EFFECTS OF FIRE AND GRAZING DRIVEN HETEROGENEITY ON N CYCLING IN TALLGRASS PRAIRIE

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EFFECTS OF FIRE AND GRAZING DRIVEN HETEROGENEITY ON N CYCLING IN TALLGRASS PRAIRIE

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PREFACE

This study was conducted as the initial investigation of belowground processes under fire-grazing interaction in tallgrass prairie. As such, N availability was chosen as the parameter of interest because of the dynamic nature of N transformations. There was also ample literature to justify our hypotheses tests. Specific objectives were to determine 1) if there were any differences in N availability between a shifting mosaic and an homogenous fire-grazing regime and to determine if those differences were more closely modeled by fire or grazing effects obtained from the literature and 2) the link between N availability and soil microbial biomass as affected by fire-grazing regime.

I sincerely thank my major advisor Dr. Sam Fuhlendorf and graduate committee members Dr. Dave Engle and Dr. Shipeng Deng for their patience through the many trials and tribulations that were encountered before compiling satisfactory versions of these manuscripts. Additionally, I would like to thank Clem Turner for his participation in laboratory analysis of samples and Dr. Carla Goad for her help in the statistical analysis of data.

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INTRODUCTION

Current management objectives on privately owned rangelands in North American tallgrass prairie are largely centered around livestock production. Often a goal of ranchers on these rangelands is to maintain dominant forage species while reducing variability in plant species composition in an attempt to optimize livestock production. Management practices including multiple water sources, herbicide application, annual prescribed fire, brush control, and rotational grazing systems are used to achieve this goal through uniform livestock distribution. Eventually, these management practices can lead to an homogeneous landscape that is moderately disturbed and where habitat is lacking for many animal species that may require undisturbed habitat as well as those that may require severely disturbed habitat. Recent studies have reported that disturbance-driven heterogeneity is critical to ecosystem function and many declining wildlife populations (Christensen 1997; Ostfeld et al. 1997; Wiens 1997). Hence, the goal of livestock production seems mutually exclusive to the goal of conservation under the current paradigm. Land management strategies are, therefore, needed that integrate profitable livestock production with disturbance-driven heterogeneity to satisfy both objectives.

Fire and grazing are considered keystone disturbance processes operative throughout the evolution of Great Plains grasslands (Collins 2000; Knapp et al. 1999). A paradigm shift in rangeland management has been proposed that integrates the use of these two paramount disturbance processes to achieve land management objectives (Fuhlendorf and Engle 2001). This new paradigm proposes an evolutionary approach to rangeland management and focuses on restoring heterogeneity critical to grassland structure and function concomitant with a profitable livestock operation. Under this regime (i.e., patch burning), localized fires are applied to the landscape, on a three-year return interval in tallgrass prairie, and grazing animals are allowed to selectively graze between burned and unburned patches. A central focal point of intense disturbance is created that can then be rotated across the landscape over several years because of the attraction localized fires have on the forage selection of large ungulates (Coppedge and Shaw 1998). The result is a shifting mosaic of vegetation structure and composition in space and time that promotes uneven grazing distribution within a year, but uniform grazing distribution over multiple years. Research thus far has resulted in positive effects on the biodiversity of plant and animal species in a variety of grassland landscapes (Fuhlendorf and Engle 2004).

Patch burning was developed with a three-year fire return interval in tallgrass prairie because of the biological responses of many organisms to fire (Collins 1990) as well as speculative accounts of how frequently fires occurred historically (Kay 1998). Research on other attributes of ecosystem function are needed that address evolutionary mechanisms of heterogeneity based management and to identity optimum fire return intervals. Specifically, soil nitrogen (N) dynamics have been shown to interact with the availability of sunlight (i.e., the Transient Maxima hypothesis) to influence aboveground net primary production in tallgrass prairie (Seastedt and Knapp 1993). We know that annual fires result in a net loss of N to the system and are not sustainable (Blair 1997; Fynn et al. 2003; Johnson and Matchett 2001; Ojima et al. 1994), but the optimum fire frequency from a production and sustainability basis is not well understood. Therefore, much research is needed to form a more ecologically sound rationale before integrating fire and grazing as a collective "dual purpose" management alternative to traditional production only based management on tallgrass prairie rangelands.

OBJECTIVES

The goal of this study was to evaluate the effects of focal fire and grazing disturbance with a three-year return interval on grassland function. Nitrogen was chosen as the variable of interest as transformations are affected by disturbance and can have dramatic broad scale implications. Specifically, this study was intended to develop an understanding of the combined interactive effect of fire and grazing on N availability under two contrasting fire-grazing management paradigms over two consecutive years.

Chapters (manuscripts) include:

- Inter and intra annual variability in N availability from pastures managed under patch burn and traditional management.
- The quantity of soil microbial biomass as a potential mechanism regulating N availability under patch burn and traditional management.

GRASSLAND N DYNAMICS

Grasslands are inherently heterogeneous landscapes where variable patterns of resource availability regulate ecosystem processes. Available nitrogen (N) is one such resource that often limits aboveground net primary productivity (Augustine et al. 2003; Blair 1998). The competitive interactions between and among native flora and microorganisms for available N results in a spatially heterogeneous and diverse indigenous plant community (Maron and Jeffries 2001; Milchunas and Lauenroth 1995;

Tilman 1987). Although N is generally considered a limiting resource, a vast amount of N present exists at all times. However, approximately 98% of the N present in grasslands is found in recalcitrant organic compounds unavailable for plant uptake (Blair 1998). Therefore, N for new plant growth must be acquired from existing soil inorganic N, atmospherically deposited N, fixed N, or mineralized N from the more readily decomposed soil organic matter fractions.

Mineralization of organic matter by the soil microbial biomass is a primary microbial process that regulates N availability in grasslands (Blair 1998; Collins 1990). Grassland soils contain large amounts of organic matter that accumulate as the production of herbaceous biomass reaches a steady state with decomposition over geologic time scales. As a result, greater quantities of microbial biomass are supported relative to forested ecosystems as microorganisms in grasslands experience less C limitation (Zak et al. 1994). Mineralization is greatly influenced by abiotic environmental conditions such as soil temperature and moisture (Drury et al. 2003; Goncalves and Carlyle 1994). As a result, average rates of N mineralization are variable over temporal scales from seasonal patterns of precipitation and temperature (Vigil et al. 2002).

Immobilization is essentially the inverse of mineralization in that inorganic N is transformed to organic N through microbial assimilation. The soil microbial biomass will immobilize inorganic N found in soil solution if they are unable to obtain sufficient amounts from the substrate they are decomposing, for example dead plant or animal residues. In grasslands, residues contain very little lignin, a large aromatic compound resistant to decomposition, but are variable in the relative proportion of N and carbon (C). The degree of C limitation relative to N limitation to decomposition is the primary determinant regulating immobilization-mineralization dynamics (Parton et al. 1987; Schimel and Parton 1986). In general, decomposing materials containing C:N ratios greater than 30:1 will typically result in immobilization and drastically reduce microbial activity that results from greater competition of existing available N. Inversely, substrates with C:N ratios less than 20:1 will result in a net increase in available N concentrations due to net N mineralization. The process of immobilization conserves N by narrowing the C:N ratio of poor quality residue (i.e., high C:N) through the release of C via respiration and the assimilation of existing soil inorganic N. Thus, immobilization reduces N losses to the environment (i.e., leaching, denitrification, etc). Immobilization will cease once the decomposing biota has narrowed the C:N ratio to a level sufficient for microbial metabolic activity. This phenomenon demonstrates the resiliency of native grasslands in conserving N and the potential for aboveground disturbances that affect plant C cycling to, therefore, affect N availability.

Fire and Grazing Effects

Nitrogen mineralization is a dynamic microbial process that is affected by disturbance (Asner et al. 1997). Numerous studies have been conducted at the Konza prairie LTER research station and in other grassland ecosystems in attempt to quantify N mineralization dynamics under a variety of disturbance regimes. This litany of research has determined that fire and grazing are the primary disturbance processes that influence N mineralization in grasslands (Blair 1998; Hobbs 1996; McNaughton et al. 1988).

Herbivory is a keystone process in grasslands and can have profound ecosystem level consequences (Collins 2000; Knapp et al. 1999). Studies on the direct effects of large ungulate grazing in grasslands have reported no detrimental effect on belowground productivity or root tissue chemistry (i.e., higher C:N) in response to repeated defoliation (Johnson and Matchett 2001; McNaughton et al. 1998; Milchunas and Lauenroth 1993). Large ungulate grazing accelerates the turnover of ecosystem N from: 1) redistribution of N in aboveground vegetation into inorganic N containing fecal material (Frank et al. 1994; Ruess and McNaughton 1987), although ammonia volatilization can result in ecosystem N loss (Sommer et al. 2001), and 2) imposing feedbacks between belowground fecal inputs and microbial activity that facilitates net N mineralization (Frank and Evans 1997; Frank and McNaughton 1993; Johnson and Matchett 2001; McNaughton et al. 1988; Risser and Parton 1982; Tracy and Frank 1998). Other studies in grasslands have reported that soil N responses following herbivory are similar for small mammalian herbivores and not restricted to large ungulates (Holland and Detling 1990; Holland et al. 1992). However, heavily grazed sites in these studies were characterized by a greater dominance of less productive forbs and dwarf shrubs that provide less belowground C to heterotrophs. As a result, feedbacks between belowground inputs and microbial processes are a more important determinant of N availability than direct fertilization effects from urine and dung deposition, although a synergistic effect is not precluded (Holland et al. 1992). In addition, N limitations can have a large effect on the behavior and productivity of domestic and wild ungulates (Augustine and Frank 2001; Augustine et al. 2003). For example, native large ungulates in the Serengeti and Yellowstone National Park have been shown to congregate on recently grazed areas which results in focal grazing and the formation of a grazing lawn that enhances plant productivity from N enrichment (Frank and McNaughton 1992; McNaughton 1984; McNaughton et al. 1997; McNaughton et al. 1988; Ruess and

McNaughton 1987; Seagle et al. 1992). Thus, herbivores respond to N limitations in a manor that enhances their carrying capacity by manipulating ecosystem structure and function (Frank and McNaughton 1992; McNaughton et al. 1988).

Fire is the most prevalent pathway of N loss in an ungrazed to moderately grazed grassland (Blair 1998; Collins 1990). Nitrogen is volatilized and lost to the atmosphere during the combustion of aboveground biomass (Hobbs et al. 1991). Annual spring burning affects the cycling of N by increasing root biomass of perennial grasses with less N allocation widening the C:N ratio of decomposable substrate available to heterotrophs (Fynn et al. 2003; Johnson and Matchett 2001; Ojima et al. 1994; Risser and Parton 1982). A slight but significant decrease in the N content of soil organic matter in the surface 2cm of soil has also been observed as a result of long term (i.e., >50 years) annual spring burning (Fynn et al. 2003). Although annual spring burning consistently results in lower N availability, no decline in aboveground net primary productivity has been observed suggesting that different factors constrain productivity and N availability in grasslands (Knapp 1998). However, this observation is the result of greater dominance of C4 grasses in annually spring burned sites responding to N limitation with greater N use efficiency (Towne and Kemp 2003) In addition, infrequent fire (i.e., >3 years) has also negatively affected the mineralizable pool of labile N as evidenced by diminished net N mineralization from in situ incubations (Blair 1997; Turner et al. 1997). These results suggest that short-term post fire microclimate effects (i.e., less soil moisture and warmer temperatures) are equally important in regulating N availability as are long-term effects of changes in the composition of flora and the subsequent interaction with soil fauna in grasslands subject to annual fire (O'Lear et al. 1996). Although these studies report a negative effect of infrequent fire when measured by in situ incubations, other studies in grasslands have reported a net increase in N availability immediately following fire when measured by other methods (Dudley and Lajtha 1993; Romanya et al. 2001). Additionally, a comprehensive meta-analysis has also reported that fire results in increase in inorganic soil N concentrations, but included a variety of ecosystems other than grassland (Wan et al. 2001). Thus, methodological and vegetation variables should be considered when comparing the results of fire effects on N availability.

The Transient Maxima Hypothesis

A nonequlibrium or abiotic driven model describing the structure and function of tallgrass prairie was proposed and identified N availability and photosynthetically active sunlight (PAR) as critically limiting resources (Seastedt and Knapp 1993). The transition between these limiting resources caused by fire was found to regulate productivity by these investigators (Fig. 1) and has been supported with subsequent research (Blair 1997). During these “transient maxima” a surge in production is observed that surpasses production during the equilibrium interval when just one essential resource is limiting. These investigators concluded that unburned prairie is energy limited as a result of the accumulation of surface litter inhibiting the penetration of sunlight through the vegetative canopy while burned prairie in non-drought years is strongly limited by N availability during post fire regrowth. The resulting pattern of N availability following fire is an initial decline immediately following fire and the eventual recovery of available N as light becomes limited once again (Fig. 1). Ultimately, these studies revealed a better understanding into the complexity of regulating factors that contribute to the function and dynamics of tallgrass prairie, a mesic grassland.

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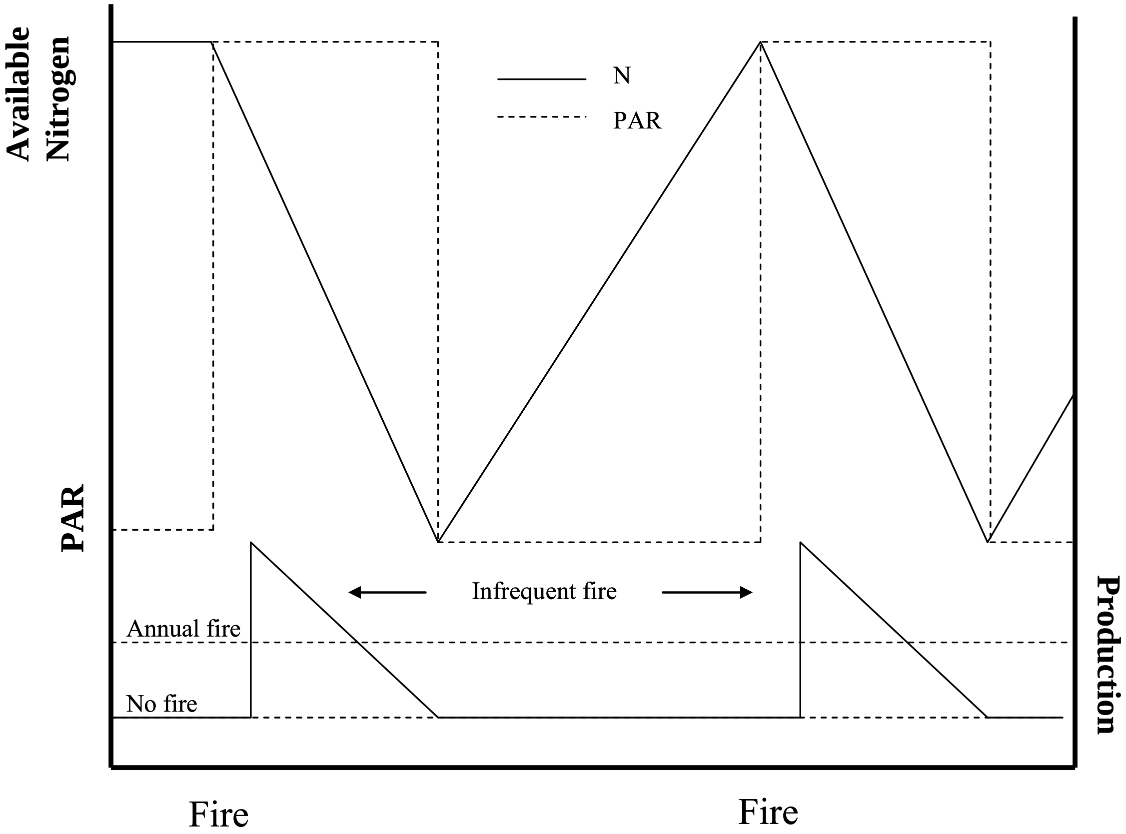
Figure 1. A graphical illustration of The Transient Maxima hypothesis that predicts a pulse in plant production following the transition between N and PAR (photosynthetic active radiation) as critically limiting resources following an infrequent fire (modified from Seastedt and Knapp 1993; Blair 1997).


Available Nitrogen
PAR
N
PAR
Infrequent fire
Annual fire
No fire
Production
Fire
Fire

CHAPTER II

NITROGEN AVAILABILITY IN A MESIC GRASSLAND UNDER A FIRE - GRAZING INTERACTION

ABSTRACT

Fire and grazing are highly interactive disturbance processes operative throughout the evolution of many grasslands. Studies on nitrogen (N) availability frequently report different effects following each disturbance and have largely neglected their interaction in time and space. Therefore, the objective of our work was to evaluate the combined interactive effect of fire and grazing on N availability in a tallgrass prairie ecosystem with a long evolutionary history of grazing. To address this, we evaluated N availability on patches within a shifting mosaic landscape where each patch varied in time since focal fire and grazing disturbance. We also evaluated N availability on a similar landscape, but where fires occurred annually and grazing pressure was moderate. Samples were collected from upland sites in May of 2003 and 2004. Total soil inorganic N was measured and a growth chamber experiment with hard red winter wheat (Triticum aestivum L. cv. Jagger) was used as a metric of net N mineralization. A pulse in N availability was commonly observed in recently burned patches consistent with ungulate foraging patterns under a shifting mosaic fire-grazing regime. Nitrogen availability was low to intermediate within the annually burned and moderately grazed landscape and although thought to contain greater mineralizable N than recently burned prairie, unburned patches were also more N limited compared to recently burned and heavily grazed sites. Overall, our study produced patterns of N availability that are more similar to grazing lawn studies where N availability is enhanced by periodic focal grazing.

Key words: Fire; grazing; tallgrass prairie; N availability; net N mineralization

INTRODUCTION

Ecosystems can be characterized by variability in space and time. Variability can be driven by spatio-temporal patterns of resource availability and by variable patterns of disturbance. In grassland ecosystems, fire and grazing are two primary disturbance processes (Collins 1990; Collins 2000; Knapp et al. 1999; McNaughton et al. 1988), and soil nitrogen (N) is frequently a resource that affects the productivity and composition of vegetation (Augustine et al. 2003; Maron and Jeffries 2001; Milchunas and Lauenroth 1995; Tilman 1987). Most studies of fire and grazing on N availability have focused on the main effects of each disturbance but have largely neglected their interaction in space and time which may have been an important evolutionary mechanism shaping grassland landscapes and providing habitat for many species (Fuhlendorf and Engle 2001). Therefore, studies of the patterns of N availability associated with fire-grazing interaction are needed to more fully understand the structure and function of grassland ecosystems.

The interaction between fire and grazing is organized around spatial and temporal variability across the landscape and has been described as a shifting mosaic (Fuhlendorf and Engle 2001; Fuhlendorf and Engle 2004). The probability of fire occurring is highest on an undisturbed grassland because of the accumulation of litter and standing biomass that that can serve as fine fuel. When a fire occurs and fuel is consumed, productivity, palatability and accessibility of forage increases. Thus, grazing animals are attracted increasing the probability and intensity of grazing. Focal grazing lowers fuel levels and reduces the probability and intensity of fire (Hobbs 1996; Steuter et al. 1995). Grazing animals will congregate on recently burned patches until fires occur in other locations. When grazing animals move to a recently burned area, the original burned patch has an increase in biomass that includes a diversity of graminoids and herbaceous dicots. Over the next several years the patch accumulates litter as grasses regain dominance again increasing the probability of fire. The result is a mosaic of patches that are recently burned and focally grazed nested within a landscape that is variable in time since focal fire and grazing. So, the landscape includes patches that are intensively disturbed, undisturbed, and many levels of recovery.

Nitrogen limitations are common in grasslands (Augustine et al. 2003; Blair 1998) and can have a large effect on the behavior and productivity of domestic and wild ungulates (Augustine and Frank 2001). For example, focal grazing by native large ungulates in the Serengeti and Yellowstone National Park has resulted in greater plant productivity from N enrichment on these grazing lawns (Frank and McNaughton 1992; McNaughton et al. 1988). Accelerated N turnover within grazing lawns has even been proposed as the mechanism by which native African ungulates have evolved on N limited grasslands (McNaughton 1984; McNaughton et al. 1997; Ruess and McNaughton 1987; Seagle et al. 1992). In fact, greater N mineralization within grazing lawns has been reported from numerous studies conducted across a variety of grassland ecosystems suggesting a consistent relationship between large ungulate grazers and grasslands (Augustine et al. 2003; Frank and Evans 1997; Frank and McNaughton 1993; Johnson and Matchett 2001; Risser and Parton 1982; Tracy and Frank 1998). A major limitation to domestic livestock enterprises that are based on native grasslands is protein and N limitations in forage during the dormant season (McCollum and Horn 1986). As a result, relationships between grazing and N availability have been investigated in the context of agriculture and native ecosystems but remains largely unevaluated in the context of fire-grazing interaction.

Fire is a common disturbance on grasslands that can influence N availability. In the absence of large ungulate grazing, annual burning has reduced net N mineralization and potentially mineralizable N (Blair 1997; Fynn et al. 2003; Turner et al. 1997). Thus, promoting N limitation and immobilization of existing soil inorganic N from turnover of lower quality (i.e., higher C:N ratio) organic matter (Fynn et al. 2003; Johnson and Matchett 2001; Ojima et al. 1994). However, infrequent fire allows accumulation of litter that can lead to limitations in productivity from reduced light availability. Immediately following fire, productivity quickly becomes limited by N availability as plant growth is quickly increased (Seastedt et al. 1991; Seastedt and Knapp 1993). The Transient Maxima hypothesis suggests that this transient release from light limited productivity to N limited productivity results in a temporary surge in overall grassland productivity (Seastedt and Knapp 1993). The resulting pattern of N availability is an initial decline immediately following fire and the eventual recovery of available N as light becomes limited once again (Blair 1997; Seastedt et al. 1991; Seastedt and Knapp 1993).

Fire and grazing are important disturbances in many grassland ecosystems regulating N availability, but most studies have focused on the main effects of fire and grazing with little attention given to their ecological interaction in space and time. The ecological interaction is different from the statistical interaction in that it is regulated by spatial and temporal patterns of fire and grazing where the probability of each disturbance is dependent on the other disturbance and a shifting mosaic pattern emerges from the interaction. Studies of the main effects of fire and grazing have generated different hypotheses describing N availability following each disturbance (Fig. 1). However, the cumulative effect when both disturbances interact in space and time remains largely unknown. We have developed a unique experiment capable of evaluating the ecological interaction of fire and large ungulate grazing on grassland structure and function (Fuhlendorf and Engle 2001; Fuhlendorf and Engle 2004). For this study we continue this focus with our primary goal of evaluating the effect of the fire-grazing interaction on soil N availability in tallgrass prairie. We specifically tested whether N availability under a fire-grazing interaction was more accurately modeled by either of two competing hypothesis of the effects of fire and grazing independent of the other disturbance. The Grazing hypothesis predicts an increase in N availability followed by a gradual decline in response to concentrated grazing pressure (McNaughton 1984; McNaughton et al. 1997; Ruess and McNaughton 1987; Seagle et al. 1992). On the other hand, the Transient Maxima hypothesis predicts that N availability will decrease immediately following fire and gradually increase over the next few years as light becomes limited once again (Blair 1997; Seastedt et al. 1991; Seastedt and Knapp 1993). To evaluate these competing hypothesis, we evaluated N availability on patches within a shifting mosaic landscape where each patch varied in time since focal fire and grazing disturbance. To evaluate the effects of focal fire and grazing disturbance, we also evaluated N availability on a landscape that had similar grazing pressure but where the entire area was burned annually and the fire-grazing interaction did not exist.

MATERIALS AND METHODS

Site Description

Our study was conducted on the Nature Conservancy's 16,000-ha Tallgrass Prairie Preserve (TGPP) located at the southern edge of the Flint Hills in the tallgrass prairie region of central North America. Mean annual precipitation of the region is 870mm with 70% occurring between April and September (Bourlier 1979). Vegetation at the TGPP is tallgrass prairie dominated by C4 grasses big bluestem (Andropogon gerardii), Indian grass (Sorghastrum nutans), switchgrass (Panicum virgatum), and little bluestem (Schizachyrium scoparium) (Hamilton 1996; Palmer 2000). Topography is gently rolling with highly variable soils derived from shale, limestone, and sandstone. Limestone is typically found interbedded between sandstone and shale with sandstone found at the surface of ridge crests. Either shale or limestone can be found as outcrops on side slopes or toe slopes as a result of geologic erosion. The result is a heterogeneous mixture of soils over multiple scales that vary in texture depending on parent material and topographic position. Site descriptions contain complexes of thermic lithic Haplustolls and thermic aquic Paleustalfs (Bourlier 1979). Upland sites contain mollic epipedons characteristic of long term perennial grassland vegetation and possess smectitic mineralogy. We limited our evaluations of N availability to upland soils.

Study Design

To evaluate the effects of the ecological interaction of fire and grazing on N availability, two contrasting fire-grazing regimes were evaluated (Fig. 2) each with two replications arranged in a completely randomized design. A shifting mosaic fire-grazing regime has fire applied to spatially discrete patches within a larger area (approx 1,200-ha) that is unburned. Fires were annually applied to one third of the landscape on a three-year return interval while grazing intensity was calculated for the entire area.

Alternatively, an homogenous fire-grazing regime was burned in its entirety each year (also approx 1,200-ha). These different fire-grazing regimes were stocked with large ungulates (Bos taurus) similarly, but previous analyses demonstrated that these grazing animals spend over 70% of their grazing time on recently burned patches and the majority of the remaining time on patches burned one year earlier avoiding most patches burned two years earlier (Fuhlendorf and Engle 2004). So, grazing pressure in the shifting mosaic fire-grazing regime varied from two to three times greater than the homogenous fire-grazing regime on recently burned patches to patches that were essentially avoided by grazing animals. Specifically, we sampled patches within the shifting mosaic fire-grazing regime in the first year of focal disturbance that were currently heavily grazed, one year since focal disturbance that were minimally grazed, and two years since focal disturbance which were avoided by grazing animals. In addition, we sampled from similar sites within the homogeneous fire-grazing regime where fire occurs annually but grazing pressure was moderate. All burns included in this study were conducted just prior to the growing season in March and grazing animals were moderately stocked for half of the growing season (April through July) based on the entire area they had access to.

Soil N Measurements

To evaluate N availability, soil samples were taken to a depth of 0-10cm using a 1.9cm diameter soil core and bulked from each experimental area in May of 2003 and 2004. If needed, litter was removed to sample mineral soil only and direct sampling of fecal pats was avoided. Total soil inorganic N (NH4+-N + NO3--N) was measured, immediately after sampling, in each year colorimetrically using a Lachat Quickchem

Autoanalyzer (Milwaukee, Wisc.) after extraction with 100ml's of 1 mol/L KCl solution (Mulvaney 1996). Additionally, a growth chamber experiment was conducted in each year as a metric of net N mineralization (Fynn et al. 2003). Four air-dried 500g subsamples from each homogenized composite sample were hand ground and placed into 1-quart polystyrene containers. Seven seeds of certified hard red winter wheat (Triticum aestivum L. cv. Jagger) were planted in each container. Hard red winter wheat was selected because of its known response to additions of N (Oscarson et al. 1995). Five plants container-1 were allowed to germinate and grow with optimal watering for seventy days with eighteen hours of light day-1 at 25ºC (Goncalves and Carlyle 1994). Half of the subsamples in each year received a basal dressing of a nutrient solution that contained macro (P, K, Ca, Mg, S) and micro (Zn, Cu, Mn, Fe, B and Mo) nutrient elements made from reagent grade chemical to ensure that other nutrients were not critically limited. The nutrient solution was supplied to bring the containers to field capacity and was also supplied half way through the growing period to avoid nutrient toxicity, but to focus on previously described N limitations in grasslands (Augustine et al. 2003; Maron and Jeffries 2001; Milchunas and Lauenroth 1995; Tilman 1987). Following each nutrient application subsamples were randomized within the growth chamber. At the end of the seventy-day growing period, roots and shoots from each container were harvested, dried for seven days at 45ºC, and weighed (Ostertag and Hobbie 1999). Tissue N (%) was determined by dry combustion with a Leco CN 2000 autoanalyzer (St. Joseph, Michigan) and plant N (mg container-1) was determined as the product of dry weight biomass (g) and tissue N (%). The recovered total (roots + shoots) plant N from each container was used as an metric of net N mineralized over the seventy day trial (Fynn et al. 2003). The relative change in total plant N from 2003 to 2004 was also computed to illustrate differences between years and to determine the relative influence of spatial variability as time since focal disturbance was different in each year for the same site within the shifting mosaic fire-grazing regime (Fig. 2).

Statistical Analyses

Each patch within the replicated shifting mosaic fire-grazing regime and the similar sites sampled within the replicated homogenous fire-grazing regime were analyzed as separate levels of the same main effect which will be referred to as treatment. Both total soil inorganic N and total plant N data were analyzed in each year separately. Total plant N data were analyzed for interaction by a two-way analysis of variance (ANOVA) where treatment and nutrient application were both main effects. There was no statistical interaction in either year, so data were combined in both years to better evaluate treatment effects on N availability. Significant differences among treatment means for total soil inorganic N data, total plant N data, and the relative change in total plant N from 2003 to 2004 were independently tested using single degree of freedom contrasts in ANOVA. Due to the extent of our study site and the small number of degrees of freedom, F values were considered significant at $P < 0.10$ throughout this paper. All analyses were conducted in SAS (SAS Institute 1989).

RESULTS

Nitrogen availability was strongly influenced by treatment. Total soil inorganic N was greatest in the focally disturbed patch in 2003 and decreased with each successive year since focal disturbance (Fig. 3), although no statistical differences were detected in either year. There was no statistical interaction between treatment and nutrient application for total plant N recovered across all subsamples in either 2003 ($P = 0.317$) or 2004 ($P = 0.938$) trials. So, total plant N for each treatment was combined across subsamples and used as a surrogate for net N mineralization. Root and shoot biomass varied in a similar manner to total plant N while the concentration of tissue N did not vary much with treatment (Tables 1 and 2). In 2003, the focally disturbed patch produced containers with the greatest total plant N while in 2004 year since focal disturbance shifted within the shifting mosaic fire-grazing regime but the same pattern was observed. Table 3 shows significant differences from all pairwise contrasts.

Change in total plant N from 2003 to 2004 (Fig. 5) from each experimental area indicates how net N mineralization changed from one year to the next relative to change in year since focal disturbance. So, the relative change is a stronger indication of the treatment effect because it reflects the change that occurred on an individual sample site that is associated with a specific treatment. The patch within the shifting mosaic regime focally disturbed between 2003 and 2004 sampling had the greatest increase (Fig. 5) indicating greater net N mineralization following focal fire and grazing disturbance and was significant from all other sites (Table 3). Patches that were 1 or 2 years since focal disturbance within the shifting mosaic regime had the lowest change while the homogenous regime increased by 27%, but was still significantly less than the increase from the patch burned and focally grazed between years. Greater total plant N was recovered in 2004 ($\bar{y}$ = 18.65mg) on average than in 2003 ($\bar{y}$ = 14.59mg) suggesting interannual variation from field conditions or from variation between trials in the growth chamber. However, the moderate increase in total plant N from the homogeneous regime is a more accurate reflection of the interannual variation that could be associated with the environment ($\bar{y}$ = 13.3mg in 2003 and $\bar{y}$ = 18.4mg in 2004).

DISCUSSION

Fire and grazing have long been recognized as dominant forces regulating the structure and function of grassland ecosystems. The main effects of these disturbances on N dynamics have been described with different conclusions while the spatially controlled interaction has largely been neglected. Focal grazing and the creation of grazing lawns are responsible for the increase in N availability in some grazed grasslands (McNaughton 1984; McNaughton et al. 1997; Ruess and McNaughton 1987; Seagle et al. 1992). On the other hand, infrequent fires have been reported to reduce N availability as grasses increase production and capture all available resources following the removal of light limitation (Blair 1997; Seastedt et al. 1991; Seastedt and Knapp 1993). So, the dominant disturbances of fire and large ungulate grazing can lead to competing hypotheses describing N availability in grassland ecosystems (Fig. 1) suggesting a potential conflict in understanding the interactive effect of the fire-grazing shifting mosaic. It was our goal in this study to determine the effect of spatially controlled fire-grazing interaction on N availability and to accurately assess the combined interactive effect of these two dominant disturbances on grassland structure and function.

Although no statistical differences were detected, greater concentration of total soil inorganic N observed in the focally disturbed patch in 2003 (Fig. 3) is consistent with the Grazing hypothesis (Fig. 1). Precipitation was greater in the spring of 2004 resulting in greater primary productivity and possibly greater plant N uptake across all sites at our study area, so the focally disturbed patch did not contain more total soil inorganic N than the other sites. Furthermore, soil inorganic N concentrations in recently burned native grasslands are typically maintained at low concentrations as a result of the competitive interactions between and among microorganisms and vigorously growing vegetation (Bardgett et al. 2003). As a result, the growth chamber experiments were conducted to evaluate the supply rate of available N over several months as opposed to an instantaneous concentration and has previously been reported from a grassland ecosystem (Fynn et al. 2003). Results from the growth chamber experiments (Figs. 4 and 5) are also consistent with the Grazing hypothesis where the creation of a grazing lawn resulted in greater total plant N recovered across all subsamples.

Differences between fire-grazing regimes are characterized by fire frequency and spatio-temporal patterns of the current years grazing intensity. The most recently burned patches within the shifting mosaic fire-grazing regime are most heavily grazed, whereas, grazing pressure within the homogenous fire-grazing regime is homogenously distributed throughout the landscape and grazing lawns do not develop. In general, focally disturbed patches were found to contain greater N availability relative to previously burned patches and the homogenous fire-grazing regime respectively. Furthermore, treatment patterns were consistent between years and through the analysis of change from year to year. Thus, our results indicate that even with variable spatial disturbance from year to year the effects persist resulting in a mosaic of N enriched patches that are recently burned and focally grazed nested within an unburned and ungrazed landscape. Our study demonstrates that fire-grazing interaction produces patterns of N availability that are more similar to grazing lawn studies where N availability is enhanced by periodic focal grazing by large ungulates while N availability in an annually burned and homogenously grazed regime is influenced more by interannual variability.

Herbivory is a keystone disturbance process in grasslands that can have profound consequences on the amount of N available to growing plants. Studies have commonly reported C translocation from roots to shoots following defoliation (Detling et al. 1979; Caldwell et al. 1981; Osterheld and McNaughton 1988) which could potentially alter the C:N ratio of senesced roots during decomposition regulating mineralization-immobilization dynamics (Parton et al. 1987; Schimel and Parton 1986). Other studies, including a comprehensive meta-analysis, have reported no decline in belowground primary productivity in grasslands with a long evolutionary history of grazing in response to periodic defoliation (McNaughton et al. 1998; Milchunas and Lauenroth 1993). However, grazing patterns in these studies differ from the effects of short duration, high intensity grazing such as what occurs under a shifting mosaic fire-grazing regime. Intense defoliation on grazing lawns may impede belowground C inputs to heterotrophs during focal disturbance reducing N immobilization by the soil microbial biomass and increasing mineralization potentials (Johnson and Matchett 2001; Sankaran and Augustine 2004). There is an apparent feedback that exists between N availability and grazing activity moderated through decomposition (Augustine et al. 2003; McNaughton et al. 1997), but the degree to which intensity and duration of grazing influences N availability is less known. Although the degree to which grazers influence decomposition is questionable, the most conspicuous effects of large herbivores commonly reported are accelerated turnover of ecosystem N from: 1) redistribution of N in aboveground vegetation into inorganic N containing excrement (Frank et al. 1994;

Ruess and McNaughton 1987), and 2) imposing feedbacks between feces and microbial activity that facilitates net N mineralization surrounding the affected microsite (Frank and Evans 1997; Frank and McNaughton 1993; McNaughton et al. 1988; Risser and Parton 1982; Tracy and Frank 1998; Ruess and McNaughton 1987; Seagle et al. 1992). It has been suggested that grazing effects on decomposition are a more important determinant of N availability than direct inorganic N deposition in excrement (Holland et al. 1992). Our data agrees with this conclusion as significant differences in total plant N, an index of net N mineralization, were observed in both years while no statistical differences occurred for total soil inorganic N data in either year. Uncoupling the relative contributions of urine, dung, and grazer-modified substrate availability to determine the actual causal mechanism behind the observed pulse in N availability in the current study remains difficult, although synergistic effect is not precluded.

Previous site management and disturbance history must also be considered to effectively interpret results. All experimental areas prior to 2000 were managed for homogeneity with frequent fire and grazing by large ungulates, similar to the homogenous fire-grazing regime. It is clear that a single rotation of localized fire on a three year return interval may not have allowed sufficient time for all ecosystem traits to stabilize to the effect of short term intensive grazing followed by periodic deferment from both fire and grazing over subsequent years within the shifting mosaic fire-grazing regime. However, in spite of the necessity of long term treatments, we were able to demonstrate significant short-term effects of focal disturbance on N dynamics.

Management Implications

Long term annual burning has consistently resulted in a reduction in N availability (Blair 1997; Fynn et al. 2003; Ojima et al. 1994; Turner et al. 1997). Plant responses have also been documented resulting in greater root primary productivity with less tissue N content (Johnson and Matchett 2001). This widens the C:N ratio of decomposable substrate available to heterotrophs which is an important control over microbial immobilization-mineralization dynamics (Parton et al. 1987; Schimel and Parton 1986). Although there has been less research, plant responses to annual burning followed by moderate to heavy grazing are significantly different. Johnson and Matchett (2001) reported that large ungulate grazing in an annually burned tallgrass prairie preserves root tissue quality (i.e., lower C:N) as vegetation allocate less C to belowground roots and rhizomes in response to repeated defoliation relative to annually burned prairie alone. Thus, grazing activity seemingly acts as a buffer against declines in N availability commonly observed in annually burned grasslands. In our study we could not identify any reduction in N availability associated with annual burning and moderate uniform grazing within the homogeneous fire-grazing regime relative to other infrequently burned sites.

Annual spring burning followed by spring and early summer grazing is a livestock enterprise system common to the Flint Hills in the tallgrass prairie region of central North America. Livestock ranchers employ annual spring burning as a means to uniformly distribute grazing pressure in order to achieve more efficient forage utilization when dominant tallgrasses are preferred forage. Tallgrasses are more productive, fire tolerant, warm season forage species that have a competitive advantage over less productive species when annually burned in spring (Seastedt et al. 1991; Towne and Kemp 2003).

Despite the compensation in root tissue chemistry that occurs when grazing animals are present in annually burned grasslands, this management regime is not without its consequences. For example, long term annual burning has resulted in loss of grassland obligate species diversity (Collins 1998; Jansen et al. 1999).

Unlike this traditional management, a rotation of localized fires concentrate livestock on post burn regrowth (i.e., fire-grazing interaction) maximizing livestock distribution over several years but minimizing distribution within individual years (Fuhlendorf and Engle 2004). Periodic deferment from fire and focal grazing under this management regime allows the accumulation of detritus in unburned patches and has resulted in positive effects on the biodiversity of plant communities in grassland landscapes (Fuhlendorf and Engle 2004). Changes in animal communities have also been demonstrated (Harrell et. al 2004; Townsend et al 2004,). In addition, a shifting mosaic application of the fire-grazing model seemingly enhances the carrying capacity in the focally disturbed patch as a result of elevated N availability observed in the current study (Frank and McNaughton 1992; McNaughton et al. 1988). Given adequate growing conditions, fire-grazing interaction may provide a management alternative that enables sustainable livestock production concomitant with a variety of species habitats in predominantly N limited grasslands.

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Table 1. Root and shoot biomass (g) and tissue N (%) from a growth chamber experiment using hard red winter wheat (*Triticum aestivum* L. cv. Jagger) as affected by an homogenous fire-grazing regime and patches within a shifting mosaic fire-grazing regime in 2003. Patches were recently disturbed by focal fire and grazing, one year since focal disturbance (YSFD), and two years since focal disturbance.

Treatment	YSFD	Biomass (g)				N (%)			
		Root		Shoot		Root		Shoot	
		Fert	Unfert	Fert	Unfert	Fert	Unfert	Fert	Unfert
Homogenous		0.86 ± 0.24	0.61 ± 0.12	0.56 ± 0.06	0.47 ± 0.10	0.98 ± 0.08	1.32 ± 0.08	0.83 ± 0.08	1.30 ± 0.19
Shifting mosaic	0	1.48 ± 0.32	1.12 ± 0.07	0.81 ± 0.35	0.65 ± 0.05	0.92 ± 0.08	1.17 ± 0.13	0.73 ± 0.02	1.07 ± 0.15
Shifting mosaic	1	1.28 ± 0.01	0.39 ± 0.18	0.66 ± 0.05	0.33 ± 0.13	0.84 ± 0.05	1.52 ± 0.26	0.63 ± 0.06	1.32 ± 0.22
Shifting mosaic	2	1.09 ± 0.16	0.61 ± 0.09	0.55 ± 0.15	0.42 ± 0.05	0.99 ± 0.05	1.12 ± 0.10	0.80 ± 0.06	0.99 ± 0.13

* "Fert" subsamples received a non-N nutrient solution

* values reported are the mean ± 1 SE

Table 2. Root and shoot biomass (g) and tissue N (%) from a growth chamber experiment using hard red winter wheat (*Triticum aestivum* L. cv. Jagger) as affected by an homogenous fire-grazing regime and patches within a shifting mosaic fire-grazing regime in 2004. Patches were recently disturbed by focal fire and grazing, one year since focal disturbance (YSFD), and two years since focal disturbance.

Treatment	YSFD	Biomass (g)				N (%)			
		Root		Shoot		Root		Shoot	
		Fert	Unfert	Fert	Unfert	Fert	Unfert	Fert	Unfert
Homogenous		1.00 ± 0.38	0.61 ± 0.02	0.96 ± 0.27	0.64 ± 0.13	1.15 ± 0.19	1.43 ± 0.06	1.06 ± 0.16	1.24 ± 0.14
Shifting mosaic	0	1.02 ± 0.03	0.70 ± 0.28	0.94 ± 0.07	0.69 ± 0.16	1.36 ± 0.01	1.51 ± 0.28	1.34 ± 0.13	1.46 ± 0.07
Shifting mosaic	1	1.45 ± 0.17	0.70 ± 0.02	1.09 ± 0.01	0.78 ± 0.04	0.87 ± 0.02	1.23 ± 0.03	0.70 ± 0.12	1.07 ± 0.04
Shifting mosaic	2	1.08 ± 0.02	0.42 ± 0.03	0.96 ± 0.28	0.55 ± 0.10	0.88 ± 0.02	1.48 ± 0.13	0.77 ± 0.06	1.28 ± 0.14

* "Fert" subsamples received a non-N nutrient solution

* values reported are the mean ± 1 SE

Table 3. Statistical contrasts for each pairwise comparision of treatment means

Contrast	2003				2004					
	Total soil inorganic N		Total plant N		Total soil inorganic N		Total plant N		Δ in total plant N	
	$F_{1,4}$	P	$F_{1,12}$	P	$F_{1,4}$	P	$F_{1,12}$	P	$F_{1,12}$	P
0 YSFD vs 1 YSFD	0.59	ns	10.94	0.006	0.46	ns	1.89	ns	20.00	< 0.001
0 YSFD vs 2 YSFD	2.88	ns	8.13	0.015	0.02	ns	6.61	0.025	7.25	0.019
0 YSFD vs Homogenous	3.98	ns	7.87	0.016	1.78	ns	2.03	ns	3.18	0.099
1 YSFD vs 2 YSFD	0.87	ns	0.21	ns	0.65	ns	1.43	ns	3.17	ns
1 YSFD vs Homogenous	1.51	ns	0.25	ns	4.04	ns	0.01	ns	7.23	0.019
2 YSFD vs Homogenous	0.09	ns	0.01	ns	1.46	ns	1.32	ns	0.83	ns

* for the Δ in total plant N, year since focal disturbance (YSFD) refers to 2004

* ns = not significant at $\alpha = 0.10$

Fig. 1. Conceptual model of the temporal dynamics of soil N availability in response to fire: Transient Maxima hypothesis (Blair 1997; Seastedt et al. 1991; Seastedt and Knapp 1993) and grazing: Grazing hypothesis (McNaughton 1984; McNaughton et al. 1997; Ruess and McNaughton 1987; Seagle et al. 1992). Samples were collected in May of 2003 and 2004 from patches recently disturbed by focal fire and grazing (A), one year since focal disturbance (B), and two years since focal disturbance (C). The effect of disturbance is a combined interactive effect of localized fire followed by focal grazing and the formation of a grazing lawn (Fuhlendorf and Engle 2001).

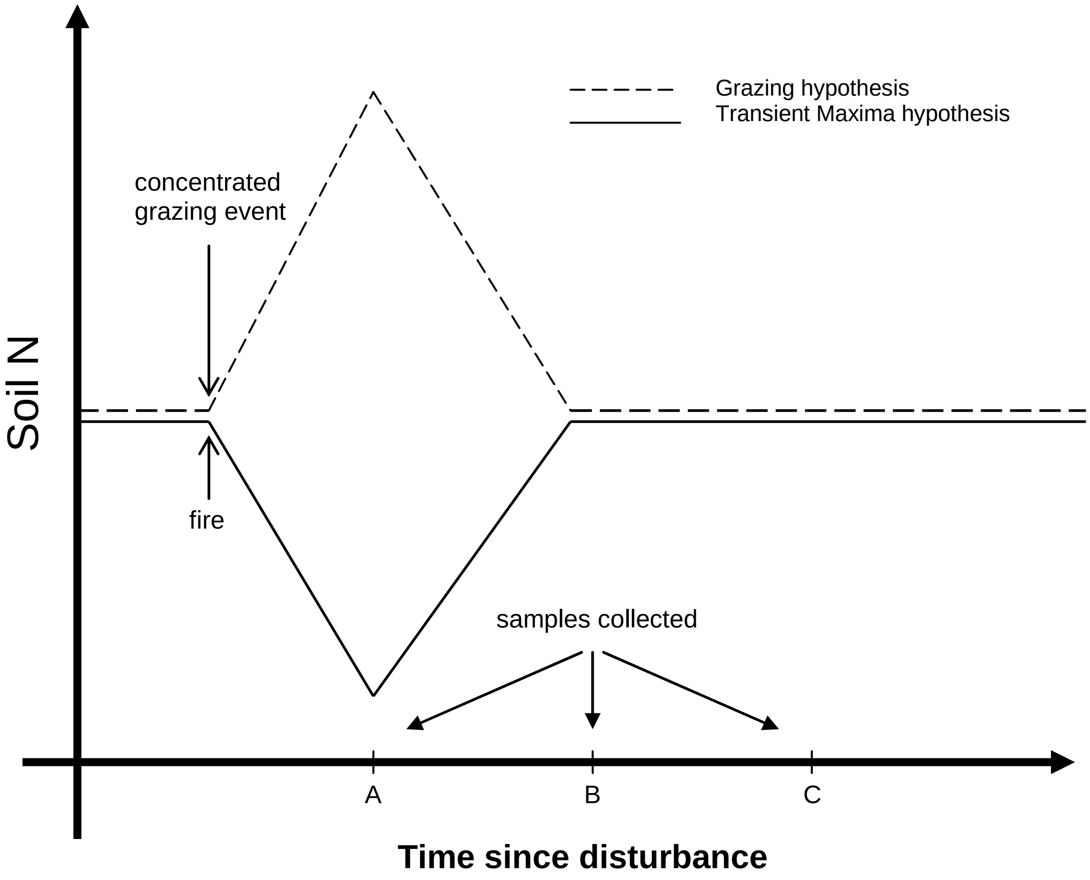

Grazing hypothesis
Transient Maxima hypothesis
concentrated grazing event
fire
Soil N
samples collected
A
B
C
Time since disturbance

Fig. 2. Graphical illustration of experimental units as sampled in 2003. Samples were collected in May of 2003 and 2004 from an homogeneous fire-grazing regime and patches within a shifting mosaic fire-grazing regime. Patches were recently disturbed by focal fire and grazing (A), one year since focal disturbance (B), and two years since focal disturbance (C). Focal disturbance within the shifting mosaic was rotated in 2004 providing replication in space and time.

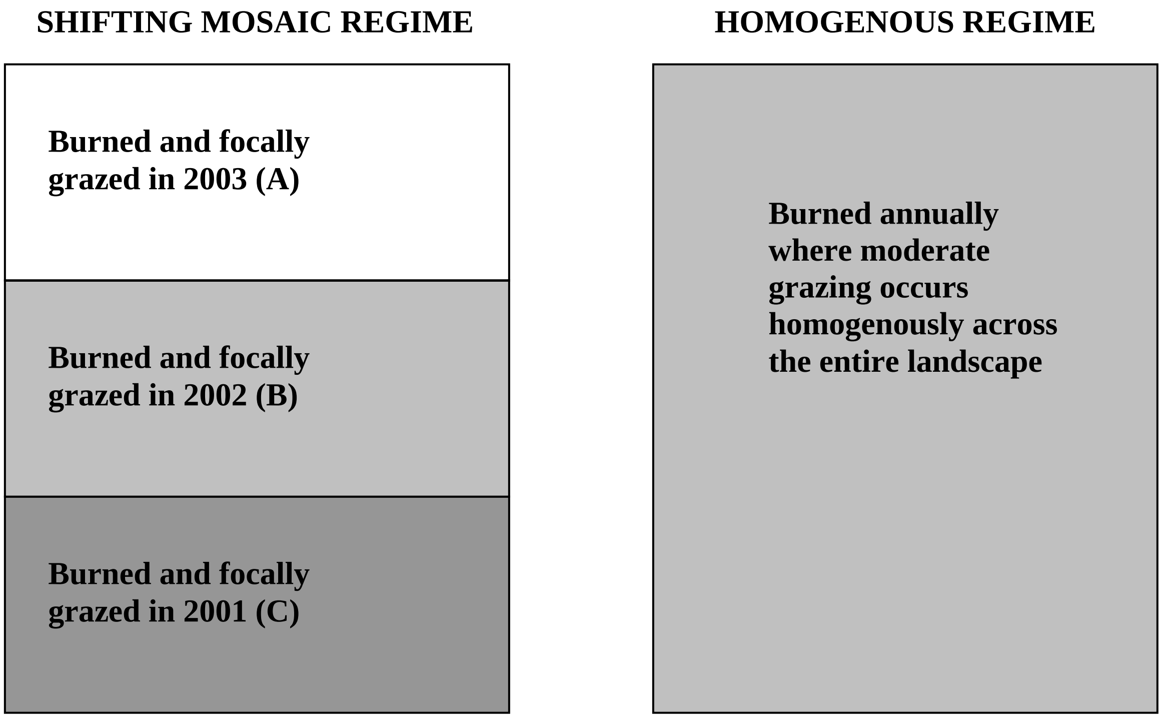

SHIFTING MOSAIC REGIME
HOMOGENOUS REGIME
Burned and focally grazed in 2003 (A)
Burned and focally grazed in 2002 (B)
Burned and focally grazed in 2001 (C)
Burned annually where moderate grazing occurs homogenously across the entire landscape

Fig. 3. Total inorganic N (NH_4^+-N + NO_3^--N) as affected by an homogenous fire-grazing regime and patches within a shifting mosaic fire-grazing regime. Patches were recently disturbed by focal fire and grazing, one year since focal disturbance (YSFD), and two years since focal disturbance. Histogram bars are least squares means (± 1 SE).

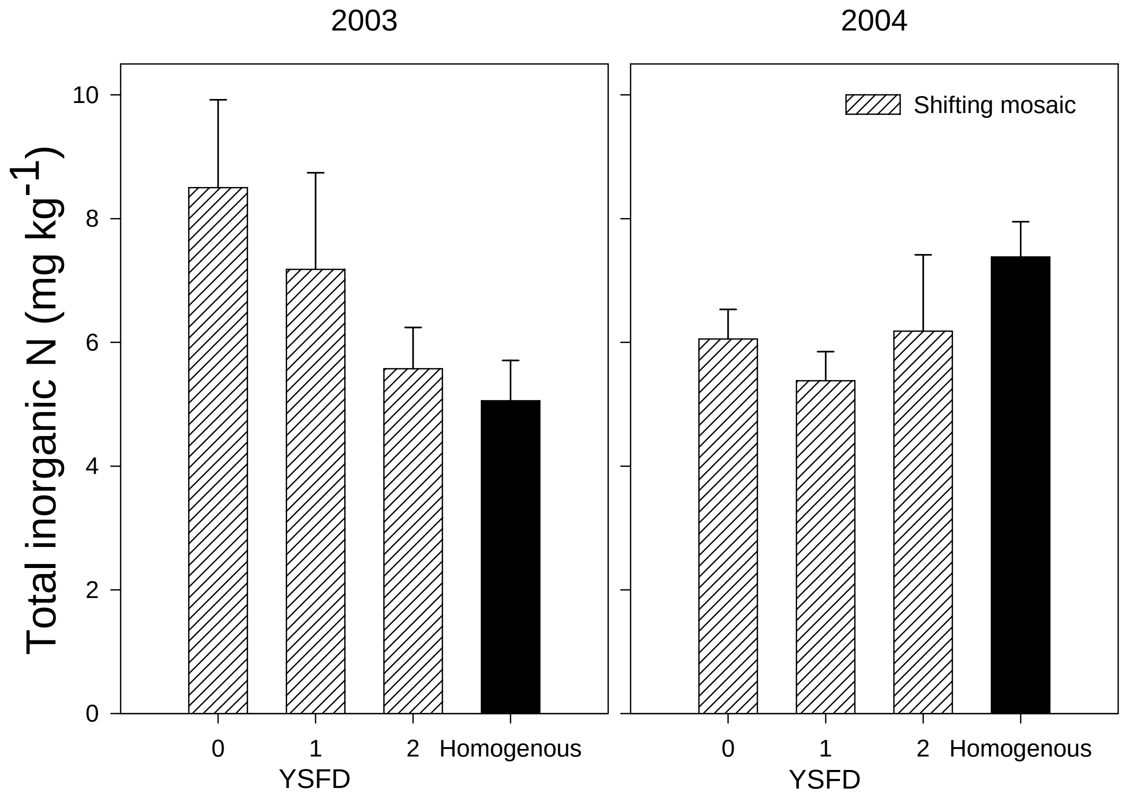

2003
2004
Shifting mosaic
Total inorganic N (mg kg^{-1})
0
2
4
6
8
10
0
1
2
Homogenous
YSFD
0
1
2
Homogenous
YSFD

Fig. 4. Total plant N (roots + shoots) recovered from a growth chamber experiment using hard red winter wheat (*Triticum aestivum* L. cv. Jagger) as affected by an homogenous fire-grazing regime and patches within a shifting mosaic fire-grazing regime. Patches were recently disturbed by focal fire and grazing, one year since focal disturbance (YSFD), and two years since focal disturbance. Histogram bars are least squares means (± 1 SE).

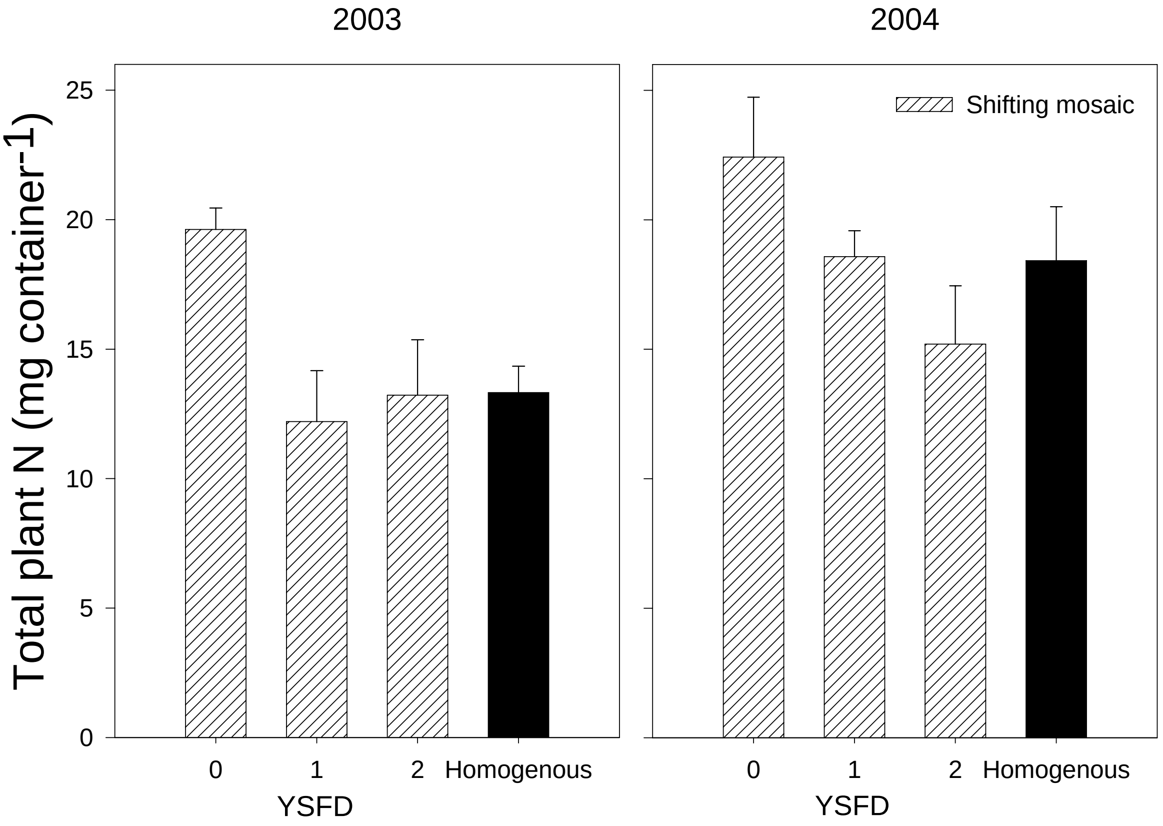
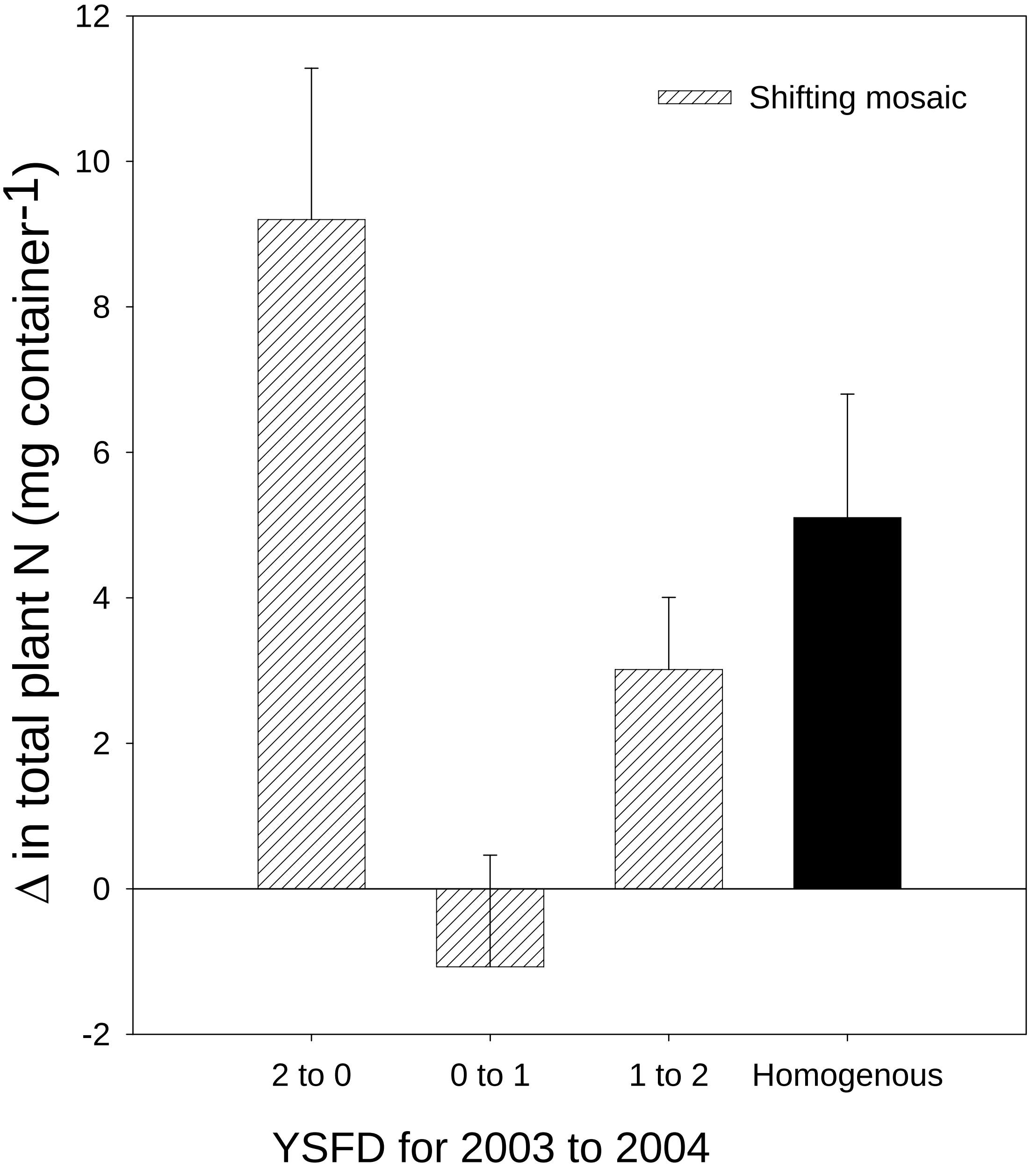

2003
2004
Total plant N (mg container^{-1})
25
20
15
10
5
0
Shifting mosaic
0
1
2
Homogenous
YSFD
0
1
2
Homogenous
YSFD

Fig. 5. Relative change in total plant N (roots and shoots) recovered from a growth chamber experiment using hard red winter wheat (*Triticum aestivum* L. cv. Jagger) as affected by an homogenous fire-grazing regime and patches within a shifting mosaic fire-grazing regime. Patches were disturbed by focal fire and grazing in the present year, one year since focal disturbance (YSFD), and two years since focal disturbance. Histogram bars are least squares means (± 1 SE).



12
10
8
6
4
2
0
-2
Δ in total plant N (mg container-1)
Shifting mosaic
2 to 0
0 to 1
1 to 2
Homogenous
YSFD for 2003 to 2004

CHAPTER III

MICROBIAL BIOMASS IN A MESIC GRASSLAND UNDER A FIRE - GRAZING INTERACTION

ABSRACT

The ecological interaction between fire and grazing (fire-grazing interaction) is an important disturbance in many grassland ecosystems regulating nitrogen (N) availability. Grazing animals congregate in recently burned patches enhancing N availability while unburned areas accumulate detritus and are N limited. We hypothesized that urine and dung deposition from congregated grazing activity following localized fire should enhance substrate quality (i.e., lower C:N) resulting in a temporary surge in the quantity of soil microbial biomass concurrent with elevated N availability. To address this, we measured soil microbial biomass C (MBC) on patches within a shifting mosaic tallgrass prairie landscape where each patch varied in time since focal fire and grazing disturbance. To evaluate the effects of focal disturbance, we also evaluated an homogenous landscape that had similar grazing pressure but where the entire area was burned annually and the fire-grazing interaction was not allowed to be expressed in spatio-temporal dynamics. MBC was positively correlated with organic C and N, pH, and clay content. Multiple regression was used to evaluate the influence of each variable relative to fire-grazing regime effects on MBC values. Most of the variance in MBC values was related to variability in organic C and pH, whereas fire-grazing regime had no detectable effect.

Key words: Fire; grazing; tallgrass prairie; microbial biomass; N availability

INTRODUCTION

Microorganisms are largely responsible for nitrogen (N) transformations and the vast majority of available N in terrestrial ecosystems. In grasslands, large amounts of organic matter accumulate as the production of herbaceous biomass reaches a steady state with decomposition over geologic time scales. Consequently, large quantities of soil microbial biomass are usually present relative to forested ecosystems as there is less C limitation (Zak et al. 1994). Mineralization of organic N by soil microbial biomass liberates N for plant uptake while immobilization serves as a sink. The balance between these two microbial processes largely regulates N availability which can have profound ecosystem level consequences in grasslands (Maron and Jeffries 2001; Milchunas and Lauenroth 1995; Tilman 1987). Therefore, the soil microbial biomass should be especially paramount in regulating N availability following disturbance in these systems.

Fire and grazing are primary disturbance processes regulating the structure and function of grassland ecosystems (Collins 1990; Collins 2000; Knapp et al. 1999; McNaughton et al. 1988). Both disturbance processes are critical to grasslands and influence ecosystem N availability (McNaughton et al. 1988; Seastedt and Knapp 1993). Thus, the role of soil microbial biomass in regulating spatial and temporal patterns of N availability as affected by fire, grazing, and the interaction between fire and grazing needs explored. However, most studies have neglected the interaction which may have been an important evolutionary mechanism shaping grassland landscapes and providing habitat for many species (Fuhlendorf and Engle 2001).

The ecological interaction of fire and grazing (fire-grazing interaction) is organized around spatial and temporal variability across the landscape that has been described as a shifting mosaic (Fuhlendorf and Engle 2001; Fuhlendorf and Engle 2004). This spatial variance is driven by inherent variability in resources and the interaction of fire and grazing disturbances. The probability of fire occurring is highest on an undisturbed grassland because of the accumulation of litter and standing biomass that can serve as fine fuel. When a fire occurs and fuel is consumed, productivity, palatability and accessibility of forage increases. Under this condition, grazing animals are attracted and can congregate increasing grazing pressure on the recently burned patch enhancing N availability (Anderson 2005). Grazing animals will congregate there until fires occur in other regions. When grazing animals move to a new, recently burned area, the original burned patch has an increase in biomass that includes a diversity of graminoids and herbaceous dicots. Over the next several years the patch accumulates litter as grasses regain dominance again increasing the probability of fire and N availability returns to pre-fire levels (Anderson 2005). The result is a mosaic of N enriched patches that are recently burned and focally grazed nested within an unburned and ungrazed landscape.

The ecological interaction between fire and grazing (fire-grazing interaction) is an important disturbance in many grassland ecosystems regulating N availability. The causal mechanism responsible for the pulse in N availability following focal disturbance previously reported, however, remains unknown. In general, annual C inputs from senesced plant litter is only adequate to meet the maintenance requirements of microorganisms (Smith 1990; Zak et al. 1994). Thus, we hypothesized that urine and dung deposition from congregated grazing activity should enhance substrate quality (i.e., lower C:N) resulting in a temporary surge in the quantity of soil microbial biomass facilitating greater N turnover. To address this we compared the quantity of soil microbial biomass from patches within a shifting mosaic fire-grazing regime where each patch varied in time since focal disturbance. To evaluate the effects of focal disturbance, we also compared the quantity of soil microbial biomass from an homogenous fire-grazing regime that had similar grazing pressure but where the entire area was burned annually and the fire-grazing interaction was not allowed to be expressed in spatio-temporal dynamics.

MATERIALS AND METHODS

Site Description

Our study was conducted on the Nature Conservancy's 16,000ha Tallgrass Prairie Preserve (TGPP) located at the southern edge of the Flint Hills in the tallgrass prairie region of central North America. Mean annual precipitation of the region is 870mm with 70% occurring between April and September (Bourlier 1979). Vegetation at the TGPP is tallgrass prairie dominated by C4 grasses big bluestem (Andropogon gerardii), Indian grass (Sorghastrum nutans), switch grass (Panicum virgatum), and little bluestem (Schizachyrium scoparium) (Hamilton 1996; Palmer 2000). Topography is gently rolling with highly variable soils derived from shale, limestone, and sandstone. Limestone is typically found interbedded between sandstone and shale with sandstone generally found at the surface of ridge crests. Either shale or limestone can be found as outcrops on side slopes or toe slopes as a result of geologic erosion. The result is a heterogeneous mixture of soils over multiple scales that vary in texture depending on parent material and topographic position. Site descriptions contain complexes of thermic lithic Haplustolls and thermic aquic Paleustalfs (Bourlier 1979). Upland sites contain mollic epipedons characteristic of long term perennial grassland vegetation and possess smectitic mineralogy. We limited our sampling to upland soils.

Experimental Design

To evaluate the effects of the ecological interaction of fire and grazing on the quantity of soil microbial biomass, two contrasting fire and grazing regimes were evaluated each with two replications arranged in a completely randomized design. A shifting mosaic fire-grazing regime has fire applied to spatially discrete patches within a larger area that is unburned. Fires were annually applied to one third of the landscape on a three-year return interval while grazing intensity was calculated for the entire area. Alternatively, an homogenous fire-grazing regime was burned in its entirety each year. These different fire-grazing regimes were stocked with large ungulates similarly but previous analyses demonstrated that these grazing animals spend over 70% of their grazing time on recently burned patches and the majority of the remaining time on patches burned one year earlier avoiding most patches burned two years earlier (Fuhlendorf and Engle 2004). So, grazing pressure in the shifting mosaic fire-grazing regime varied from two to three times greater than the homogenous fire-grazing regime on recently burned patches to patches that were essentially avoided by grazing animals. Specifically, we sampled patches within the shifting mosaic fire-grazing regime that were currently being heavily grazed as a grazing lawn, one year since fire which were minimally grazed, and two years since fire which were avoided by grazing animals. In addition, we sampled from the homogeneous fire-grazing regime where fire occurs annually but grazing pressure was moderate. Burns included in this study were either conducted in spring (in March) or summer (in August) and grazing animals were moderately stocked for half of the growing season (April through July) based on the entire area they had access to.

Soil Analysis

Soil microbial biomass C (MBC) was determined using the chloroform fumigation extraction method (Horwarth 1996; Jenkinson 1987). Field moist samples were sieved with a 4mm screen to remove roots, rocks, and other debris. Moisture was determined gravimetrically after drying 100g of field moist soil at 75ºC for twenty four hours. Duplicate 20g dry weight equivalent aliquots were placed in 170mm glass desiccators, sealed under pressure, and exposed to chloroform vapor for five days. Fumigated samples were extracted with 100ml of 0.5M K2SO4 by vigorously shaking for thirty minutes followed by filtration using Whatman #2 filtration paper. Extracts were back titrated after a dichromate digestion with 0.017M Fe(NH4)2(SO4)2 to an end point using Ferroin indicator solution. Total extracted C was quantified with a calibrated regression curve generated using known concentrations of sucrose-C solution digested and titrated as standards (Heanes 1984).

Additional soil properties were measured because the quantity of soil microbial biomass is often affected by topoedaphic factors (Schimel and Parton 1986; Tracy and Frank 1998). Total organic C and N in original composite samples were determined by dry combustion with a Leco CN 2000 autoanalyzer (St. Joseph, Michigan) and soil C:N ratios were calculated. Soil reaction was determined using a 1:1 ratio of deionized water to dry soil on a Metler Toledo pH meter (Columbus, Ohio) and particle size analysis was conducted using the hydrometer method (Day 1965).

Statistical Analysis

To evaluate the response of spring and summer burns, MBC from each patch within the shifting mosaic fire-grazing regime was averaged across subsamples and analyzed for interaction by two way analysis of variance (ANOVA) where season of burn and year since focal disturbance were both main effects. No season of burn effects were detected so data were combined. Each year since focal disturbance within the shifting mosaic fire-grazing regime and the similar sites sampled within the homogenous fire-grazing regime were analyzed as separate levels of the same main effect and will be referred to as treatment. Significant differences among treatment means for MBC and selected soil properties were independently tested using single degree of freedom contrasts in ANOVA. Multiple regression was then used to determine the dominant variables affecting the variance in MBC values. Due to the extent of our study site and the small number of degrees of freedom, F values were considered significant at $P < 0.10$ throughout this paper. All analyses were conducted in SAS (SAS Institute 1989).

RESULTS

MBC was strongly affected by site variability but not by treatment. Across all sites, MBC values ranged from 137.99 to 913.15 mg C kg-1 and were positively correlated with organic C ($r = 0.74$, $P < 0.001$), organic N ($r = 0.45$, $P = 0.081$), pH ($r = 0.74$, $P = 0.001$), and clay content ($r = 0.65$, $P = 0.006$). There was no statistical interaction between season of burn and treatment on the response of MBC values (P =

0.343) so data were combined to better evaluate treatment effects. No main effects were observed for either the season of burn ($P = 0.760$) or treatment ($P = 0.279$) on MBC. Table 1 shows selected soil properties for each site samples were collected. Additionally, no treatment effects were detected for any of the response variables measured.

Multiple regression analysis was performed using all correlated variables and treatment as main effects model parameters. Organic N, clay content, and treatment were not significant and were removed from the model. Results from the subsequent analysis revealed that organic C ($P > 0.001$) and pH ($P = 0.018$) were dominant variables explaining the variance in MBC values (R2 = 0.73). Clay content was not significant, presumably from mulitcolinearity with organic C ($r = 0.833$, $P < 0.001$) and pH ($r = 0.747$, $P < 0.001$). So, treatments were not significant and the majority of the variability in MBC was explained by site variability associated with organic C and pH.

DISCUSSION

Grasslands are heterogeneous landscapes where variable patterns of resource availability regulate ecosystem processes. Decoupling inherent landscape variability from that driven by disturbance has long been an objective of ecologists. In this paper we evaluated the impact of two contrasting fire-grazing regimes on the quantity of soil microbial biomass as a mechanism regulating N dynamics relative to inherent landscape variability. Under a shifting mosaic fire-grazing regime, grazing animals congregate in the most recently burned patch leading to the formation of a grazing lawn (Fuhlendorf and Engle 2004). Accelerated N turnover within grazing lawns has been proposed as the mechanism by which native African ungulates have evolved on N limited grasslands

(McNaughton 1984; McNaughton et al. 1997; Ruess and McNaughton 1987; Seagle et al. 1992). In fact, greater N mineralization within grazing lawns has been reported from numerous studies conducted across a variety of grassland ecosystems suggesting a consistent relationship between large ungulate grazers and grasslands (Augustine et al. 2003; Frank and Evans 1997; Frank and McNaughton 1993; Johnson and Matchett 2001; Risser and Parton 1982; Tracy and Frank 1998). Thus, we hypothesized that urine and dung deposition from congregated grazing activity should enhance substrate quality (i.e., lower C:N) resulting in a temporary pulse in the quantity of soil microbial biomass concomitant with that observed for N availability (Anderson 2005). Our results indicate that the quantity of soil microbial biomass is more affected by landscape variability while N dynamics are related more to variable patterns of disturbance.

Soil samples were restricted to upland sites but did little to mitigate the influence of spatial variability. The extent of experimental units and the distance between units made it difficult to find compatible sites, although treatments were randomly applied to the landscape. As such, variability among organic C and N were considered inherent to the region as no treatment effects were detected. Soil reaction and surface texture were also measured because both fundamental soil properties have been shown to influence the function of grassland ecosystems. For example, species richness has been negatively correlated with soil reaction in a tallgrass prairie landscape (Palmer et al. 2003). The effect of pH on soil microbial biomass, however, has been less studied. Inversely, surface texture has received much attention where studies commonly report that finer textured soils support greater quantities of soil microbial biomass than do coarse textured soils given comparable climates (Burke et al. 1989; Merckx et al. 1985; Muller and

Hoper 2004; Ruess and Seagle 1994; Schimel and Parton 1986). Our data are consistent with these studies and suggest that the relative influence of pH, clay content, and organic C on soil microbial biomass can be considered equivocal because all soil properties are inter-related as a result of long-term soil forming processes.

Two contrasting fire-grazing regimes were evaluated in this study. The lack of a significant treatment effect is evidence that neither fire, regardless of season, nor grazing, regardless of intensity, has an effect on the quantity of soil microbial biomass in grasslands. However, previous research in the Serengeti reported a positive independent effect on the quantity of soil microbial biomass with increasing large ungulate grazing intensity and organic C content (Ruess and McNaughton 1987). Although a similar trend with organic C was observed in the current study (Fig. 1), we suggest that the discrepancy between grazing effects may be related to the degree of spatial variability associated with our two study sites. Research from a European grassland has also reported an increase in the quantity of soil microbial biomass on intensively grazed sites (Patra et al. 2005). However, this conclusion was the result of long-term continuous grazing which differs from high intensity-short duration grazing such as what occurs under a shifting mosaic fire-grazing regime. Inversely, research in an African grassland has shown a negative effect of grazing on the quantity of soil microbial biomass suggesting a potential conflict in understanding grazing effects on the soil microbiota (Sankaran and Augustine 2004). Grazing effects on microbial biomass have also been studied in a northern grassland inside Yellowstone National Park and reported results consistent with the current study. These investigators reported that topography and

ANPP were dominant variables regulating the quantity of soil microbial biomass whereas grazing activity had no effect (Tracy and Frank 1998).

Studies reporting the effects of fire on soil microbial biomass in grasslands are also confounding. Research from tallgrass prairie has reported that the quantity of microbial biomass varied from year to year and that infrequent fires had no effect (Garcia and Rice 1994). However, an additional study from the same site reported that annual burning resulted in a net reduction in the quantity of soil microbial biomass, although these sites were also N fertilized (Ajwa et al. 1999). A study from a New Zealand grassland reported that infrequent fire also resulted in a reduction in microbial biomass values (Ross et al. 1997). Thus, direct fire effects on microbial biomass in native grasslands are seemingly influenced by other factors.

In general, C inputs from vegetation constrain the growth of microorganisms (Smith 1990; Zak et al. 1994) making detection of direct aboveground disturbance effects on microbial biomass operationally difficult. Disturbance regimes that affect plant C allocation should thus be most easily detected. For example, long term (i.e., > 10 years) annual burning in tallgrass prairie has resulted in compensatory C allocation to belowground productivity (Johnson and Matchett 2001). However, studies on the direct effects of large ungulate grazing in grasslands have reported no effect on belowground productivity or root tissue chemistry (i.e., higher C:N) even when grasslands are annually burned (Johnson and Matchett 2001; McNaughton et al. 1998; Milchunas and Lauenroth 1993). It appears that grazing activity may, therefore, mitigate any indirect effects of annual fire on the quantity of soil microbial biomass. In the current study, all experimental areas prior to 2000 were managed for homogeneity with frequent fire and grazing by large ungulates, similar to the homogenous fire-grazing regime. It is clear that a single rotation of localized fire on a three year return interval may not have allowed sufficient time for all ecosystem traits to stabilize to the effect of short term intensive grazing followed by periodic deferment from both fire and grazing over subsequent years within the shifting mosaic fire-grazing regime.

In summary, we found that the quantity of soil microbial biomass on upland sites in tallgrass prairie was strongly regulated by variability in organic C and pH. Neither the effects of focal fire and grazing disturbance nor annual burning and moderate uniform grazing, however, had a detectable effect. Organic C was also unaffected by fire and grazing but was significantly correlated to pH and clay content suggesting that the relative effects of each soil property on microbial biomass should be considered equivalent. Overall, our results indicate that the quantity of soil microbial biomass in tallgrass prairie was regulated by inherent topoedaphic variability rather than disturbance.

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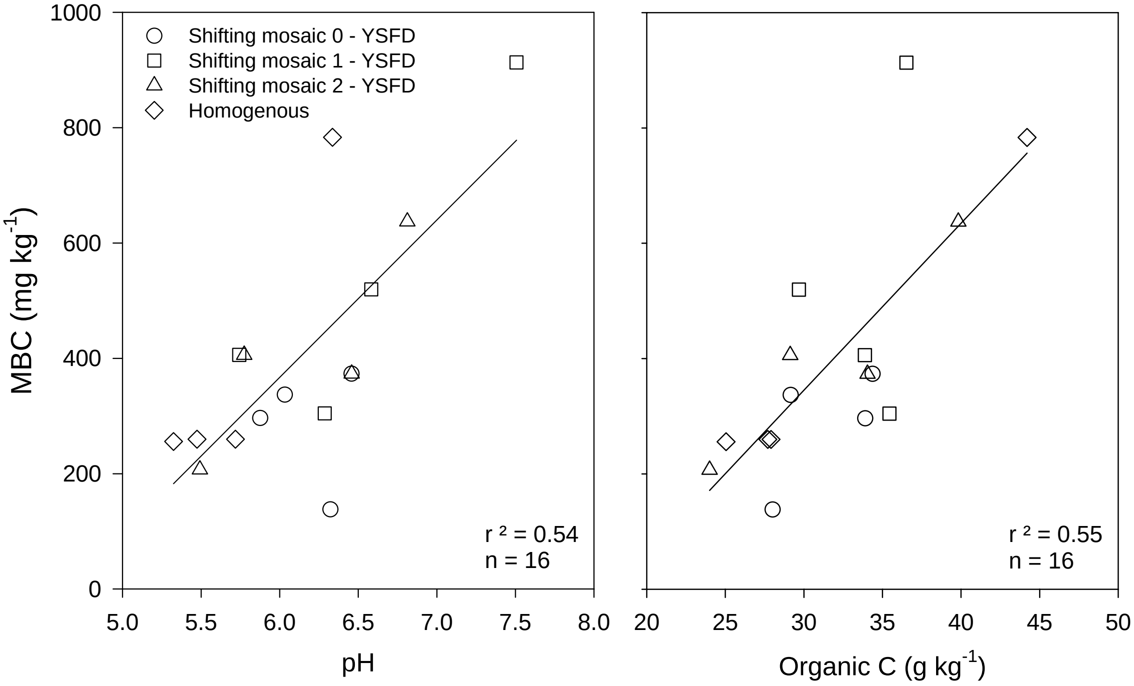
Table 1. Selected soil propterties of the respective sites sampled.

Treatment	YSFD	Rep	Burn	pH	Organic C	Organic N	C:N	Sand	Silt	Clay	USDA Textural Class
					g kg-1	g kg-1		%	%	%	
Homogenous		1	Spring	5.3	25.1	3.5	7.2	37.5	40.0	22.5	Loam
Homogenous		1	Spring	5.5	27.7	2.3	12.0	42.5	37.5	20.0	Loam
Homogenous		2	Spring	6.3	44.2	3.3	13.4	17.5	42.5	40.0	Sandy Clay Loam
Homogenous		2	Spring	5.7	27.9	2.2	12.7	22.5	50.0	27.5	Clay Loam
Shifting mosaic	0	1	Spring	5.7	33.9	3.8	8.9	22.5	42.5	35.0	Clay Loam
Shifting mosaic	0	2	Spring	7.5	36.5	3.4	10.7	20.0	40.0	40.0	Clay Loam
Shifting mosaic	0	1	Summer	6.6	29.7	3.5	8.5	30.0	40.0	30.0	Clay Loam
Shifting mosaic	0	2	Summer	6.3	35.4	2.6	13.6	20.0	45.0	35.0	Clay Loam
Shifting mosaic	1	1	Srping	6.8	39.8	4.5	8.8	17.5	42.5	40.0	Sandy Clay Loam
Shifting mosaic	1	2	Srping	6.5	34.1	2.5	13.6	22.5	42.5	35.0	Clay Loam
Shifting mosaic	1	1	Summer	5.5	24.0	1.8	13.3	40.0	37.5	22.5	Loam
Shifting mosaic	1	2	Summer	5.8	29.1	3.6	8.1	20.0	47.5	32.5	Clay Loam
Shifting mosaic	2	1	Spring	5.9	33.9	2.5	13.6	35.0	32.5	32.5	Clay Loam
Shifting mosaic	2	2	Spring	6.0	29.6	5.0	5.9	22.5	42.5	35.0	Clay Loam
Shifting mosaic	2	1	Summer	6.5	34.4	2.7	12.7	17.5	40.0	42.5	Silty Clay
Shifting mosaic	2	2	Summer	6.3	28.1	2.3	12.2	25.0	45.0	30.0	Clay Loam

* YSFD refers to years since focal disturbance within the shifting mosaic fire-grazing regime

Fig. 1. Relationships among microbial biomass C (MBC), pH (A), and organic C (B) for an homogenous fire-grazing regime and patches within a shifting mosaic fire-grazing regime. Patches were recently disturbed by focal fire and grazing, one year since focal disturbance (YSFD), and two years since focal disturbance


1000
800
600
400
200
0
MBC (mg kg^{-1})
○ Shifting mosaic 0 - YSFD
□ Shifting mosaic 1 - YSFD
△ Shifting mosaic 2 - YSFD
◇ Homogenous
r ² = 0.54
n = 16
5.0
5.5
6.0
6.5
7.0
7.5
8.0
pH
r ² = 0.55
n = 16
20
25
30
35
40
45
50
Organic C (g kg^{-1})

APPENDIX A

Chapter II raw data by site

Year	Condition	Treatment	YSFD	SB (g)	RB (g)	SN (%)	RN (%)	SN (g)	RN (g)	Total N (g)	NO3 (mgl^{-1})	NH4 (mgl^{-1})
2003	Fertilized	Homogenous		0.494	0.619	0.903	1.060	0.004	0.007	0.011	2.350	1.680
2003	Unfertilized	Homogenous		0.368	0.484	1.490	1.400	0.005	0.007	0.012	2.350	1.680
2003	Fertilized	Homogenous		0.621	1.106	0.753	0.900	0.005	0.010	0.015	4.615	1.470
2003	Unfertilized	Homogenous		0.568	0.727	1.120	1.240	0.006	0.009	0.015	4.615	1.470
2003	Fertilized	Shifting mosaic	0	0.841	1.164	0.717	1.000	0.006	0.012	0.018	6.510	3.410
2003	Unfertilized	Shifting mosaic	0	0.601	1.054	1.210	1.300	0.007	0.014	0.021	6.510	3.410
2003	Fertilized	Shifting mosaic	0	0.771	1.805	0.747	0.843	0.006	0.015	0.021	4.210	2.870
2003	Unfertilized	Shifting mosaic	0	0.695	1.194	0.920	1.040	0.006	0.012	0.019	4.210	2.870
2003	Fertilized	Shifting mosaic	1	0.616	1.274	0.570	0.787	0.004	0.010	0.014	1.360	7.380
2003	Unfertilized	Shifting mosaic	1	0.195	0.216	1.530	1.780	0.003	0.004	0.007	1.360	7.380
2003	Fertilized	Shifting mosaic	1	0.711	1.276	0.680	0.893	0.005	0.011	0.016	3.190	2.430
2003	Unfertilized	Shifting mosaic	1	0.463	0.571	1.100	1.260	0.005	0.007	0.012	3.190	2.430
2003	Fertilized	Shifting mosaic	2	0.403	0.924	0.737	0.933	0.003	0.009	0.012	1.320	3.590
2003	Unfertilized	Shifting mosaic	2	0.366	0.520	1.120	1.220	0.004	0.006	0.010	1.320	3.590
2003	Fertilized	Shifting mosaic	2	0.705	1.251	0.860	1.040	0.006	0.013	0.020	5.100	1.140
2003	Unfertilized	Shifting mosaic	2	0.470	0.705	0.870	1.020	0.004	0.007	0.011	5.100	1.140
2004	Fertilized	Homogenous		0.688	0.626	1.228	1.346	0.008	0.008	0.016	3.713	3.673
2004	Unfertilized	Homogenous		0.509	0.586	1.379	1.368	0.007	0.008	0.015	3.713	3.673
2004	Fertilized	Homogenous		1.230	1.380	0.906	0.963	0.011	0.013	0.024	5.800	1.575
2004	Unfertilized	Homogenous		0.778	0.634	1.095	1.493	0.008	0.009	0.018	5.800	1.575
2004	Fertilized	Shifting mosaic	0	1.010	1.048	1.209	1.354	0.012	0.013	0.025	2.422	3.151
2004	Unfertilized	Shifting mosaic	0	0.526	0.422	1.536	1.794	0.008	0.008	0.016	2.422	3.151
2004	Fertilized	Shifting mosaic	0	0.872	0.992	1.468	1.367	0.013	0.013	0.026	4.914	1.620
2004	Unfertilized	Shifting mosaic	0	0.850	0.982	1.391	1.233	0.012	0.012	0.024	4.914	1.620
2004	Fertilized	Shifting mosaic	1	1.078	1.613	0.592	0.846	0.006	0.014	0.020	4.250	1.601
2004	Unfertilized	Shifting mosaic	1	0.744	0.687	1.034	1.227	0.008	0.008	0.016	4.250	1.601
2004	Fertilized	Shifting mosaic	1	1.100	1.281	0.823	0.886	0.009	0.011	0.020	2.357	2.554
2004	Unfertilized	Shifting mosaic	1	0.821	0.721	1.111	1.283	0.009	0.009	0.018	2.357	2.554
2004	Fertilized	Shifting mosaic	2	0.681	1.055	0.710	0.865	0.005	0.009	0.014	1.789	3.155
2004	Unfertilized	Shifting mosaic	2	0.449	0.395	1.002	1.345	0.004	0.005	0.010	1.789	3.155
2004	Fertilized	Shifting mosaic	2	1.242	1.089	0.830	0.897	0.010	0.010	0.020	3.835	3.581
2004	Unfertilized	Shifting mosaic	2	0.645	0.446	1.556	1.614	0.010	0.007	0.017	3.835	3.581

APPENDIX B

Chapter III raw data by site

Treatment	Burn	YSFD	pH	TotalC (g kg^{-1})	TotalN (g kg^{-1})	CN	Clay (%)	MBC
Homogenous	Spring		5.3	2.51	0.35	7.18	22.50	255.68
Homogenous	Spring		5.5	2.77	0.23	12.09	20.00	259.74
Homogenous	Spring		6.3	4.42	0.33	13.45	40.00	783.28
Homogenous	Spring		5.7	2.79	0.22	12.95	27.50	259.74
Shifting mosaic	Spring	0	5.9	3.39	0.25	13.35	32.50	296.27
Shifting mosaic	Spring	0	6.0	2.96	0.50	5.88	35.00	336.85
Shifting mosaic	Summer	0	6.5	3.44	0.27	12.73	42.50	373.38
Shifting mosaic	Summer	0	6.3	2.81	0.23	12.44	30.00	137.99
Shifting mosaic	Spring	1	7.5	3.65	0.34	10.81	40.00	913.15
Shifting mosaic	Spring	1	5.7	3.39	0.38	8.91	35.00	405.84
Shifting mosaic	Summer	1	6.6	2.97	0.35	8.54	30.00	519.48
Shifting mosaic	Summer	1	6.3	3.54	0.26	13.53	35.00	304.38
Shifting mosaic	Spring	2	5.5	2.40	0.18	13.17	22.50	206.98
Shifting mosaic	Spring	2	5.8	2.91	0.36	8.04	32.50	405.84
Shifting mosaic	Summer	2	6.5	3.41	0.25	13.79	35.00	373.38
Shifting mosaic	Summer	2	6.8	3.98	0.45	8.85	40.00	637.18

VITA

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