# FIRE AND GRAZING IN THE TALLGRASS PRAIRIE: CONTINGENT EFFECTS ON NITROGEN BUDGETS[1]

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*Abstract.* Fire and grazing occur together in many of the world's grasslands, but their effects on nutrient cycling have usually been studied as if they acted separately. We hypothesized that grazing by large herbivores results in conservation of nitrogen that would otherwise be lost from burned grasslands. We tested this hypothesis in a series of experiments on burned and unburned tallgrass prairie grazed by cattle. We manipulated grazing using exclosures and mowing. Combustion losses of N from ungrazed plots (1.8 $g \cdot m^{-2} \cdot yr^{-1}$) burned in the spring were double those from similarly burned, grazed plots (0.9 $g \cdot m^{-2} \cdot yr^{-1}$). These losses represented about half of the preburn, aboveground stocks of N. The magnitude of N loss was proportional to the standing crop biomass available for combustion. Fire temperatures and energy release were reduced by grazing. We used mowing to simulate locally heavy grazing in patches. In the absence of burning, mowing patches increased the likelihood that a patch would be regrazed and caused persistent reductions in the residual biomass remaining in a patch at the end of the growing season. Mowing did not influence patch utilization or residual biomass when pastures were burned. Thus, the effects of fire on grassland N budgets were modified by grazing, and the effects of grazing on the patch structure of grasslands were modified by fire. We conclude that accurately predicting volatile losses of nutrients from grassland ecosystems resulting from biomass burning may depend on understanding effects of grazing.

*Key words: burning; cattle; fire; grazing; herbivory; nitrogen budgets; nutrient cycling; patch dynamics; spatial variation.*

## INTRODUCTION

Fire and grazing are known to influence nitrogen (N) budgets in grassland ecosystems by affecting the spatial distribution of N and by mediating its addition and loss. Although these influences act together in many of the world's grasslands, studies of the effects of herbivores on ecosystem N dynamics (Brockman et al. 1971, Woodmansee 1978, Stillwell and Woodmansee 1981, Coppock et al. 1983a, Lambert et al. 1985, Schimel et al. 1986, Agrawal and Tiwari 1987, Detling 1988, Jaramillo and Detling 1988, McNaughton et al. 1988, Jarvis et al. 1989) have usually proceeded apart from studies of the effects of fire (Cook 1939, Norman and Wetselaar 1960, Kucera and Ehrenreich 1962, Grant et al. 1963, Lloyd 1971, Christensen 1976, Wells et al. 1979, Woodmansee and Wallach 1981, Boerner 1982, Schimel 1982, Hobbs and Schimel 1984, Robertson

and Rosswall 1986, Agrawal and Tiwari 1987). As a result, our current understanding of the role of fire and grazing in grassland N cycling may overemphasize the independence of these processes, and may fail to recognize the contingency that one process creates for the other.

Interactions between fire and grazing may regulate grassland nutrient cycling in ways that depart qualitatively from their individual, regulating effects. We hypothesize that fire and grazing are interactive processes as a result of their impacts on the spatial distribution of accumulated plant biomass. Grazing removes plant tissue from landscapes in a heterogeneous pattern. This removal increases spatial heterogeneity in the behavior of fire by increasing spatial variation ("patchiness") in the amount of organic matter available for combustion. When grazers prefer one patch of grasses over another, they increase the disparity of fuels between those patches, and thereby cause fire to burn less intensely in grazed patches than in ungrazed ones

(Conrad and Poulton 1966, Norton-Griffiths 1979, Mandany and West 1983, Zimmerman and Neuenschwander 1984).

We propose that fire acts to reduce the level of spatial heterogeneity caused by grazing. Grazed patches are apparent on the landscape. They contrast with the surrounding matrix by virtue of phenological differences in plant color, structure, and chemistry (McNaughton 1984, Gordon 1988). In productive grasslands, large herbivores may gain nutritional benefits from feeding in grazed patches (McNaughton 1984, Gordon 1988, Hobbs and Swift 1988), may prefer them over ungrazed ones (Vesey-Fitzgerald 1974, Coppock et al. 1983b, McNaughton 1984, Gordon 1988), and hence, may accentuate the disparity between grazed and ungrazed patches over time. Fire may eliminate the contrast between grazed patches and the ungrazed matrix by returning the grazed landscape to a more uniform phenological and structural state. Thus, fire interrupts the short-term positive feedback that results when feeding by herbivores produces apparent and attractive grazed patches (Coppock and Detling 1986).

Moreover, fire may make ungrazed patches more attractive in burned, grazed grasslands, thereby reversing the spatial effects of grazing. When herbivores reject patches as places for feeding, organic matter accumulates that would otherwise be eaten. Consequently, if accumulated fuel allows those areas to burn more intensely than grazed areas, and if forage quality is enhanced by increased availability of mineral N following burning (Willms et al. 1981a, Hobbs and Schimel 1984, Hobbs and Swift 1985), then herbivores may obtain nutritional benefits from feeding in burned patches (Woolfolk et al. 1975, Hobbs and Spowart 1984, Svejcar 1989) and may be attracted to them following fire (Daubenmire 1968, Willms et al. 1980, 1981b, Coppock and Detling 1986).

These hypothesized spatial patterns have important implications for estimating losses of N from grassland ecosystems to the atmosphere. Fire intensity and combustion losses of mineral stocks from burned grasslands are proportionate to the aboveground biomass burned (Stronach and McNaughton 1989). Removal of biomass by herbivores may decrease fire intensity in grazed patches and may also move N from above- to belowground pools (via urinary and fecal excretion) where it is less susceptible to volatilization during burning. Thus, the feeding patterns of large herbivores may act to conserve ecosystem N stocks that would otherwise be lost from ungrazed, burned grasslands.

These ideas can be stated more formally in the following hypotheses:

Hypothesis 1: Grazing moderates combustion losses of N resulting from fire by reducing the biomass of herbage available for burning. As a result, N is conserved in burned, grazed grasslands relative to burned grasslands that are not grazed.

Hypothesis 2: Grazing regulates herbaceous bio-mass and, therefore, fire intensity. Moderately grazed patches burn less completely and less intensely than ungrazed ones; heavily grazed patches will not burn at all.

Hypothesis 3: In the absence of fire, grazing increases the likelihood that a patch will be regrazed. In the presence of fire, there is no effect of grazing on patch use. As a result, grazing history influences accumulation of biomass in patches on unburned landscapes, but not on burned ones.

Hypothesis 4: Grazing intensity at the patch level is modified by the effects of fire on herbage nutritional quality. Because fire enhances forage quality, burned patches are grazed more heavily than unburned ones.

Here, we report experiments designed to test these hypotheses and to reveal interactions between fire and grazing in a tallgrass prairie ecosystem.

## MATERIALS AND METHODS

Our experiments were conducted at the Kansas State University Donaldson Research area in the Flint Hills of eastern Kansas, USA, ≈10 km northwest of Manhattan, Kansas. The site is an area of native tallgrass prairie with vegetation dominated by *Andropogon gerardii* Vittm., *Sorghastrum nutans* (Michx) Nash, and *Panicum virgatum* L. The Flint Hills are steep and rocky, and unsuitable for conventional farming. The region is used primarily for cattle production. The climate is continental with 835 mm mean annual precipitation.

### Experimental design

Our experiment was designed to include three spatial scales: pastures, plots, and patches (Fig. 1). At the landscape scale, we observed responses to treatments in two pastures. Both were moderately grazed between 1 May and 1 October at a rate of ≈1.4 ha per 250 kg steer over this interval. One of the two grazed pastures (44 ha) was burned on 1 May 1985, 16 April 1986, and 23 April 1987. The other pasture (60 ha) was not burned. These landscape units have been treated in this manner for the last 27 yr and thus offer annually burned and unburned conditions that were well established before our experiments. Although we were not able to achieve replication of landscapes, our experimental pastures were sufficiently large to contain all of the major landscape features identified in the Flint Hills (Anderson and Fly 1955, Schimel et al. 1991), including multiple first-order drainages, scarps, and uplands. Thus, we believe they are generally similar to each other and are representative of the range of variation within tallgrass prairie in the Flint Hills.

To study the effects of presence or absence of grazing, we constructed two 15 × 15 m grazing exclosures within each pasture to provide two replications of ungrazed treatments within the burned and unburned pastures (Fig. 1). These plots were established in 1985 imme-

diately after that year's prescribed burn. Adjacent plots were chosen to study the grazed condition.

To study the effect of heavy defoliation within patches, we established pairs of mowed and unmowed patches within each pasture immediately before the first year's burn (Fig. 1). We randomly chose 10 pairs of 2 × 2m patches within grazed–burned and grazed–unburned pastures during early March 1985. One member of each pair was chosen by coin flip and mowed to a height of 5 cm to simulate effects of locally heavy grazing. Mowed herbage was raked and removed. This provided two levels of defoliation (moderate/variable in the unmowed patch, and heavy/uniform in the mowed one). These patches were permanently marked with steel pins driven to ground level at each corner. Their locations were not changed during the three study years. They were mowed only during the initial year.

### Procedures

To determine effects of grazing on combustion losses of N (Hypothesis 1), we estimated aboveground standing stocks of N before and after burning on grazed and ungrazed plots (Fig. 1) during 1986. We randomly placed four 0.2-m$^2$ quadrats within each grazed and ungrazed plot. Quadrats were divided in half and marked with fireproof stakes. Immediately before the fire, aboveground live herbage, standing dead, and litter were collected from half of the quadrat (0.1 m$^2$). Following the burn, ash was collected from the adjacent 0.1 m$^2$ using a vacuum cleaner. Any unburned residue was collected and bagged separately. Samples were analyzed for total N (AOAC 1980) and total C (Snyder and Trofymow 1984); $NH_4^+$ and $NO_3^-$ were also extracted from ash with 2 mol/L KCl and analyzed colorimetrically using a Lachat Flow Injection Analyzer. Losses were computed by subtracting postburn amounts from total preburn pools (Ojima 1987). We do not include losses of N from soil pools in these estimates because the maximum fire temperatures we observed at the ground surface (<350°C, see Results) failed to exceed those needed for volatilization from the soil (>400°; Kenworthy 1963).

To study effects of defoliation on fire behavior (Hypothesis 2), we observed the extent of burning on mowed and unmowed patches (Fig. 1) during 1985. Immediately after burning pastures we visually classified each mowed and unmowed patch into one of four categories on the basis of the area of the patch that was blackened by fire (0–25 vs. 26–50 vs. 51–75 vs. 75–100%).

In addition, we used water-can analogs (Beaufait 1966) to provide an index of fire intensity (Hypothesis 1) within the moderately grazed and the ungrazed plots (Fig. 1) during 1986. Tared, steel soil cans (8 cm diameter × 4 cm high) were filled with 200 mL of distilled water. Lids punctured with a vent (≈3 mm) were fit tightly to the cans. We placed five cans at random locations within each of the grazed and ungrazed plots. Immediately before and after burning, cans were
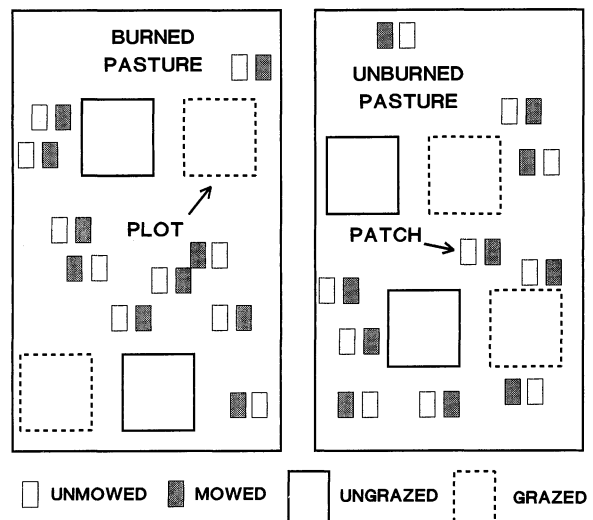


Fig. 1. Schematic of the experimental layout, not drawn to scale. The outer rectangles represent two pastures (≈50 ha each), one of which was burned during the spring of each year. The other was left unburned. Both pastures were moderately grazed. Within each pasture, there were two grazing exclosures (15 × 15 m) paired with grazed areas of equal size. We refer to these areas as "plots." We also created 10 pairs of mowed and unmowed "patches" (2 × 2 m) in each pasture to simulate locally heavy grazing.

weighed, and the temperature of the water in each can was measured to the nearest degree Celsius. Energy release (in joules) was calculated as the heat required to vaporize the water that disappeared during the fire plus the heat required to change the temperature of the residual water in the can. This index integrates effects of fire temperature and residence time (Beaufait 1966). It is dimensionless because the area over which the can integrates remains unknown. Maximum fire temperature was also estimated using 20 color-coded pellets (Fisher Scientific), each of which melted at a different temperature (52°–399° in ≈20° increments). Two sets of pellets were set within ≈1 m of each can on steel rulers on the ground surface. The five energy release values and the 10 maximum temperatures were averaged for each plot before analysis, thereby providing two independent replications for each treatment (one per plot, Fig. 1).

To examine the effects of fire and defoliation on aboveground biomass present at the end of the growing season (Hypotheses 2 and 3), we harvested and weighed the aboveground standing crop from a 60 × 60 cm frame placed at random locations within each mowed and unmowed patch within the burned and unburned pastures. These measurements were taken at the end of the second and third growing seasons (15 October 1986 and 20 October 1987) following the mowing treatment (June 1985), and therefore reflected effects of grazing by cattle on the current year's production rather than the direct effects of removal due to mowing.

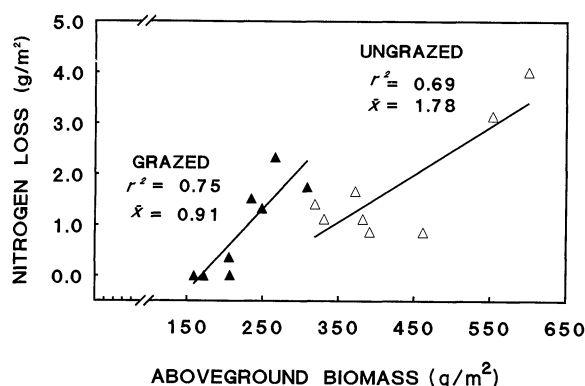To examine the effects of defoliation and forage qual-

FIG. 2. Combustion losses of nitrogen from grazed (▲) and ungrazed plots (△) in relation to preburn biomass (measured as dry mass). Data points represent four subsamples from each of two grazed and ungrazed plots in the burned pasture.

ity on grazing intensity (Hypotheses 3 and 4), we visually estimated the proportion of the current year's production that was consumed by cattle on each pair of mowed and unmowed patches within the burned and unburned pastures. Estimates were made on the 1st d of each month following burning (1 June–1 October) during the first (1985), second (1986), and third (1987) growing seasons after mowed patches were established. We visually categorized forage removal on four 60 × 60 cm square frames placed randomly within each mowed and unmowed patch. Categories included five levels of removal (<19, 20–39, 40–59, 60–79, and >79%).

To study fire-induced changes in the nutritional value of forage (Hypothesis 4), we collected the aboveground parts of plants every 2 wk during June–September 1985 from five randomly chosen locations (≈0.1 × 0.1 m) within burned and unburned pastures. Samples from unburned pastures were separated into live and dead; samples from burned pastures consistently included only green material. Forage samples were analyzed for N concentration using Kjeldahl procedures (AOAC 1980). Dry matter content was determined gravimetrically (AOAC 1980). We analyzed samples for in vitro dry matter digestibility following the method of Tilley and Terry (1963) as modified by Pearson (1970).

### Statistical analysis

Because our design does not include multiple replications of our experiment at the level of the landscape, statistical inferences on the burning treatment are strictly limited to a "population" of repetitions of our experiment at the specific site we studied. We used a paired $t$ test to analyze differences in N losses between grazed and ungrazed plots. To examine effects of fire and grazing on residual biomass at the end of the growing season, we used an analysis of variance for a randomized complete block design with 2 × 2 factorial layout (grazed vs. ungrazed crosses with burned vs.

unburned) and a repeated-measures structure (repeating over years). We used chi-square contingency tables (mowed vs. unmowed for five categories in two tables controlling for two levels of fire) to analyze forage utilization scores in response to mowing in the burned and unburned pastures. We used $t$ tests to test for differences in energy release between grazed and ungrazed treatments and used a Wilcoxon rank-sum test to compare ranks of areas burned in the mowed and unmowed treatments. Forage quality responses to the burning treatment were analyzed with a one-way analysis of variance for a blocked design with repeated measures (repeating over sample date).

### RESULTS

Grazing influenced combustion losses of N. Nitrogen losses due to burning in the absence of grazing were almost double those observed when grazing was present (Fig. 2, $P = .001$, one-tailed $t$ test, df = 2, $t = -10.8$). Nitrogen losses were directly proportional to the aboveground standing crop available for burning in the spring. Thus, to the extent that the previous year's grazing reduced herbage biomass aboveground, it also reduced the aboveground stocks of N ($\bar{X}$ and 95% CI, grazed: 2.27 ± 0.28 g/m², ungrazed: 3.78 ± 2.45 g/m²), and reduced N lost via combustion. In some grazed quadrats that failed to carry a fire, N losses were nil. N losses per unit of dry biomass were higher in the grazed plots relative to the ungrazed ones (Fig. 2), reflecting slightly higher preburn N concentrations in grazed standing biomass and litter (grazed: 7.9 ± 0.16 g dry mass/100 g, ungrazed: 7.6 ± 0.05 g/100 g dry mass). However, slopes of the regression lines did not differ significantly (Fig. 2, grazed slope and 95% CI = 0.016 ± 0.02, ungrazed = 0.0094 ± 0.008). Forty percent of the preburn, standing stocks of N were lost via combustion in the grazed plots, and 47% were lost in the ungrazed plots.

Defoliation influenced fire behavior. None of the mowed patches burned in excess of 25% of their area; almost all of the unmowed patches burned in excess of 75% (Fig. 3, Wilcoxon rank-sum test: $P = .0001$, df = 1, $Z = -3.9$). Thus, removal of aboveground biomass to simulate heavy grazing imposed strong spatial limits on the distribution of fire in the tallgrass prairie. As noted above, N losses were influenced by the failure of fire to carry uniformly.

Maximum temperatures achieved by fire were lower in the grazed than the ungrazed plots, but this difference was not significant (grazed $\bar{X} = 180°C$, ungrazed $\bar{X} = 241°$, one-tailed $t$ test, $P = .12$, df = 2, $t = -1.65$). Although fire burned more intensely, releasing more heat within grazing exclosures than outside of them, this difference only approached significance (energy release based on water-can analogs: grazed $\bar{X} = 267$ J, ungrazed $\bar{X} = 581$ J, one-tailed $t$ test, $P = .07$, df = 2.0, $t = -2.24$). Differences in energy release were roughly proportional to the differences in preburn
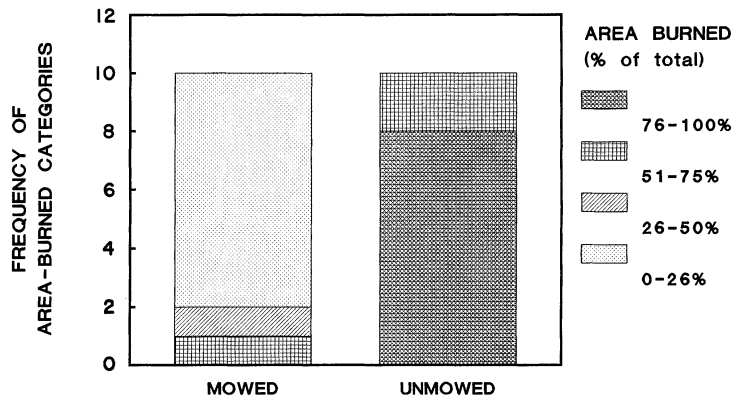
Fig. 3. Frequency of area-burned categories (estimated visually) on mowed and unmowed patches ($n = 10$) within the burned pasture. Patches were mowed immediately before spring burning to simulate locally heavy grazing.

standing biomass between grazed ($\bar{X} = 285$ g/m²) and ungrazed ($\bar{X} = 476$ g/m²) plots.

Spring burning influenced the effects of mowing on the aboveground standing crop of biomass at the end of the growing season on grazed plots (Fig. 4, fire × mowing $P = .049$, ANOVA, df = 1, $F = 4.12$). The magnitude of this interaction did not depend on year (Fig. 4, fire × grazing × year, $P = .20$, df = 1, $F = 1.69$). Averaged across interactions, standing crop biomass at the end of the growing season was greater in the burned than in the unburned pasture (main effect $P = .002$, ANOVA, df = 1, $F = 11.05$), but we observed no effect of mowing alone (main effect $P = .31$, ANOVA, df = 1, $F = 1.02$). Note that the mowing treatment took place at least 16 mo previous to biomass measurements. Thus, effects of heavy grazing on standing crops in the unburned pasture persisted from one growing season into the next. These effects did not persist in the burned pasture.

The dependence of the effect of mowing on burning was attributable to increased rates of utilization of forage on mowed patches in unburned pastures. Within burned pastures, we found no discernible difference in



Fig. 4. Average standing crop biomass (dry mass) at the end of the growing season on mowed and unmowed patches within burned–grazed and unburned–grazed pastures. Patches were mowed to simulate locally heavy grazing at the beginning of the growing season, 1985. Error bars are 1 SE ($n = 10$).

the frequency of utilization scores attributable to mowing (Fig. 5, $P = .51$, chi-square test, df = 4, $\chi^2 = 3.2$). However, in the unburned pasture, mowing patches resulted in large increases in forage utilization (Fig. 5, $P < .0001$, chi-square test, df = 4, $\chi^2 = 92.9$). Mowed patches in the unburned pasture were often visually discernible from a distance of 50 m or more. Because these patches were maintained in green, growing condition as a result of grazing, they increasingly contrasted with the surrounding matrix as the growing season progressed and the surrounding vegetation matured. In contrast, mowed patches in the burned pasture could not be visually distinguished from the surrounding matrix. Locating the corners of mowed patches in the burned pastures required the use of a metal detector throughout the season. Thus, mowed patches were visually apparent and were preferentially grazed in the unburned pasture but were not apparent and were not preferred by grazers in the burned pasture.

Fire influenced the nutritional value of herbage. Burning increased the N concentration (Fig. 6, main effect $P = .005$, ANOVA, df = 2, $F = 182.1$) and in vitro dry matter digestibility (main effect $P = .043$, ANOVA, df = 2, $F = 21.83$) of standing herbage on grazed landscapes. In both cases, the magnitude of treatment effects diminished as season advanced (Fig. 6). With the exception of forage N concentration during the early growing season, the major differences in forage quality were due to age of the plant material (green vs. dead), rather than to the burning treatment (Fig. 6).

DISCUSSION

Fire and grazing acted together to influence the N budget of the tallgrass prairie. We estimate that grazing conserved $\approx 1$ g·m⁻²·yr⁻¹ N that would have otherwise been lost as a result of combustion. However, for net conservation of N to occur, N conserved by grazing on burned landscapes must exceed losses resulting from grazing itself. This includes N lost from harvested animals and from NH₃ volatilization from excreta. Given
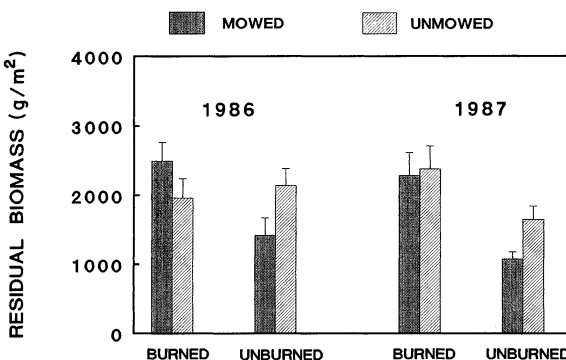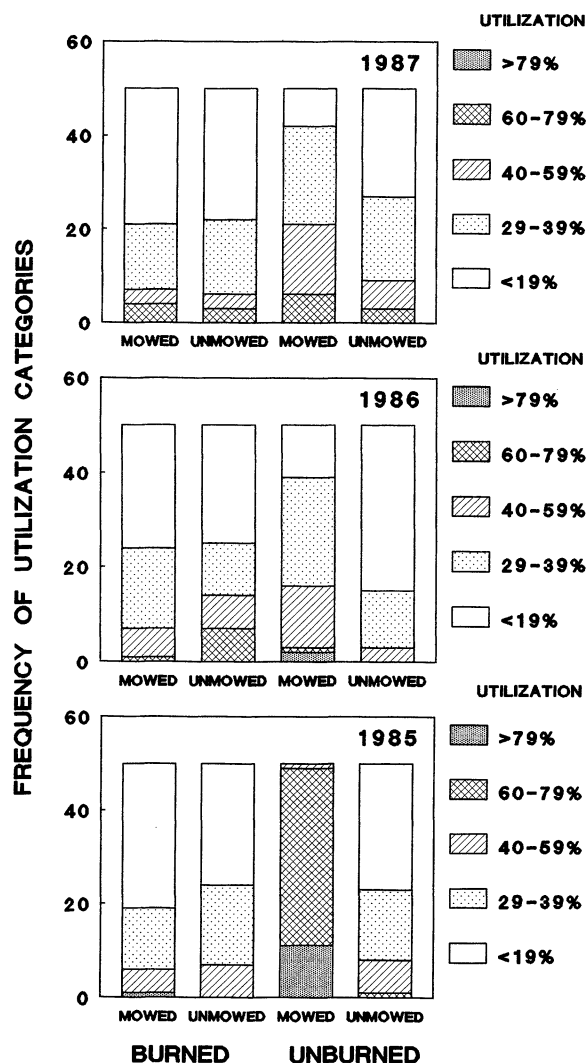
FIG. 5. Frequency of visually estimated categories of forage utilization (percent of current production removed by cattle) during the growing season on mowed and unmowed patches within burned and unburned pastures. Within each treatment combination we categorized 10 patches once each month for 5 mo ($n = 50$). Patches were mowed to simulate locally heavy grazing at the beginning of the growing season, 1985.

the stocking rates typical of this area of the tallgrass prairie, removal of N in animal biomass is small, amounting to $\approx 0.06$ g·m$^{-2}$·yr$^{-1}$ of N assuming 60 kg mass gain per animal per year (Parton and Risser 1980, Svejcar 1989) and an N concentration in gained tissue of 0.014 g/g fresh body mass (Berg and Butterfield 1976:52). Volatilization of N from urine and dung may not represent a net loss because volatilization from unconsumed vegetation may exceed losses from animal excreta (Schimel et al. 1986, Detling 1988). However, even if we include gross values for excretion losses of $\approx 0.2$–$0.3$ g·m$^{-2}$·yr$^{-1}$ (Schimel et al. 1986, Jarvis et al. 1989), the mass of N conserved by grazing exceeds the amount lost by three- to fivefold.

This has important implications for the N balance of this prairie. Net annual deposition inputs of N to the tallgrass prairie have been estimated variously from 0.44 g/m$^2$ (wet fall only: NADP 1987) to 1.7 g·m$^{-2}$·yr$^{-1}$ (bulk precipitation including organics: Seastedt 1985). High dry deposition and organic inputs may result from redeposition of suspended ash upwind. Estimating inputs of N via fixation is problematical, but these additions are probably small in most years (Hobbs and Schimel 1984, Eisele et al. 1989). Although our current estimates of N losses via combustion averaged 1.8 g·m$^{-2}$·yr$^{-1}$ for the ungrazed condition, those losses may frequently exceed 2 g·m$^{-2}$·yr$^{-1}$ (Ojima 1987). It is possible that inputs of N ($\approx 1$ g·m$^{-2}$·yr$^{-1}$) will exceed combustion losses from a grazed grassland (0.9 g·m$^{-2}$·yr$^{-1}$, Fig. 2), but will be less than combustion losses from an ungrazed grassland (1.8 g·m$^{-2}$·yr$^{-1}$, Fig. 2). Thus, grazing may determine whether N stocks accumulate or decline in an annually burned tallgrass prairie. This effect of grazing on ecosystem N stocks may help to explain the sustained fertility (Owensby and Anderson 1967) of annually burned grazing lands in the tallgrass prairie, despite N fertility data from ungrazed experimental plots (Ojima 1987) that suggest burning may deplete N stocks over time. Ruess and McNaughton (1988) have also observed that grazing by ungulates can conserve N that would otherwise be volatilized and lost from grassland ecosystems.

The mechanisms by which this conservation is achieved depend strongly on spatial scale. Although N stocks may be conserved by grazing at the level of the landscape (thousands of square metres), this influence depends on dynamics at the level of the patch (tens of square metres). Grazers create patches by preferring one area for feeding over another, and they apparently are attracted to the patches they create (McNaughton 1984). It is the collective effect of reduced fuels in grazed patches that contributes to the spatial heterogeneity of fire and its behavior. In aggregate, it is this variability that reduces N losses at larger scales.

Annual burning erased the patch mosaic created by herbivores, but in the absence of fire, the mosaic persisted. As a result, large herbivores used burned landscapes more uniformly than unburned landscapes. This created divergent patch structures between grazed landscapes that were burned and those that were not. Reduction in spatial variability of the previous year's patches and the resulting increased uniformity of utilization by cattle that resulted from spring burning may partially explain the substantial improvements in animal performance that results from burning in the tallgrass prairie (Woolfolk et al. 1975, Parton and Risser 1980, Svejcar 1989).

The interdependent behavior of fire and grazing within patches has been noted by others (Campbell 1954, Conrad and Poulton 1966, Daubenmire 1968, Vesey-Fitzgerald 1974, Norton-Griffiths 1979, Ma-
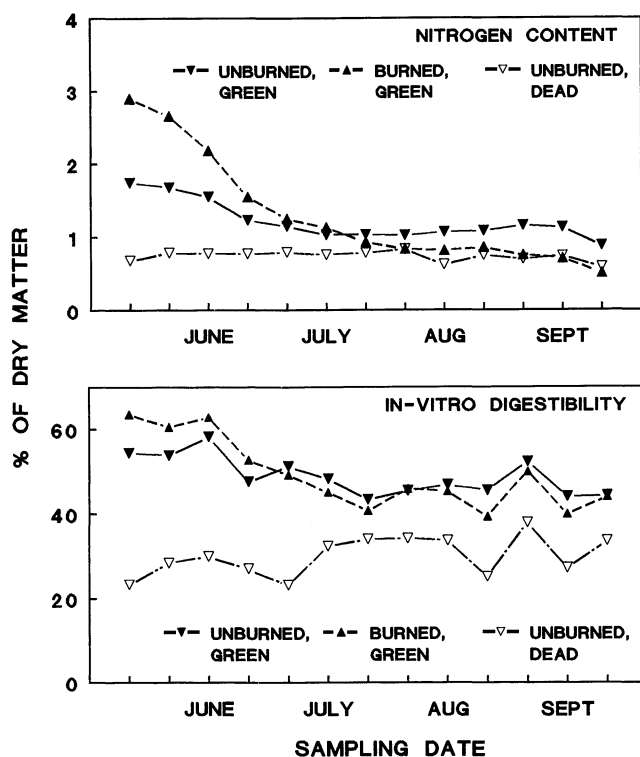
FIG. 6. Average nitrogen concentration and in vitro dry matter digestibility of the standing crop biomass from burned and unburned pastures. Standard errors were too small to plot for most sample dates ($n = 5$ per date).

dany and West 1983, McNaughton 1983, 1985, Zimmerman and Neuenschwander 1984, Hobbs and Gimingham 1987). Patches that are intensely grazed fail to burn as a result of insufficient fuel, while ungrazed patches accumulate fuel and burn intensely. Similar to our findings, Stronach and McNaughton (1989) observed that aboveground biomass was directly related to fire intensity.

When patches burn in grasslands, plant responses to the fertilizing effect of readily available mineral N (Hobbs and Schimel 1984) may attract herbivores (Daubenmire 1968, Coppock and Detling 1986). However, we found the local effects of burning did not increase the likelihood that a patch would be grazed in the tallgrass prairie, despite demonstrable improvements in forage quality. We suggest that this occurred because burning reduced the structural differences between the mowed and unmowed patches, and the nutritional differences induced by fire were insufficient to drive discernible differences in grazing behavior. Hobbs and Spowart (1984) also observed that chemical differences were less important than structural ones in influencing the feeding behavior of large vertebrate herbivores in burned grasslands.

Herbage removal was an important influence on grazing behavior of large herbivores in an unburned tallgrass prairie. Removal of residual biomass clearly attracted grazers. Our observations of increased use of grazed patches by large herbivores are consistent with

findings of others in a variety of grassland ecosystems (Vesey-Fitzgerald 1974, Coppock et al. 1983b, McNaughton 1984, Gordon 1988). There was a marked difference in nutritional quality between live and dead forage from unburned pastures that was evident during the early growing season for N, but was seen throughout the season for dry matter digestibility. Perhaps removal of the previous year's growth may allow herbivores to consume higher quality diets by providing green tissue that is undiluted and unobstructed by standing dead tissue (Willms et al. 1980, McNaughton 1984).

Effects of grazing on combustion losses of N may parallel effects on losses of other materials to the atmosphere. Burning in grasslands has emerged as a major terrestrial source of atmospheric methane and CO, particularly in tropical areas (Crutzen et al. 1985, Kirchhoff and Rasmussen 1990). Recent assessments have concluded that more biomass is burned in grasslands and savannas than in any other type of ecosystem (Kirchhoff and Rasmussen 1990, P. J. Crutzen and M. O. Andreae, personal communication). Current estimates of additions of materials to the atmosphere from these systems are calculated by multiplying an emission factor by the biomass at risk of burning, the latter quantity being currently obtained from estimates of net primary production in many cases (Seiler and Crutzen 1980). However, most grasslands and savannahs are grazed. Our findings illustrate that understanding the grazing–burning interaction is essential to

estimating the contributions of grassland fires to atmospheric chemistry. We suggest that calculation of atmospheric additions of materials from burning in grasslands must carefully consider reductions of combustible biomass resulting from grazing.

McNaughton (1983) emphasized that the potency of a single ecological influence may depend on its interactions with other influences. We conclude that the effects of grazing on grassland spatial pattern are relatively weak in the presence of fire but may be strong when fire is absent. Grazing weakened the relatively strong effects of fire on ecosystem N budgets. The influence of fire on ecosystem N budgets was altered by grazing to the extent that grazing may control whether burned tallgrass prairie gains or loses N.

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