The Ecology of Plants, Large Mammalian Herbivores, and Drought in Yellowstone National Park

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THE ECOLOGY OF PLANTS, LARGE MAMMALIAN HERBIVORES, AND DROUGHT IN YELLOWSTONE NATIONAL PARK[1]

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Abstract. The purpose of this study was to examine the effect of abundant native large herbivores on ecosystem function of a spatially and temporally heterogeneous temperate grassland. Net aboveground primary production (ANPP), large herbivore consumption (*C*), and dung deposition (*D*), an index of nutrient flow from herbivores to the soil, were measured in grassland and shrub–grassland habitat on winter, transitional, and summer range used by herds of elk (*Cervus elaphus*) and bison (*Bison bison*) in northern Yellowstone National Park. Temporary exclosures (5–7 per site) were moved every 4 wk during the snow-free season to determine ANPP and *C*. Data were collected during 1988, a year of drought and unusually high elk and bison population levels, and 1989, a climatically near-average year, with dramatically fewer elk and bison.

All three processes, ANPP, *C*, and *D*, varied widely among sites: ANPP range: 16–589 g/m², *C* range: 0–306 g/m², and *D* range: 0–68 g/m². An average of 45% of ANPP was consumed by herbivores. Production and consumption, and consumption and dung deposition were positively correlated across all sites. In addition, sites were grazed when plants were growing.

There was a 19% reduction in ANPP from 1988 to 1989, likely caused by death or injury to plants during the 1988 drought. Drought also appeared to be partially responsible for reductions in elk and bison from 1988 to 1989, which were coincident with declines in *C* and *D*. Results indicate direct effects and suggest indirect effects of a single-season drought on grassland function that will persist for several years after the event.

Key words: bison; consumption; drought; elk; forage quality; grassland function; grasslands; herbivory; landscape ecology; primary production; ungulate migration; ungulates; Yellowstone National Park.

INTRODUCTION

Grasslands supporting abundant herds of large mammalian herbivores sustain the highest chronic rates of herbivory of any terrestrial ecosystem (Detling 1988, McNaughton et al. 1989). The effects of grazers on grasslands are profound and cascade through all trophic levels (McNaughton 1985, Detling 1988, McNaughton et al. 1988). When herbivores are migratory, their effects include additional spatial and temporal components (Senft et al. 1987, McNaughton 1989, 1990). A variety of large herbivores have been shown to exhibit habitat preferences with landscapes, including bison, *Bison bison* (Coppock et al. 1983, Norland et al. 1985), feral horses, *Equus caballus* (Turner and Bratton 1987), eastern gray kangaroos (*Macropus giganteus*), wallaroos (*M. robustus robustus*) (Taylor 1984), and both resident (McNaughton 1988) and migratory (McNaughton 1990) African ungulates. As a result, large herbivores can play an important role in

determining landscape patterns of energy and nutrient fluxes. Furthermore, since the composite effects of herbivores are partially dependent on other trophic processes (McNaughton 1985) that vary temporally (e.g., soil processes; Birch 1958, Burke 1989, Burke et al. 1989), the timing of herbivore use is an important determinant of the impact of grazers on ecosystem processes.

In precolonial times as much as 25% of the terrestrial habitats were grasslands (Shantz 1954), 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 grazers with domesticated grazers has severely reduced the extent of these areas (Risser 1988).

Although much is known about the functional properties of grasslands in general (Coupland 1979, French 1979, Huntley and Walker 1982), and about 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 large grassland ecosystems with large herds of Pleistocene mammalian herbivore fauna. The tropical savanna habitat of east
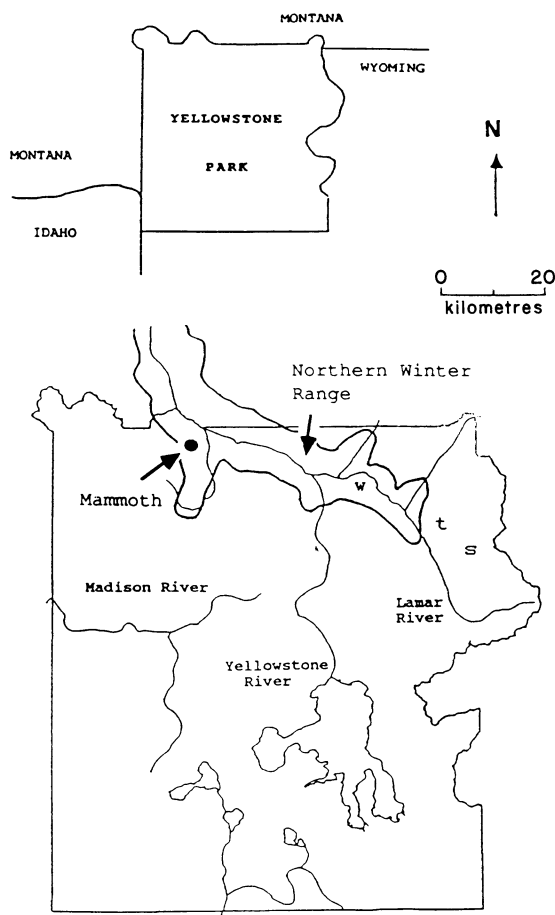
FIG. 1. Map of study region, indicating delineation of the northern winter range and the winter (w), transitional (t), and summer (s) range study site locations. Adapted from Houston (1982).

Africa, until now, has been our only point of reference (Lock 1972, Sinclair 1975, Edroma 1981, McNaughton 1983, 1985). Here we present a second example from the grasslands and shrub–grasslands of Yellowstone National Park, a North temperate mountainous reserve, with one of the highest concentrations of native ungulates in North America.

An important question facing ecologists today is how ecosystem processes vary both spatially and temporally in terrestrial habitats (Turner 1989). In this paper we examine the effect of large herds of native ungulates on the functional organization of temperate grasslands. We ask: (1) how do plant aboveground production, ungulate consumption, and amounts of dung deposited at sites vary across a temperate grassland landscape, and (2) how are these processes spatially and temporally linked. Our measurements span two disparate years: (1) 1988, a year of drought and landscape-scale wildfires, when elk and bison populations were at their highest levels in recent decades, and (2) 1989, a near-average year in terms of temperature and precipitation,

with lower elk and bison populations. Consequently, we also address how functional properties of this temperate grassland dominated by native herbivores responded to a severe, one-year drought.

METHODS

Study area

Yellowstone National Park occupies 8995 km² between 44°08' and 45°07' N and 111°10' and 110° W in the northwest corner of Wyoming, USA (Fig. 1). Elevations in the Park range from 1500 m to over 3000 m, though much of the area is a gently rolling plateau between 1200 and 2600 m (Meagher 1973, Houston 1982). The Park is covered mostly by tertiary and quarternary volcanic deposits that have been glaciated several times since their deposition (Keefer 1987). The climate of the Park features long, cold winters and short, dry summers. Eight ungulate species occur in Yellowstone: 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 this study was non-forested habitat in the northeastern portion of Yellowstone used primarily by northern range elk and bison. Herds of northern elk and bison migrate between low-elevation northern winter range and high-elevation summer range. The northern winter range is ≈1000 km² in area, comprised of the lower stretches of the Yellowstone River and Lamar River drainages and their tributaries (Fig. 1, Houston 1982). Summer range for northern bison includes ridges and plateaus in the Lamar drainage (Meagher 1973). Northern elk summer range includes high elevations throughout all but extreme southern portions of Yellowstone, and some ridges and plateaus north of the Park (Houston 1982).

Vegetation of the northern winter range is grassland and shrub–grassland with isolated stands of trees. Summer range is dominated by lodgepole pine (*Pinus contorta*) forest. Grassland and shrub–grassland on the summer range can be spatially extensive on ridge lines and in perched drainages on plateaus (e.g., on Mirror Plateau). Most elk and bison summer grazing is concentrated in grassland and shrub–grassland habitat (Cole 1969, Meagher 1973). Non-forested vegetation throughout the study area was markedly heterogeneous due to steep soil and moisture gradients created by uneven topography.

Ungulate management

Management of northern range elk and bison herds has varied considerably, reflecting the evolution of national park policy. Meagher (1973) and Houston (1982) provide thorough histories of bison and elk management in the Park. After 1969, when population reductions (culling) ceased, elk and bison levels were allowed

TABLE 1. Topographic position, elevation, and vegetation of study sites in the northeast portion of Yellowstone National Park (Wyoming, USA).

Site	Topographic position	Elevation (m)	Vegetation	Herbaceous dominants
Winter range				
w1	Bench	1909	Grassland	*Festuca idahoensis, Lupinus sericeus*
w2	River terrace	1998	Grassland	*Phleum pratense, Poa pratensis*
w3	Valley bottom	1999	Grassland	*Bromus inermis*
w4	River terrace	1888	Sedge Meadow	*Carex rostrata*
Transitional range				
t1	Ridgetop	2342	Grassland	*Koelaria cristata, Astragulus miser*
t2	Slope	2318	Grassland	*Phleum pratense, Juncus hallii*
t3	Slope	2294	Shrub–grassland	*Phleum pratense, Agropyron caninum*
Summer range				
s1	Ridgetop	2575	Grassland	*Danthonia unispicata, Poa scabrella*
s2	Slope	2450	Shrub–grassland	*Stipa occidentalis, Bromus carinatus*
s3	Bench	2355	Grassland	*Phleum pratense, Carex* sp.*
s4	Bench	2428	Grassland	*Poa* sp.**, *Stipa occidentalis*
s5	Bench	2428	Forest	*Calamagrostis rubescens*

 * Includes *C. xerantica* and *C. raynoldsii.*
** Includes *Poa nevadensis* and others.

to fluctuate without human interference within the Park (Cole 1971, Meagher 1973, Houston 1982). Northern range elk increased from about 4000–5000 in 1968 to 12 000–16 000 individuals by the late 1970s (Houston 1982). In 1988, after several consecutive years of wet summers and mild winters, northern elk numbered 22 500 (Singer et al. 1989). Meanwhile, northern bison increased from ≈200 in the late 1960s (Meagher 1973) to >577 in 1988 (M. M. Meagher, *personal communication*).

It is impossible to know how current elk and bison population levels compare to those prior to the arrival of white trappers and settlers in the northern Rockies. However, numerous accounts indicate that both elk (Russell 1965, see Houston 1982) and bison (Roe 1951, Meagher 1973, Dary 1974) were abundant in Yellowstone at the time of the Park's establishment in 1872.

Study sites

Study sites were selected to represent a spectrum of topographic positions, primary productivities, and plant community species compositions of nonforested habitat in winter, transitional, and summer range areas (Fig. 1, Table 1). In addition, we studied one summer range forest understory (s5, Table 1). Winter range sites were located in the upper northern winter range, near Crystal Creek (w1), in the Lamar Valley (w2, w3), and along Slough Creek (w4). Transitional (t1–3) and summer range (s1–5) sites were on the same ridge, between Cache and Calfee Creeks, i.e., Cache-Calfee Ridge. All transitional range communities were within 0.5 km of each other, and summer range sites were separated by no more than 1 km.

Sampling period

Measurements were concentrated during the snow-free periods of two climatically different years: (1) in

1988, a drought year with large landscape-scale wildfires (Romme and Despain 1989), when northern range elk and bison populations were at their highest levels in recent decades, and (2) in 1989, a near-average year in terms of precipitation, when northern range elk were ≈40% (Singer et al. 1989) and bison ≈50% (M. M. Meagher, *personal communication*) of their 1988 levels. The 1988 drought began in early June after above-average moisture in April and May (Singer et al. 1989). Precipitation at Mammoth in the northwest corner of the Park (Fig. 1) was 24% of the 53-mm June (30-year) average, 76% of the 31-mm July average, and 9% of the 38-mm August average (NOAA 1988), resulting in the summer of 1988 being the driest on record (Schullery 1989). In contrast, precipitation at Mammoth for June, July, and August of 1989 was 100%, 99%, and 83% of average, respectively (NOAA 1989). Additionally, in 1988 ≈400 000 ha (45%) of the Yellowstone National Park burned (Schullery 1989). Although no study site burned, fire occurred within 1 km of each site.

Sampling methods, derived variables, and data analysis

Net aboveground primary production (ANPP) and large-herbivore consumption were measured at each site. Aboveground biomass was estimated with the canopy intercept method (Frank and McNaughton 1990), except at a wet sedge meadow (w4) where vegetation was too high for canopy intercept and therefore was clipped instead. The canopy intercept method relates standing crop to the number of hits a pin makes when passed at an angle through vegetation. The technique is affected strongly by plant growth form. Slopes of the regressions of standing crop (g/m²) on the mean number of contacts for five functional groups encoun-

TABLE 2. Measured vegetation state variables and derived variables.

	State variables
g	Green standing crop
ht	Vegetation canopy height
pg	Standing crop inside movable exclosures
	Derived variables
ANPP	Net aboveground primary production = sum of pg increments
dANPP	Rate of production per day during a sampling interval = (pg increment)/(no. of days in the sampling interval)
C	Consumption during the snow-free season = sum of differences between g and pg
gC	Growing season consumption = sum of differences between g and pg during the growing season*
lC	Late-season consumption = sum of differences between g and pg during the late-season†
dC	Rate of consumption per day during a sampling interval = (consumption)/(no. of days in the sampling interval)
GBC	Green biomass concentration (mg/cm³) = g/ht
D	Dung deposited at sites during the snow-free period (Eq. 1)

* That period when green biomass was at least 20% of total standing crop.

† The period between the end of the growing season and snowfall.

tered in this study ranged from 0.175 to 0.853, and r^2 of the relationships ranged from 0.83 to 0.96.

Temporary exclosures (1.5 × 1.5 m, $n = 5$–7 per site) were used to determine ANPP under grazing and large-herbivore consumption (McNaughton 1985). Exclosures were established at snowmelt and moved at random approximately every 28 d until snow accumulation. During relocation, standing crop was estimated in 0.5-m² quadrats in the center of each exclosure and quadrats randomly located in grazed vegetation. Production at each site was calculated as the sum of significant ($P < .05$, one-way ANOVA) increments of standing crop inside exclosures. Consumption was defined as a significant difference ($P < .05$) in standing crop inside vs. outside the exclosures. Consumption for a period greater than one sampling interval at a site was calculated as the sum of the differences during that interval. Variances of production and consumption for periods greater than one sampling interval were calculated by summing interval variances, since variance is additive.

The 28-d sampling interval was a compromise between limiting fencing effects (intensive sampling) and the desire to embrace system diversity (extensive sampling). Notable exceptions to the normal sampling regimen were 34–36 d intervals for the five summer range sites during July–August 1988, due to restricted backcountry access during wildfires. Since most of the vegetation had senesced and no detectable plant growth occurred during these periods, fencing effects were likely negligible. ANPP of *Artemisia tridentata,* a shrub,

was taken as peak biomass, since it was not grazed at the two study sites, t3 and s2, where it occurred (Cole 1969, D. A. Frank, *personal observation*). Aboveground biomass of *A. tridentata* was determined with clipped quadrats (0.5 m², $n = 10$), because bushes were too tall to be sampled with the canopy intercept method.

Canopy height of herbaceous vegetation was estimated in 1989 as the resting height of a styrofoam sheet (5.0 g, 26 × 21 cm, $n = 10$) when laid gently on the vegetation (McNaughton 1976, 1984). Canopy height and standing-crop estimates were made simultaneously at each site throughout the snow-free season. The concentration of green biomass (GBC, in milligrams per cubic centimetre) was calculated as the quotient of green standing crop (converted to milligrams per square centimetre) divided by canopy height (in centimetres; McNaughton 1976, 1984).

Dung deposition during the snow-free season was calculated as

$$D = \left(\sum_{i=1}^{m} \sum_{j=1}^{10} p_{ij} b_i \right) \Big/ 200 \qquad (1)$$

where D (in grams per square metre) is dung deposited during the snow-free period at a site, and p_{ij} and b_i are the number of fecal piles in a 10 × 2 m transect and the mean dry mass of a fecal pile, respectively, for the ith of m ungulate species (e.g., elk, bison) and the jth of 10 transects.

Measured vegetation state variables were standing crop inside movable exclosures (pg), standing crop of grazed vegetation (g), and vegetation height (ht). A list of the derived variables is included in Table 2.

Nitrogen concentrations were determined on aboveground biomass of select grass forages with a Carlo Erba CNS Analyzer using standard protocol. Harvested samples were oven-dried at Yellowstone Park, then shipped to Syracuse where they were rinsed with distilled water, re-oven-dried, and ground to pass a 500-μm mesh screen using a Wiley Mill. Samples were mixed thoroughly before single subsamples were collected from each for analysis.

All the relationships between processes (ANPP, C, gC, lC, dC, dANPP, D) are least-square fits. Between-year differences in processes were examined with paired t tests. Proportions were always arcsine-transformed to satisfy parametric test requirements, except forage nitrogen data, which met assumptions. Nonparametric analyses were used only when satisfying these requirements was impossible. Plant species diversity was indexed with H' (Pielou 1966).

RESULTS

Soils within the major rooting zone (0–10 cm) at the sites were loams, silt loams, and sandy loams (Table 3). Soil pH values were all slightly acidic, ranging from

TABLE 3. Soil properties at study sites in Yellowstone National Park.

Site	pH	Bulk density (g/cm³)	Field capacity (% H₂O)	OM* (%)	N (%)	USDA texture categories (%)			Soil classification
						Sand	Silt	Clay	
Winter range									
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
Transitional range									
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
Summer range									
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

* Percentage of organic matter from loss on ignition.

5.14 in a summer range lodgepole pine forest (the only forest sampled) to 6.75 at the summer range ridgetop site. Bulk density, field capacity, organic matter, and soil nitrogen (N) ranged between 0.83 and 1.32 g/cm³, 16.0–65.2%, 5.2–25.5%, and 0.1–0.9%, respectively. There was a tendency for pH and bulk density to increase, and field capacity, percentage of organic matter, and percentage of soil N to decline from the base to the top of slopes. A wet sedge meadow in the winter range (w4, Table 1) was notable as having the lowest bulk density and the highest field capacity, percentage of organic matter, and percentage of soil N.

Rates of ecosystem processes

Net aboveground primary production.—An initial objective of the study was to select sites representative of the spectrum of herbaceous aboveground primary productivities (ANPP) encountered by elk and bison. Ranges for ANPP were 27–539 g/m² in 1988 and 16–589 g/m² in 1989 (Table 4). The least productive community in both years was a summer range ridgetop site (s1, Table 4); the most productive community was a winter range wet sedge meadow (w4, Table 4). Herbaceous production declined from 1988 to 1989 at 6 of 11 sites (Table 4). Moreover, mean ANPP of sites where ANPP was measured during both years declined from 278 g/m² in 1988 to 226 g/m² in 1989 ($t_{10} = 3.3$, $P < .08$, paired t test), a decrease of 19%. This indicates that the decline in herbaceous production was a landscape phenomenon. Production of *Artemisia tridentata* at two shrub–grassland sites did not differ between years and averaged 55 ± 12 g/m² (mean $\pm$ 1 SE, $n = 20$) and 77 ± 14 g/m² ($n = 20$) at t3 and s2, respectively.

Production was associated with several soil properties in both years. For example, Spearman rank correlations showed 1989 ANPP was negatively correlated with bulk density ($P = .05$, $n = 12$, $r_s = -0.56$) and

percentage of sand ($P = .03$, $n = 12$, $r_s = -0.67$), and weakly positively related to percentage of silt ($P = .06$, $n = 12$, $r_s = 0.57$).

The frequency distributions of daily production (dANPP) for both years were distinguished by the large number of zero growth intervals (Fig. 2). For sites sampled in both years (paired sites) no significant growth occurred during 66% and 63% of the intervals in 1988 and 1989, respectively. Daily productivity at paired 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. The highest dANPP measured during 1989 occurred at a wet sedge meadow (w4) not sampled in 1988. Mean detectable dANPP at paired sites was 5.7 g·m⁻²·d⁻¹ in 1988 and 3.2 g·m⁻²·d⁻¹ in

TABLE 4. Herbaceous net aboveground primary production (ANPP, means $\pm$ 1 SE) and probabilities that 1988 and 1989 values are from the same sample populations. NS denotes nonsignificance ($P > .05$).

Site	ANPP (g/m²)		P
	1988	1989	
Winter range			
w1	a*	85 ± 7	···†
w2	513 ± 27	380 ± 21	<.001
w3	232 ± 19	204 ± 19	NS
w4	539 ± 31	589 ± 31	NS
Transitional range			
t1	145 ± 23	60 ± 5	<.001
t2	343 ± 19	297 ± 15	NS
t3	241 ± 38	163 ± 37	NS
Summer range			
s1	27 ± 3	16 ± 1	<.01
s2	112 ± 11	84 ± 12	<.01
s3	278 ± 33	248 ± 18	NS
s4	238 ± 22	136 ± 5	<.001
s5	247 ± 18	198 ± 17	<.05

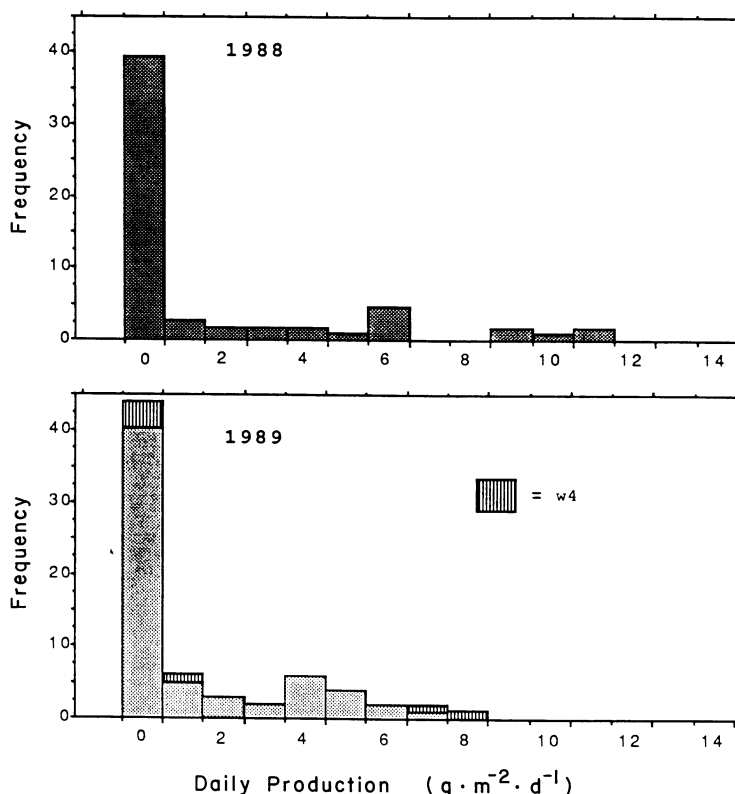* a = data not available.
† Not applicable.

FIG. 2. Frequency histograms of daily aboveground net primary production (*d*ANPP) in 1988 and 1989 at Yellowstone National Park study area. Gray bars represent samples from sites where measurements were made both years.

1989 ($F_{1,42} = 2.83$, $P = .11$). Maximum *d*ANPP at each of the sites sampled during both years was greater in 1988 than 1989 ($t_8 = 5.09$, $P < .001$, paired *t* test).

Plant growth in Yellowstone occurs locally as a brief, strong pulse, and regionally as a landscape-level wave. Production at the sites began after snowmelt and lasted for 1–2 mo, except in mesic–wet valley-bottoms (w2 and w4) where growth was measured for up to 4 mo (Frank 1990). As in other temperate mountainous regions, the spatial shift of aboveground production in Yellowstone follows the pattern of snowmelt, progressing up elevational gradients, influenced locally by topography, with the advancing season. Plant growth normally begins in March on the lower winter range and sweeps upslope to the upper summer range, lasting in most years into August (D. Despain, *personal communication*).

Nitrogen content of dominant grasses harvested at the same time as biomass estimates declined through the growing season. During the first harvests, ≈28 d after snowmelt, plant nitrogen concentration ranged from 2.5 to 3.7% and was significantly greater than harvests later in the year ($F_{1,31} = 53.3$, $P < .0001$), which ranged from 1.1 to 2.4% (Fig. 3). The percentage of nitrogen (%N) was related to the number of days

after snowmelt (d_{as}) ($r^2 = 0.66$, df = 30) by

$$\log \%N = -0.46(\log d_{as}) + 1.15.$$

Implicit in this relationship is a nitrogen wave that is tied to the spatiotemporal pattern of plant growth presented above.

Green biomass concentrations (GBC, in grams per cubic centimetre) and the number of days after snowmelt (d_{as}) were negatively related ($r^2 = 0.470$, df = 56, $P < .001$) by

$$GBC = 106.3 - 0.640 (d_{as})$$

(Fig. 4). Highest values for GBC occurred during the first sample, ≈28 d after snowmelt, at all sites except two, a summer-range ridgetop (s1) and a summer range forest (s5). Restricting analysis to the earliest samples at each site, 32.9% of the variation in GBC was explained by ANPP ($F_{1,9} = 4.41$, $P = .065$), in contrast to ANPP explaining only 4% of the variance ($F_{1,55} = 3.3$, $P = .075$) when both d_{as} and ANPP were included as variables in a multiple regression over the entire snow-free season. From Fig. 4 it is clear that ANPP explains little variation in GBC during the snow-free season, because of a homogenization among sites, e.g.,
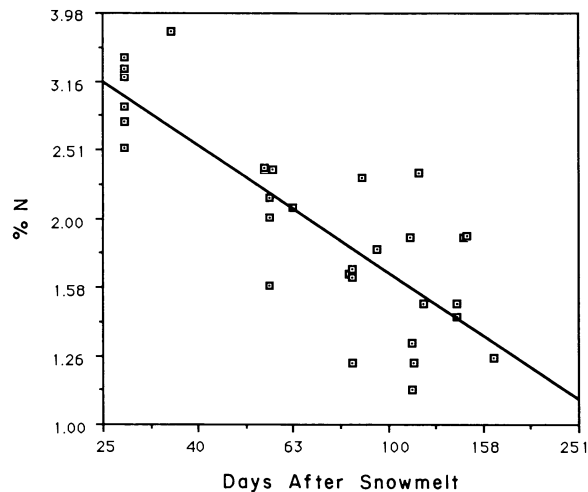
FIG. 3. Relationship of the percentage of nitrogen (%N) of dominant grasses at seven sites in Yellowstone National Park study area and number of days after snowmelt. Note that both axes are log-scaled.
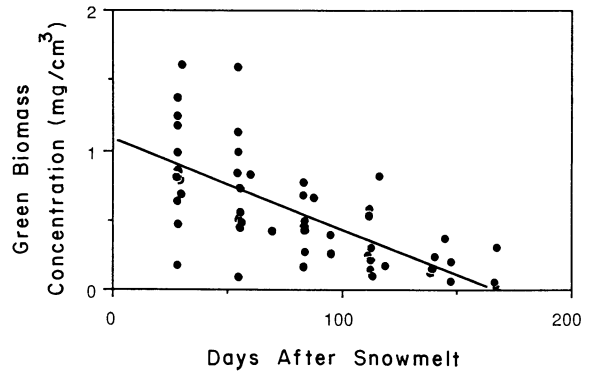

FIG. 4. Relationship between green biomass concentration (GBC) and number of days after snowmelt (d_{as}) at Yellowstone National Park study area.

an across-site reduction in GBC, as the season progresses.

Correlation analyses of the relationship between d_{as} and the two components of GBC, green biomass and canopy height (Table 2), showed the decline in GBC with length of season was due to a contemporaneous decline in standing green biomass and an increase in canopy height. Days after snowmelt was negatively related to green biomass ($P = .02$, $r = -0.31$, df = 56) and positively related to canopy height ($P = .002$, $r = 0.41$, df = 56).

Herbivore consumption (C). — Whether a herbivore grazes live or dead tissue has important implications

for both the herbivore and the plant that is grazed. Therefore, in addition to presenting consumption data for the entire snow-free period, we report offtake during the growing season, arbitrarily defined as that portion of the season when green biomass comprised at least 20% of the standing crop, and the late season, that period after the growing season until snowfall.

Consumption varied widely and was affected strongly by northern-range herd size. Growing-season consumption (gC) at sites sampled in both years and grazed in at least one year ranged between 32 and 249 g/m² in 1988 and 20–137 g/m² in 1989 (Table 5). At w1, where only 1989 data exist, offtake was 20 g/m², the lowest of any site sampled that year. Mean gC for grazed sites measured in both years declined from 111 g/m² in 1988 to 63 g/m² in 1989 ($t_7 = 2.5$, $P < .04$, paired t test), a decrease of 43%. Reductions in gC occurred at six of eight sites (Table 5). Most notable

TABLE 5. Consumption during the growing season (gC), late-season consumption (lC) and consumption during the snow-free season (C) during 1988 and 1989, all as means $\pm$ 1 SE. Probabilities and units as in Table 4.

Site	gC 1988	gC 1989	P	lC 1988	lC 1989	P	C 1988	C 1989	P
Winter range									
w1	a*	20 $\pm$ 6	$\cdots$†	a	0	$\cdots$	a	20 $\pm$ 6	$\cdots$
w2	249 $\pm$ 49	86 $\pm$ 25	<.01	0	0	NS	249 $\pm$ 49	86 $\pm$ 25	<.01
w3	50 $\pm$ 11	0	$\cdots$	56 $\pm$ 21	0	$\cdots$	106 $\pm$ 16	0	$\cdots$
w4	0	0	$\cdots$	0	0	$\cdots$	0	0	$\cdots$
Transitional range									
t1	47 $\pm$ 13	0	$\cdots$	63 $\pm$ 6	0	$\cdots$	111 $\pm$ 46	0	$\cdots$
t2	199 $\pm$ 19	137 $\pm$ 15	<.05	107 $\pm$ 14	0	$\cdots$	306 $\pm$ 15	137 $\pm$ 15	<.001
t3	90 $\pm$ 28	53 $\pm$ 15	NS	0	0	NS	90 $\pm$ 28	53 $\pm$ 15	NS
Summer range									
s1	0	0	$\cdots$	0	0	$\cdots$	0	0	$\cdots$
s2	32 $\pm$ 3	20 $\pm$ 2	<.01	0	0	NS	32 $\pm$ 3	20 $\pm$ 2	<.01
s3	97 $\pm$ 24	127 $\pm$ 15	NS	51 $\pm$ 8	0	$\cdots$	148 $\pm$ 20	127 $\pm$ 15	NS
s4	124 $\pm$ 15	77 $\pm$ 5	<.01	24 $\pm$ 8	0	$\cdots$	149 $\pm$ 23	77 $\pm$ 13	<.001
s5	0	0	$\cdots$	0	0	NS	0	0	$\cdots$

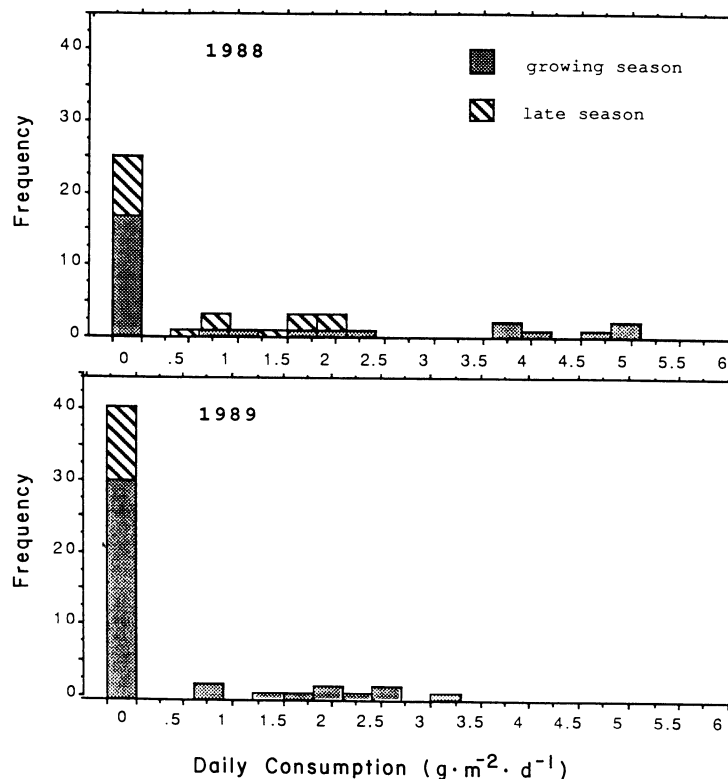* a = data not available
† Not applicable.

FIG. 5. Frequency histograms of daily consumption (dC) by large herbivores in Yellowstone National Park study area in 1988 and 1989.

was a 65% decline at w2, which in 1988 had the highest rate of gC.

At t3 and s2, shrub–grassland sites where *A. tridentata* occurred, herbaceous vegetation between and under shrubs was sampled separately. At no time did significant consumption occur under *A. tridentata,* or did we find evidence of browsing on *A. tridentata* (D. A. Frank, *personal observation*). This suggests a negative relationship between sagebrush abundance and herbivory across the landscape.

The percentage of ANPP consumed during the growing season at grazed sites ranged between 22 and 58% in 1988 and 23–51% in 1989. Mean percentage of herbivory for sites grazed in either year declined somewhat from 39.2% in 1988 to 29.0% in 1989 (t_7 = 2.17, P = .07, paired *t* test), and the number of sites that were not grazed increased from three in 1988 to five in 1989.

Offtake late in the season (*lC*) differed markedly between years. In 1988, detectable *lC* occurred in five communities, ranging between 24 and 107 g/m², and averaging 60 g/m² (Table 5). In contrast, no grazing occurred during the late season at any site during 1989.

Consumption during the entire snow-free season (*C*) at grazed sites ranged between 32 and 306 g/m² in 1988 and 20–137 g/m² in 1989 (Table 5). Herbivory declined from 1988 to 1989 at six of eight sites (Table 5). Mean *C* for sites grazed during at least one of the years de-

clined from 149 g/m² in 1988 to 63 g/m² in 1989 (t_7 = 3.9, P < .006, paired *t* test), a reduction. Note that since no late-season consumption occurred during 1989, gC equalled C during that year.

Daily consumption (*dC*) was calculated as the amount consumed during an interval divided by the number of days of the interval. Frequency histograms of *dC* at grazed sites for 1988 and 1989 (Fig. 5) are similar to those for *d*ANPP (Fig. 2). In both years no significant offtake occurred during the majority of the sampling intervals: for 61% and 76% of the growing season samples, and 57% and 76% of all samples in 1988 and 1989, respectively. The range of *dC* in 1988 was 0.5–5.0 g·m⁻²·d⁻¹ and in 1989 was 0.7–3.1 g·m⁻²·d⁻¹. Mean detectable *dC* 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, mean detectable *dC* 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). This indicates the offtake rate in 1988 among the sites was greater during the growing season than after it.

Flux of dung from ungulates to the soil.—Oven-dry masses of elk, bison, and pronghorn fecal piles randomly collected near the study sites were 92 ± 10.6 g (mean ± 1 SE, *n* = 38), 294 ± 25.6 g (*n* = 36), and 37 ± 4.2 g (*n* = 10), respectively. Maximum values of *D* during the snow-free periods of both years occurred at

TABLE 6. Dung deposited during 1988 and 1989. Probabilities and units as in Table 4.

	Dung deposited, D (means ± 1 SE)		
Site	1988	1989	P
Winter range			
w1	22 ± 6	7 ± 3	<.04
w2	28 ± 8	12 ± 3	NS
w3	15 ± 5	12 ± 4	NS
w4	0	0	···†
Transitional range			
t1	22 ± 4	2 ± 2	<.0001
t2	41 ± 7	20 ± 5	<.03
t3	4 ± 2	8 ± 3	NS
Summer range			
s1	2 ± 1	0	···
s2	18 ± 5	6 ± 1	<.03
s3	68 ± 9*	21 ± 6	<.001
s4	14 ± 3	45 ± 9*	<.001
s5	4 ± 2	1 ± 1	NS

* Site used as elk bedding area.
† Not applicable.

sites that, in addition to receiving inputs while animals were grazing, were used as bedding areas by elk: s3 received 68 g/m² in 1988 and s4 received 45 g/m² in 1989 (Table 6). For the remaining communities, fecal return ranged between 2 and 41 g/m² in 1988 and 0–21 g/m² in 1989 (Table 6). Mean D at those sites declined from 15 g/m² in 1988 to 8 g/m² in 1989 (P < .02, F_8 = 3.1, paired t test), a decrease of 48%. This indicates that the reduction of herbivores from 1988 to 1989 dramatically depressed the flux of dung from grazers to the soil across the Yellowstone landscape.

During the snow-free season, D did not differ between seasonal-use areas ($F_{2,217}$ = 0.26). However, over the entire year it is likely that D varied substantially at this spatial scale, since herbivores concentrate in the winter range for at least 5 mo (November to March). During the winter of 1988–1989, dung deposited at winter range sites w1, w2, w3, and w4 equalled 35.5 ± 8.0, 48.2 ± 4.5, 57.7 ± 7.1, and 166.1 ± 14.1 g/m², respectively (means ± 1 SE). These amounts were 160%, 170%, 380%, and 791% of the quantities deposited at the same sites during the snow-free season. Site w4, a wet sedge meadow, was grazed intensely by elk and bison during the winter. The dung deposited at w4 appeared to be as concentrated as at any site we observed in the northern range.

Relationships between processes

Net aboveground primary production and herbivory. —In an effort to understand fully the link between plants and herbivores, consumption was related to vegetation in several ways. Consumption during the growing season (gC) was associated with ANPP and community species diversity (H') in 1988 (r^2 = 0.63, P = .0002, df = 8) by

$$gC = -108.9 + 0.33(ANPP) + 68.8(H'),$$

and in 1989 (r^2 = 0.53, P = .006, df = 10) by

$$gC = -68.3 + 0.16(ANPP) + 47.9(H'),$$

with ANPP 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' in predicting gC is almost solely due to a summer-range forest, s5, and a winter-range wet sedge meadow, w4. If these sites are omitted in the analysis, H' no longer is significant and gC becomes linearly and positively associated with ANPP among sites where the variables were measured during both years, in 1988 (r^2 = 0.90, P = .0001, df = 7) by

$$gC = -30.8 + 0.55(ANPP)$$

and in 1989 (r^2 = 0.53, P = .025, df = 7) by

$$gC = -4.0 + 0.34(ANPP)$$

(Fig. 6A). Slopes of the relationship could not be discriminated from one another ($F_{1,14}$ = 2.47, P = .14) and intercepts were indistinguishable from zero (t_7 = −1.61 for 1988; t_7 = −0.16 for 1989). A winter range grassland sampled only in 1989 (w1) lies well within 95% confidence limits calculated from other samples that year.
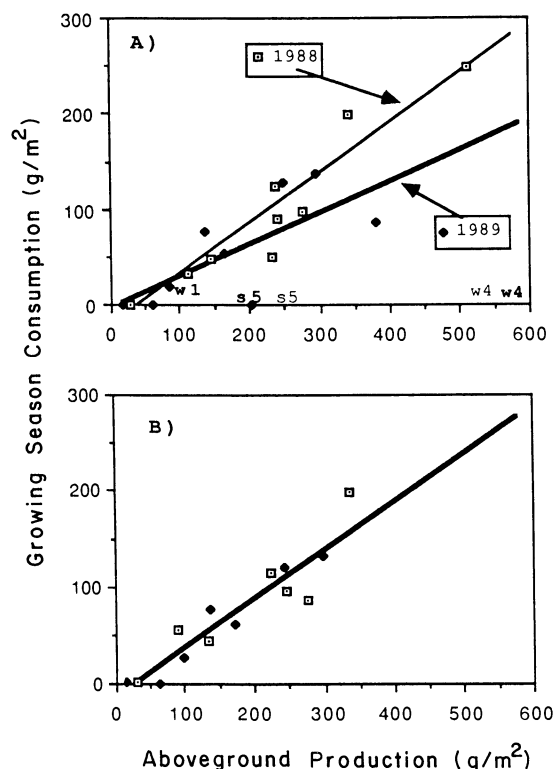

FIG. 6. Relationship of growing-season consumption (gC) on aboveground net primary production (ANPP) during 1988 and 1989 at Yellowstone National Park study area for (A) all sites, and (B) transitional and summer range sites only. Alphanumerically coded samples were not used to calculate regression equations. For w4 and s5, 1989 samples are in bold lettering.
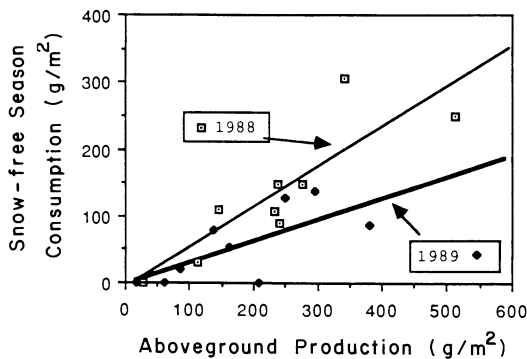
FIG. 7. Relationship of consumption during the snow-free season (C) to aboveground net primary production (ANPP) for 1988 and 1989 at the Yellowstone National Park study area.

It is clear from Fig. 6A that w4 and s5 were not grazed, despite exhibiting high productivities. Both sites were dominated by single graminoid species that represented >90% of the total standing crop: *Carex rostrata* at site w4, and *Calamagrostis rubescens* at site s5. Furthermore, w2, a relatively productive winter range grassland (two-year mean ANPP equalled 218 g/m²) was not grazed in 1989 and had one grass, *Bromus inermis*, contributing >90% of the aboveground biomass. The nearly monospecific composition of these communities was profoundly different from that of other communities. This is reflected in the low H' values for the three sites, ranging from 0.37 to 0.71, compared with values from 1.41 to 2.74 for other sites. These results suggest there are two different types of plant communities in Yellowstone, distinguished by both their structure and function: one of low species diversity avoided by large herbivores during the snow-free season, and a second possessing higher species diversity and grazed by large herbivores during the snow-free year. Although only 3 of 12 sites studied here exhibited near-monospecific compositions, sites dominated by single species in this fashion are common in lodgepole pine forests throughout Yellowstone Park, and therefore constitute an important structural and functional component of Yellowstone at the ecosystem level.

For sites that were grazed during the study, in 1989 there was a weakly significant lower slope for the relationship between gC and ANPP for winter-range sites compared to the slope calculated from higher elevation sites ($F_{1,6} = 5.20$, $P < .06$). In contrast, during 1988 there was no difference between winter and other seasonal ranges ($F_{1,5} = 0.76$, $P < .42$).

To examine rates of herbivory at sites off the winter range, the relationship between gC and ANPP was reevaluated for transitional and summer range sites only. Because we were just interested in grazed vegetation, the ungrazed forest summer range site, s5, and ungrazed areas beneath *A. tridentata* were omitted. There was a positive relationship between gC and ANPP in

1988 ($r^2 = 0.86$, $P = .003$, df $= 5$) with

$$gC = -14.8 + 0.53(\text{ANPP})$$

and in 1989 ($r^2 = 0.94$, $P = .0003$, df $= 5$) with

$$gC = -17.4 + 0.54(\text{ANPP})$$

(Fig. 6B). Two points should be noted. First, ANPP was a precise predictor of gC, explaining 86% and 94% of the variation in gC in 1988 and 1989, respectively. Second, the regression lines are so similar that they cannot be visually distinguished in Fig. 6B. This indicates that, despite the great differences in climate and ungulate numbers between years, the rate of grazing per unit of production was the same in transitional and summer range areas.

Consumption during the snow-free season (C) and site production (ANPP) in 1988 were positively related ($r^2 = 0.74$, $P = .003$, df $= 7$) by

$$C = -8.50 + 0.60(\text{ANPP})$$

(Fig. 7). The relationship between C and ANPP in 1989 was the same as that for gC and ANPP. The difference in late-season consumption between years, high in 1988 vs. none in 1989, was not enough to differentiate slopes of C on ANPP for the two years ($F_{1,14} = 2.02$, $P = .18$). In addition, intercepts could not be discriminated from zero ($t_7 = -0.24$ for 1988; $t_7 = 0.16$ for 1989).

To explore temporal interactions between herbivores and vegetation, daily consumption (dC) was re-
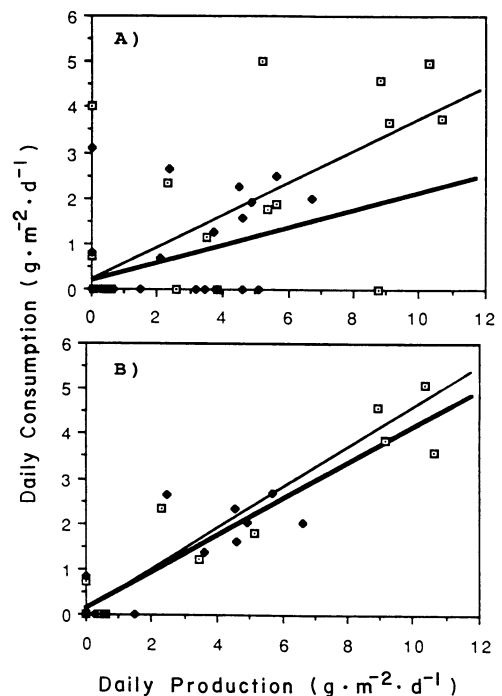

FIG. 8. Relationship of growing season daily consumption (dC) to daily aboveground net primary production (dANPP) at the Yellowstone National Park study area for (A) all grazed sites and (B) transitional and summer range grazed sites only. Symbols and lines as in Fig. 6.

lated to a variety of seasonally fluctuating plant variables. Correlation analyses performed on 1989 data revealed no association between daily consumption (dC) and either green standing crop ($P = .40$) or total standing crop ($P = .44$). Instead, dC was positively associated with both daily production, (dANPP, $r = 0.54$, $P < .0001$) and green biomass concentration (GBC, $r = 0.45$, $P < .003$). A stepwise regression with dC as the response variable and dANPP and GBC as independent variables loaded dANPP only, indicating that GBC did not explain any further variance in dC. Among grazed sites that were sampled in both years, daily consumption (dC) during the growing season and daily production were positively related in 1988 ($r^2 = 0.50$, $P < .0001$, df = 26) with

$$dC = 0.25 + 0.34(d\text{ANPP})$$

and in 1989 ($r^2 = 0.30$, $P < .0003$, df = 39) with

$$dC = 0.13 + 0.23(d\text{ANPP})$$

(Fig. 8A). Much of the dispersion of the samples around the regression lines was due to animals leaving the winter range early in the growing season when plants were growing. When the relationship was reevaluated for transitional and summer ranges only, dC was related to dANPP in 1988 ($r^2 = 0.92$, $P < .0001$, df = 16) by

$$dC = 0.082 + 0.42(d\text{ANPP})$$

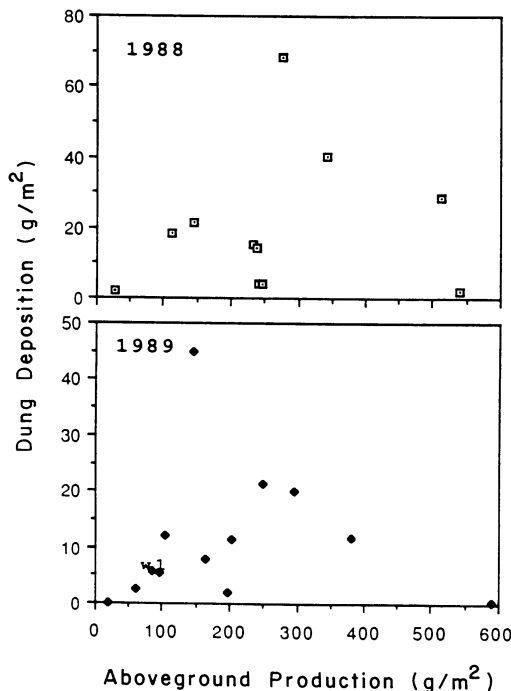and in 1989 ($r^2 = 0.79$, $P < .0001$, df = 28) by

FIG. 9. Scattergram of dung deposition (D) relative to aboveground production (ANPP) for 1988 and 1989 at the Yellowstone National Park study area. Symbols are sites sampled in both years.
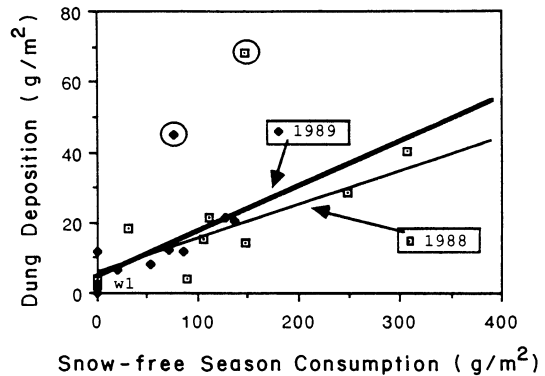

FIG. 10. Relationship of dung deposition (D) to consumption during the snow-free season (C) for 1988 and 1989 at the Yellowstone National Park study area. Circled samples were elk-bedding areas and were not included in calculations.

$$dC = 0.048 + 0.385(d\text{ANPP})$$

(Fig. 8B). Slopes for the two years were the same ($F_{1,34} = 0.59$) and intercepts could not be discriminated from zero ($t_{16} = 0.53$ for 1988; $t_{28} = 0.55$ for 1989).

Dung deposition, herbivory, and aboveground net primary production. — There was no first- or second-order polynomial relationship between D and ANPP (Fig. 9). However, D and consumption during the snow-free season (C), omitting elk bedding areas that were statistical outliers (outside the 95% prediction limits of the regressions), were positively related in 1988 ($r^2 = 0.79$, $P < .0001$, df = 8) by

$$D = 3.99 + 0.11(C),$$

and in 1989 ($r^2 = 0.81$, $P = .0004$, df = 8) by

$$D = 2.94 + 0.12(C)$$

(Fig. 10). Slopes could not be discriminated between years ($F_{1,16} = 0.20$, $P = .66$), and intercepts for both years were indistinguishable from zero ($t = 1.44$ for 1988; $t = 1.09$ for 1989).

If the relationship between D and ANPP is considered only for sites that were grazed and where elk did not bed, D was positively related to ANPP for pooled 1988 and 1989 data ($r^2 = 0.47$, $P = .003$, df = 14) by

$$D = 2.84 + 0.05(\text{ANPP}).$$

The intercept could not be differentiated from zero ($t = 0.75$). Therefore, in areas that they graze, large herbivores return nutrients to the system at a constant rate per unit ANPP.

DISCUSSION

Temporal association between processes: plant growth and ungulate grazing

Aboveground net primary production (ANPP) in Yellowstone occurs as a brief pulse locally and region-

ally as a nitrogen-rich wave that follows the elevational gradient. ANPP begins in the low winter range in the early spring and ends in the high summer range in late summer. There is a link between the timing of plant growth and the timing of consumption. Since forage nitrogen content (%N) and green biomass concentration (GBC) are highest during plant growth, ungulates increase forage quality and the yield of high-quality forage per bite by grazing young vegetation. Yellowstone may be able to support large herds of herbivores because of its size, the elevation gradient that makes this young, nutritious, and concentrated forage available for up to 6 mo/yr, and the migratory behavior of the most abundant grazers.

In the Serengeti ecosystem, ungulate migration is also associated with animals following a seasonal wave of green vegetation (McNaughton 1979). However, in contrast to the predictable pattern of plant growth along an elevational gradient in Yellowstone, production in the Serengeti is distributed stochastically in space according to rainfall events. The high level of concordance between Yellowstone and the Serengeti with reference to grazer migration suggests that the spatial and temporal dynamics of primary production is a fundamental factor in the functional organization of grassland ecosystems with abundant large herbivore populations.

There was evidence for functional dissimilarity between the winter range and other seasonal ranges. During 1989 the rates of herbivory (slope of the relationship between consumption during the growing season, gC, and ANPP) were lower at winter range sites than at transitional and summer range sites. There was no difference between seasonal ranges in 1989, suggesting that grazing intensity during the growing season may be lower on the winter range than other areas of the Park during years of moderate elk and bison population levels (1989), and the same when populations are large (1988). Seasonal segregation of grazing leading to forage conservation during the food-limiting period of the year, e.g., winter in temperate grasslands and the 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). These results indicate a potential interaction between herbivore population size and winter forage quantity in Yellowstone.

Spatial associations of ecosystem processes

The non-forested landscape of Yellowstone's northern range is functionally heterogeneous. All three processes measured in this study, aboveground net primary production (ANPP), ungulate consumption (C), and dung deposition (D) ranged widely among study sites. Aboveground productivity varied by $\approx$ 20-fold in 1988 and by >35-fold in 1989. Consumption ranged from 0 to 306 g/m² in 1988 and 0 to 137 g/m² in 1989.

Fecal deposition at study sites ranged from 2 to 68 g/m² in 1988 and 0 to 45 g/m² in 1989.

The spatial pattern of ecosystem processes in semi-arid habitats is tied to soil properties, which are influenced by topography (Schimel et al. 1985, Burke 1989, Burke et al. 1989). In Yellowstone, aboveground production was associated with several soil characteristics. However, since large herbivores have profound direct and indirect effects on ecosystem processes (Detling 1988, McNaughton et al. 1988, Pastor et al. 1988), grazers may alter the spatial pattern of energy and nutrient fluxes by their pattern of landscape utilization. In this study, consumption was positively and linearly associated with site aboveground production. This indicates that as production of a landscape patch increases, so too does consumption at a constant rate per unit of productivity. In addition, the fecal return by ungulates was positively and linearly linked to both production and consumption, except in elk-bedding areas. Ungulates excrete >90% of the phosphorous they ingest, $\approx$99% of which is fecal, and 65-95% of their ingested nitrogen, $\approx$85% of which is urinary (Ruess 1987). Excretal phosphorous and nitrogen are in forms readily available to plants and soil microbes (Wilkinson and Lowery 1973, Floate 1981). If dung deposited at the sites is used as an index of nutrient return from ungulates to the soil, the positive association between dung deposition and both aboveground grassland production and grazing suggests that production and grazing are coupled to herbivore-facilitated nutrient cycling in Yellowstone.

It is notable that a winter range wet sedge meadow (w4) and a summer range forest (s5) exhibited dramatically different relationships between ANPP and consumption than other sites. Although both sites were productive, neither was grazed. In addition, a productive winter range grassland site, w3, was avoided in 1989. All three communities were quasi-monocultures, with a single species contributing >90% of the standing crop. Ungulates grazed areas adjacent to each site, suggesting the communities were avoided because of their low forage quality or palatability. The environmental factors promoting both exceptionally high species dominance in the vegetation and low herbivore utilization is not clear.

Consumption in Yellowstone's northern range compared to other ecosystems

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

Here we compare herbivory in Yellowstone with other ecosystems using a previously reported data set

(McNaughton et al. 1989) of coupled aboveground production and herbivore consumption (by both insects and large herbivores) for a variety of terrestrial habitats. Herbivore consumption (C) and net foliar production (NFP) were strongly and positively related in that data set. Foliar production equalled ANPP for all habitats except forests, where it did not include wood production, which is considered largely unavailable to herbivores. The relationship was heavily influenced by samples from East African parks and game reserves (Sinclair 1975, McNaughton 1985) that had greater proportions of their primary production grazed than all other ecosystems. Superimposing samples of grazed sites in Yellowstone, representing single-year measurements or, when available, two-year averages (Fig. 11), it is clear that rates of herbivory at Yellowstone 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 proportion-consumed data, grouped African and Yellowstone samples together, which verifies statistically what is visually apparent from Fig. 11: the percentage of NFP consumed in these two ecosystems is similar and higher than in other terrestrial ecosystems. Yellowstone was also grouped with the salt marsh, indicating offtake in salt marshes can also be high. Consumption averaged 62% at African game reserve sites and 45% at grazed northern-range Yellowstone sites. Herbivory was over six times as high in Yellowstone as in other temperate grassland sites (consumption = 7.9%), which were small reserves with, likely, small populations of large herbivores.

These results suggest that grassland ecosystems with abundant large herbivores are functionally similar to aquatic systems that support high chronic levels of herbivory (Carpenter and Kitchell 1984, Berquist and Carpenter 1986, Detling 1988), and an understanding of these terrestrial grazing ecosystems can come only from their direct study and not by 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 grassland ecosystems that, prior to the spread of European influence, supported large herds of ungulates throughout all of Africa (Ford 1971), North America (Roe 1951, Dary 1974), and Eurasia (Bannikov et al. 1961), and Macropods in Australia (Newsome 1971, 1975).

The effect of drought on ecosystem processes

Climate is the principal driving variable of ecosystem processes. We documented dramatic reductions in aboveground primary production, consumption, and the flux of nutrients from ungulates to the soil, one year after a major drought in the Yellowstone grasslands.
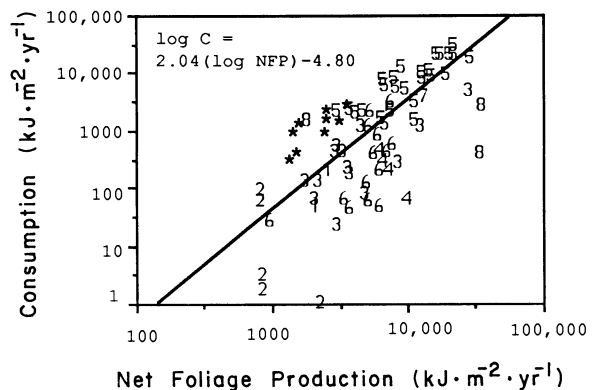

FIG. 11. Relationship of herbivore consumption, C, to net foliage production, NFP, for terrestrial ecosystems. Codes are: 1 = desert; 2 = tundra; 3 = temperate grassland; 4 = temperate successional old field; 5 = unmanaged tropical grassland; 6 = temperate forest; 7 = tropical forest; 8 = salt marsh; 9 = agricultural tropical grassland; and * = Yellowstone grassland. Yellowstone samples were not included in the regression. Adapted from McNaughton et al. 1989, 1990.

The frequently reported relationship between grassland production and climatic estimates of water balance using temperature and precipitation (Lieth 1973, Sims and Singh 1978, Lauenroth 1979, Stephenson 1990), and the demonstrated stimulation of grassland production by irrigation (Dodd and Lauenroth 1979), implicates moisture as an important limiting factor of grassland productivity. We thus were surprised that production in Yellowstone was higher in 1988, a year of drought, than in 1989, a year of near-average precipitation. A likely principal contributing factor in the decline was the death or injury of plants during the 1988 drought, which reduced the productivity potential at the sites in 1989. Grasses that possess belowground perennating structures are considered protected from drought (Coughenour 1985). The near disappearance of some dominant grass species from 1988 to 1989, e.g., peak biomass decline of *Danthonia unispicata* from 16.7 g/m² to 0.7 g/m² at an ungrazed summer range site, s1 (Frank 1990), is testimony to the severity of the 1988 drought in some parts of the northern range.

The 1988 drought affected herbivores by reducing the duration of nutritious forage late in the season (Frank 1990), which likely led to ungulates entering the ensuing winter in relatively poor condition. Furthermore, drought-induced wildfire burned portions of the northern winter range and limited winter forage. These direct (reduced late-season forage quality) and indirect (reduced winter range) drought effects interacted with a severe 1988–1989 winter that produced: (1) a large number of winter-killed elk and (2) a larger-than-normal winter migration out of the Park where many elk and bison were shot (Singer et al. 1989). The result was dramatic declines in northern-range elk and bison pop-

ulations, and, consequently, reductions in average growing season consumption by 43%, and dung deposition by 47%. Because large herbivores have effects on ecosystems that pervade all trophic levels (McNaughton et al. 1988), factors that determine the numbers of grazers have important indirect effects on ecosystem function. The reduction in nutrient fluxes through herbivores may have reduced rates of nutrient cycling across the landscape in 1989.

A second potential type of functional response to drought is its effect on the relationship between processes. Although results must be interpreted cautiously since data are limited, there were between-year consistencies in the relationships of three pairs of processes: (1) growing season consumption (gC) and aboveground production (ANPP), particularly on transitional and summer ranges, (2) daily aboveground production (dANPP) and daily consumption (dC), and (3) dung deposition (D) and consumption during the snow-free season (C). These results suggest grassland functional integrity through time in reference to the relationships between trophic levels. However, information from years of high ungulate numbers and low plant production, or vice versa, are needed to thoroughly explore this phenomenon. In contrast, there was a marked difference in grazing during the late season between years. During 1988 five sites were grazed at an average rate of 60 g/m², while in 1989 no site was grazed. An explanation for this stark between-year distinction stems from the 1988 fires that concentrated ungulates on unburned areas in late summer and fall 1988, and in 1989 may have drawn grazers away from the study sites into burned valleys that provided high-quality forage (Knight and Wallace 1989). Wildfire did not appear to affect ungulate foraging patterns during the growing season of either year (Frank 1990).

Synthesis

Large mammalian herbivores are mobile and functionally integrated components of the semiarid habitats that they dominate. By tracking young vegetation in Yellowstone, herbivores prolong a nutritionally rich diet while simultaneously maintaining high foraging efficiency. Topographically determined edaphic patterns are important determinants of energy- and nutrient-flux patterns in most semiarid habitats. Because of the direct and indirect effects large herbivores impart on semiarid landscapes, their pattern of landscape use can bear substantially on patterns of ecosystem processes. Processes measured in this study (ANPP, C, D) varied widely among sites in Yellowstone. Furthermore, there were positive spatial associations between (1) aboveground production and consumption, and (2) consumption and nutrient return to sites from herbivores. These results suggest native herbivores may steepen gradients of energy and nutrient fluxes in landscapes, beyond those gradients induced by topography alone.

Drought had a severe effect on grassland and shrub–grassland ecosystem function. Results indicate large direct and indirect effects of drought on net energy and nutrient flux in Yellowstone. Direct drought-induced death and injury of plants reduced the base of the food web, and, thus, the energy- and nutrient-capturing capacity of the ecosystem. Direct effects on ungulate condition and indirect effects through wildfire were likely involved in the decline in elk and bison numbers, which in turn meant reductions in both consumption and nutrient flux through grazers (indexed with dung deposited at sites). The decline in grazers probably had indirect cascading effects on trophic processes that should be expected to reverberate in this grazing-dominated ecosystem until herbivore populations recover. These results show how dramatically a severe drought of one-year duration can alter ecosystem function.

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