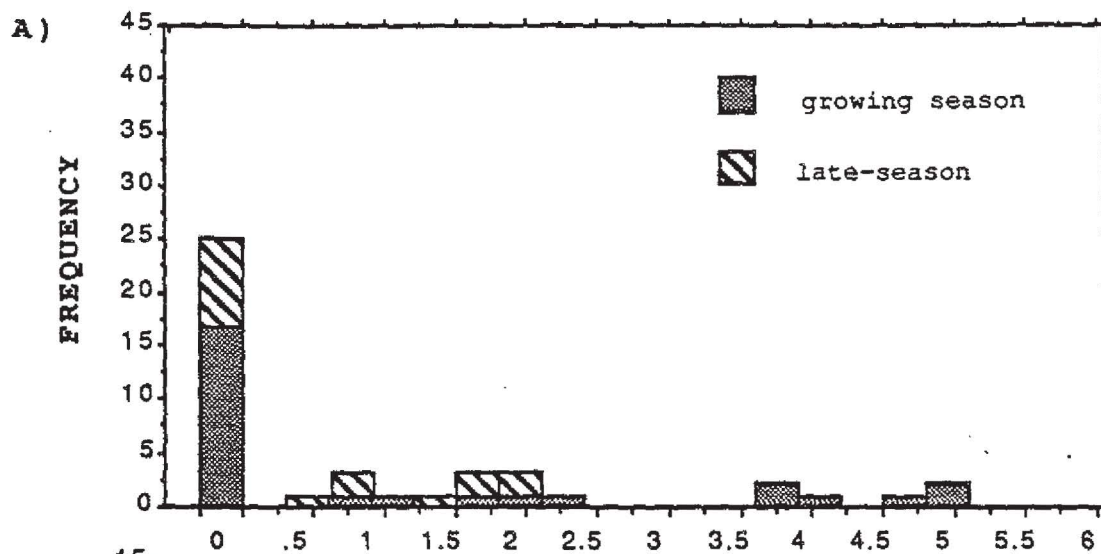


Fig. 16. Frequency histograms of dH, daily consumption, in A) 1988 and B) 1989. Gray and striped bars are from sites there are data for both years. Values for tb calculated from vegetated areas only.



For positive values, dH ranged from 0.5-5.0 g m⁻² d⁻¹ in 1988 and 0.7-3.1 g m⁻² d⁻¹ in 1989. Mean detectable dH during the growing season declined from 3.1 g m⁻² d⁻¹ in 1988 to 1.9 g m⁻² d⁻¹ in 1989 ($F_{1,19}=4.80$, $P=.04$). In 1988, the mean positive dH was lower in the late-season, 1.7 g m⁻² d⁻¹, than during the growing season ($F_{1,17}=8.92$, $P=.008$). The greater number of late-season samples in 1988 was due to the relatively early senescence of vegetation during the drought.

The relationship between plants and herbivores

In an effort to understand the multidimensional link between plants and herbivores, consumption was related to vegetation in several ways. Consumption during the growing season (gH) was associated with aPn and plant community species diversity (H') in 1988 ($r^2=0.633$, $df=8$) by

$$gH = -108.9 + 0.33(aPn) + 68.8(H'),$$

and in 1989 ($r^2=0.533$, $df=10$) by

$$gH = -68.3 + 0.16(aPn) + 47.9(H'),$$

with aPn and H' explaining 36.7% and 26.6% of the variation in 1988, and 19.7% and 33.6% of the variation in 1989, respectively.

The contribution of H' to predicting gH is virtually solely due to sites s5 and w4. If they are omitted in the analysis, H' no longer is significant and gH becomes linearly and positively related to aPn among paired sites, sites where aPn and gH were sampled during both years, in 1988 ($r^2=.896$, $df=7$) by

$$gH = -30.8 + .548(aPn)$$

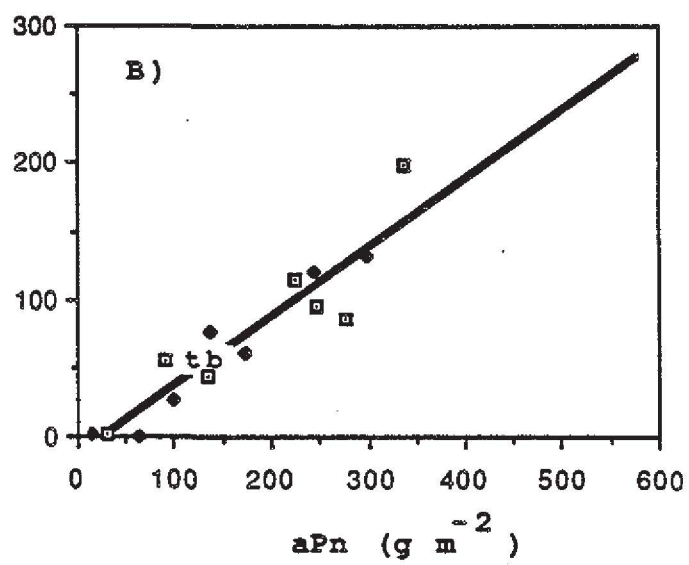
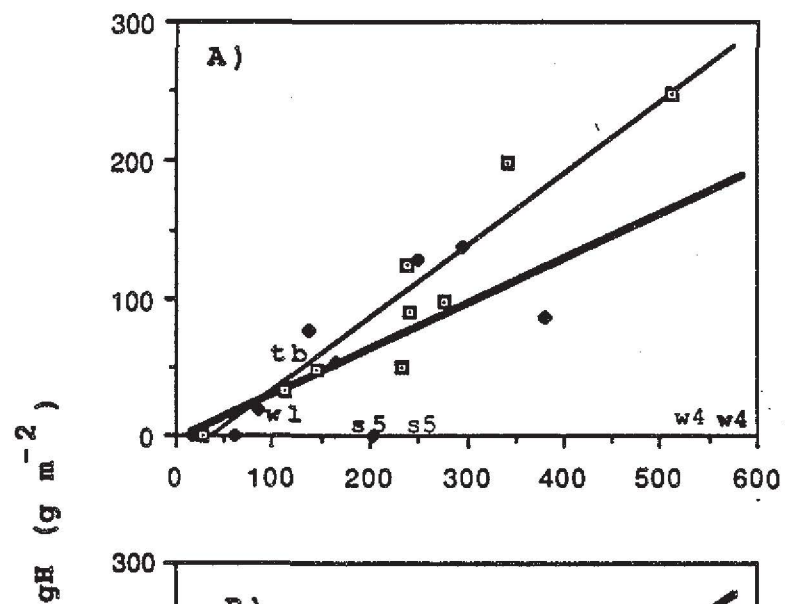
and in 1989 ($r^2=.534$, $df=7$) by

$$gH = -4.0 + .337(aPn)$$

(Fig. 17a). Slopes in this relationship could not be discriminated from one another ($F_{1,16}=.825$) and intercepts were indistinguishable from zero. The 1989 samples for w1, a site incompletely studied in 1988, and tb, a burned community added in 1989, lie well within the 95% confidence limits calculated from other samples that year.

Returning, however, to w4 and s5, it is clear from Fig. 17a that that they are abberant in reference to the relationship between gH and aPn for other sites. Both communities were not grazed the entire snowfree season,

Fig 17. Relationship of gH, growing season consumption, on aPn, net aboveground primary production for A) all sites, and B) transitional and summer range sites only during 1988 (■, —) and 1989 (●, —). Alphanumerically coded samples were not used to calculate regression equations. For w4 and s5, 1989 samples are in bold.



yet they had high levels of aPn. Both sites were dominated by single graminoid species that represented more than 95% of the total standing crop: Carex rostrata at site w4, and Calamagrostis rubescence at site s5. Furthermore, a third relatively productive community, w3, remained ungrazed in 1989 and had one grass, Bromus inermis, contributing over 90% of the aboveground biomass. The quasi-monoculture structure of these communities was profoundly different from that of other communities, reflected by their low values for H' , ranging from 0.37 to 0.71, compared to 1.41 to 2.74 for other sites. These results suggest that there are two fundamentally different types of plant communities in Yellowstone distinguished by both their structure and function: one of low species diversity and avoided by large herbivores during the snowfree year, and a second possessing higher species diversity and grazed by large herbivores during the snowfree year. Although only 3 of 13 sites studied here exhibited monospecific compositions, sites dominated by single species in this fashion are common in lodgepole pine forests throughout the Yellowstone landscape, and, therefore, may constitute an important structural and functional component of Yellowstone at the ecosystem level.

It is not suprising that grazing intensity (gH%) was the same in all seasonal ranges in 1988 given the low dispersion of samples around the 1988 regression line (see

Fig. 17a). In contrast, in 1989, winter range sites were grazed less per unit production than transitional and summer range sites ($F_{1,7}=9.40$, $P<.02$).

To compare herbivory between years off the winter range, the relationship of gH on aPn was reevaluated for transitional and summer range sites only. Because I was only interested in grazed vegetation, s5 and areas below A. tridentata were omitted. There was a positive relationship between gH and aPn in 1988 ($r^2=.860$, $df=5$) by

$$gH = -14.8 + .530(aPn)$$

and in 1989 ($r^2=.937$, $df=5$) by

$$gH = -17.4 + .538(aPn)$$

(Fig. 17b). Two points are remarkable. First, aPn was a precise predictor of gH, explaining 86% and 94% of the variation in gH in 1988 and 1989, respectively. Secondly, the slopes of the regression lines are so similar that they cannot be visually distinguished in Fig 17b. This indicates that despite the profound differences in climate and ungulate numbers between years the flux from plants to large herbivores per unit aPn was the same in transitional and summer range areas that were grazed. The proportion of aPn consumed was the same in tb as in unburned

communities.

Consumption during the snowfree season (H) and site production (aPn) in 1988 were positively related ($r^2=.743$, $df=7$) by

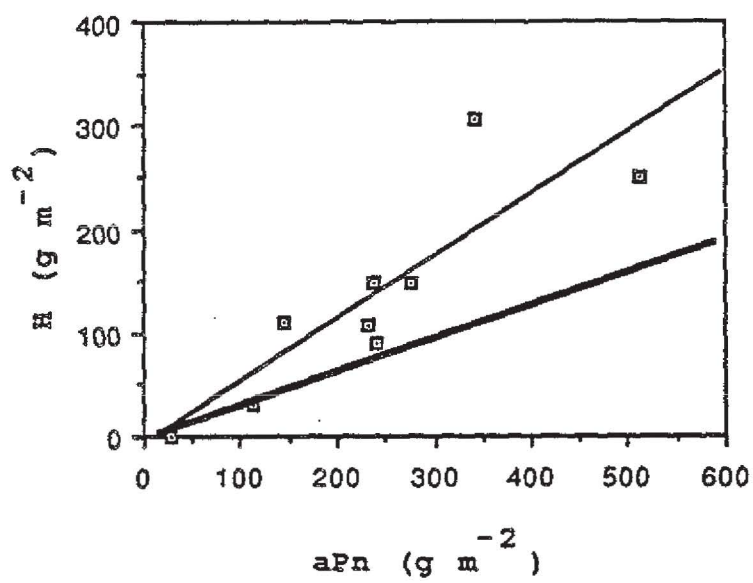
$$H = -8.50 + .60(aPn)$$

(Fig. 18). The relationship between H and aPn in 1989 was the same as that for gH on aPn. Slopes for H on aPn were different between years ($P=.05$, $df=16$), and intercepts could not be discriminated from zero.

To explore temporal interactions between herbivores and plants, daily consumption (dH) was related to a variety of seasonally fluctuating variables. Daily production (dPn) explained more of the variance in daily consumption (dH) during the growing season than concentration of green biomass (C), amount of green standing biomass, or amount of total standing biomass, and no other variable explained any further variation. Correlation analyses performed on 1989 data revealed positive associations between daily aboveground production and green biomass concentration ($r=.760$, $P<.0001$), green standing crop ($r=.486$, $P=.0001$), and total standing crop ($r=.237$, $P=.073$).

Among grazed sites that were sampled in both years daily growing season consumption (dH) and daily production

Fig. 18. Relationship of H, consumption in the snow-free season, on aPn, net aboveground primary production, for 1988 and 1989. Symbols and lines as Fig. 17.



(dPn) were positively related in 1988 ($r^2=.495$, $P<.0001$, $df=26$) by

$$dH = .25 + .34(dPn)$$

and in 1989 ($r^2=.293$, $P<.0003$, $df=39$) by

$$dH = .13 + .23(dPn)$$

(Fig. 19a). Much of the dispersion of the samples around the regression lines was due to animals not grazing sites in the winter range during periods of plant growth. If the relationship is reevaluated for transitional and summer ranges only, dH is related to dPn in 1988 ($r^2=.917$, $P<.0001$, $df=16$) by

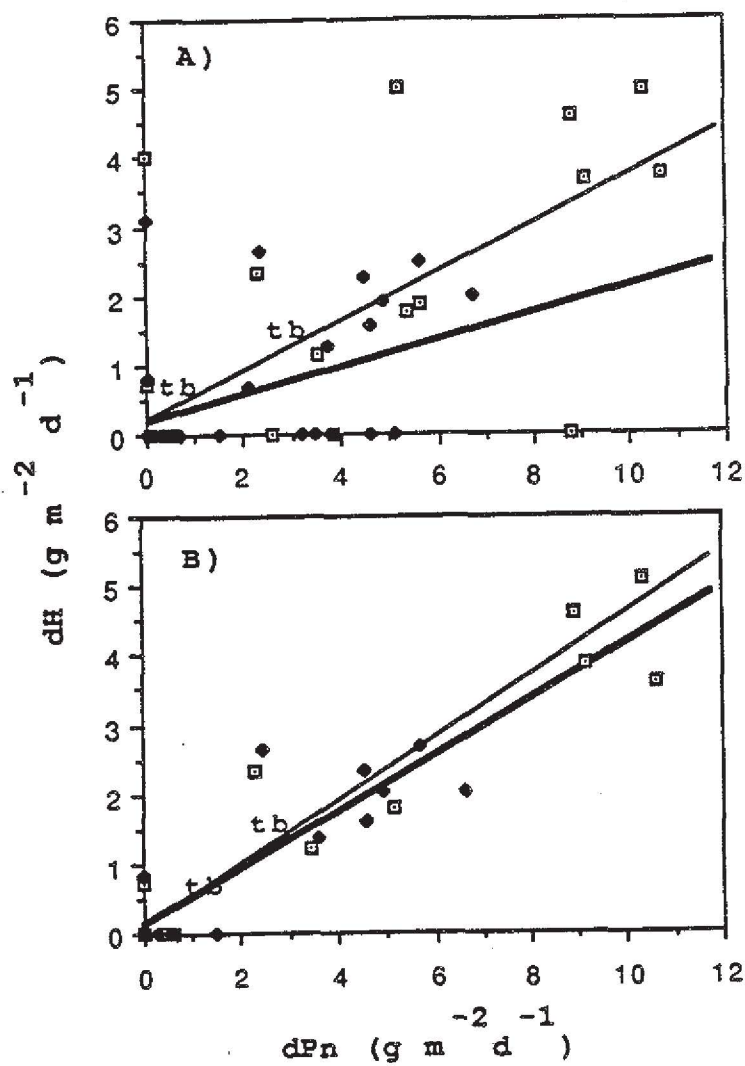
$$dH = .082 + .42(dPn)$$

and in 1989 ($r^2=.795$, $P<.0001$, $df=28$) by

$$dH = .048 + .385(dPn)$$

(Fig. 19b).

Fig. 19. Relationship between dH, growing season daily consumption, on dPn, daily net aboveground primary production, for A) all grazed sites and B) transitional and summer range grazed sites only. Site tb was sampled in 1989 only and was not used in calculations. Symbols and lines as Fig. 17.

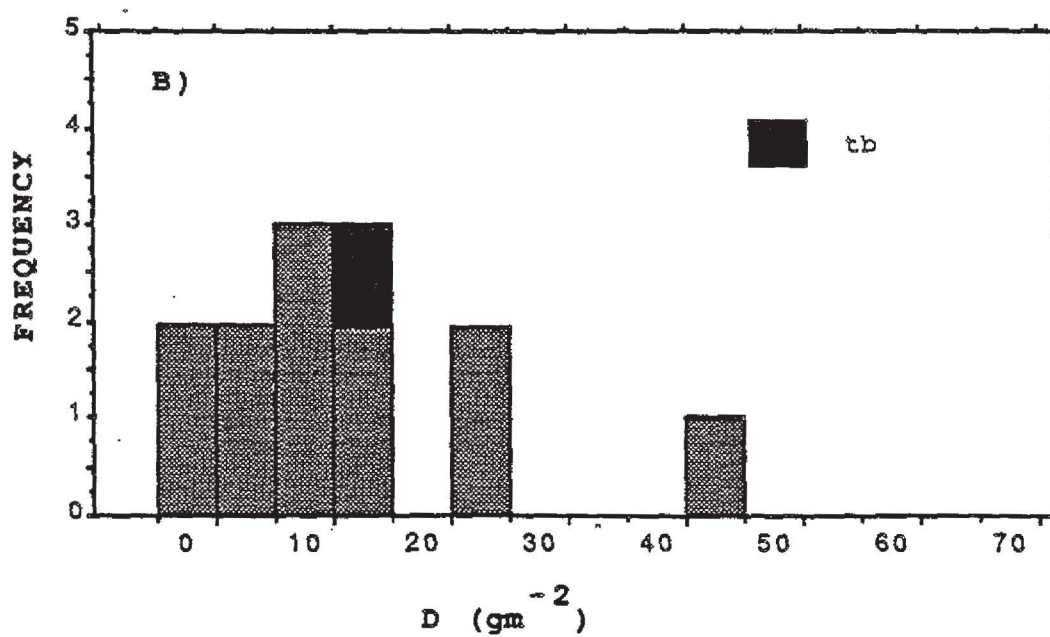
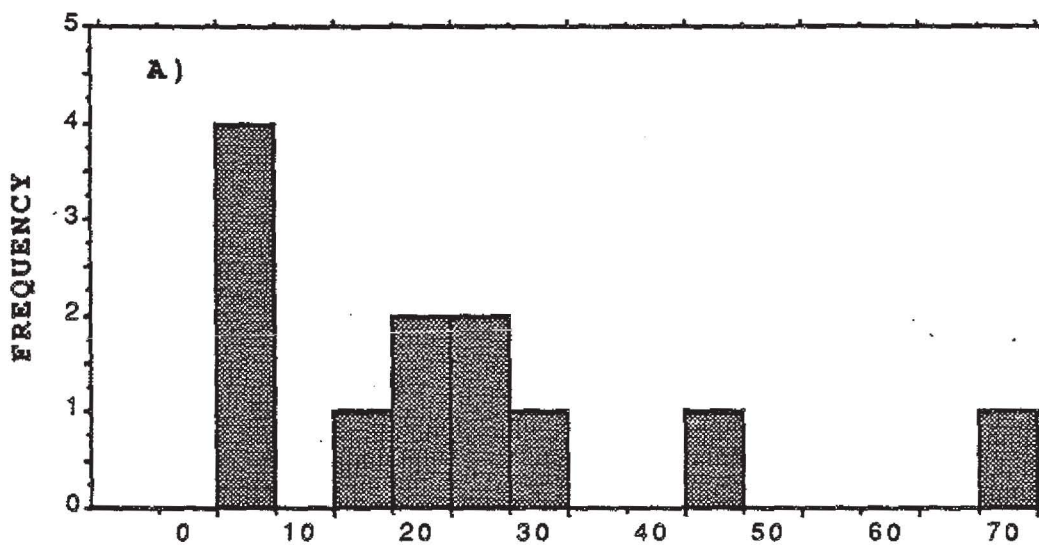


Nutrient flow from large herbivores to the soil

Nutrient flow from herbivores to soil was indexed with dung deposition (D , g m^{-2}) during the snow-free season at each site during both years. Maximum values for D during each year occurred at sites that, in addition to receiving inputs while animals were grazing or travelling, were used as bedding areas by elk: s3 received 68.5 g m^{-2} in 1988 and s4 received 45.0 g m^{-2} in 1989. For the remaining communities, fecal return ranged from $2\text{--}40 \text{ g m}^{-2}$ in 1988 and $0\text{--}21 \text{ g m}^{-2}$ in 1989 (Fig. 20). Mean deposition for all sites declined from 22 g m^{-2} in 1988 to 12 g m^{-2} in 1989 ($P < .0001$, $F_{1,198} = 17.8$), indicating that decreased herbivore numbers reduced the flow of nutrients from herbivores to soil across the Yellowstone landscape.

During the snow-free season, D did not differ between seasonal-use areas ($F_{2,217} = .26$). However, over the entire year it varied substantially at this spatial scale, since herbivores concentrate in the winter range from November–April. During the winter, dung was added at rates of 35.5 , 48.8 , 57.7 and 166.1 g m^{-2} in w1, w2, w3, and w4, respectively. These fluxes were 160%, 170%, 380% and 791% of the amounts deposited in the same sites during the snow-free season. Site w4 was intensely grazed by elk and bison during the winter. The quantity (g m^{-2}) of winter-time dung deposition at w4 appeared to be as high as any

Fig. 20. Frequency histograms of D, dung deposition, for
A) 1988 and B) 1989. Codes for bars are as Fig.
3.



site observed in the northern range.

There was no first or second order polynomial relationship between D and aPn (Fig. 21). However, D and consumption during the snow-free year (H), omitting elk bedding areas that were statistical outliers (outside the 95% prediction limits of the regressions), were positively related in 1988 ($r^2=.795$, $P<.0001$, $df=8$) by

$$D = 3.99 + .11(H),$$

and in 1989 ($r^2=.809$, $P=.0004$, $df=8$) by

$$D = 2.94 + .12(H)$$

(Fig. 22). Slopes could not be discriminated between years ($F_{1,17}=.02$, $P=.89$), and intercepts for both years were indistinguishable from zero ($t=1.44$ for 1988; $t=1.09$ for 1989). This indicates herbivores are returning nutrients to plant communities they remove them from, and grazing and nutrient cycling are closely coupled in the Yellowstone landscape, except where elk bed.

If the relationship between D and aPn is reevaluated only for sites that were grazed and where elk did not bed, D was positively related to aPn for pooled 1988 and 1989 data ($r^2=.47$, $P=.003$, $df=14$) by

Fig. 21. Scattergram of D, dung deposition, on aPn, net aboveground primary production for A) 1988 and B) 1989. Symbols are sites sampled in both years.

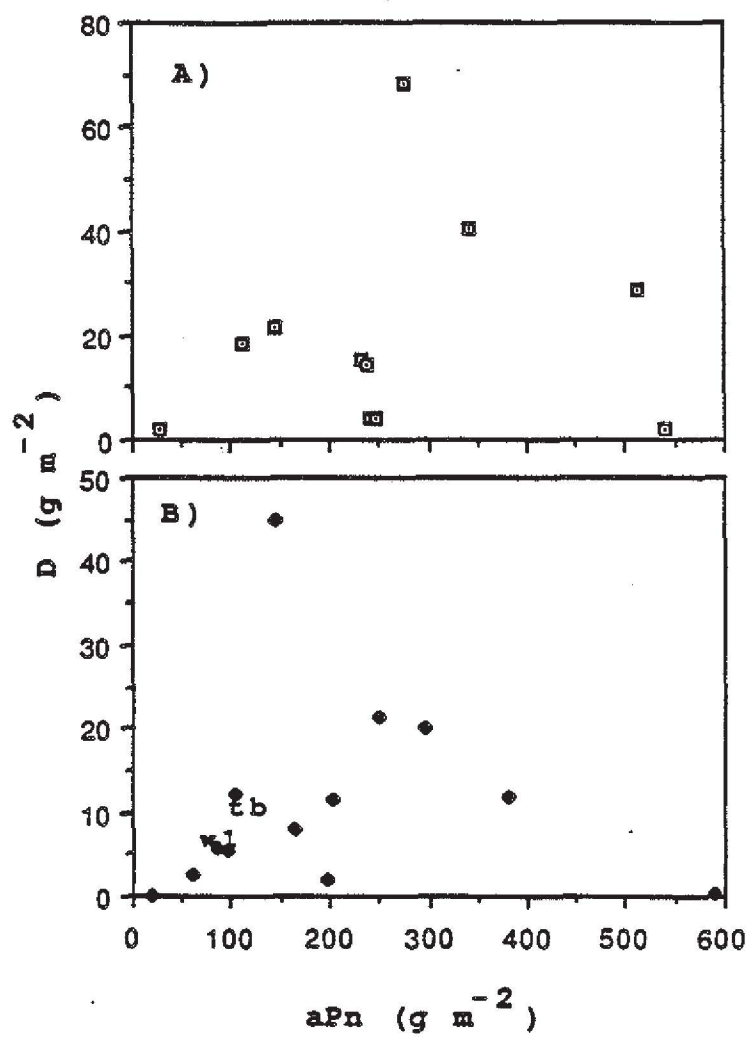
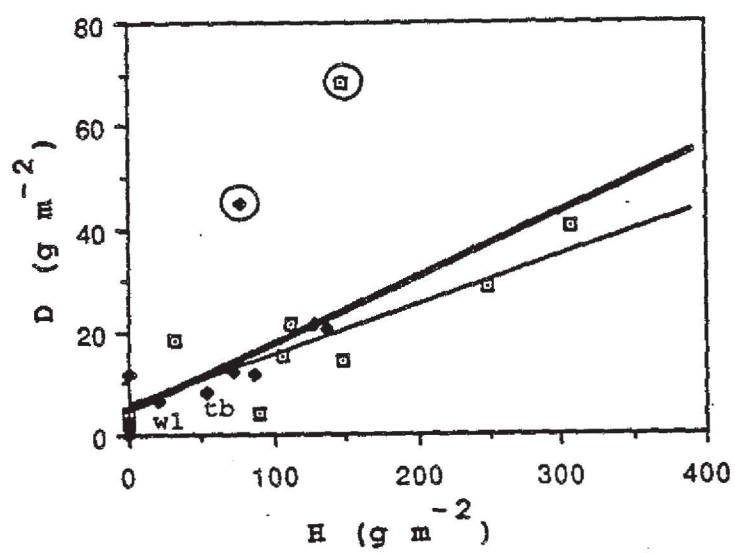


Fig. 22. Relationship of D, dung deposition, on H, consumption during the snow-free season, for 1988 and 1989. Symbols and lines as Fig. 17. Circled samples were elk bedding areas and were not included in calculations.



$$D = 2.84 + .05(aPn).$$

The intercept could not be differentiated from zero ($t=.75$). Therefore, in areas where they graze, large herbivores add nutrients at a constant rate per aPn.

RESULTS: SPECIES COMPOSITION

Climate and large herbivores are important determinants of grassland species composition. The sharp disparity in prevailing climatic conditions during the 2 years of this study and the maintenance of fenced, ungrazed areas at 3 sites in otherwise heavily grazed vegetation, provide a rare opportunity to examine the comparative effects of grazing and weather on plant community species composition. For each site a discriminant analysis of grazed and ungrazed vegetation at peak standing crop in 1989 (w1), or 1988 and 1989 (t2 and s4) was performed using arcsine-transformed relative species abundance data. For 7 other sites, where there were no permanent fences, the singular effect of climate was examined with discriminant analysis of 1988 and 1989 species composition at peak standing crop.

In the interest of simplicity, I have limited discussing details of function loading and individual species responses to sites with large herbivore and climate treatments. Furthermore, to clarify interpretation and avoid the meaningless discrimination of treatments using rare species, the analyses included only species that represented at least 2% of the standing crop for a treatment.

For w1, a xeric winter range site, the analysis

clearly discriminated 1988 from 1989 samples (Fig. 23). The first discriminant function (DF) explained 87.8% of the variation in the analysis, and nearly completely separated 1988 and 1989 samples ($\chi^2=50.3$, $df=18$, $P=.00007$). The second function was not significant, although it tended to separate 1989, grazed from 1989, fenced vegetation ($\chi^2=12.22$, $df=8$, $P=.25709$). Only 1 of 12 1988, grazed samples was misclassified, while 4 of 12 1989, grazed and 3 of 12 1989, fenced samples were misclassified.

Nine of 15 species found at the site were used in the analysis. Two species, Poa sandbergii and Lupinus sericeus, in order of declining importance, were loaded positively and heavily on DF1; and Festuca idahoensis and Koeleria cristata received extreme negative loadings (Table 4). Agropyron spicatum and Koeleria cristata were weighted positively and heavily on DF2; and Chrysothamnus viscidiflorus received the only negative score.

Results from univariate F tests indicated 4 species were sensitive to prevailing conditions (Table 5). Scheffe range tests showed Festuca idahoensis was relatively more abundant in 1988, grazed vegetation than 1989 vegetation, Linanthus septentrionalis and Lupinus sericeus were more abundant in 1989, fenced vegetation than 1988 grazed vegetation, and Poa sandbergii was more abundant in 1989, grazed vegetation than 1988, grazed

Fig. 23. Discriminant analysis of 1988, grazed (1); 1989, grazed (3); and 1989, fenced (4) vegetation at w1 using relative abundance of most common species. Group centroids (+) for DF1,DF2 are: 1988, grazed = -2.34, -0.05; 1989, grazed = 1.29, -0.73; and 1989, fenced = 1.06, 0.78.

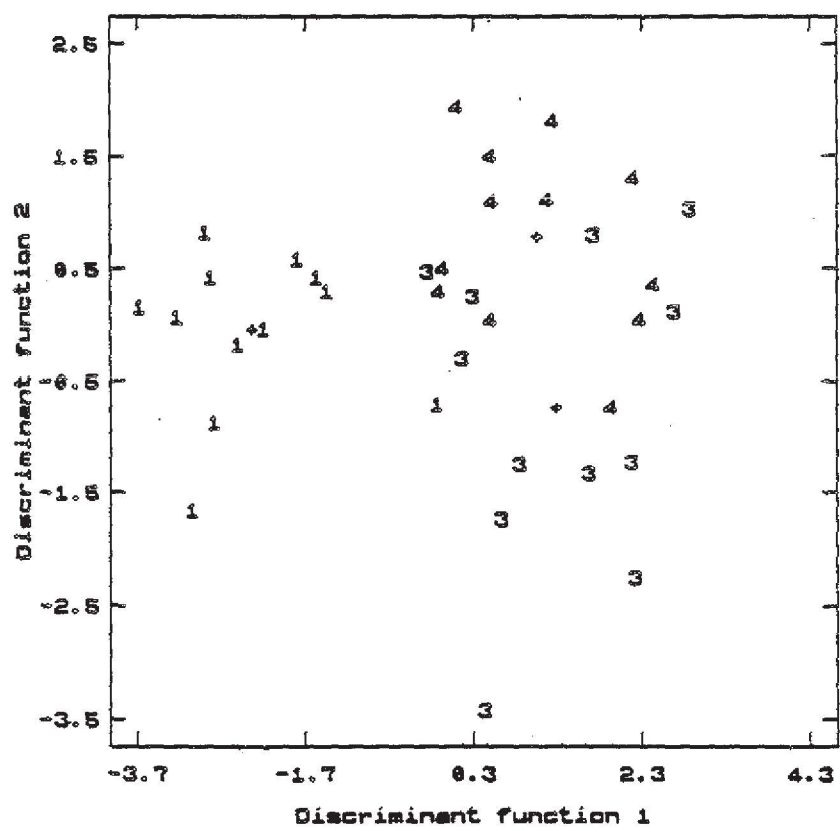


Table 4. Standardized coefficients of common species at w1 for the first (DF1) and second (DF2) discriminant functions.

SPECIES	DF1	DF2
<u>Agropyron spicatum</u>	0.303	0.842
<u>Chrysothamnus viscidiflorus</u>	0.303	-0.090
<u>Festuca idahoensis</u>	-0.699	0.450
<u>Koelaria cristata</u>	-0.293	0.768
<u>Linanthus septentrionalis</u>	0.289	0.595
<u>Lupinus sericeus</u>	0.592	0.407
<u>Poa sandbergii</u>	0.626	0.238
<u>Phlox hoodii</u>	0.019	0.088
<u>Stipa viridula</u>	0.044	0.284

Table 5. Mean relative species abundance of grazed vegetation in 1988 and grazed and fence vegetation in 1989 at w1. Significance testing includes F tests, F statistic and probability (P), and Scheffe range tests. Means with the same letter are statistically cannot be distinguished.

Species	Percent abundance			F	P<
	1988 grazed	1989 grazed	1989 fenced		
<u>Agropyron spicatum</u>	9.8a	12.4a	17.8a	1.76	NS
<u>Chrysothamnus viscidiflorus</u>	5.6a	12.0a	5.3a	1.20	NS
<u>Festuca idahoensis</u>	30.6b	10.4a	11.1a	27.7	0.0001
<u>Koeleria cristata</u>	9.4a	7.6a	13.7a	1.91	NS
<u>Linanthus septentrionalis</u>	0.1a	1.9ab	3.7b	3.43	0.04
<u>Lupinus sericeus</u>	12.3a	23.2ab	25.7b	4.43	0.02
<u>Poa sanbergii</u>	3.2a	9.6b	8.1ab	4.92	0.01
<u>Phlox hoodii</u>	2.8a	2.1a	1.9a	0.01	NS
<u>Stipa viridula</u>	23.1a	16.9a	9.2a	3.26	NS

vegetation. No species was affected by large herbivores.

For t2, a mesic transitional range site, 4 distinct species compositions were identified (Fig. 24). Discriminant function 1, explaining 65.5% of the variation in the analysis, almost discretely separated 1988 vegetation from 1989 vegetation ($x^2=114.7$, $df=36$, $P<0.00001$). Discriminant function 2, explaining 19.5% of the variation, tended to separate 1988, grazed and 1989, fenced vegetation from 1988, fenced and 1989, grazed vegetation ($x^2=54.8$, $df=22$, $P<0.0002$). Discriminant function 3 explained 15.0% of the variation and separated 1989, grazed from 1989, fenced vegetation ($x^2=24.9$, $df=10$, $P<0.006$). The analysis misclassified 1 of 11 1988, grazed; 1989, grazed; and 1989, fenced samples. All 1988, fenced samples were correctly reclassified.

Twelve of 25 species found at t2 were used in the analysis. Two species, Perideridia gairdneri and Achillea millifolium, loaded positively and heavily on DF1; and Stipa occidentalis was a strong negatively loaded species (Table 6). Discriminant function 2 used Agropyron caninum as a strong positive weight, and Stipa occidentalis as an extreme negative weight. Discriminant function 3 weighted Trifolium longipes strongly and positively, and opposite Danthonia intermedia.

All 6 species receiving extreme weights for 1 or more discriminant functions exhibited significant differences

Fig. 24. Discriminant analysis of 1988, grazed (1); 1988, fenced (2); 1989, grazed (3); and 1989, fenced (4) vegetation at t2. Group centroids for DF1,DF2,DF3 (not shown) are: 1988, grazed = -1.81, 1.50, 0.59; 1988, fenced = -2.20, -1.22, -0.76; 1989, grazed = 1.60, -0.89, 1.28; and 1989, fenced = 2.41, 0.61, -1.10.

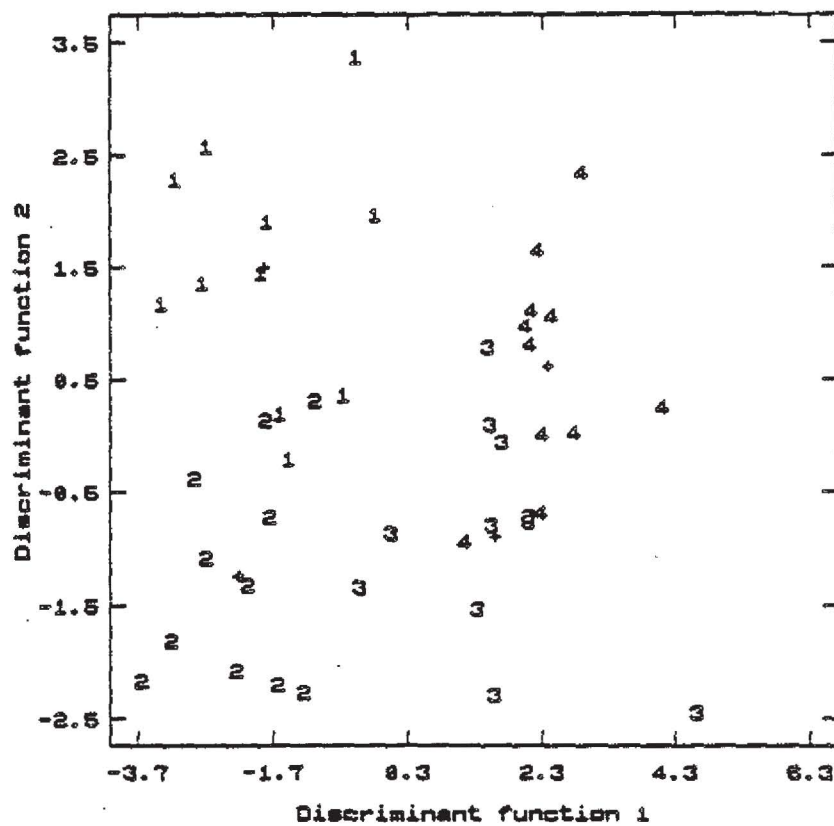


Table 6. Standardized coefficients of common species at t2 for the first (DF1), second (DF2), and third (DF3) discriminant functions.

Species	DF1	DF2	DF3
<u>Achillea millefolium</u>	0.839	0.410	0.068
<u>Agropyron caninum</u>	-0.180	0.854	0.032
<u>Bromus carinatus</u>	-0.251	0.430	-0.340
<u>Carex spp.</u>	-0.413	0.592	0.055
<u>Danthonia intermedia</u>	-0.145	-0.117	-0.994
<u>Funcus hallii</u>	0.043	0.166	-0.431
<u>Perideridia gairdneri</u>	1.046	-0.358	-0.101
<u>Phleum pratense</u>	-0.185	-0.216	-0.162
<u>Potentilla spp.</u>	0.651	-0.300	-0.062
<u>Stipa occidentalis</u>	-0.678	-0.870	-0.286
<u>Tharaxacum officinale</u>	-0.235	-0.053	-0.109
<u>Trifolium longipes</u>	0.359	-0.066	0.798

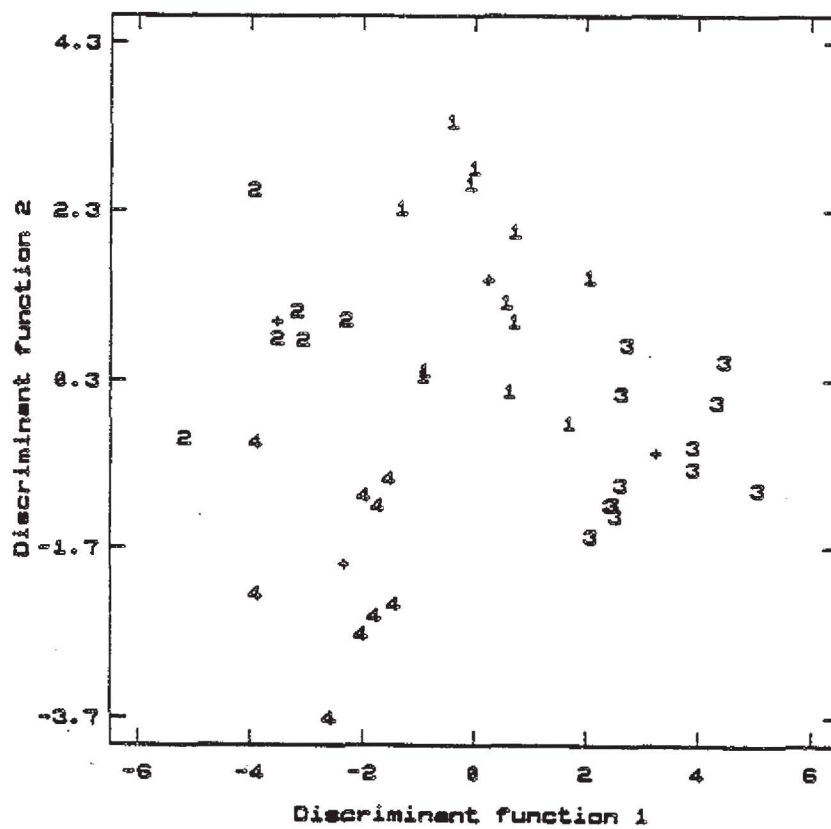
between treatments (Table 7). Phleum pratense, an introduced species and dominant at t2, also responded differently to treatments, yet was not an important discriminating variable of any function. Scheffe range tests indicated that 6 species were variably affected by treatments. Trifolium longipes was more abundant in 1989 grazed vegetation than fenced vegetation in both year and Danthonia intermedia was more abundant in fenced vegetation than grazed vegetation during both years. Perideridia gairdneri increased in the presence and absence of herbivores from 1988 to 1989 and Phleum pratense was relatively rarer in 1989 fenced vegetation than 1988 fenced or grazed vegetation. Achillea millifolium was more abundant in 1989 fenced vegetation than 1988 grazed vegetation, and Stipa occidentilis was positively affected by fencing in 1988.

For s4, a forest opening in the summer range, as in the case of t2, the analysis clearly distinguished all 4 treatments (Fig. 25). Discriminant function 1 explained 76.9% of the variation in the analysis, and primarily separated grazed vegetation from fenced vegetation, and secondarily discriminated 1988, grazed from 1989 grazed vegetation ($x^2=96.7$, $df=48$, $P=0.00004$). Although DF2, explaining 20.7% of the variation, was not significant, it helped distinguish 1988, fenced vegetation from 1989, fenced vegetation ($x^2=37.8$, $df=30$, $P=0.15$). Discriminat

Table 7. Mean relative species abundance of grazed and fenced vegetation in 1988 and 1989 at t2. Significance testing is as Table 5.

Species	Percent abundance				F	P<
	1988		1989			
	grazed	fenced	grazed	fenced		
<u>Achillea millifolium</u>	0.5a	0.7ab	0.6ab	2.1b	3.83	0.0
<u>Agropyron caninum</u>	4.0a	1.2a	1.4a	2.5a	3.24	0.0
<u>Bromus carinatus</u>	7.8a	3.1a	3.0a	2.6a	2.09	N
<u>Carex spp.</u>	8.3a	4.1a	3.7a	6.5a	1.53	N
<u>Danthonia intermedia</u>	1.5a	2.8ab	2.5a	15.1b	4.26	0.0
<u>Juncus hallii</u>	5.7a	5.6a	7.5a	9.5a	0.86	N
<u>Perideridia gairdneri</u>	0.2a	0.1a	2.2b	2.7b	17.3	0.0
<u>Phleum pratense</u>	57.1b	59.6b	51.3ab	41.4a	5.32	0.0
<u>Potentilla spp.</u>	4.1a	5.0a	5.1a	5.7a	0.491	N
<u>Stipa occidentalis</u>	3.0a	12.0b	2.7a	2.8a	4.17	0.0
<u>Taraxacum officinale</u>	4.4a	4.0a	5.6a	5.7a	0.569	N
<u>Trifolium longipes</u>	1.8ab	0.1a	4.5b	1.1a	9.57	0.0

Fig. 25. Discriminant analysis for site s4. Symbols are as Fig. 24. Group centroids for DF1, DF2, DF3 (not shown) are: 1988, grazed = 0.23, 1.49, -0.52; 1988, fenced = -3.52, 0.99, 0.91; 1989, grazed = 3.26, -0.57, 0.33; and 1989, fenced = -2.32, -1.88, -0.36.



function 3 only contributed 3% of the variation ($x^2=7.4$, $df=14$, $P=0.92$) and does not warrant any interpretation. Together, the 3 functions reclassified the samples perfectly.

Sixteen of 34 species were used in the analysis. Two species, Taraxacum officinale and Stipa occidentalis were weighted positively and heavily on DF1, and Agrostis exarta and Trifolium longipes were loaded strongly negative (Table 8). Five species, Poa spp., Stipa occidentalis, Taraxacum officinale, Danthonia intermedia, and Carex spp., loaded positively and heavily on DF2, and Bromus carinatus was loaded heavily negative.

Eight of the 16 species displayed significant differences between treatments (Table 9). Six were strongly positively or negatively loaded on 1 or more functions. The remaining two species, Antennaria microphylla and Juncus hallii, were not particularly important for discriminating groups. Range tests showed that grazing increased Antennaria microphylla, Juncus hallii, and Taraxacum officinale; Poa spp. declined from 1988 to 1989 in grazed vegetation; and Stipa occidentalis was more abundant in grazed 1989 vegetation than fenced 1988 vegetation.

At 5 of 7 other sites, species composition was significantly affected by climate (Table 10). Sites unaffected were: w3, a winter range community dominated by

ble 8. Standardized coefficients of common species at s4 for first (DF1) and second (DF2) discriminant functions. Discriminant function 3 was uninformative and not considered.

Species	DF1	DF2
<u>Procyon caninum</u>	-0.066	-0.034
<u>Procyon exarata</u>	-0.657	-0.239
<u>Tennaria microphylla</u>	0.505	0.580
<u>Onoclea carinata</u>	-0.399	-0.768
<u>Rex spp.</u>	-0.178	1.105
<u>Scirpus scariosus</u>	0.686	-0.059
<u>Anthoxanthus intermedia</u>	0.208	1.166
<u>Stipa idahoensis</u>	0.309	0.290
<u>Agrostis virginiana</u>	-0.375	0.701
<u>Trisetum hallii</u>	0.763	0.920
<u>Leum pratense</u>	0.063	0.532
<u>Trisetum spp.</u>	-0.082	1.601
<u>Centilla spp.</u>	0.417	0.220
<u>Stipa occidentalis</u>	1.255	1.265
<u>Trisetum officinale</u>	1.371	1.171
<u>Trisetum longipes</u>	-0.544	0.317

Table 9. Mean relative species abundance of grazed and fenced vegetation in 1988 and 19 at s4. Significance testing as in Table 5.

Species	1988		Percent abundance 1989		F	P<
	grazed	fenced	grazed	fenced		
<u>Agropyron caninum</u>	4.7a	6.0a	5.5a	9.9a	2.31	NS
<u>Agrostis exarata</u>	1.6a	2.8a	0.5a	0.1a	2.97	0.05
<u>Antennaria microphylla</u>	2.9b	1.7ab	2.5b	0.2a	4.34	0.01
<u>Bromus carinatus</u>	13.9a	15.2a	12.4a	16.9a	0.245	NS
<u>Carex spp.</u>	9.0a	14.7a	7.8a	14.4a	3.10	0.05
<u>Cirsium scariosum</u>	2.4a	1.0a	3.1a	1.2a	1.42	NS
<u>Danthonia intermedia</u>	3.7a	5.9a	1.5a	8.5a	1.98	NS
<u>Festuca idahoensis</u>	0.5a	0.7a	1.3a	3.4a	0.889	NS
<u>Fragaria virginiana</u>	2.2a	1.4a	2.7a	1.8a	1.42	NS
<u>Juncus hallii</u>	6.7ab	2.2a	9.9b	2.1a	4.75	0.01
<u>Phleum pratense</u>	2.2a	4.0a	0.0a	1.7a	4.07	0.02
<u>Poa spp.</u>	13.0b	21.7b	4.0a	9.9ab	7.83	0.001
<u>Potentilla spp.</u>	4.1a	7.2a	5.7a	7.2a	1.40	NS
<u>Stipa occidentalis</u>	18.3ab	10.4a	28.2b	16.9ab	4.56	0.01
<u>Taraxacum officinale</u>	8.4ab	1.6a	11.4b	1.6a	5.68	0.003
<u>Trifolium longipes</u>	2.1a	0.9a	0.6a	0.8a	1.23	NS

Table 10. Discriminant analyses on species composition of 1988 and 1989 grazed vegetation at 7 sites using relative dry-weight abundance of common species. Degrees of freedom (df) equals number of species used in the analysis, and S equals species richness at the site.

Site	Chi-square value	df	P<	S
w3	1.8	2	NS	8
t1	32.7	7	0.00003	18
t3	32.5	9	0.0002	25
s1	26.6	6	0.0002	11
s2	24.2	14	0.05	32
s3	24.6	12	0.02	22
s5	5.01	2	NS	13

a single nonnative grass species, Bromus inermis; and s5, a summer range lodgepole pine understory community dominated by Calamagrostis rubescence. Dominants at both sites represented over 90% of the total standing crop.

DISCUSSION

Within climatic and edaphic constraints, large herbivores have profound direct and indirect effects on ecosystem processes (McNaughton et al. 1988, Naiman 1988, Naiman et al. 1988, Pastor et al. 1988, Whicker and Detling 1988). To understand how large herbivores, primarily elk and bison in this study, affect the structural and functional organization of grasslands in Yellowstone's northern range, it is necessary to bear in mind seven factors. First, aboveground primary production in Yellowstone occurs locally as a strong, brief pulse, and regionally as a nitrogen rich "green wave" (McNaughton 1979) that follows an elevational gradient beginning in the lower-winter range in the spring and ending in the high-summer range in the late summer. Second, ungulates have evolved the capacity to increase utilization of this nutritious and highly concentrated food source at the ecosystem level by following the wave as it sweeps across the ecosystem. The ability of Yellowstone Park to support large migratory herds of ungulates may be tied to its climatic (Dirks and Martner 1982, Despain 1987), geologic, elevational, and vegetative diversity that makes available this young, nutritious forage for up to 6 months a year someplace in the park. Third, uneven topography in Yellowstone has established complex resource gradients and

heterogeneous landscapes composed of patches that vary in primary production. Fourth, grassland patch production is positively associated with both herbivore consumption and nutrient flow from herbivores to the soil. Grazing, therefore, is coupled spatially to nutrient cycling in the northern range. Fifth, the myriad of effects large herbivores have on ecosystem processes in Yellowstone result in an increase in aboveground primary production. Sixth, nonuniform herbivore utilization patterns in the landscape, in conjunction with the many herbivore effects on ecosystem structure and function, lead to greater environmental heterogeneity at all spatial scales in the ecosystem. Seventh, climate, the principal driving variable of ecosystem function, can modify the effect large herbivores have on ecosystem processes by controlling herbivore numbers and/or affecting their regulatory influence on trophic processes.

Large herbivore migration and forage quality

Escape from predators or access to high quality forage are the two prevailing explanations for the migratory behavior of large herbivores (Kruuck 1970, 1972, Maddox 1979, Fryxell and Sinclair 1988, Fryxell et al. 1988). In Yellowstone, seasonal migration is likely driven by foraging decisions, since bison have had no

effective predators after the ecological elimination of the gray wolf (Canis lupus) in the 1920s (Meagher 1973), and elk movements generally coincide with those of many of their predators, including cougar (Felis concolor), coyotes (Canis latrans), black bear (Ursus americanus), and grizzly bear (U. arctos). Therefore, migratory elk in Yellowstone should not be any less vulnerable to predation than resident animals (Fryxell et al. 1988). Predator avoidance, however, may play a role in ungulates selecting habitats within seasonal ranges. Elk calving is closely associated with shrub communities, where vulnerable newborn calves may be less detectable to predators than in open steppe (F. Singer, per. comm.), and elk daytime, summer bedding usually occurs in shaded, forested areas.

Elk and bison migration during the growing season in the northern range is closely tied to a wave of young vegetation as it moves from the winter range to summer range. Nitrogen concentration, generally considered limiting to large herbivores (Mattson 1980), was highest in young tissue and declined quickly with tissue age. By preferentially grazing young vegetation in the landscape, herbivores increased forage quality, the duration of a high quality diet, and their yield per bite, since concentration of green biomass was also highest at sites supporting young vegetation.

In the Serengeti ecosystem, ungulate migration during

the wet season is also associated with animals following patches of young vegetation (McNaughton 1979). However, in contrast to the predictable pattern of green up along an elevational gradient in Yellowstone, plant growth in the wet season in the Serengeti is stochastically distributed in space in accordance with rainfall events. This high level of concordance between Yellowstone and the Serengeti in regards to factors associated with movement of migratory herds of grazers suggests that the spatiotemporal dynamics of primary production is a fundamental factor determining the structural and functional organization of ecosystems dominated by large vertebrate herbivores.

Since the mid-1980s, several hundred bison have descended in the summer to the upper northern winter range, principally the Lamar Valley and areas west to Junction Butte (M. Meagher per. comm.). Bison are aggregated at this time into large groups for the rut, which begins in mid-July (Meagher 1973). Their summer movement to the Lamar Valley in both years in this study coincided with a prevalent community type in the Lamar Valley, w2, having the highest level of green biomass among all sites sampled. Site w2 was grazed in August and July of 1988, and August of 1989. Available ground water at w2, as well as other valley bottom areas throughout the Lamar Valley, may sustain plant growth and green biomass

well into the summer, even during severe drought. Bison likely grazed in the Lamar Valley from mid- to late-summer because of the lack of large areas of high quality grassland in transitional and summer ranges at this time of year. Large grasslands may be of distinct importance to bison during the rut when they have formed large groups. Therefore, access to high quality forage can be invoked to explain both seasonal movements of entire herds, and some long distance intra-seasonal movements of herd segments.

Elk and bison spend the winter foraging on rank vegetation in the winter range, where temperatures are higher and snow accumulation is lower than at upper elevations. Winter-time migration to the northern winter range, therefore, confers on animals reduced energy demands and greater access to forage, since snow limits forage availability (Meagher 1973, Houston 1982).

Large herbivores in heterogeneous environments

The interplay between herbivores and their landscape is largely driven by grazers striving to meet dietary needs in ecosystems offering patchy forage, and modified by other behaviors, such as predator avoidance or bedding (Turner 1989). Foraging decisions by herbivores are a series of hierarchical alternatives that vary at spatial

scales ranging from the region to the individual plant (Senft et al. 1987, McNaughton 1989). Because of the patchiness of their utilization and their vast effects on functional and structural properties of sites that they use, large herbivores increase ecosystem heterogeneity at all spatial scales.

At the level of the seasonal range, it is clear from this study that the winter range is functionally distinguished from other seasonal ranges in two important respects. First, ungulates graze the winter range for 6 months when other seasonal ranges receive no or negligible use. During the winter, ungulates obtain energy, but few nutrients by consuming rank vegetation, while continuing to lose nutrients through excretion. Consequently, there is likely a net transport of nutrients from transitional and summer range areas where ungulates graze high quality forage and gain condition in the spring and summer, to the winter range where condition is lost. The nutrient influx can be especially high in communities where winter use is extreme, such as w4 where 166 g m^{-2} of dung was deposited during the winter of 1988-89.

Second, these results suggest that during years of near-average weather and low or moderate elk and bison herd sizes (e.g. 1989), the winter range is grazed less intensively during the growing season than other seasonal ranges. This is because elk and bison move off the winter

range during spring to graze at higher elevations. As a result, winter forage, generally thought to be a principal limiting factor to herbivores in the northern range (Meagher 1973, Houston 1982) is conserved. Seasonal segregation of grazing leading to conservation of forage during the food limiting period of the year, e.g, winter in temperate grasslands, dry season in tropical grasslands, is a feature common to ecosystems supporting large herds of migratory herbivores (Sinclair and Norton-Griffiths 1979, Morgantini and Hudson 1988) and has long been a practice of animal husbandary (McNaughton 1985).

In 1988 when elk and bison populations in the northern range were at their highest levels in recent history, the winter range was grazed during the growing season at the same intensity as other seasonal ranges. This phenomenon may have been a consequence of a portion of the ungulates delaying migration from the winter range during the spring because of grazer satiation at higher elevations and/or a particularly early return by over 300 bison to the Lamar Valley, which may have been drought-induced. Climate has long been recognized as a determinant of winter forage quantity, both by influencing primary production during the growing season, and by regulating forage availability as a result of snow accumulation and density in the winter (Meagher 1973). The interaction of ungulate number and climate on winter

forage availability as inferred in this study, indicates the complex and partially ungulate dependent nature of carrying capacity of the northern range.

The next hierarchical level is landscapes (Senft et al. 1987), of which there are several per seasonal range (e.g., valleys, ridges, or plateaus), and between which ungulates likely decide at a rate of several times each season. A variety of large wild herbivores have been shown to exhibit landscape preference, including bison (Coppock et al. 1983, Norland et al. 1985), feral horses (Turner and Bratton 1987), eastern grey kangaroos, and wallaroos (Taylor 1984). Herbivores select landscapes according to forage quality (Senft et al. 1987), water availability (Valentine 1947, McNaughton and Georgiadis 1987), and presence of salt licks (Jones and Hanson 1985).

All sites in the present study were confined to a single landscape per seasonal range: the Lamar Valley and adjacent terrain in the winter range, and Cache-Calfee Ridge, on which transitional and summer range sites were located. However, ample information on elk and bison utilization of the park (Meagher 1973, Houston 1982) clearly indicates their nonuniform distributions. Transitional and summer range study areas were selected for their high elk and bison densities. Bison tend to concentrate during the growing season in localized areas, such as Cache-Calfee and adjacent ridges, the Mirror

Plateau, Hayden Valley, and Pelican Valley (Meagher 1973). Distributions of elk during the growing season tend to be more dispersed, although some landscapes support high concentrations of elk, including all the high bison-use areas mentioned above, while other areas may support negligible elk, such as some forested areas on the central plateau of the park (F. Singer pers. comm.).

The distribution of ungulates at the landscape scale may reflect underlying differences in geologies, which influence soil fertility, vegetation structure, and forage quality (Chapin 1980, Coley et al. 1985, 1988). Differential herbivore utilization of these landscape units may increase their structural and functional dissimilarities well beyond levels stemming from geological differences alone; thus, leading to greater landscape-scale heterogeneity in the park.

The third level is the plant community (Senft et al. 1987). In Yellowstone, elk and bison appear to have a two-class system for selecting plant communities: (1) those that should be grazed at levels according to the community's primary production, and (2) those that should be avoided. This study documents positive linear relationships for both herbivore consumption and nutrient return by grazers with grassland production (see Figs. 17, 18, and 22). These results indicate close linkages between production, consumption, and nutrient cycling in

grasslands and shrub-grasslands across Yellowstone's northern range. Three sites, a sedge meadow, w4, forest, s5, and nonnative grassland, w3, were avoided by grazers during the snowfree season in this study. All communities were quasi-monocultures, with a single species contributing over 90% of the standing crop. Ungulates grazed areas adjacent to each of these sites, suggesting the communities were avoided because of their low forage quality. What environmental factors that couple exceptionally high species dominance and low forage quality at ecological and evolutionary time scales are not clear. Similar to landscape units that are not used by herbivores, the avoidance of some plant communities likely increases their differences from other communities that are grazed.

Herbivores can make decisions at the level of the plant at rates as high as 10^7 /yr, the estimated number of bites per year (Chacon et al. 1976). Patchy within community grazing alters plant competitiveness according to the degree a plant is defoliated in relation to its neighbors, and the plant's physiological attributes (Wareing et al. 1968, Hodgkinson 1974, Detling et al. 1979, Caldwell et al. 1981, McNaughton et al. 1983, Oosterheld and McNaughton 1988). Superimposed upon patterns of grazing is patchy deposition of herbivore feces and urine (Carren et al. 1982, McNaughton 1983,

1985, Day and Detling 1989, 1990), which further diversifies the availability of resources and plant competitiveness, and may lead to increased species diversity in some plant communities (Sala et al. 1986, Milchunas et al. 1988, Noy-Meir et al. 1989).

The movement of substantial resources across patch boundaries by herbivores is a unique property that separates grazing ecosystems from other terrestrial habitats, which in Yellowstone, may primarily occur at the scales of the seasonal range and microsite. Interactions of herbivores with their spatial environment is largely determined by the distribution of forage. Forage patchiness leads to patchy utilization by grazers and increased heterogeneity of grazing ecosystems at all spatial scales.

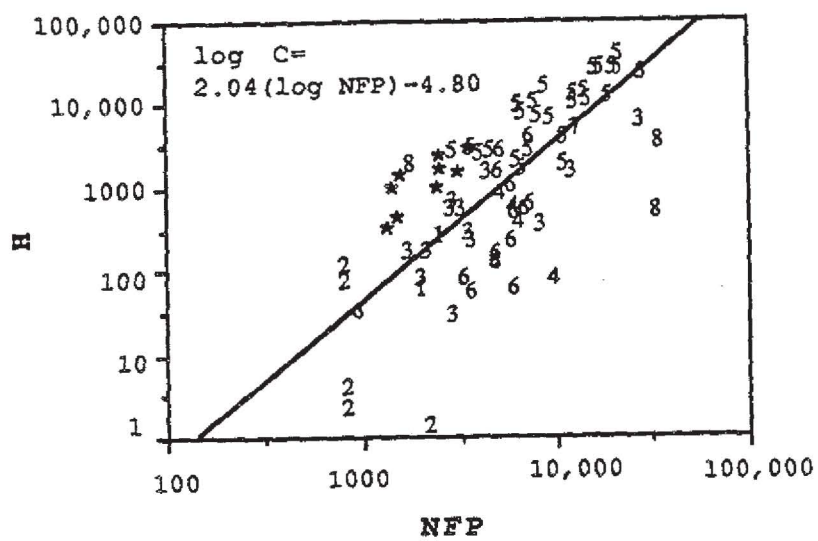
Consumption in Yellowstone's northern range compared with other ecosystems

Rates of primary production and herbivore consumption are fundamental properties of ecosystem food web structure and function. Although aboveground production and herbivory have been examined in most terrestrial habitats, these measurements are rare for areas such as Yellowstone that support large populations of native large herbivores.

A data set of coupled net primary production and

herbivore consumption from a variety of terrestrial ecosystems was compiled from the literature by McNaughton et al. (1989, 1990). They found that herbivore consumption and foliar production were strongly and positively related, where foliar production was aboveground production, except in forest ecosystems when it equalled aboveground production minus wood production. The relationship was heavily influenced by a large number of samples ($n=31$) from East African game reserves (Sinclair 1975, McNaughton 1985), which had a greater proportion of their primary production grazed than all other ecosystems. If average values for consumption and production of grazed sites in Yellowstone's northern range determined in this study are superimposed on the relationship (Fig. 26), it is clear that, like African game reserves, rates of herbivory at Yellowstone sites lie consistently above the best fit line determined by McNaughton et al. (1989) for terrestrial ecosystems in general. A Waller-Duncan Bayes LSD range test, adjusted for unequal sample sizes (Kramer 1956), on arcsine transformed values for the proportion of aboveground production consumed, lumped African and Yellowstone samples into one group, which statistically indicates what is visually apparent from Fig. 26, that consumption in these two ecosystems are similar, and higher than other terrestrial ecosystems. (Yellowstone was also grouped

Fig26. Relationship of herbivore consumption, H , on net foliage production, NFP, for terrestrial ecosystems. Codes are: 1, desert; 2, tundra; 3, temperate grassland; 4, temperate successional old field; 5, unmanaged tropical grassland; 6, temperate forest; 7, tropical forest; 8, salt marsh; 9, agricultural tropical grassland; and, *, Yellowstone grassland. Yellowstone samples were not included in the regression. Units are $\text{kJ m}^{-2} \text{yr}^{-1}$. Adapted from McNaughton et al. 1989, 1990.



with salt marshes, indicating offtake in salt marshes can also be high). Consumption averaged 62% at African sites and 45% in Yellowstone's northern range steppe and shrub-steppe. Herbivory was over six times as intense in Yellowstone as in other temperate grassland sites, primarily relatively small reserves possessing small populations of native ungulates (French 1979), where consumption averaged 7.9%.

These results suggest that grassland ecosystems with abundant large herbivores are structurally and functionally more similar to aquatic grazing systems that support high chronic levels of herbivory (Carpenter and Kitchell 1984, Berquist and Carpenter 1986), than to other terrestrial ecosystems (McNaughton 1983, 1985), and understanding these terrestrial, grazing ecosystems can only come from their direct study and not extrapolation from other ecosystems. Furthermore, these findings suggest that high rates of herbivory and concomitant structural and functional food web properties may have been typical for grasslands that, prior to the spread of European influence, supported large herds of ungulates throughout all of Africa (Ford 1971), North American (Roe 1951, Dary 1974), and Eurasia (Bannikov et al. 1961) and macropods in Australia (Newsome 1971, 1975). It is suprising that this study represents only the second ecosystem possessing a large complement of its native large herbivore fauna where

primary production and consumption have been measured. The novelty of such data is likely a reflection of the woeful worldwide rarity of these ecosystems.

Large herbivore regulation of primary productivity

Defoliation, trampling, urination, and defecation by large herbivores have profound effects on carbon, nutrient, and water flows in biotic communities, which together, interactively determine plant growth (McNaughton et al. 1982, McNaughton 1985, 1988, Ruess 1987). The removal of photosynthetic tissue by grazers influences plant physiological processes in several ways.

Defoliation opens the canopy allowing greater light penetration (Laude 1972, Monsi et al. 1973), and causes plants to allocate a greater proportion of photosynthate to aerial parts (Gifford and Marshall 1973, Detling et al. 1979, 1980, Oesterheld and McNaughton 1988), usually at the expense of root growth (Davidson and Milthorpe 1966, Evans 1973a, 1973b, Hodgkinson and Baas Becking 1977). Regrowth after defoliation has higher nitrogen content (Detling and Painter 1983, McNaughton 1983, Ruess et al. 1983, Ruess 1984) and higher photosynthetic rates (Parsons and Penning 1988, Gold and Caldwell 1989b, Wallace 1990), which lead to higher growth rates for grazed plants compared to ungrazed plants (Oesterheld and McNaughton

1988, Caldwell 1989a, Polley and Detling 1990). Removal of transpiring tissue results in soil moisture conservation (McNaughton 1985, Wraith et al. 1987), greater regrowth promotion, and higher plant water use efficiency (McNaughton 1985). Furthermore, grazing stimulates tillering (McNaughton 1983, Kotanen and Jefferies 1987, Butler and Briske 1988, Milchunas and Lauenroth 1989) and promotes a short and concentrated canopy structure, e.g. a grazing lawn (McNaughton 1984). In Yellowstone, green biomass of grazed vegetation was more concentrated than for ungrazed vegetation at all three grazed sites where permanent fences were maintained. Grazing, therefore, maintains vegetation at a young, productive stage, and initiates a positive feedback loop to herbivores that confers lasting nutritious forage that can be efficiently exploited.

Soil processes are also dramatically affected by large herbivores. Grazers indirectly influence soil dynamics by limiting the accumulation of standing dead and litter, thereby allowing greater soil irradiation and warming (Ruess 1987). Because decomposition is positively related to temperature and moisture (Waksman and Gerretsen 1931), grazing, which increases both factors, should stimulate decomposition rates. Trampling can also stimulate decomposition rates by fragmenting plant tissue and incorporating it into the soil (Ruess 1987).

Large herbivores remove nutrient poor material (plant tissue) and add material that is nutrient rich (feces and urine). Ungulates excrete 90% of their ingested phosphorus, 99% of which is lost as feces, and 65-95% of their ingested nitrogen, 85% of which is urinary (McDonald et al. 1973, Wilkinson and Lowery 1973, Day and Detling 1990). The C/N ratio of litter is an important determinant of microbial mineralization-immobilization dynamics (Paul and Juma 1981). As the ratio increases, microbial immobilization rates increase, and net mineralization and nutrient availability to plants declines. Because urine and feces have narrow C/N ratios, net mineralization in urine and feces amended soils increases, making nutrients more available to plants. Since grasslands are nitrogen (Owensby et al. 1970, McNaughton 1985) and/or phosphorus (Keya 1973, Penning de Vries et al. 1980, Bremen and de Wit 1983, McNaughton and Chapin 1985, Mott et al. 1985) limited, it follows that grazing, if associated with fecal and urinal return, may indirectly promote growth by increasing nutrient availability. Banyikwa (1976) showed that addition of dung to Serengeti shortgrass plains increased plant growth late in the wet season when, presumably, plants were nutrient limited (McNaughton 1985). In Yellowstone, I found a positive association between consumption at the plant community level and nutrient return, indexed by dung

deposition. Consequently, grazing and nutrient cycling should be coupled spatially in the Yellowstone landscape.

Grazers, therefore, stimulate plant aboveground growth by causing plants allocate to aboveground parts, while making all resources, light, water, and nutrients, more available. However, whether herbivores enhance, inhibit, or have no affect on production depends on several interacting factors, including soil fertility (McNaughton and Chapin 1983), soil mineralogy (Ruess 1987), plant-herbivore evolutionary history (Mack and Thompson 1982, Milchunas et al. 1988), and grazing intensity (McNaughton 1979a, 1985, Hilbert et al. 1981).

Grazer stimulation of aboveground productivity is a second similarity that can be drawn between Yellowstone and the Serengeti (McNaughton 1979a, 1979b, 1985). In both ecosystems, large herbivores concentrate their grazing during a period after the onset of the growing season, initiated in the Serengeti by spatially stochastic rains at the beginning of the wet season, and in Yellowstone by snowmelt. Because a pulse of mineralization likely accompanies the first rains breaking a protracted drought (Birch 1958a, 1958b), and mineralization rates of temperate semiarid habitats are highest early in the growing season (Burke 1989), grazing by native ungulates in both ecosystems coincides with high soil moisture and nutrient availability, which would favor

regrowth of grazed plants. Thus, stimulation of aboveground production may be an emergent functional property of grassland ecosystems dominated by native migratory herds of large herbivores that seek to increase their diet quality in landscapes with marked spatiotemporal shifts of forage quality.

In the Serengeti, stimulation declined with declining rainfall at sites throughout the ecosystem (McNaughton 1985). In Yellowstone, the only community not stimulated was the summer range site, s4, where the 1988 drought was severest. The unusually xeric conditions at s4 may have negated the mechanisms that normally would have caused herbivores to enhance plant growth in years of more normal moisture. Interestingly, the drought effect carried over to the next year, 1989, when again there was no stimulation at the site. These results indicate what may be expected to happen during normal years when grazing occurs late in the growing season while soil moisture is usually low - grazers will not stimulate primary production (Detling 1988, Maschinski and Whitman 1989, Olson et al. 1989). Alternatively, the lack of stimulation at s4 may have been a site effect, an inherent property of the community, rather than an effect from severe moisture stress.

Herbivores increased production at w4, a Carex rostrata community, even though grazing occurred at this

site only during the winter. Consequently, production must have been stimulated by factors other than plant regrowth after defoliation, e.g., fertilization or standing dead removal. This bolsters the contention a thorough understanding of mechanisms underpinning the facilitation of production by grazers cannot be achieved by examining singular responses alone, e.g., clipping, but must be sought in an integrated approach that takes into account the many direct and indirect effects herbivores have on a plant's physiology and the growing environment.

The grazing optimization model (McNaughton 1979a, Hilbert et al 1981), predicting maximum aboveground production at some intermediate level of grazing intensity and a decline to below control (ungrazed) levels at higher grazing intensities, has been demonstrated for ecosystems ranging from ungulate-grazed tropical savannas (McNaughton 1979a, 1979b, 1985) to goose-grazed tundra (Hik and Jefferies 1990). In Yellowstone, herbivores stimulated production at sites that were explicitly selected at the beginning of the study for their high herbivore use. Moreover, stimulation occurred in 1988 when elk and bison populations were at their highest levels in recent history. The only exception was the summer range site, mentioned above, where the drought was the severest and, notably, grazers had no affect on production. Some (Chase 1986) have argued that the increase of northern range elk

since Yellowstone Park's implementation of the "natural regulation" policy in 1969 (Cole 1971, Houston 1982) has led to grassland deterioration in the northern range. These data clearly refute this argument by demonstrating no evidence for ecosystem process degradation, and show that quite the contrary, even during a year of unusually high elk and bison numbers, grazers stimulated grassland production in the northern range.

The effects of fire on ecosystem processes

Fire is an important natural component of the Yellowstone ecosystem (Romme and Despain 1989). Pre-European fire frequency varied markedly between regions of the ecosystem, from intervals of 20-40 years in the steppe and shrub-steppe habitats in the northern range (Houston 1973) to 200-400 year intervals in some forested areas on the central plateau (Romme 1982). The ecological consequences of fire are numerous (Daubenmire 1968, Romme and Despain 1989). Nutrient dynamics are altered directly due to greater volatilization of C compared to N; thus reducing C/N ratios of burned residue, and increasing net mineralization rates (Hobbs and Schimel 1983) and plant nutrient concentrations in burned areas (Woolfolk et al. 1975, Allen et al. 1976, Wood 1988, Knight and Wallace 1989). Herbivores are attracted to post-fire regrowth

(McNaughton 1985, Knight and Wallace 1989), which results in an increase in their productivity (Hilmon and Hughes 1965, Svejcar 1989). Longer term effects of fire are changes in vegetation structure and species composition, which can vary in duration from several years in grasslands, where most of the vegetation resprouts from perennating structures (Daubenmire 1968), to many decades in forests, where more vigorous herbaceous growth may persist until canopy closure (Knight and Wallace 1989, Romme and Despain 1989). This shift in vegetative structure following fire confers indirect fire impacts on ecosystem function (Knight and Wallace 1989).

The 1988 Yellowstone fires were at the scale of the ecosystem (Schullery 1989). Ungulates may respond in the short term by concentrating their grazing in areas that recently burned, and in the long term by continuing for decades to utilize burned forests that support abundant herbaceous growth (Knight and Wallace 1989). Changes in the spatial pattern of ungulate-landscape interactions will result in an alteration of ungulate-mediated nutrient transport in the ecosystem, and a spatial redistribution of ungulate-regulated ecosystem processes.

Grassland production has been shown to increase, decline, and not change after fire (Daubenmire 1968, Anderson et al. 1970, James 1985, McNaughton 1985). The inconsistent effect of fire on production may be caused by

variability of available soil moisture to support regrowth (Risser et al. 1981). The post-1988 fire productivity of Artemisia tridentata communities in Yellowstone likely declined due to mortality of Artemisia and nearby herbaceous plants, creating barren areas that were described previously for site tb. The herbaceous production at these sites should recover to prefire levels within several years as bare areas are recolonized. Although no recolonization of bare areas occurred one year after the fire at the burned Artemisia site in this study, by early-summer of 1990, bare areas in burned Artemisia communities throughout the northern range supported substantial, and, in some cases, dense vegetation, which started principally from seed (per. obs.).

Grazing intensity, the proportion of primary production consumed, was the same at tb as other transitional and summer range sites during the growing season when forage quality on unburned sites was high. However, in the late-season, tb was the only site of the 13 sampled in 1989 that was grazed, leading to its highest overall grazing intensity of any site during the snowfree season. These results suggest that: (1) any improvement in forage quality of burned vegetation early in the season is too small to alter ungulate site selection when forage quality at all sites, burned and unburned, is high, and (2) plants in burned areas retain more nutrients in aerial

parts late in the season when vegetation dries compared to plants of unburned areas, resulting in higher forage quality and greater herbivore consumption.

The fires had unknown direct and indirect effects on ungulate foraging patterns during the study. Although no 1988 study site burned, fire approached to within 1 km of all sites, primarily burning forested areas in drainages, and a portion of nonforested habitat in the upper winter range. Probably most severely affected was late-season consumption, since animals in 1988 concentrated on unburned sites where there was forage, and, in 1989, may have concentrated off the study sites in burned drainages where forage quality was high. Thus, the fire likely increased the between-year difference in late-season consumption. Growing season consumption for 1988 was unaffected, since the fires occurred after the animals moved off the study sites seeking green vegetation at higher elevations. During the 1989 growing season, elk and bison used traditional migration routes after leaving the winter range, concentrating their grazing on unforested high elevation habitats that was largely unburned. These observations, in addition to data for site tb showing growing season consumption was the same as unburned sites, suggests 1989 consumption measurements during the early season were not significantly affected by the fires.

The effect of drought on ecosystem processes

The frequently reported relationship between grassland production and a climatic estimate of water balance, e.g., precipitation and temperature (Lieth 1973, Sims and Singh 1978, Lauenroth 1979, Stephenson 1990), and the demonstrated stimulation of grassland production by irrigation (Dodd and Lauenroth 1979) both implicate moisture as an important limiting factor of grassland productivity. Therefore, it was surprising that in this study production in the northern range was higher in 1988, a period of high temperature and drought, compared to 1989, a year of near-average precipitation and temperature. The reason for the decline was likely the death or injury of plants during the drought, which would have reduced the production potential at the sites in 1989. Grasses which possess belowground perennating structures are considered protected from drought (Coughenour 1985). The near complete disappearance of some dominant grass species from 1988 to 1989, e.g., peak biomass decline of Danthonia uniflora from 16.7 to 0.7 g m⁻² at an ungrazed summer range site, s1, is testimony to the severity of the 1988 drought in some parts of the ecosystem.

However, an explanation of the between-year reduction

in production cannot be sought by solely considering direct climatic effects on plants. Productivity of the northern range is, in part, regulated by grazers; therefore, indirect drought effects on herbivores are also important. The duration of high quality forage was low in 1988, which may have caused herbivores to enter the winter in relatively poor condition. Poor animal condition, loss of a portion of the winter range to fire, and a colder than average winter, likely all contributed to the large elk 1988-89 winter kill and large numbers of elk and bison exiting the park where many were shot (Singer et al. 1989). From 1988 to 1989, elk in the northern range declined by approximately 40% (Singer et al. 1989), and bison by approximately 50% (Meagher pers. com.). It was gratifying, therefore, that average consumption at the study sites declined from 154 g m^{-2} in 1988 to 71 g m^{-2} in 1989. Reduced herbivory in 1989 could have resulted in a concomitant reduction in stimulation and, therefore, production. However, this only would have been possible in the winter range where grazing intensity, the proportion of primary production grazed, declined from 1988 to 1989, and the 1988 drought was not harsh enough to obviate regrowth. So, the 1988 drought could have affected net energy and nutrient flux in the Yellowstone grasslands by: (1) killing plants, the base of the food web, thus, reducing the energy and nutrient capturing

capability of the ecosystem, and/or (2) changing herbivore stimulation of plants directly through ecosystem function, or indirectly by reducing the numbers of grazers.

At transitional and summer range sites, both production and growing season consumption declined equally, so the proportion of production grazed remained the same between years. The consistency of this relationship during two profoundly different years suggests a robust property of herbivory in Yellowstone: a constant percent of production is grazed in transitional and summer range areas regardless of weather or herbivore numbers. Although an enticing idea that would greatly simplify modeling system processes, the proof for a constant rate of herbivory, in my view, is incomplete, since the two years of measurements include a year of high production and high ungulate numbers, and a second year of low production and low ungulate numbers. Clearly, measurements during years of low production and high herbivory, and vice versa are needed before the relationship between production and consumption can be thoroughly described.

Effect of drought and herbivores on species composition

The 1988 drought also had a tremendous effect on plant community species composition throughout the

northern range. Discriminant analyses of 1988 and 1989 grazed vegetation at 6 of 8 sites were significantly different. At 3 other sites, w1, t2, and s4, discriminant analyses of grazed and ungrazed vegetation separated completely grazed 1988 samples from grazed 1989 samples, and at t2 and s4, ungrazed 1988 and 1989 samples were separated. The only sites plant community composition did not change between years were 2 quasi-monoculture communities, w3 and s5, where single grass species contributed over 90% of the total biomass. Elsewhere, Frank and McNaughton (1990) showed that plant community species composition change at the sites declined with plant community species diversity (H'), except for sites w3 and s5. Therefore, resistance to drought-induced plant community species composition change, a form of plant community stability, increased with species diversity.

Species that declined in relative abundance from 1988 to 1989 in grazed vegetation were likely particularly susceptible to drought-induced death or injury. At the xeric winter range site for example, Festuca idahoensis in grazed vegetation declined significantly from 31% in 1988 to 11% in 1989; a change in relative abundance associated with a reduction in peak standing crop from 18 g m^{-2} in 1988 to 6 g m^{-2} in 1989. Poa declined in grazed vegetation at s4, and the probable mortality-caused

disappearance of Danthonia uniflora at a summer range ridgetop site, s1, in 1989 already has been mentioned.

Species that increased from 1988 to 1989 in grazed vegetation were resistant to drought-induced mortality or injury and/or benefited from the relatively moist growing conditions and reduced competition in 1989. This latter factor was likely important for Poa sandbergii at w1, which in 1988 had nearly completely browned by the end of June and in 1989 continued tillering through most of July. Relative abundance of P. sandbergii increased from 3.2% in 1988 to 9.6% in 1989. Perideridia gairdneri, an important staple for grizzly bears, increased at t2.

Changes in species abundance inside fenced areas are more difficult to decipher. By 1988, one year after fencing was erected at site t2, Stipa occidentalis was more abundant inside compared to outside exclosures, indicating a negative response to grazing (Table 7). However, in 1989 Stipa declined inside exclosures to a level equivalent to that of grazed vegetation, suggesting ungrazed plants were more sensitive than grazed plants to drought. A particularly noteworthy species is the nonnative Phleum pratense, which was introduced in Lamar Valley for hay in 1926, and has since expanded its range throughout the northeastern portion of the park. P. pratense exhibits vigorous vegetative growth and is normally found at mesic sites with well developed soils,

where it often dominates. Grime (1979) predicted a species with these "competitive" attributes will be detrimentally affected by moisture stress. At the mesic transitional range site, t2, P. pratense declined in ungrazed vegetation from 1988 to 1989, while in grazed vegetation it was unchanged, probably as a result of it responding favorably to the combination of grazing and the near-average moisture regime in 1989. These results, which may be of particular interest to managers concerned with the spread of this species in the park, suggest that P. pratense moisture sensitive and grazer promoted.

The effect of grazing on plant community species composition appeared to increase from the winter range to the summer range; a gradient of increasing drought intensity. At w1 in the winter range, 1989 grazed and ungrazed vegetation was indistinguishable. In the transitional range, all 4 vegetation treatments (1988, grazed; 1988, ungrazed; 1989, grazed, 1989, ungrazed) were separated by discriminant analysis, and DF1, which explained 65.5% of the variation of the analysis, separated species composition by year, while DF2, which explained only 19.5% of the variation, separated grazed and ungrazed samples. At s4 in the summer range, discriminant analysis again separated all four treatment combinations, however, this time the differences in species composition were primarily segregated by the

presence or absence of grazers, and secondarily by year.

A possible explanation for the increasing effect of grazing on plant community species composition with increasing drought lies in understanding plant-herbivore interactions at ecological and evolutionary time scales. Migratory large herbivores evolved in grassland ecosystems with shifting forage bases. To increase their diet quality in such ecosystems, herbivores preferentially graze young plant tissue as it appears across the ecosystem. Plants that are grazed at this time can regrow because of sufficient available soil moisture and nutrients. Thus, herbivore foraging decisions link plants and grazers spatiotemporally in a way that increases diet quality for herbivores and decreases the net impact of herbivores on plants. The 1988 drought decoupled this link and, as a result, increased the effect of grazers on plants. Low soil moisture in 1988 likely prevented defoliated plants from regrowing (production stimulation did not occur at s4, the site most droughty) and, worse, may have injured or killed them. Studies of Kyllinga nervosa (McNaughton et al. 1983), Hyparrhenia filipendula (Coughenour et al. 1985a), Themeda triandra (Coughenour et al. 1985b), and Sporobolus kentrophyllus (Georgiadas et al. 1989), all Serengeti graminoids, show that combining clipping and low or infrequent watering reduces residual plant biomass, which corroborates field observations

herein if herbivores selectively forage species in the Yellowstone grasslands. Furthermore, the findings herein indicate differences in grazed and ungrazed vegetation during drought do not dampen after a single year, but instead may represent the beginnings of different species composition trajectories through time.

Drought has long been known to have a strong effect on plant community species composition (Nelson 1934, Weaver and Albertson 1944, Tannehill 1947). Buffington and Herbel (1965) described and Schlesinger et al. (1990) further discussed a dramatic shift from grassland to shrubland at the Jornada Experimental Range in the Chihuahuan Desert as a result of heavy cattle grazing and drought. In contrast, Houston (1982) after reviewing results from several long term studies in the northern winter range, some of which used exclosures, concluded that climatic variation had a substantial effect, and elk and bison had little effect on plant species composition of the winter range. The results of this study support Houston's conclusions, with the addendum that there is an interaction between grazing and climate, e.g., drought, on plant community species composition. These findings suggest the temporal link between native herbivores grazing phenologically young vegetation is fundamentally important in limiting herbivore impact on plant community species composition during normal years, and the great

species changes of rangeland grazed by cattle may be reduced by mimicing foraging patterns of native ungulates and restricting grazing to the early growing season.

Synthesis

Native large mammalian herbivores in grassland ecosystems are inextricably enmeshed in a complex web of energy and nutrient flows. The effect of herbivores on the structural and functional organization of grazing ecosystems is to a great extent determined by the foraging decisions of migratory grazers as they attempt to maintain a quality diet in ecosystems with shifting forage bases. In Yellowstone, grazing is spatiotemporally linked to plant growth in the landscape. By preferentially grazing young vegetation, herbivores increase the duration of a nutritiously rich diet and their foraging efficiency. Herbivores promote the availability of light, nutrients, and water to plants, resulting in the stimulation of aboveground productivity in Yellowstone, a positive causal feedback from herbivores to plants that is enhanced by defoliation occurring early in the season when soil moisture and nutrient availability is high and regrowth potential is great. This positive feedback on range production and a possible interaction of climate and ungulate numbers on winter range forage quantity, indicate

that carrying capacity of the northern range cannot be determined independently of herbivores (McNaughton 1985).

During a severe drought, the normal temporal link between plants and herbivores is decoupled changing the functional relationship between herbivores and the rest of the ecosystem. Herbivores no longer regulate production through trophic-level interactions, but instead become passive channels for energy and nutrients through the food web. An emergent structural consequence of the functional impact of drought on grazing ecosystems is the greater influence herbivores exert on plant community species composition. These results indicate the primary and secondary roles of climate and herbivores, respectively, in regulating grazing ecosystem organization. These findings additionally show how dramatically a severe drought of one year duration can alter ecosystem function and structure, and suggest a likely rapid terrestrial biosphere response to global climate change.

BIBLIOGRAPHY

- Allen, L.J., L.H. Harbers, R.S. Schalles, C.E. Owensby, and E.F. Smith. 1976. Range burning and fertilizing related to nutritive value of bluestem grass. *Journal of Range Management* 29:306-308.
- Anderson, K.L., E.F. Smith, and C.E. Owensby. 1970. Burning bluestem range. *Journal of Range Management* 23:81-91.
- Anderson, R.C. 1982. An evolutionary model summarizing the roles of fire, climate, and grazing animals in the origin and maintenance of grasslands: an end paper. pp. 297-308 in J.R. Estes, R.J. Tylr, and J.N. Brunken (editors). *Grasses and Grasslands*. University of Oklahoma Press, Norman, Oklahoma.
- Bannikov, A.G., L.V. Zhirnov, L.S. Lebedeva, and A.A. Fandeev. 1961. *Biology of the Saiga*. Englis translation. Department of Commerce, Springfield, Va.
- Banyikwa, F.F. 1976. A quantitative study of the ecology of the Serengeti short grasslands. Dissertation. University of Dar es Salaam, Dar es Salaam, Tanzania.
- Berquist, A.M., and S.R. Carpenter. 1986. Limnetic herbivory: effects on phytoplankton populations and primary production. *Ecology* 67:1351-1360.
- Bremen, H., and C.T. de Wit. 1983. Rangeland productivity and exploitation in the Sahel. *Science* 221:1341-1347.
- Buffington, L.C. and C.H. Herbel. 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. *Ecological Monographs* 35:139-164.
- Burke, I.C. 1989. Control of nitrogen mineralization in a sagebrush steppe landscape. *Ecology* 70:1115-1126.
- Butler, J.L., and D.D. Briske. 1988. Population structure and tiller demography of the bunchgrass Schizachyrium scoparium in response to herbivory. *Oikos* 51: 306-312.
- Caldwell, M.M., J.H. Richards, D.A. Johnson, R.S. Nowak, and R.S. Dzurec. 1981. Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid Agropyron bunchgrasses. *Oecologia* 50:14-24.

- Carpenter, S.R., and J.F. Kitchell. 1984. Plankton community structure and limnetic primary production. *American Naturalist* 124:157-172.
- Carran, R.A., P.R. Ball, P.W. Theobald, and M.E.G. Collins. 1982. Soil-nitrogen balances in urine-affected areas under two moisture regimes in Southland. *New Zealand Journal of Experimental Agriculture* 10:377-381.
- Chacon, E., T.H. Stobbs, and R.L. Sandland. 1976. Estimation of herbage consumption by grazing cattle using measurements of eating behavior. *Journal of the British Grassland Society* 31:81-87.
- Chapin, F.S. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* 11:261-285.
- Chase, A. 1986. *Playing God in Yellowstone: the destruction of America's first National Park.* Atlantic Monthly Press, Boston.
- Cole, G.F. 1971. An ecological rationale for the natural or artificial regulation of native ungulates in parks. *Transactions of the 36th North American Wildlife and Natural Resources Conference* 36:417-425.
- Coley, P.D., J.P. Bryant, and F.S. Chapin. 1985. Resource availability and plant antiherbivore defense. *Science* 230:895-899.
- Collins, S.L. and S.C. Barber 1985. Effects of disturbance on diversity in mixed-grass prairie. *Vegetatio* 64:87-94.
- Coppock, D.L., J.E. Ellis, J.K. Detling, and M.I. Dyer. 1983. Plant-herbivore interactions in a North American mixed grass prairie. II. Responses of bison to modification of vegetation by prairie dogs. *Oecologia* 56:10-15.
- Coughenour, M.B. 1985. Graminoid responses to grazing by large herbivores: adaptations, exaptations, and interacting processes. *Annals of the Missouri Botanical Garden* 72:852-863.
- Coughenour, M.B., S.J. McNaughton, and L.L. Wallace. 1985a. Responses of an African tall-grass (*Hyparrhenia filipendula* stapf.) to defoliation and limitations of water and nitrogen. *Oecologia* 68:80-86.

- Coughenour, M.B., S.J. McNaughton, and L.L. Wallace. 1985b. Responses of an African graminoid (Themeda triandra Forsk.) to frequent defoliation, nitrogen, and water: a limit of adaptation to herbivory. *Oecologia* 68:105-110.
- Coupland R.T. 1979. Grassland ecosystems of the world; International Biological Programme, Cambridge University Press, Cambridge.
- Cowlinshaw, S.J. 1951. The effect of sampling cages on the yields of herbage. *Journal of Range Management* 18:126-128.
- Dary, D.A. 1974. The Buffalo Book. Avon, New York.
- Daubenmire, R. 1968. Ecology of fire in grasslands. *Advances in Ecological Research* 5:209-266.
- Davidson, J.L., and F.L. Milthorpe. 1966. the effect of defoliation on carbon balance in Dactylis glomerata. *Annals of Botany* 30:185-198.
- Day, T.A., and J.K. Detling. 1989. Changes in grass leaf water relations following bison urine deposition. *American Midland Naturalist* 123:171-178.
- Day, T.A., and J.K. Detling. 1990. Grassland patch dynamics and herbivore grazing preference following urine deposition. *Ecology* 71:180-188.
- Demment, M.W., and P.J. van Soest. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *American Naturalist* 125: 641-672.
- Despain, D.G. 1987. The two climates of Yellowstone National Park. *Proceedings of the Montana Academy of Sciences* 47:11-19.
- Detling, J.K. 1988. Grasslands and savannas: Regulation of energy flow and nutrient cycling by herbivores. *Ecological studies* 67. in L.R. Pomeroy, and J. J. Alberts (editors). *Concepts of Ecosystem Ecology: A Comparative View*. Springer-Verlag, New York.
- Detling, J.K., M.I. Dyer, C. Procter-Gregg, and D.T. Winn. 1980. Plant-herbivore interactions: Examination of potential effects of bison saliva on regrowth of Bouteloua gracilis. *Oecologia* 45:26-31.

- Detling, J.K., M.I. Dyer, and D. Winn. 1979. Net photosynthesis, root respiration and regrowth of Bouteloua gracilis following simulated grazing. *Oecologia* 41:127-134.
- 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.
- Dirks, R.A. and B.E. Martner. 1982. The climate of Yellowstone and Grand Teton National Parks. Natural Resource Report. National Park Service. 26 pp.
- Dodd, J.L., and W.K. Lauenroth. 1979. Analysis of a grassland ecosystem to stress. pp. 43-58 in N.R. French (editor). *Perspectives in Grassland Ecology*. Springer-Verlag, New York.
- Duncan, P. 1983. Determinants of the use of habitat by horses in a Mediterranean wetland. *Journal of Animal Ecology* 52:93-109.
- Edroma, E.L. 1981. The role of grazing in maintaining high species composition in Imperata grassland in Rwenzori National Park, Uganda. *African Journal of Ecology* 19:215-233.
- Evans, P.S. 1973a. The effect of repeated defoliation to three different levels on root growth of five pasture species. *New Zealand Journal of Agricultural Research* 16:31-34.
- Evans, P.S. 1973b. Effect of seed size and defoliation at three development stages on root and shoot growth of seedlings of some pasture species. *New Zealand Journal of Agricultural Research* 16:389-399.
- Ford, J. 1971. *The Role of Trypanosomiasis in African Ecology*. Clarendon, Oxford.
- Frank, D.A., and S.J. McNaughton. 1990. Stability increases with diversity in plant communities: empirical evidence from the Yellowstone drought. In review.
- Frank, D.A., and S.J. McNaughton. 1990. Aboveground biomass estimation with the canopy intercept method: a plant growth form caveat. *Oikos* 57:57-60.
- French ed., N.R. 1979. *Perspectives in grassland ecology*. Springer-Verlag, New York.

- Fryxell, J.M., J. Greever, and A.R.E. Sinclair. 1988. Why are migratory ungulates so abundant?. *American Naturalist* 131:781-798.
- Fryxell, J.M., and A.R.E. Sinclair. 1988. Causes and consequences of migration by large herbivores. *Trends in Ecology and Evolution* 3:237-241.
- Georgiadas, N.J., R.W. Ruess, S.J. McNaughton, and D. Western. 1989. Ecological conditions that determine when grazing stimulates grass production. *Oecologia* 81:316-322.
- Gifford, R.M., and C. Marshall. 1973. Photosynthesis and assimilate distribution in Lolium multiflorum Lam. following differential tiller defoliation. *Australian Journal of Biological Science* 26:517-526.
- Gold, W.G., and M.M. Caldwell. 1989. The effects of the spatial pattern of defoliation on regrowth of a tussock grass. *Oecologia* 80:289-296.
- Gold, W.G., and M.M. Caldwell. 1990. The effects of the spatial pattern of defoliation on regrowth of a tussock grass III. Photosynthesis, canopy structure and light interception. *Oecologia* 82:12-17.
- Grime, J.P. 1979. *Plant Strategies and Vegetation Processes*. John Wiley and Sons, New York.
- Heady, H.F. 1957. Effect of cages on yield and composition in the California annual type. *Journal of Range Management* 10:175-177.
- Hik, D.S., and R.L. Jefferies. 1990. Increases in net above-ground primary production of a salt-marsh forage grass: a test of the predictions of the herbivore-optimization model. *Journal of Ecology* 78:180-195.
- Hilbert, D.W., D.M. Swift, J.K. Detling, and M.I. Dyer. 1981. Relative growth rates and the grazing optimization hypothesis. *Oecologia* 51:14-18.
- Hilmon, J.B., and R.H. Hughes. 1965. Fire and forage in the wiregrass type. *Journal of Range Management* 18:251-254.
- Hitchcock, C.L., and A. Cronquist. 1973. *Flora of the Pacific Northwest*. University of Washington Press, Seattle, Washington.

- Hobbs, N.T., and D.S. Schimel. 1983. Fire effects on nitrogen mineralization and fixation in mountain shrub and grassland communities. *Journal of Range Management* 37:402-404.
- Hodgkinson, K.C. 1974. Influence of partial defoliation on photosynthesis, photorespiration by lucerne leaves of different ages. *Australian Journal of Plant Physiology* 1:561-578.
- Hodgkinson, K.C., and H.G. Baas Becking. 1977. Effect of defoliation on root growth of some arid zone perennial plants. *Australian Journal of Agricultural Research* 29:31-42.
- Hofmann, R.R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* 78:443-457.
- Houston, D.B. 1973. Wildfires in northern Yellowstone National Park. *Ecology* 54: 1111-1117.
- Houston, D.B. 1982. *The Northern Yellowstone Elk: Ecology and Management*. Macmillan Publishing, New York.
- Huntley, B.J. and B.H. Walker. 1982. *Ecology of Tropical Savannas*. Springer-Verlag, New York.
- Huntly, N., and R. Inouye. 1988. Pocket gophers in ecosystems: patterns and mechanisms. *Bioscience* 38:786-793.
- James, S.W. 1985. An unexpected effect of autumn burning on total grass production. *American Midland Naturalist* 114:400-403.
- Jones, R.L., and H.C. Hanson. 1985. Mineral licks, geophagy, and biogeochemistry of North American ungulates. Iowa State University Press, Ames, Iowa.
- Keya, N.C.O. 1973. The effect of N. P. fertilizers on the productivity of Hyparrhenia grasslands. *East African Agriculture and Forestry Journal* 39:195- 200.
- Knight, D.H., and L.L. Wallace. 1989. The Yellowstone fires: issues in landscape ecology. *Bioscience* 39:700-706.
- Kotanen, P., and R.L. Jefferies. 1987. The leaf and shoot demography of grazed and ungrazed plants of Carex subspathacea. *Journal of Ecology* 75:961-975.

- Kramer, C.Y. 1956. Extension of multiple range tests to group means with unequal numbers of replications. *Biometrics* 12:307-310.
- Krueger, K. 1986. Feeding relationships among bison, pronghorn, and prairie dogs: an experimental analysis. *Ecology* 67:760-770.
- Kruuk, H. 1970. Interactions between populations of spotted hyenas (Crocuta crocuta Erxleben) and their prey species. pp. 359-374 in A. Watson (editor). *Animal populations in relation to their food resources*. Blackwell Publishers, Oxford.
- Kruuk, H. 1972. *The spotted hyena*. University of Chicago Press, Chicago.
- Laude, H.M. 1972. External factors affecting tiller development. pp. 146-154 in V.B. Youngner, and C.M. McKell (editors). *The Biology and Utilization of Grasses*. Academic Press, New York.
- Lauenroth, W.K. 1979. Grassland primary production: North American grasslands in perspective. pp. 3-24 in N.R. French (editor). *Perspectives in grassland ecology*. Springer-Verlag, New York, New York.
- Lauenroth, W.K., H.W. Hunt, D.M. Swift, and J.S. Singh. 1986. Estimating aboveground net primary production in grasslands: a simulation approach. *Ecological Modelling* 33:297-314.
- Lieth, H. 1973. Primary production: terrestrial ecosystems. *Human Ecology* 1:303-332.
- Lock, J.M. 1972. The effect of Hippopotamus grazing on grasslands. *Journal of Ecology* 60: 445-467.
- Love, R.M. 1972. Selection and breeding of grasses for forage and other uses. pp. 66-73 in V.B. Youngner, and C.M. McKell (editors). *The biology and utilization of grasses*. Academic Press, New York.
- MacArthur, R.H. 1955. Fluctuations of animal populations and a measure of stability. *Ecology* 36:533-536.
- Mack, R.N., and J.N. Thompson. 1982. Evolution in steppe with few large, hooved mammals. *American Naturalist* 119:757-773.

- Maddock, L. 1979. The "migration" and grazing succession. pp. 104-129 in A.R.E. Sinclair, and M. Norton-Griffiths (editors). *Serengeti: dynamics of an ecosystem*. University of Chicago, Chicago.
- Maschinski, J., and T.G. Whitman. 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. *American Naturalist* 134:1-19.
- Mattson, W.J. 1980. Herbivory in relation to plant nutrient content. *Ann. Rev. Ecol. Syst.* 11:119-161.
- McDonald, P., R.A. Edwards, and J.F.D. Greenhalgh. 1973. *Animal Nutrition*. Longman, London.
- McNaughton, S.J. 1976. Serengeti migratory wildebeest: facilitation of energy flow by grazing. *Science* 191:92-94.
- McNaughton, S.J. 1979a. Grazing as an optimization process: Grass-ungulate relationships in the Serengeti. *American Naturalist* 113:691-703.
- McNaughton, S.J. 1979b. Grassland-herbivore dynamics. pp. 46-81 in A.R.E. Sinclair, and M. Norton-Griffiths (editors). *Serengeti: dynamics of an ecosystem*. University of Chicago, Chicago.
- McNaughton, S.J. 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. *Ecological Monographs* 53:291-320.
- McNaughton, S.J. 1984. Grazing lawns: animals in herds, plant form, and coevolution. *American Naturalist* 124:863-886.
- McNaughton, S.J. 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecological Monograph* 55:259-295.
- McNaughton, S.J. 1989. Interactions of plants of the field layer with large herbivores. *Symposium of the Zoological Society of London*. 61:15-29.
- McNaughton, S.J. 1990. Mineral nutrition and seasonal movement of African migratory ungulates. *Nature* 345:613-615.
- McNaughton, S.J., and F.S. Chapin. 1985. Effects of phosphorus nutrition and defoliation on C4 graminoids from the Serengeti plains. *Ecology* 66:1617-1629.

- McNaughton, S.J., M.B. Coughenour, and L.L. Wallace. 1982. Interactive processes in grassland ecosystems. in J.R. Estes, R.J. Tylr, and J.N. Brunken (editors). Grasses and Grasslands. University of Oklahoma Press, Norman, OK.
- McNaughton, S.J., and N.J. Georgiadis. 1986. Ecology of African grazing and browsing mammals. Annual Review of Ecology and Systematics 17:39-65.
- McNaughton, S.J., M. Oesterheld, D.A. Frank, and K.J. Williams. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. Nature 341:142-144.
- McNaughton, S.J., M. Oesterheld, D.A. Frank, and K.J. Williams. 1990. Relationships between primary and secondary production in terrestrial ecosystems. in J.J. Cole, S. Findlay, and G.M. Lovett (editors). Comparative Analyses of Ecosystems: Patterns, Mechanisms, and Theories. Springer-Verlag, New York.
- McNaughton, S.J., R.W. Ruess, and S.W. Seagle. 1988. Large mammals and process dynamics in African ecosystems. Bioscience 38:794-800.
- McNaughton, S.J., L.L. Wallace, and M.B. Coughenour. 1983. Plant adaptation in an ecosystem context: effects of defoliation, nitrogen, and water on growth of an African C4 sedge. Ecology 64:307-318.
- Meagher, M.M. 1973. The bison of Yellowstone National Park. National Park Service Scientific Monograph Series No. 1.
- Milchunas, D.G., and W.K. Lauenroth. 1989. Three-dimensional distribution of plant biomass in relation to grazing and topography in the shortgrass steppe. Oikos 55:82-86.
- Milchunas, D.G., O.E. Sala, and W.K. Lauenroth. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. American Naturalist 132:87-106.
- Monsi, M., Z. Uchijima, and T. Oikawa. 1973. Structure of foliage canopies and photosynthesis. Annual Review of Ecology and Systematics 4:301-327.

- Morgantini, L.E., and R.J. Hudson. 1988. Migratory patterns of the wapiti, Cervus elaphus, in Banff National Park, Alberta. Canadian Field-Naturalist 102: 12-19.
- Morton, J.K. 1972. Phytogeography of the West African mountains. pp. 221-236 in D.H. Valentine (editor). Taxonomy, phytogeography, and evolution. Academic Press, New York.
- Mott, J.J., J. Williams, M.H. Andrew, and A.N. Gillison. 1985. Australian savanna ecosystems. pp. 56-82 in J.C. Tothill, and J.J. Mott (editors). Ecology and Management of the World's Savannas. The Australian Academy of Science, Canberra, Australia.
- Naiman, R.J. 1988. Animal influences on ecosystem dynamics. Bioscience 38:750-752.
- Naiman, R.J., C.A. Johnston, and J.C. Kelly. 1988. Alteration of North American streams by beavers. Bioscience 38:753-763.
- Nelson, E.W. 1934. The influence of precipitation and grazing upon black grama grass range. U.S. Department of Agriculture Technical Bulletin 409:1-32.
- Newsome, A.E. 1971. The ecology of red kangaroos. Australian Zoologist 16:32-50.
- Newsome, A.E. 1975. An ecological comparison of the two arid-zone kangaroos of Australia and their anomalous prosperity since the introduction of ruminant stock to their environment. Quarterly Review of Biology 50:389-424.
- Norland, J.E., L.R. Irby, and C.B. Marlow. 1985. Determination of optimum bison stocking rate in Theodore Roosevelt National Park, North Dakota. Journal of Environmental Management 21:225-239.
- Noy-Meir, I., M. Gutman, and Y. Kaplan. 1989. Responses of Mediterranean grassland plants to grazing and protection. Journal of Ecology 77:290-310.
- Oosterheld, M., and S.J. McNaughton. 1988. Intraspecific variation in the response of Themeda triandra to defoliation: the effect of time of recovery and growth rates on compensatory growth. Oecologia 77:181-186.

- Olson, B.E., R.L. Senft, and J.H. Richards. 1989. A test of grazing compensation and optimization of crested wheatgrass using a simulation model. *Journal of Range Management* 42:458-467.
- Owensby, C.E., R.M. Hyde, and K. Anderson. 1970. Effects of clipping and supplemental nitrogen and water on loamy upland bluestem range. *Journal of Range Management* 23:341-346.
- Parsons, A.J., and P.D. Penning. 1988. The effect of the duration of regrowth on photosynthesis, leaf death and the average rate of growth in a rotationally grazed sward. *Grass and Forage Science* 43:15-27.
- Pastor, J., R.J. Naiman, B. Dewey, and P. McInnes. 1988. Moose, microbes, and boreal forests. *Bioscience* 38:770-777.
- Paul, E.A., and N.G. Juma. 1981. Mineralization and immobilization of soil nitrogen by microorganisms. pp. 179-195 in F.E. Clark and T. Rosswall (editors). *Terrestrial nitrogen cycles*. Royal Swedish Academy of Sciences, Stockholm, Sweden.
- Penning de Vries, F.W.T., J.M. Krul, and H. van Keulen. 1980. Productivity of Sahelian rangelands in relation to the availability of nitrogen and phosphorus from the soil. pp. 95-113 in T. Rosswall (editor). *Nitrogen Cycling in West African Ecosystems*. Royal Swedish Academy of Sciences, Stockholm, Sweden.
- Polley, H.W., and J.K. Detling. 1990. Grazing-mediated differentiation in Agropyron smithii: evidence from populations with different grazing histories. *Oikos* 57:326-332.
- Polley, H.W. and L.L. Wallace. The relationship of plant species heterogeneity to soil variation in buffalo wallows. *Southwestern Naturalist* 31:493-501.
- Raven, P.H., and D.I. Axelrod. 1974. Angiosperm biogeography and past continental movements. *Annals of the Missouri Botanical Gardens* 61:539-673.
- Risser, P.G., E.C. Birnsy, H.D. Blocker, S.W. May, W.S. Parton, and J.A. Wiens. 1981. *The True Prairie Ecosystem*. Hutchinson Ross Publishing Company, Stroudsburg, PA.
- Roe, F.G. 1951. *The North American Buffalo*. University of Toronto Press, Toronto.

- Romme, W.H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. *Ecological Monographs* 52:199-221.
- Romme, W.H., and D.G. Despain. 1989. Historical perspective on the Yellowstone fires of 1988. *Bioscience* 39:695-699.
- Ruess, R.W. 1984. Nutrient movement and grazing: experimental effects of clipping and nitrogen source on nutrient uptake in *Kyllinga nervosa*. *Oikos* 43: 183-188.
- Ruess, R.W. 1987. The role of large herbivores in nutrient cycling of tropical savannas. pp. 67-91 in B.H. Walker (editor) *Determinants of tropical savannas*. IRL Press Limited, Oxford.
- 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.
- Sala, O.E., M. Oesterheld, R.J.C. Leon, and A. Soriano. 1986. Grazing effects upon plant community structure in subhumid grasslands of Argentina. *Vegetatio* 67:27-32.
- Schimel, D., M.A. Stillwell, and R.G. Woodmansee. 1985. Biogeochemistry of C, N, and P in a soil catena of the shortgrass steppe. *Ecology* 66:276-282.
- Schlesinger, W.H., J.F. Reynolds, G.L. Cunningham, L.F. Huenneke, W.M. Jarrell, R.A. Virginia, and W.C. Whitford. 1990. Biological feedbacks in global desertification. *Science* 247:1043-1048.
- Schullery, P. 1989. The fires and fire policy. *Bioscience* 39:686-694.
- Senft, R.L., M.B. Coughenour, D.W. Bailey, L.R. Rittenhouse, O.E. Sala, and D.M. Swift. 1987. Large herbivore foraging and ecological hierarchies. *Bioscience* 37: 789-799.
- Sims, P.L., and J.S. Singh. 1978. The structure and function of ten North American grasslands. III. Net primary production, turnover, and efficiencies of energy capture and water use. *Journal of Ecology* 66:573-597.

- Sinclair, A.R.E. 1975. The resource limitation of trophic levels in tropical grassland ecosystems. *Journal of Animal Ecology* 44:497-520.
- Sinclair, A.R.E. 1977. *The African Buffalo*. University of Chicago Press, Chicago.
- Sinclair, A.R.E., and M. Norton-Griffiths. 1979. *Serengeti: Dynamics of an Ecosystem*. University of Chicago Press, Chicago.
- Singer, F.J., W. Schreier, J. Oppenheim, and E.O. Garton. 1989. Drought, fires, and large mammals: evaluating the 1988 severe drought and large-scale fires. *Bioscience* 39:716-722.
- Stebbins, G.L. 1981. Coevolution of grasses and herbivores. *Annals of the Missouri Botanical Garden* 68:75-86.
- Stephenson, N.L. 1990. Climatic control of vegetation distribution: the role of the water balance. *American Naturalist* 135:649-670.
- Svejcar, T.J. 1989. Animal performance and diet quality as influenced by burning tallgrass prairie. *Journal of Range Management* 42:11-15.
- Tannehill, I.R. 1947. *Drought: its causes and effects*. Princeton University Press, Princeton, New Jersey.
- Taylor, R.J. 1984. Foraging in the eastern grey kangaroo and wallaroo. *Journal of Animal Ecology* 53:65-74.
- Turner, M.G. 1989. Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* 20:171-198.
- Turner, M.G., and S.P. Bratton. 1987. Fire, grazing, and the landscape heterogeneity of a Georgia barrier island. in M.G. Turner (editor). *Landscape Heterogeneity and Disturbance*. Springer-Verlag, New York.
- U. S. Department of Commerce. 1988. Climatological Data for Wyoming. U.S. Department of Commerce, Washington D.C.
- U.S. Department of Commerce. 1989. Climatological Data for Wyoming. U.S. Department of Commerce, Washington D.C.

- Valentine, K.A. 1947. Distance from water as a factor in grazing capacity of rangeland. *Journal of Forage* 45:749-754.
- Waksman, S.A. and F.C. Gerretsen. 1931. Influence of temperature and moisture upon the nature and extent of decomposition of plant residues by microorganisms. *Ecology* 12: 33-60.
- Wallace, L.L. 1990. Comparative photosynthetic responses of big bluestem to clipping versus grazing. *Journal of Range Management* 43:58-61.
- Wareing, P.F., M.M. Khalifa, and K.H. Treharne. 1968. Rate limiting processes in photosynthesis at saturating light intensities. *Nature* 22:19-21.
- Weaver, J.E., and F.W. Albertson. 1944. Nature and degree of recovery of grassland from the great drought of 1933 to 1940. *Ecological Monographs* 14:393- 479.
- Welsh, A.H., A.T. Peterson, and S.A. Altman. 1988. The fallacy of averages. *American Naturalist* 132:277-288.
- Whicker, A.D., and J.K. Detling. 1988. Ecological consequences of prairie dog disturbances. *Bioscience* 38:778-785.
- Wilkinson, S.R., and R.W. Lowrey. 1973. Cycling of mineral nutrients in pasture ecosystems. pp. 247-315 in G.W. Butler, and R.W. Bailey (editors). *Chemistry and Biochemistry of Herbage*. Volume 2. Academic Press, New York.
- Wood, G.W. 1988. Effects of prescribed fire on deer forage. *Wildlife Society Bulletin* 16:180-186.
- Woolfolk, J.S., E.F. Smith, R.S. Schalles, B.E. Brent, L.H. Harbers, and C.E. Owensby. 1975. Effects of nitrogen fertilization and late-spring burning of bluestem range on diet and performance of steers. *Journal of Range Management* 28:190-193.
- Wraith, J.M., D.A. Johnson, R.J. Hanks, and D.V. Sisson. 1987. Soil and plant water relations in a crested wheatgrass pasture: response to spring grazing by cattle. *Oecologia* 73:573-578.

APPENDIX A: EXECUTIVE SUMMARY

The principal objectives of this study were measuring aboveground net primary production, large herbivore consumption, and fecal deposition in a variety of winter, transitional, and summer range sites in Yellowstone Park's northern range. This summary is meant to explicitly address the major findings of the study, which I feel would be of particular interest to park managers. I have organized this summation into 3 sections: (1) the effect of large herbivores on grassland production, (2) how elk and bison interact with their heterogeneous landscape, and (3) effects of the 1988 drought on ecosystem structure and function.

Ungulates and grassland production: To examine how elk and bison affect grassland production, aboveground primary production of grazed vegetation, determined with small exclosures moved every 4 weeks, was compared with aboveground primary production of permanently fenced, and thus, ungrazed, vegetation at two sites in 1988 and four sites in 1989. At three of the sites, a transitional range site in 1988 and 1989 and two winter range sites, one wet and one dry, in 1989, grazers increased aboveground production. In contrast, at a summer range site, herbivores had no effect on aboveground production

in both 1988 and 1989 (see Fig. 10). The summer range site experienced the most severe drought of any site in 1988, which may have nullified the stimulatory influence by ungulate on aboveground production. These data clearly indicate that ungulates are having no detrimental effect on grassland function in Yellowstone Park.

Ungulates and heterogeneous landscapes: The grasslands of the northern range are very heterogeneous, comprising patches that vary in their level of production. Findings herein indicate that patch production and herbivore consumption are positively and linearly related, meaning that as patch production increases, so too does herbivore consumption at a constant rate (see Fig. 17). Furthermore, herbivore consumption and nutrient deposition from ungulates to the soil (indexed by fecal deposition) are positively and linearly related (see Fig. 22). Because nutrients of urine and feces are in a readily available form to plants and microbes, these results suggest that grazing and nutrient cycling are coupled in the Yellowstone landscape. Finally, there was a positive and linear relationship between the timing of production and the timing of consumption, e.g., elk and bison grazed the sites when plants were growing. This suggests that grazers are following a wave of plant growth as it sweeps across the park, from the lower winter range to the upper

summer range.

The 1988 drought and ecosystem structure and function: Both aboveground primary production and herbivore consumption declined from 1988 to 1989. The decline in production was likely a result of death and/or injury to plants during the 1988 drought. The decline in consumption was due to the reduction in elk and bison numbers, which largely was a result of the drought-induced winter-kill (elk), and migration out of the park where animals were shot (elk and bison). As noted above, the drought appeared to negate the stimulatory effect of ungulates on grassland production. Lastly, drought profoundly altered plant community species composition throughout the northern range.