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COMPARATIVE EFFECTS OF ELK HERBIVORY AND 1988 FIRES ON NORTHERN YELLOWSTONE NATIONAL PARK GRASSLANDS[1]

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Abstract. The drought, frequent lightning strikes, and resultant large fires of 1988 in Yellowstone National Park were considered a several-century event for the area. They presented an unparalleled opportunity to document the effects of large fires on forage production, forage quality, and herbivory for the largest elk (*Cervus elaphus*) population in a natural area in North America. We documented elk–grassland dynamics on the Blacktail Plateau on Yellowstone's northern elk winter range following the burning of 25% of the study area in 1988.

Contrary to predictions of earlier scientists, grazing of the grasslands by elk prior to the fires did not result in warmer, drier, or less productive bunchgrass communities. Soil moisture was equivalent, soil temperatures were cooler, aboveground grass biomass was equivalent in two of three years, and N, macronutrients (Ca, Mg, P, K), and digestibility concentrations were higher on grazed than ungrazed grasslands. Forb biomass, *Poa sandbergii* biomass, and litter accumulations, however, were less on grazed sites, and more bare ground occurred on grazed (35%) than on ungrazed (24%) grasslands ($P < 0.05$). Elk herbivory resulted in more documented ecosystem effects for Blacktail Plateau elk than did burning.

Two years postfire, burning had increased aboveground biomass of grasslands by 20%. However, digestibility of only one (*Festuca idahoensis*) of three grass species (*F. idahoensis*, *Pseudoroegneria spicata*, and *Koeleria macrantha*) was enhanced. N, cellulose, and macronutrient concentrations in grasses, and digestibility in *P. spicata*, *K. macrantha* were unaffected by the fires. In grazed vs. ungrazed areas *F. idahoensis*, *P. spicata*, and *K. macrantha* averaged a 21% higher N concentration, and a 7% higher digestibility. Aboveground herbaceous biomass was greater in grazed than ungrazed areas in one of three years, and total aboveground N yield was greater in two of three years. Forage biomass did increase postfire and could have benefited elk foraging efficiency. Elk use of burned grasslands increased following the fires ($P < 0.05$). Elk avoided burned forests during the first three winters postfire ($P < 0.05$), but elk obtain few of their forages from forest communities on the northern Yellowstone winter range (<10% of feeding observations prefire). The possibility exists that shrub and herbaceous biomass in forest understories will increase after ≥3 yr postfire. Other studies suggest slower recovery, or increases to preburn levels in forests after ≈6–8 yr. Eventually, the elk might benefit from increased quality and biomass of forages in burned forests. Grazing, by reducing fuels, can alter the extent of burning and create a more patchy fire pattern than occurs on ungrazed areas, thus conserving N that would otherwise be volatilized by burning. We observed no such interaction between elk herbivory and burning, in spite of a sixfold reduction in litter on grazed sites. Burning did not affect N concentrations on either grazed or ungrazed study sites, apparently because accumulations of dead aboveground plant material were still very light on both treatments in comparison to, e.g., tallgrass or mixed-grass prairies in the Great Plains. The relatively minor effects of the fires of 1988 on the grassland study sites were probably a result of the relatively fast front fires, with little residual burning, and the relatively small dead plant accumulations in bunchgrass communities.

Key words: Cervus elaphus; *elk; fire effects; forage quality; grasslands; grazing; herbivory; ungulate winter range; Yellowstone.*

INTRODUCTION

The large fires in Yellowstone National Park (YNP) in 1988 provided an opportunity to study the effects of a large wildfire on a relatively self-regulated population of elk (*Cervus elaphus*). Effects of the elk on park vegetation are equivocal and controversial (Skinner 1928, Cole 1971, Beetle 1974, Houston 1982, Chase 1986, Baur 1987, Patten 1993). Artificial controls on elk were terminated in 1968, under the assumption that the ungulates, even in the absence of gray wolves (*Canis lupus*), would be naturally regu-

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lated at levels with acceptable effects on the park vegetation (Cole 1971, Houston 1976, 1982). Some critics have argued that the park's "natural regulation" experiment has failed: the elk population has grown without constraint and the vegetation has been severely affected by ungulates (Beetle 1974, Chase 1986, Kay 1987, 1990, Patten 1993). Others suggest that the experiment is incomplete without gray wolves or wildfires (Peek 1980); or that no scientific experiment exists, but rather a paradigm in management (Kay 1990, Chadde and Kay 1991). Here, we present data on effects of elk herbivory and the fires of 1988 on aboveground biomass production, nitrogen (N) and macronutrient concentrations, percent digestibility, and plant species composition in bunchgrass and big sagebrush (*Artemisia tridentata*) communities, and on effects of the fires on elk habitat preferences. Frank and McNaughton (1992) documented plant responses to elk and bison grazing on Yellowstone's northern range, but they studied more mesic meadows, mostly on higher elevation transition and summer ranges, where elk densities were only ≈1/10th of the ungulate densities of our study area, but herbaceous biomass production was much greater. Consumption by bison was approximately equivalent to that by elk on their study sites, while our sites were almost exclusively affected by elk herbivory. On their sites, ungulate herbivory occurred during the growing season, whereas we studied only winter-grazed sites. Coughenour (1991) studied plant responses to ungulates on lower elevation, semiarid portions of the winter range, but he studied only major plant groups. Neither author studied effects of burning.

The climatic, lightning, and wind patterns of 1988, which ultimately led to the burning of 1 405 775 ha in the Greater Yellowstone area, were considered a 250–400 year event for the area (Despain et al. 1989, Schullery 1989, Millspaugh 1995). The low winter snowpack of 1987–1988 was only 31% of normal, and the June-July-August rainfall was only 36% of normal, the lowest precipitation for those months recorded in 112 years of park records (Singer et al. 1989). Temperatures were elevated in June and July (2.7°C above normal), and moisture levels in fine fuels were reduced to only 2–3% by late July (Schullery 1989). Nearly all of the burning on the northern range occurred during a single 24-h period on the afternoon and night of 9 September and the morning of 10 September 1988, during a spectacular, fast-moving, 34-km run of the North Fork fire. About 27 000 ha (27%) of the 140 000-ha ungulate northern winter range burned, including ≈11 427 ha of grasslands and 15 580 ha of forest. The Blacktail Plateau study area was burned mostly by an accidental man-caused fire (North Fork fire) that could not be suppressed, and by a naturally ignited fire that was suppressed (Lava Creek fire).

The large Yellowstone fires of 1988 presented the opportunity to evaluate a number of questions dealing with the management of fire and elk in large natural areas. The elk population was suspected to be at or above ecological carrying capacity (ECC) in 1988 (Boyce and Merrill 1989, Merrill and Boyce 1991). The immediate decline of elk following the fires and subsequent predicted increase in elk, due to increased biomass and quality of forages, presented an opportunity to evaluate the ECC for the population (Boyce and Merrill 1989, Christensen et al. 1989). Increases in grassland biomass and plant tissue concentrations, forage digestibility, diet quality, and body condition were predicted for elk following the fires (Rowland et al. 1983, Hobbs and Spowart 1984, Boyce and Merrill 1989, Christensen et al. 1989). The fires might alter elk–grassland interactions. For example, elk diets might change following the fires, as previously unpalatable forages might become more palatable to elk following burns (Leege 1969, Asherin 1976); green-up might occur earlier and senescence might occur later (Peet et al. 1975, Hobbs and Spowart 1984); and N may be more concentrated in grass biomass on burned areas. Although elk might prefer burned grasslands, they might avoid burned forests during winter because of deeper and more crusted snows under burned canopies (Meiman 1968, Skovlin and Harris 1970, Jones 1974, Davis 1977).

Most studies in grasslands have investigated the effects of prescribed burning: typically slow burning, hot backfires, conducted during the spring (Hobbs and Spowart 1984, Seip and Bunnell 1985, Canon et al. 1987). Wildfires in grasslands are more typically fast frontfires, which are cooler than backfires (Daubenmire 1968). Burning in autumn typically results in less enhancement of aboveground herbaceous plant production when compared to spring burning (Anderson 1965, Owensby and Anderson 1967). Greater enhancement of production from spring burning is probably due to larger increases in soil temperatures.

Our objectives were to document the effects of elk herbivory on grassland species composition, biomass production, and forage quality, and to document any changes in ungulate–grassland interactions caused by the autumn wildfires of 1988.

We hypothesized that:

1) Herbivory by elk at densities of 14–19 elk/km^2 would result in a warmer, drier grassland with more bare ground, reduced plant biomass, and altered plant species composition (Beetle 1974, Chase 1986, Kay 1990).

2) Burning of Yellowstone's grasslands would increase biomass, nutritional quality, and digestibility of forages consumed by elk (DeWitt and Derby 1955, Miller 1963, Lyon and Stickney 1976, Keay and Peek 1980, Rowland et al. 1983). As a consequence, elk should prefer burned over unburned grassland habitats (Rowland et al. 1983, Hobbs and Spowart 1984, Canon et al. 1987) and their diets should be altered as some burned forages become more palatable (Leege 1969, Asherin 1976).

3) The autumn Yellowstone fires of 1988 (all frontfires) would increase quantity and quality of grassland forages relatively less than prescribed spring burns (mostly backfires; Anderson 1965, Owensby and Anderson 1967, Smith and Owensby 1972, Canon et al. 1987), due to cooler burning of frontfires, a longer time interval between autumn burning and initiation of plant growth, and less enhancement of the soil temperatures during the growing season (Aldous 1934, Smith and Owensby 1972).

Study Area

The northern Yellowstone elk herd is one of eight migratory elk herds that spend part of the year in Yellowstone National Park (YNP), and is one of only two elk herds that winter primarily within the boundaries of YNP (Singer and Mack 1993). The northern Yellowstone elk herd is one of the most populous in North America, and is the largest elk herd in Montana. From 1975 to 1990, harvest of elk (mostly antlerless), which occurs when elk migrate north of the park, averaged 1056 ± 725 elk/yr ($\bar{X}$ ± 1 SE) from the northern herd (harvest of adult cows is 559 ± 467 elk/yr, $\bar{X}$ ± 1 SE), or 5–8% of the population each year, insufficient to limit or regulate the elk population (Houston 1982, Merrill and Boyce 1991, Singer and Mack 1993). The northern Yellowstone elk herd is presumed to be regulated primarily by natural processes (Houston 1982, Coughenour and Singer 1995). The combination of the events of 1988–1989, including the most severe drought on record, the fires of 1988, and a severe winter with three arctic storm fronts (rated −2.5 on a scale from +4, mildest, to −4, most severe; Farnes 1995) contributed to unprecedented elk migrations, large elk harvests outside of the park, and a large winterkill of elk. During the winter of 1988–1989, ≈38–43% of the northern elk population died, ≈14–16% of the population was harvested north of the park (typical harvests are 6–8%), and 24–27% of the population died of winter malnutrition both within and north of the park (Singer et al. 1989).

Our study was conducted on the 97.7-km² Blacktail Plateau, located in the approximate geographic center of the northern winter range. Elevation is ≈2040 m above sea level and average annual precipitation at the nearest weather station at Mammoth, 8 km distant, is ≈400 mm/yr. Aerial counts of the northern Yellowstone elk herd ranged from 14 800 to 18 900 during the winters of 1985–1990, and an average of 1470 ± 345 elk ($\bar{X}$ ± SE, range 223–2969) was counted on the Blacktail Plateau area during that period. Average elk densities on the Blacktail Plateau during this study, 15.0 ± 3.6 elk/km², were representative of densities (13–16 elk/km²) on the entire northern range at the same time (Singer 1991, Singer and Mack 1993).

The Blacktail Plateau is composed mostly of open grassland habitat types, e.g.: Idaho fescue–bearded wheatgrass *Festuca idahoensis–Agropyron smithii, Geranium* phase (8.5%); Idaho fescue–bluebunch wheatgrass *Pseudoroegneria spicata* (1.4%); Idaho fescue–bearded wheatgrass (1.5%); big sagebrush *Artemisia tridentata* types, mostly big sagebrush–Idaho fescue (11.1%); big sagebrush–Idaho fescue, *Geranium* phase (8.5%); and of coniferous forest types, mostly Douglas-fir–snowberry *Pseudotsuga menziesii–Symphorocarpus albus* (16.9%) and Douglas-fir–pinegrass *Calamogrostis rubescens* (4.5%) (Despain 1991). The remainder of the study area is a variety of wet coniferous forests (*Pinus contorta, Picea engelmanii*) little used by elk. Dominant grasses are Idaho fescue, bluebunch wheatgrass, prairie Junegrass (*Koeleria macrantha*), bearded wheatgrass–wildrye (*A. smithii–Elymus cinereus*), and Sandberg's bluegrass (*Poa sandbergii*). Dominant shrubs are big sagebrush, common rabbitbrush (*Chrysothamnus nauseosus*), and green rabbitbrush (*C. viscidiflorus*). A variety of forbs exists on the sites, but forbs apparently are of limited availability to elk during winter because of their desiccation and the extensive snow cover. From 1985 through 1988, forbs comprised only 3% of the winter diet of elk, whereas grasses and sedges comprised 83% and shrubs 8% (Singer and Norland 1994). Soils at the Blacktail sites are Pinedale glacial till derived from Absaroka volcanics, limestone, precambrian crystalline rocks and tuff (Pierce 1973, U.S. Geological Survey 1975).

Two 2-ha ungulate exclosures were erected (one in 1958, one in 1962) near Blacktail Deer Creek to evaluate the effects of elk grazing (Barmore 1980, Houston 1982). Both are located on open, rolling, shrubsteppe habitats. Most winter ungulate herbivory on the Blacktail Plateau is by elk; a few bison seen on the area concentrate their feeding in the swales and sedge meadows (Barmore 1980, Meagher 1989). Winter consumption by elk on similar grassland sites averaged 55% over eight winters, 1971–1979 (Houston 1982:147). A few elk linger each spring in the vicinity of the exclosures to graze on early green-up of grasses before migrating to subalpine summer ranges.

Measurements of aboveground biomass and forage quality were obtained from a series of marked plots located in grazed and ungrazed sites in 1986 and 1987. Some of these plots burned opportunistically when 49% of the Blacktail Plateau study area burned on 9 September 1988, as the North Fork fire made its last major run (Despain et al. 1989). Extensive mosaics of unburned areas occurred within the fire perimeter (Despain et al. 1989) and provided representative burned and adjacent unburned plots both inside and outside the exclosures. The mosaic pattern of burning was primarily due to erratic winds at the time of the fires; no known differences existed between the burned and unburned patches (D. Despain, *personal communication*, November 1988, Yellowstone National Park).

Methods

Sampling design and biomass measures

Different, but comparable, sample designs were used before and after the fires to measure the effects of the

treatments on plant biomass. In 1986 and 1987, prior to the fires, 20 1 × 1 m plots were randomly located on ungrazed (= exclosed) sites and 20 plots on grazed sites adjacent to the 2-ha elk exclosures (n = 40 plots total). Percent cover of plant basal area, bare ground, rocks (>6 cm diameter), pebbles (<6 cm diameter), pavement, moss, lichens, elk dung, litter, and dead bunchgrass clumps were sampled on each plot using a 1-m² gridded frame. All herbaceous and subshrub aboveground biomass was then clipped from the 1-m² plots at peak standing crop (late July) and sorted by species. Green vs. dead components of each species were separated, oven-dried for 48 h at 60°C, and weighed.

During the fires of 1988, about one-half of the ungrazed and one-half of the grazed areas burned. Following the fires, a 20-ha area in and near the exclosures was stratified into burned and unburned areas of grazed and ungrazed sites within two habitats, grass and big sagebrush. Twelve 1-m² plots were randomly located within each stratum for a balanced ANOVA design of the two treatments, burning and grazing (n = 48 plots total). Temporary grazing cages (1.5 m²) were placed at each of the grazed plots, and 1990 offtake was sampled from paired plots using the difference method. Plots within the burn were separated by either a swale, fire boundary, or both, and the plots were treated as independent samples under the assumption that movements by elk between sites required a foraging decision. Plant species biomass in 1990 was sampled three times during the growing season, using the canopy-intercept method with hits by a pin passed through vegetation (Frank and McNaughton 1990). We clipped 12 plots in 1990 to calibrate the number of hits with clipped biomass, and we compared 1990 to prefire sampling because plot size was identical (1 m²) and because Frank and McNaughton (1990) reported good correlations between biomass and pin hits of narrow-bladed (r = 0.846) and medium-bladed grasses (r = 0.896) from the area using this technique. All subsequent samples of grass morphology and forage quality and all subsequent soil measures were taken from these same plots, unless otherwise indicated.

Grass morphology

Vegetative and reproductive culm numbers and heights were recorded for bluebunch wheatgrass in 1986, 1987, 1989, and 1990 on 20 × 30 cm subplots located within the same 48 1-m² plots sampled for biomass. The circumference and heights of the tallest vegetative and reproductive culms were measured, and the numbers of vegetative and reproductive culms and seeds of each individual plant were counted.

Forage quality

Forage quality was sampled in mid-July 1986, 1989, and 1990 for *Pseudoroegneria spicata*, *Festuca idahoensis*, and *Koeleria macrantha* by collection of randomly located grass clumps in each treatment (n = 24 clumps/species). These grasses were the three most common grasses (*P. spicata*, 12%; *F. idahoensis*, 18%; and *K. macrantha*, 7%) in the elk diet (Singer and Norland 1995). Fiber (analyzed by proximate analysis: Van Soest 1981), total ash, gross energy, and N, Ca, P, K, Mn, and Mg concentrations of the grasses were analyzed by the Composition Analysis Laboratory, Colorado State University, Fort Collins, Colorado (Association of Official Analytical Chemists 1970). In vitro digestible organic matter (IVDOM, hereafter digestibility) was determined by the method of Tilley and Terry (1963), as modified by Pearson (1970).

Soil moisture and temperature

Soil moisture and temperature were recorded biweekly from late April through early September of 1990 within the same 48 plots sampled for biomass. Soil moisture was measured gravimetrically from three random points at depths of 5 and 15 cm within the same plots. Soil temperatures were obtained using a soil thermometer at a depth of 12 cm at three random points within the plots.

Statistical analyses

Nutritional levels of grass forages and standing crop biomass were first compared among years with ANOVA. Burning and grazing treatments were compared with a two-way (burning × grazing) ANOVA. Three-way ANOVAs (date × grazing × burning) were used to compare production between treatments within each habitat type. The Bartlett's test was conducted to test for equal variances; normality and equal variances were found except where otherwise noted. Tukey's W procedure was used for pairwise comparisons in those cases when variances were equal, the F statistic was significant, and the interaction was not significant. Numbers, heights, and seed production of bluebunch wheatgrass were tested among treatments with a two-way ANOVA. All statistical differences were at the $P < 0.05$ level, except where otherwise indicated.

Soil moisture and temperature data were analyzed using two-way ANOVA (date × burning) for each habitat type. Soil measurements on permanently exclosed grass sites were compared to grazed sites with a three-way ANOVA (date × burning × grazing).

Elk selection for habitats

Seven aerial counts of elk were made from fixed-wing aircraft (Super Cub) during midwinter (December to February), two winters prefire (1986–1987, 1987–1988) and three winters postfire (1988–1989, 1989–1990, 1990–1991). The entire Blacktail Plateau elk study area was censused during each survey, and group size and location (UTMGS) of each elk group were plotted on a topographic map (1:62 500). Elk were counted in the mornings, mostly between 0730 and 1030; nearly all elk groups were feeding or were lo-

cated near feeding sites. Habitat preference tests, therefore, largely represent feeding habitats. Elevation, slope, aspect, vegetative cover type, habitat type, and burn category (burned, unburned, mosaic burn; Mattson and Despain 1984, Despain et al. 1989) were later generated for each elk location using the YNP Geographic Information System (GIS). The availability of each cover type and burn category type on the study area was generated from the GIS system. We used the Bonferroni approach (Neu et al. 1974, Miller 1981, Byers et al. 1984) to calculate confidence intervals on the proportional use of vegetation cover and burn areas by elk. The technique is used in conjunction with a chi-square test, after the chi-square has led to rejection of the null hypothesis that a set of observations does not follow an expected occurrence pattern. The technique involves the use of a Bonferroni z statistic in estimating whether more or fewer elk groups than expected occur in a habitat, based on availability of that habitat. Confidence intervals on elk use were compared with availability of habitats to evaluate disproportionate use by elk. Elk use "greater than" (selection), "less than," or "equal to" habitat availability was tested at the $P < 0.10$ level, following suggestions of Neu et al. (1974).

Results

Elk herbivory in grasslands

In contrast to our hypotheses, bunchgrass communities on the Blacktail Plateau that were grazed mostly in winter were not less productive, and plant species composition, with few exceptions, was not altered by elk herbivory restricted mostly to winter. In 1986, less total aboveground standing green biomass, total grass biomass, and *Pseudoroegneria spicata* biomass were produced in grazed areas, but in 1987 and 1990, there were no other consistent trends in these variables due to elk herbivory ($P > 0.05$; Fig. 1). Less forb, *Poa sandbergii*, and litter and standing dead biomass were sampled on grazed vs. ungrazed sites during all three years (Fig. 1). Less *Koeleria macrantha* was produced on grazed sites (both burned and unburned) in 1990, but there was no difference in the other two years ($P > 0.05$; Fig. 1). More *Festuca idahoensis* was produced on grazed sites in 1987 and 1990, but not in 1986, and total production of grasses was higher on grazed sites in 1987 ($P < 0.05$; Fig. 1). No other differences attributable to elk herbivory were detected in the biomass of any other plant species. A total of 23 grass species, 87 forb species, and 22 shrub/subshrub species were sampled on the study sites.

Elk herbivory did not influence total species richness; an average of 4.5 grasses, 17.5 forbs, and 3.5 shrubs and subshrubs were identified on each 1 × 1 m plot (t tests, $P > 0.05$). Three forbs (*Tragopogon dubius, Arabis holboelii,* and *Allium cernum*) were found more often than expected on ungrazed sites (χ^2 tests, $P < 0.05$), although none of these species was eliminated from grazed sites. Two grasses (*P. spicata* and *A. dasystachum*) were found more often than expected on grazed sites ($P < 0.05$).

Ground cover was altered by elk herbivory. Moss cover was significantly greater on ungrazed sites (10.4 ± 3.9, $\bar{X}$ ± 1 SE) than on grazed sites (1.7 ± 0.2, $P < 0.05$). All unvegetated surfaces (bare ground and pebble cover combined) averaged 35% cover on grazed plots vs. 24% cover on protected plots (Fig. 1, $P < 0.05$). Litter and standing dead vegetation averaged 6.0 times more biomass on ungrazed than grazed plots ($P < 0.05$), which explained differences in estimates of bare ground cover (Fig. 1). Elk herbivory did not affect lichen cover ($P > 0.05$). Dung from ungulates and rabbits provided a minor amount of ground cover (1–4%) on both grazed and ungrazed sites.

Although recently overgrazed ranges typically possess large numbers of dead bunchgrass clumps (Mueggler 1969), we observed no significant increase in bunchgrass mortality due to elk herbivory ($t = 0.54$, $P > 0.05$). Dead bunchgrass clumps averaged 4.3% of ground cover on both treatments.

Effects of burning on plant biomass

The effects of habitat, burning, and date on plant production were significant (three-way ANOVA, $P < 0.05$). Burning enhanced total plant and grass production in both grass and sage habitats by ≈20% ($P < 0.05$). Burning enhanced grass production in May and June in grass habitats and in July in sage habitats (Tukey's multiple comparison tests, $P < 0.01$). Burning did not affect forb production in either habitat ($P > 0.05$).

Spring and summer consumption by elk was zero in 1990 ($P > 0.05$), according to our sampling program. At least one group of elk was seen feeding in the area during spring 1990, however, and limited spring consumption was known to occur.

Effects of elk herbivory and burning on forage quality

Grazed grasses were more nutritious, elemental concentrations were higher, and total nitrogen yield was enhanced by elk herbivory during two of three years. Percent N was higher in *P. spicata* and *F. idahoensis* on grazed than on ungrazed sites ($P < 0.05$), but there were no differences for *K. macrantha* ($P > 0.05$). In 1986, nitrogen yield (biomass × % N) on grazed sites was only 50% of that on ungrazed sites, but in 1987 and 1990, respectively, grazed sites yielded 56% and 10% more N than ungrazed sites. Nitrogen concentration varied among years for all three grasses ($P < 0.05$). Each grass species had a higher N concentration in 1989 than in 1986 or 1990 (Fig. 2). Elk herbivory did not influence fiber, lignin, cellulose, or ash concentration in any of the grasses (Table 1). Calcium, phosphorus, magnesium, potassium, and manganese levels

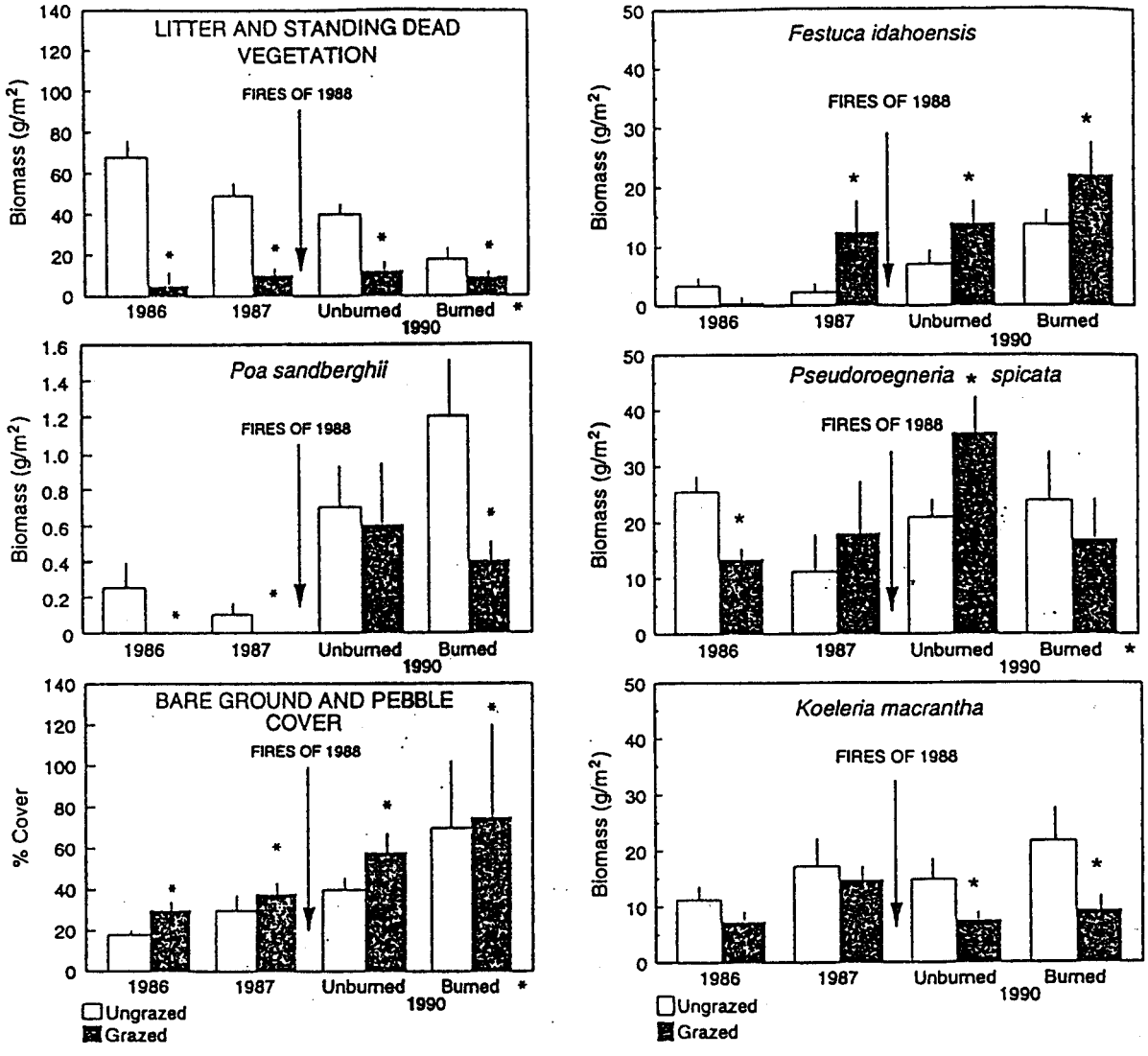

FIG. 1. Aboveground standing crop biomass in late July for functional plant groups, plant species, and ground cover in bunchgrass communities inside (ungrazed) and outside (grazed) two large ungulate exclosures on the Blacktail Plateau, 1986, 1987, and 1990. An * above means indicates significant difference due to grazing, while an * following the Burned label (x-axis) denotes a difference in biomass due to burning ($P < 0.05$, ANOVA). Error bars indicate 1 SE.

were higher in grazed than in ungrazed *F. idahoensis*. Potassium levels were also higher in grazed than in ungrazed *P. spicata*, but manganese levels were lower in grazed *P. spicata*. No differences due to elk herbivory were observed in element concentrations in *K. macrantha*.

Burning influenced nutritional and elemental concentrations of grasses far less than did grazing. Percent N in grasses on the study sites was not influenced by burning (two-way ANOVA, burning × grazing, $P > 0.05$). Burning elevated digestibility in both grazed and ungrazed *F. idahoensis* ($P < 0.05$), but we did not find evidence that burning influenced IVDOM levels in either *P. spicata* or *K. macrantha* ($P > 0.05$). Burning increased fibrous constituents in grasses. Cellulose and ash levels were higher in burned than unburned samples of grasses (Table 1; $P < 0.05$). Burning increased lignin and fiber in *P. spicata* and *F. idahoensis* ($P < 0.05$). Nutrient levels were largely unaffected by burning. Calcium, Mg, K, and P levels did not differ between burned and unburned grasses ($P > 0.05$; Table 1), except that K increased in burned and grazed *K. macrantha*. Magnesium levels were lower in burned than in unburned *F. idahoensis* and *K. macrantha* ($P < 0.05$).

Effects of elk herbivory and burning on grass morphology

The height of reproductive culms of *P. spicata* was increased by both elk herbivory and burning (three-

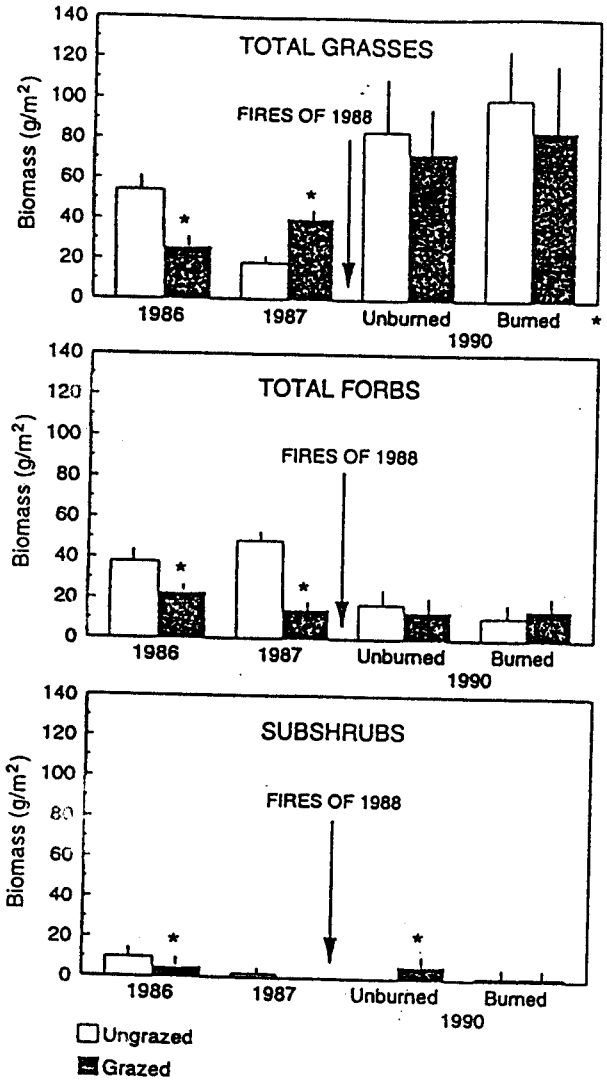

FIG. 1. Continued.

way ANOVA, year × burning × grazing, $P < 0.05$; Fig. 3), but there was no effect of either treatment on height of vegetative culms (three-way ANOVA, year × burning × grazing, $P > 0.05$). Reproductive culm heights of *P. spicata* were shorter in 1986 than during the other three years ($P < 0.05$; Fig. 3), and were taller on grazed than ungrazed sites ($P < 0.05$). Burning increased reproductive culm heights on both ungrazed and grazed sites in 1990 ($P < 0.05$; Fig. 3) but not in 1989 ($P > 0.05$).

There was a lower density of *P. spicata* clumps on grazed than ungrazed sites ($F = 18.5$, $P < 0.001$; Table 2), but burning did not effect clump density ($F = 0.03$, $P = 0.86$, two-way ANOVA). Elk herbivory did not influence the number of seeds produced per *P. spicata* clump ($F = 1.5$, $P = 0.23$), but burning increased seeds produced per clump twofold on grazed sites and fourfold on ungrazed sites ($F = 10.8$, $P < 0.01$, two-way ANOVA; Table 1). Circumference of clumps did not differ due to elk herbivory or burning ($P > 0.05$).

Soil microclimate

Soil temperatures were higher on ungrazed than grazed sites (three-way ANOVA, elk herbivory × burning × month, $P < 0.05$; Fig. 4). Soil moisture levels were not influenced by elk herbivory, burning, or habitat (three-way ANOVA, $P > 0.05$).

Elk use of burned areas

Elk use of the Blacktail Plateau dropped drastically during the first postfire winter. Prior to the fires of 1988, ≈15% of the northern Yellowstone elk herd wintered on the Blacktail Plateau study area. Following the fires, only 8% of the elk population used the area in January 1989, and only 3% of the population was present in April 1989 (Fig. 5). By the second and third winters postfire, proportional elk use of the study area recovered, averaging 14% of the counted population. These year-to-year differences in elk use of the study area were significant ($\chi^2 = 1721$, $P < 0.0001$).

In the prefire winter of 1986–1987, elk use of the same grassland areas that later burned in the 1988 fires was greater than expected based on habitat availability (active selection), but elk use of these areas was equal to their availability during the prefire winter of 1987–1988 (Neu et al. 1974 test, $P \leq 0.10$; Fig. 6). These same grasslands were used at less than their availability during the first postfire winter (1988–1989), but more than their availability during the second postfire winter (1989–1990), and during February of the third postfire winter (1990–1991). Forests that later burned were used at less than and equal to their availability during prefire winters, but burned forests were used at less than their availability during all three postfire winters. Elk selected unburned grasslands during all three winters postfire, while unburned forest–grassland mosaic was used at less than availability during both pre- and postfire winters.

DISCUSSION

Effects of elk herbivory on grasslands

Contrary to our hypotheses, winter elk herbivory of ≈55% consumption of the aboveground herbaceous standing crop on Yellowstone's northern winter range did not cause grasslands to be drier, warmer, less productive, or altered in their species composition. The exception was 1986, when total herbaceous and grass biomass amounts were less on grazed than ungrazed sites. Height of grass reproductive culms, an index of grass vigor, was shorter on grazed sites during only one of four years in 1986, suggesting that 1986 was suboptimal for grass growth. No increases in bunchgrass mortality, no differences in species diversity, and no difference in soil moisture due to winter elk herbivory were documented. Reproductive stalks of

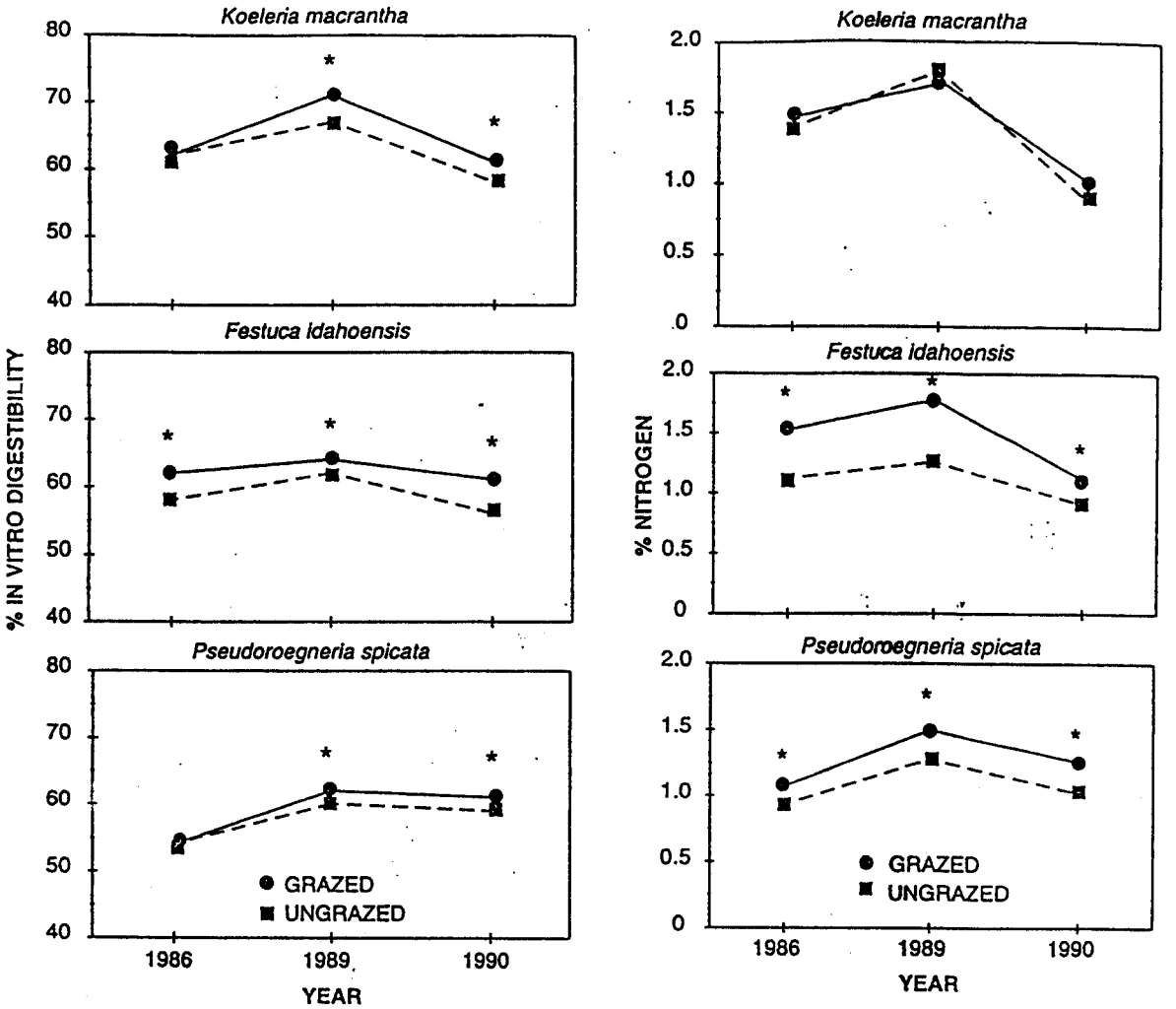

FIG. 2. In vitro digestible organic matter (IVDOM) content (left panels), and (right panels) nitrogen content of unburned *Pseudoroegneria spicata*, *Festuca idahoensis*, and *Koeleria macrantha* forages in grazed and ungrazed sites, 1986, 1989, and 1990. Asterisks indicate means that differ at the $P < 0.05$ level.

P. spicata were taller on grazed sites in two of four years, and number of individuals of *P. spicata* and biomass of *F. idahoensis*, a grazing-sensitive grass (Daubenmire 1940, Young 1943, Evanko and Peterson 1955, Pond 1960), were greater on grazed sites. Soil temperature responses were the opposite of predictions (Beetle 1974): soils were warmer on ungrazed sites. We speculate that warmer soils on ungrazed sites were due to lower wind speeds and resultant lower heat loss rates caused by more standing dead vegetation (Old 1969, Smith et al. 1983, Knapp 1984). Cooler soil temperatures on grazed sites might counteract the drying effects of 11% more bare ground and resultant increases in solar radiation on grazed soil surfaces.

Maintenance of aboveground biomass on grazed sites in Yellowstone may be due to: (1) reduced competition from adjacent grazed plants (Mueggler 1969, 1975, Archer and Detling 1985), (2) grazing during winter when plants are senescent (Mueggler 1975), (3) positive effects of ungulate herbivory, defecation, and urination on nutrient cycling rate (Williams 1966, McNaughton 1979), and (4) decomposition of plant material (Gusev and Gusev 1983).

Several lines of evidence suggest that grass growth was even stimulated by elk herbivory. Reproductive culms of *P. spicata* were taller on grazed sites in two of four years, and seed production was greater on grazed sites during one of four years when seeds were counted. Height of reproductive culms and production of seeds are indicators of vigor in grasses, and grazing typically reduces both (Jameson 1963, McNaughton 1979, Owen and Wiegart 1981). In addition, N concentrations in three grasses were, on average, 21% higher on grazed than ungrazed areas during three years, and total N yield was greater on grazed areas during two of three years of study. Increased foliar concentrations of N on grazed areas (Jameson 1963,

TABLE 1. Fibrous concentrations (% dry mass) of three grass species from grazed and protected grassland sites in 1990 influenced by burning in the Yellowstone fires of 1988. Significance level: * $P < 0.05$; ** $P < 0.01$.

	Ungrazed		Grazed		Two-way ANOVA P		
	Unburned	Burned	Unburned	Burned	Grazing	Burning	Interaction
Lignin							
Pseudoroegneria spicata	5.3	6.5	5.2	7.0	0.78	0.03*	0.66
Festuca idahoensis	4.1	6.1	3.6	6.1	0.72	0.001**	0.68
Koeleria macrantha	5.4	6.0	5.5	7.3	0.26	0.08	0.27
Cellulose							
P. spicata	16.2	29.0	18.0	28.9	0.74	0.000**	0.72
F. idahoensis	12.9	29.6	15.7	28.8	0.76	0.000**	0.56
K. macrantha	17.0	26.9	20.1	30.1	0.26	0.002**	0.95
AD Fiber							
P. spicata	33.8	37.9	33.4	38.2	0.98	0.03*	0.87
F. idahoensis	24.7	38.9	29.2	38.2	0.56	0.000**	0.56
K. macrantha	31.1	34.9	35.9	39.4	0.09	0.20	0.95
Ash							
P. spicata	4.0	7.2	4.2	10.0	14.00	0.005**	0.04
F. idahoensis	2.1	5.6	1.9	6.2	15.63	0.05*	0.18
K. macrantha	3.8	7.7	5.2	8.3	17.74	1.44	0.07
Ca							
P. spicata	0.3953	0.4222	0.4332	0.3712	0.04*	0.32	3.71
F. idahoensis	0.3525	0.2911	0.4079	0.3684	6.08	3.52	0.17
K. macrantha	0.4756	0.4254	0.4817	0.4533	0.18	0.95	0.07
Mg							
P. spicata	0.0734	0.1010	0.0798	0.0751	1.86	1.34	3.71
F. idahoensis	0.0766	0.0853	0.0976	0.0940	0.12	0.04*	0.69
K. macrantha	0.1141	0.1157	0.1218	0.1098	0.22	0.01*	0.38
K							
P. spicata	0.8307	0.9586	1.0242	0.8370	0.41	0.28	7.91
F. idahoensis	0.8790	0.6890	1.0373	1.0302	12.18	1.90	1.63
K. macrantha	1.0689	1.0144	1.0828	1.1639	0.93	0.02*	0.64
P							
P. spicata	0.1060	0.1218	0.1367	0.1091	1.31	0.56	7.6
F. idahoensis	0.1370	0.1367	0.1591	0.1689	9.88	0.31	0.34
K. macrantha	0.1554	0.1392	0.1789	0.1834	8.73	0.26	0.81
Mn							
P. spicata	0.0030	0.0032	0.0029	0.0021	3.97	1.28	2.68
F. idahoensis	0.0014	0.0025	0.0018	0.0018	1.23	9.68	11.29
K. macrantha	0.0046	0.0034	0.0041	0.0030	1.27	7.57	0.01**

Chapin 1980, Detling and Painter 1983) may be due to greater proportions of younger shoots, which tend to be higher in N (Jameson 1963, Owensby et al. 1970), higher uptake rates of N by grazed plants (Wallace et al. 1982, Ruess et al. 1984), and higher rates of decomposition (Holland and Detling 1990). Frank and McNaughton (1993) reported the promotion of aboveground grassland production by elk and bison herbivory in Yellowstone National Park. The average protein content of the three most common grasses averaged 7.6% on ungrazed sites but 9.1% on grazed sites. Mould and Robbins (1981) indicated that dry matter intake of forage by elk (initially) increased rapidly when dietary protein fell below 8%, suggesting that grazing enhancement of protein on Yellowstone's northern range might enhance elk winter survival, since elk are under nutritional stress during winter (DelGuidice and Singer 1995) in certain threshold situations. We observed enhanced mineral concentrations (Ca, Mg, K, P) in grazed grasses, as did Georgiadis and McNaughton (1990). These increases will also likely benefit elk. Ca and P metabolism are closely related and both are essential to elk (Robbins 1983). P is often limiting to elk and can limit N cycling in elk.

In agreement with our hypotheses, less forb biomass was found on grazed than ungrazed sites during two of three years, there was less litter and standing dead biomass, there was 11% more bare ground on grazed sites all years, and the grazing-sensitive (Smith 1960) grass, *Poa sandbergii*, was less abundant on grazed sites. In agreement with our findings, Jameson (1963) concluded that forbs were more sensitive to grazing and clipping than were grasses. Removal of accumulated litter and standing dead vegetation might reduce the growth of grasses and forbs (Weaver and Rowland 1952, Jameson 1963); alternatively, litter removal might benefit the growth of grasses and forbs (Hulbert 1969, Dahl and Hyder 1977).

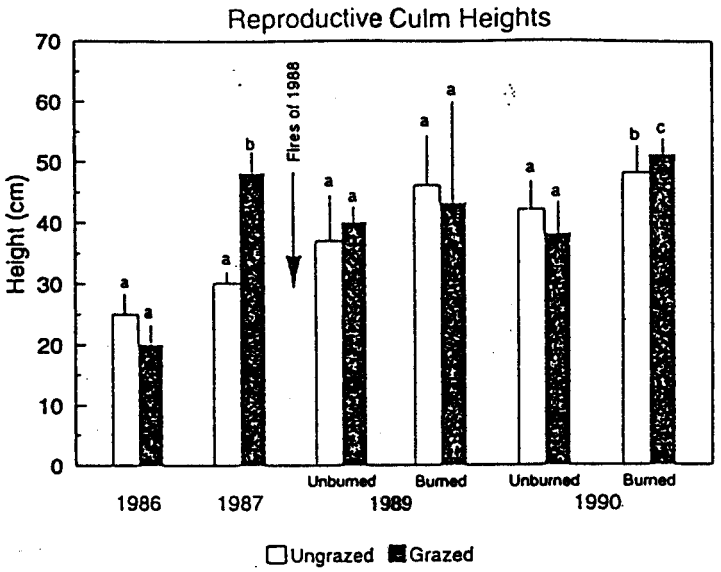

FIG. 3. Reproductive clum height of *Pseudoroegneria spicata*, July 1986 to 1990, on long-term exclosed sites and grazed sites. Years 1989 and 1990 i clude burned plots. Different letters (a, b, c) above bars denote statistically different means (ANOVA, $P < 0.05$).

Effects of burning on grasslands

Contrary to our hypotheses, burning did not reduce soil moisture, it only slightly increased the aboveground biomass of grasses, and did not affect percent N, macronutrient concentrations, or digestibility of grasses. Most authors report warmer soils (Aldous 1934, Ehrenreich and Aikman 1963, Anderson 1965, West 1965), large biomass increases of grasses (Blaisdell 1953, Mueggler and Blaisdell 1958), increased forb biomass (Antos et al. 1983), increased concentrations of Ca, P, Mg, and K (Old 1969, Lloyd 1971, Willms et al. 1981, Umoh et al. 1982, Ohr and Bragg 1985), and higher digestibility in grasses following burning (Daubenmire 1968, Pearson 1970, Grelen and Whitaker 1973, Rowland et al. 1983). Rowland et al. (1983) and Seip and Bunnell (1985), however, reported no effect of burning on crude protein concentrations in grasses. The higher fiber and lignin levels we observed following burning are in contrast to most reports of lower levels (Willms et al. 1981). We speculate that the relative lack of positive benefits from burning on the Blacktail Plateau forages was due to the rapid speed (2.4 km/h), relative coolness (542 J/m²), and lack of residual burning of the 1988 fires in grasslands (P. Perkins, *unpublished data*, Yellowstone National Park, Wyoming). The Yellowstone fires were cool, fast frontfires; most other comparative studies report on hot, slow backfires (prescribed burns) and most other published studies are in grassland regions (tallgrass, mixed-grass prairie) with greater litter accumulations than for the northern Yellowstone winter range (Old 1969, Lloyd 1971, Uresk et al. 1975, Umoh et al. 1982). We observed enhanced seed production in grasses due to burning, as have many workers (Uresk et al. 1975, Patten et al. 1988).

Condition of wintering ungulates is typically enhanced on burned grasslands, even when burning does not increase protein concentrations in grassland forages (Rowland et al. 1983, Hobbs and Spowart 1984, Seip and Bunnell 1985). On a burned range in British Columbia, spring grass growth was initiated one week earlier, forage abundance was greater, the horns of mountain sheep grew faster, and sheep had fewer lungworm larvae (Seip and Bunnell 1985). Elk ate more grass and less browse, and they weighed more and were in better condition on a burned winter range in New Mexico (Rowland et al. 1983), even though neither protein concentration nor digestibility of the grasses was enhanced by burning. Foraging efficiency of elk was enhanced in burned aspen forests, even though forage nutritional concentrations were not enhanced by burning (Canon et al. 1987). Diet quality of mountain sheep and mule deer (*Odocoileus hemionus*) was substantially higher on burned grassland–shrubland, due

TABLE 2. Numbers of *Pseudoroegnaria spicata* clumps and numbers of seeds per clump on grazed and burned treatments, Blacktail Plateau study area in 1990. Different letters indicate significant differences with two-way ANOVA and pairwise Tukey's comparisons at $P < 0.05$.

Pseudoroegnaria spicata	Ungrazed				Grazed			
	Unburned		Burned		Unburned		Burned	
	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
No. clumps/m²	13.9[a]	1.0	16.7[a]	1.8	10.6[b]	1.8	7.2[b]	1.3
No. seeds/clump	85[a]	25	392[b]	115	209[a]	74	481[b]	111

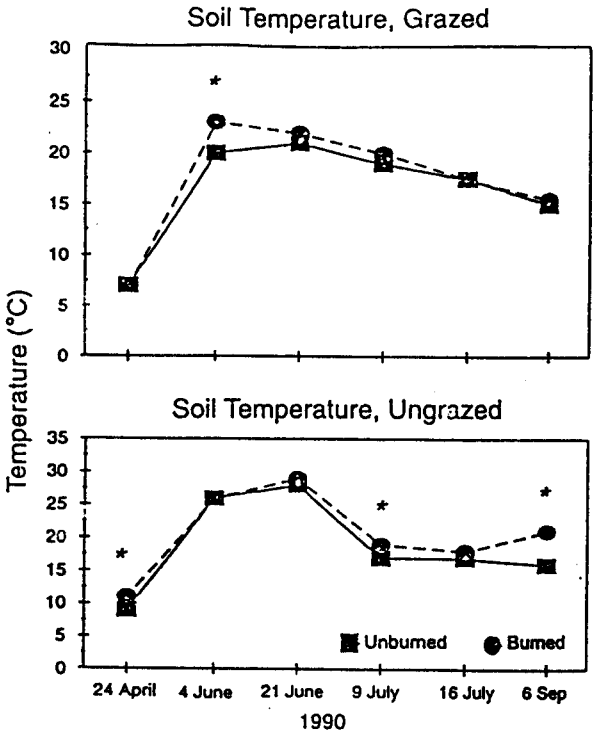

FIG. 4. Mean daily soil temperatures from burned and unburned (control), grazed and ungrazed sites on the Blacktail Plateau. An * denotes statistical differences between dates using Tukey's multiple comparisons ($P < 0.05$).

to an increased proportion of green grasses in their diets (Hobbs and Spowart 1984), although N concentration of grasses was unaffected by the burning. Turner et al. (1994) and DelGuidice and Singer (1995) reported improved condition of Yellowstone elk following the fires of 1988, and we observed elk preference for burned grasslands, both of which suggested that elk derived some benefits from the fires.

Elk use of burned forests

Elk avoided burned forests during the first three winters postfire, apparently because of deeper, more dense accumulation of snow and reduced forage biomass. Snow depths were greater in total canopy burns than in partial canopy burns in conifer forests on the northern Yellowstone winter range, and snow was more dense in burned than unburned forests, as Skovlin and Harris (1970) and Meiman (1968) observed. However, the differences were small during our study (2.5 cm deeper snows and 11% greater snow density; Norland et al. 1995). Herbaceous biomass declines in the hotter-burned conifer forests on the study area were still dramatic during the second postfire winter; 61% less herbaceous biomass was sampled in burned vs. unburned forests (Norland et al. 1995). Elk almost completely avoided the Blacktail Plateau during the first postfire winter (winter 1988–1989, when 25% of the available foraging area burned). Those animals that remained, mostly adult bulls, died at a high rate (Singer et al. 1989). Turner et al. (1994) and Coughenour and Singer (1995) concluded that the severe winter of 1988–1989 and the mosaic burning pattern of the fires contributed to the high mortality in elk during the first postfire winter. They concluded that winter severity was the dominant influence on ungulate survival.

Elk use of burned forests will probably increase four or more years postfire, following recovery of the herbaceous biomass, at least during periods of shallow snow. Protein concentrations in burned understory forages from conifer forests were 12.5% higher than in unburned forages in the northern Yellowstone winter range, and dry matter digestibilities were 4.6% higher (Norland et al. 1995), suggesting considerable advantages to elk of foraging in the forests. Forest understories recover more slowly following fire than do grasslands, but fire effects last longer, primarily due to higher fuel loadings and greater fire intensity. Herbaceous biomass in burned forests required six to eight years to equal or exceed that in unburned forests (Vogl and Beck 1970, Lyon and Stickney 1976). This increase in burned over unburned herbaceous biomass lasted 12 years in one instance (Bartos et al. 1994). Since our observations ended at only the third postfire winter, greater use of burned forests by elk is likely to be

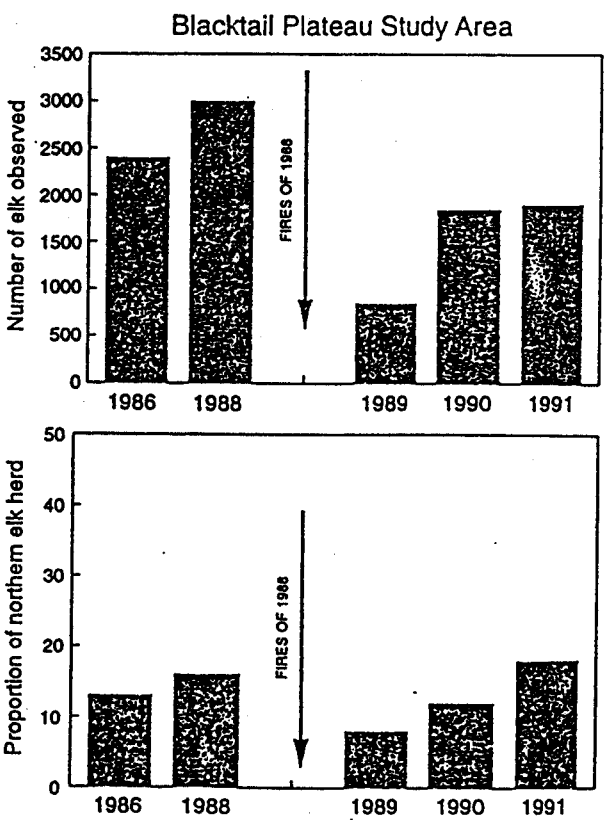

FIG. 5. Number of elk and proportion of total northern Yellowstone herd observed on the Blacktail Plateau study area during the winters 1986 to 1991.

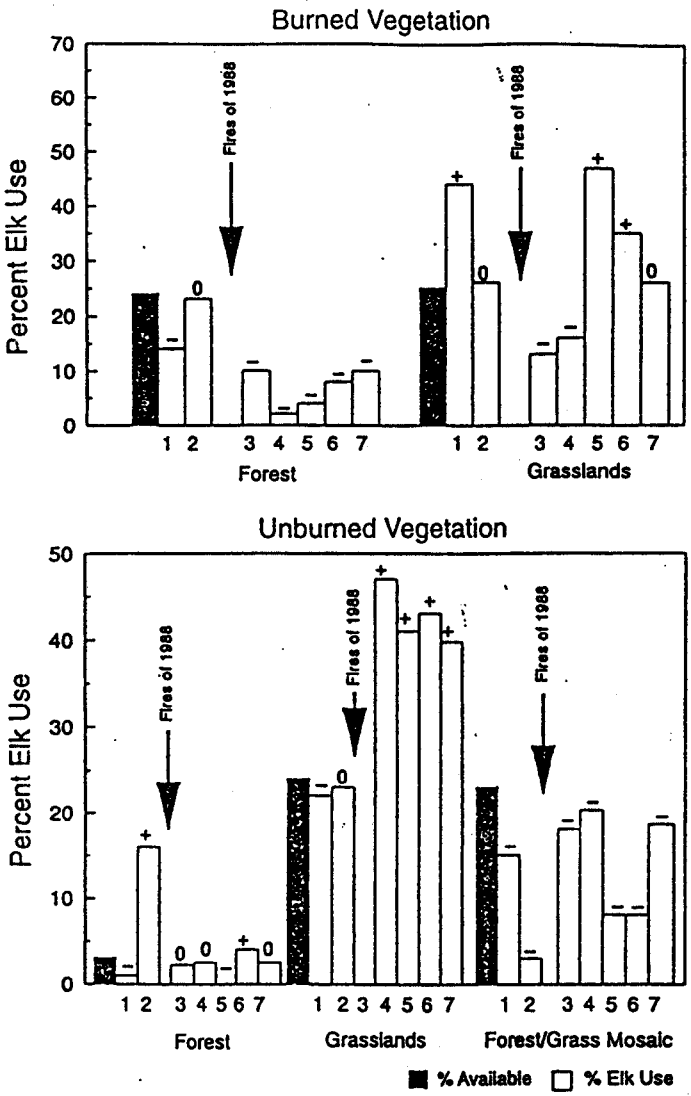

FIG. 6. Percentage of elk use of habitats in comparison to habitat availability, using the Neu et al. (1974) procedure before and after the 9 September 1988 fires on the Blacktail Plateau study area. The symbols +, 0, and − above the bars refer to use greater than expected, proportionate use, and use less than expected, respectively, at the $P < 0.10$ level. Numbers on the x-axis refer to observation flight dates: 1, 10 December 1986; 2, 19 January 1988; 3, 26 January 1989; 4, 11 and 14 April 1989 (pooled); 5, 18 January 1990; 6, 6 February 1991; and 7, 22 April 1991.

observed in subsequent years, especially during winters when snow depths are not excessive.

CONCLUSIONS

The ecological effects of the fires of 1988 on elk forages were minor. Grass biomass increased ≈20% and digestibility increased in one of three grasses. Protein, cellulose, and macronutrients in grasses were unaffected by fire. Elk preference for burned grasslands during the second and third winters following the fires, however, suggested that elk gained some benefits from burned grasslands, perhaps due to greater foraging efficiency. Canon et al. (1987) reported greater foraging efficiency by elk in burned vs. unburned habitats: more bites per minute, larger bite sizes, and less travel time by elk were observed in burned habitats.

Elk herbivory caused more documented ecological effects on vegetation of the Blacktail Plateau than did burning. Protein concentration was enhanced an average of 21%, digestibility was increased 7%, macronutrients concentrations were increased, and N yield was increased an average of 22% on grazed vs. ungrazed areas. Forage digestibility of 5–7% is needed for maintenance of elk during winter (Robbins 1983). The increase in forage digestibility we observed on elk-grazed areas might therefore raise elk forages above critical levels in some winters. The enhanced digestibility of grasses due to elk herbivory could also be ecologically important for elk during critical periods on the Blacktail Plateau; an increase in dietary digestibility from 50 to 55%, similar to what we observed, increased body weight gain by almost 100% in domestic sheep (Blaxter et al. 1961).

No interactions were observed between elk herbivory and burning on the Blacktail Plateau. Frequent, hot fires in ungrazed or lightly grazed shortgrass and tallgrass prairie, with much heavier litter accumulations than our study sites, reduce N (Parton and Risser 1980, Ojima 1987). Grazing on tallgrass prairie, by reducing litter, reduces the extent of burning and creates a patchy

fire pattern (Hobbs et al. 1991), thereby conserving N. Burning did not affect N levels in either grazed or ungrazed grasslands on the Blacktail Plateau, probably because litter accumulations on our study sites, even unprotected sites, were still far less than in tallgrass prairie. Hotter fires result in a larger increase in nutrient enhancement of forages (Dewitt and Derby 1955). We attribute the lack of nutrient enhancement by the fires of 1988 on the Blacktail Plateau to elk herbivory, the relatively low accumulation of aboveground material, the relative high speed of the frontfire, and the resultant cool burning.

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